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Supplementary information

Argentine fossil rewrites evolutionary history of a baffling dinosaur clade

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SUPPLEMENTARY INFORMATION FOR:

Argentine fossil rewrites evolutionary history of a baffling dinosaur clade

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SI GUIDE

1. Locality and Stratigraphic Information:

Both known specimens of *Alnashetri cerropoliciensis* come from the La Buitrera Paleontological Area (8) in Río Negro Province in northern Patagonia, Argentina (Fig S1a). The La Buitrera Paleontological Area is a Konservat-Lagerstätte which preserves part of a paleoerg (59) in which articulated, three dimensional skeletons of small to mid-sized tetrapods are common, including eilenodontine sphenodontians (60), limbed snakes (61), chelid turtles (62), uruguaysuchid crocodyliforms (63), dromaeosaurid and alvarezsaurid dinosaurs (7,64), dryolestoid mammals (35), and dinosaur tracks (65). The new specimen, MPCA Pv377 was collected at the Cerro Policia Locality about 15 km from the site that produced the holotype (La Buitrera Locality, lower star in Extended Data Fig. 1b). Both specimens were found in interdune deposits of aeolian sandstones referred to the upper section of the Candeleros Formation. The Cerro Policía Locality is named for a prominent hill (in Extended Data Fig. 1c), where aeolian Candeleros Formation exposures crop out at its base and are conformably overlain by fluvial and overbank deposits of the Huincul Formation (in Extended Data Fig. 1c). A ~2m thick tuff layer near the base of the Huincul Formation has been dated at 88 ± 3.9 MYA (57, 66) using fission tracks, indicating that the underlying Candeleros Formation beds are upper Cenomanian or lowermost Turonian in age. The Candeleros Formation is the oldest unit within the Neuquén Group, which is the source for all South American alvarezsauroid remains collected to date, with *Alnashetri* as the first occurrence date for the continent (Extended Data Figure 1d).

2. Referral of MPCA Pv 377 to *Alnashetri cerropoliciensis*:

The holotype of *Alnashetri cerropoliciensis* is fragmentary, comprising only hindlimb material. However, these remains are virtually identical in size and anatomy to those of the referred specimen, which along with their co-occurrence in the dune facies of the Candeleros Formation, provides strong grounds to consider them conspecific.

Preserved elements of both specimens show consistent anatomy in overlapping regions. Both specimens feature a femur in which the proximal half of the shaft is mediolaterally compressed and has a subtriangular cross-section that is distinctly taller than it is wide. Both specimens have a pyramidal femoral head that lacks a neck where it meets the shaft, a characteristics shared with alvarezsaurids like *Mononykus* and *Xixianykus*. Unlike *Alvarezsaurus* and *Achillesaurus* (26), neither specimen of *Alnashetri* has a ridge extending from the ventral surface of the femoral head onto the shaft. The lesser (= anterior) trochanter is pillar-like and confluent with the proximal femoral region in both specimens, though only its base is preserved in the holotype (Extended Data Figure 2a-b). Just posterior to the base of the lesser trochanter where it meets the femoral shaft, both specimens exhibit a low trochanteric shelf that borders a prominent fossa for insertion of the m. ischiofibularis ventrally ((7), Extended Data Figure 2a-b). Another muscle scar is present posteroventral to the trochanteric shelf, extending down the posterolateral surface of the shaft. Neither specimen possesses a posterior trochanter—a widespread ancestral trait among non-pennaraptorans—nor a fourth trochanter, which is absent in many parvicursorines, although present in a reduced form in *Patagonykus* and *Mononykus* (1, 67).

The tibiae of both specimens are long and straight, each displaying a distal groove for reception of astragalar ascending process (Extended Data Figure 2c-d). This groove is also observed in *Mononykus*, *Bannykus*, *Aorun*, but not in *Shuvuuia, Alvarezsaurus*, or *Achillesaurus*. It is also present in *Tugulusaurus*, which is not recovered as an alvarezsauroid in our analysis, though other researchers have considered it as such (e.g. 11). In MPCA Pv 377, the absence of the astragalus exposes the groove as a paired structure, divided by a central raised area into medial and lateral sulci, a unique feature among alvarezsauroids (Extended Data Figure 2e). This double groove is challenging to identify in the holotype due to the preserved articulation with the astragalus; however, under oblique lighting, the proximal end of the lateral groove is more visible, with a shallow adjacent sulcus representing the medial component of the double groove on the right ankle (Extended Data Figure 2c). The distinctive double-groove morphology on the distal end of the tibia appears to be an autapomorphy of *Alnashetri* present on both specimens but not yet reported in other alvarezsauroids.

Makovicky et al. (7) described a longitudinal ridge near the distal end of the tibia, which divides the anterior and lateral surfaces, extending to twice or more the height of the astragalar ascending process (Extended Data Figure 2c-d). This ridge is also visible on the right tibia of MPCA Pv 377, where it reinforces the anterior surface of the fibular shaft, a character also observed in the less complete right fibula of the holotype (Extended Data Figure 2c). Such a ridge is absent in *Alvarezsaurus* (Extended Data Figure 2f) and cannot be evaluated in *Patagonykus* (Extended Data Figure 2g) or *Achillesaurus*, as they are incomplete.

The metatarsi of both MPCA Pv 477 and 377 are identical in dimensions and shaft curvature and very close in size (Extended Data Figure 2h-j). Proximally, metatarsal IV is the broadest of the three major metatarsals in plantar view, while metatarsal III is the narrowest. The latter element appears rectangular in end view, as seen in *Patagonykus* and *Bannykus,* and other maniraptorans, contrasting with the notched metatarsal observed in ornithomimosaurs and tyrannosauroids. Metatarsal III is gently bowed laterally at midshaft to a similar degree in both specimens, but unlike the mt III of *Bonapartenykus* and *Bannykus*. The metatarsal shafts are considerably more slender in proportions and curved than those of *Alvarezsaurus* (Extended Data Figure 2k), although comparisons to other Argentine alvarezsauroids are limited. Unlike *Alvarezsaurus*, in which mt II is notably shorter than mt IV, those of *Alnashetri* are subequal in length.

3. Revised diagnosis of *Alnashetri cerropoliciensis*

In their description of the holotype, Makovicky et al. (7) provided a diagnosis that listed two autapomorphies: a sharp ridge separating the rostral and lateral surfaces of the distal tibial end, and paired notches just proximal to the ventral ends of the distal hemicondyles on the penultimate phalanx of digit III. Of these, only the lateral ridge near the distal end of the tibia can be observed in MPCA Pv 377, whereas, the last two phalanges of digit III are not preserved, preventing comparisons of the second autapomorphic trait. The increase in alvarezsauroid diversity since the initial description on *Alnashetri* along with the discovery of a much more complete specimen mandates a re-evaluation of the original diagnosis. For example, a lateral ridge on the distal end of the tibia separating the anterior and lateral surfaces is also observed in the holotype of *Bannykus* and is therefore no longer a valid autapomorphy of *Alnashetri.*

With an eye to the ever-increasing knowledge and discovery of alvarezsauroid diversity including several undescribed Argentinean specimens currently under study, we provide here a more extensive differential diagnosis that will hopefully remain current even as more specimens are discovered and described. The revised diagnosis includes and extensive list of both plesiomorphic, synapomorphic, and potentially autapomorphic characters in order to avoid overreliance on a few potentially autapomorphic traits whose distribution is heavily affected by missing data for many anatomical regions such as the braincase.

Revised diagnosis: subnarial process of premaxilla broad and triangular (plesiomorphic relative to parvicursorines, which have a slender reduced process); teeth unserrated (derived character shared with alvarezsaurids), relatively large (plesiomorphic as compared to parvicursorines, and possibly *Bannykus*) and set within individual sockets (plesiomorphic for alvarezsauroids), lateral surface of braincase with two pneumatic depressions rostral to CN VII exit (potential autapomorphy not observed in *Shuvuuia*); cervical vertebrae amphiplatyan (plesiomorphic as compared to the opsithocoelous of patagonykines and parvicursorines); last sacral centrum with ventral tubercle (currently an autapomorphy of *Alnashetri* and an intermediate character state between unkeeled outgroup condition and the deeply keeled sacrals of alvarezsaurids); distal caudals deeply furrowed ventrally (autapomorphy; the distal caudals of many alvarezsaurids including *Xiyunykus* and *Bonapartenykus* bear a pronounced ventral sulcus emarginated by sharp ridges on either side; by contrast this sulcus is deep but lacks the bordering ridges in *Alnashetri*); distal humerus expanded but lacking distinct condyles, a flexor fossa, and epicondylar processes (distal condyles are generally poorly developed in alvarezsauroids relative to outgroups, but their absence as discrete structures in *Alnashetri* is an autapomorphy). Like alvarezsaurids, but not basal alvarezsauroids and outgroups, the humerus of *Alnashetri* lacks a distal flexor fossa. Unlike *Bannykus, Xiyunykus* and Alvarezsauridae, the distal humerus of *Alnashetri* is plesiomorphic in that it does not bear hypertrophied entepicondylar and ectepicondylar processes); manual digit I ungual with medial claw sheath groove terminating proximally in a fully enclosed canal (derived character state shared with some but not all alvarezsaurids; a fully enclosed canal is observed in *Mononykus* and *Bonapartenykus*; in *Shuvuuia*, *Trierarcunchus*, and *Jaculinykus* the canal ends in a partially enclosed notch; in *Alvarezsaurus*, *Bannykus*, and earlier diverging taxa, the claw sheath groove is fully open throughout its length); ilium with cuppedicus shelf exending onto pubic peduncle (plesiomorphic trait lost in alvarezsaurids); pubic peduncle of ilium larger than ischiadic peduncle (plesiomorphic trait relative to alvarezsaurids, which have peduncles of subequal size); proximal femur with a full trochanteric crest (autapomorphy of *Alnashetri*, convergent on the condition seen in parvicursorines, but absent in *Bannykus* and *Patagonykus*); digit IV pedal phalanges not abbreviated (plesiomorphic relative to alvarezsaurids.)

4. Nomenclatural note

We maintain the use of the name Alvarezsauroidea for the rankless clade defined phylogenetically as all taxa closer to *Alvarezsaurus calvoi* than to *Passer domesticus* as originally defined by Choiniere (68). Agnolin et al. (19) renamed the clade with the same definition and specifiers as Alvarezsauria in order to bring it in line with older ranked Linnean classification (24), and to emphasize the distinctness of the clade. However, as neither of these are valid arguments for renaming a clade under the rules guiding phylogenetic nomenclature, the use of the name Alvarezsauria in this manner renders it a junior synonym of the established name Alvarezsauroidea.

5. Additional Anatomical Description and Comparisons to other alvarezsauroids

MPCA Pv 377 was collected in a single block. The skeleton was articulated and is missing only extremities (Extended Data Fig. 1e). Some parts of the skull and skeleton appear to have suffered scavenging by arthropods, which is common in La Buitrera fossils (69, 70). Such scavenging probably contributed to the loss of the skull roof and the major joint surfaces of the hindlimb bones. Measurements of individual bones are provided in Tables S2 and S3.

5.1. SKULL

The rostrum is preserved anterior to the lacrimal, the ascending bar of which is partially preserved on the right side of the skull (Fig. 1a; Extended Data Fig. 3a-b). In dorsal view the rostrum is notably wider than in *Shuvuuia*, with broad nasals and also a broad, triangular exposure of the maxillary processes of the premaxillae within the narial floor, similar to the condition in *Haplocheirus* (68), but unlike the short pointed one in *Shuvuuia* (Fig. 1a; Extended Data Fig. 3a). The premaxilla bears four small teeth that are not recurved and lack serrations. The internarial process appears to be short and inserted between the tips of the nasals above the caudal end of the naris. Its base is gently curved and there is a wide subnarial shelf next to the front of the naris.

The maxilla is triangular in lateral view with a straight nasal-narial border (Extended Data Fig. 3a-b). The ascending process is short and terminates at about 2/3 of the length of the tooth row. The subnarial region forms a wide, convex shelf along the entire ventral edge of the naris together with the premaxilla, unlike in parvicursorines. The lateral surface of the maxilla is smooth except for a series of relatively large mental foramina dorsal to the tooth row. A narrow interfenestral bar separates the small maxillary fenestra from the much larger antorbital fenestra. It is deeply inset, but this is the result of crushing to a degree. The bar is wider at its base, narrows dorsally, and is inclined anterodorsally. The only development of an antorbital fossa is a weak depression on the ascending process just below the nasal, and the apparent slight inset of the interfenestral bar. The dentigerous ramus of the maxilla tapers caudally. The articulation for the jugal is marked by a notch in its caudodorsal surface that terminates just behind the level of the toothrow.

The left maxilla bears 26 teeth, while 25 teeth/alveoli can be counted on the right side. The rostralmost nine teeth are the smallest in the upper jaws, closely packed, only weakly recurved, and lacking root-crown constrictions (Fig. 1a; Extended Data Fig. 3a-b). Posterior to that the teeth are more widely spaced and become more recurved and angled backward. The largest teeth appear to be nearer the caudal end of the maxillary tooth row around positions 17-20 after which they get smaller, but not to the degree seen in the rostralmost maxillary teeth. This contrasts with the homodont and minute teeth of *Shuvuuia* (9) and *Jaculinykus* (13). The teeth of *Alnashetri* are set in discrete alveoli, whereas those of *Shuvuuia* are set in a long and continuous groove (9,10). None of the teeth of MPCA Pv 377 exhibit serrations, as is typical of alvarezsaurids (13).

Both nasals are preserved from their contact with the premaxillae and above the antorbital fossa but do not preserve their contact with the frontals and prefrontals. The lacrimal is not well preserved on the right and is lost on the left side. The narial end of the nasal has a concave border where it contributes to the narial margin but is straight posterior to that. The nasals are broad in dorsal view and widen posteriorly, unlike the much narrower and tapered nasals of parvicursorines. They are slightly concave along the midline but curve ventrally at their lateral edges where they roof over the antorbital fenestra behind the ascending process of the maxilla. Several small nutrient foramina are present on the dorsal surface including one just behind the naris, one above the interfenestral bar, and one above the caudal end of the antorbital fenestra. Only a short section of the ascending bar of the right lacrimal is preserved. It is located inset within the antorbital fenestra and at the level of the jugal contact. It is similar to *Shuvuuia* in being very slender.

The right palatine is laterally exposed within the antorbital fenestra. The interchoanal process arises from about halfway between the interfenestral bar of the maxilla and the lacrimal, and projects rostrodorsally. The lateral surface of the main moiety of the palatine that gives rise to its processes is perforated but with irregular edges rendering it difficult to determine the exact outline of the dorsal pneumatic recess is present. The left palatine is displaced and is exposed in medial view along the lower edge of the left dentary (Extended Data Fig. 3a). It bears an elliptical pneumatic pocket with a well-preserved rim. The medial surface of the interchoanal bar has a small foramen at its base. Although broken, sufficient parts of the anterior, caudal, and lateral edges of the element are preserved to substantiate that the palatine had all 4 processes common to non-avian theropods.

The jugal process of the ectopterygoid process is preserved, along with a part of the main body near its base. The process is markedly curved and U-shaped, with a shallow pneumatic pocket located at its base. The left quadrate is preserved beneath the anterior cervical series, adhering to the centra of the axis and C3. Although the tip of the quadrate head is missing, it is evident that it was monostylic. The quadrate shaft is strongly arched in lateral view, such that the head would have projected posteriorly well beyond the level of the distal condyles. The pterygoid wing forms an expanded, lobate sheet of bone, and the quadrate shaft is deeply concave in posterior view. The distal condyles are strongly asymmetrical, with the lateral condyle much smaller and narrower than the medial one. As in other alvarezsauroids, the quadrate is apneumatic.

The braincase floor and sides are preserved (Extended Data Fig. 3c-d), although the roof is missing. The occipital condyle is abraded and poorly preserved but is clearly angled relative to the braincase floor and much smaller than the foramen magnum, as seen in *Shuvuuia* (IGM 100/977). The foramen magnum (Extended Data Fig. 3d) is proportionately large, consistent with alvarezsaurids (11). The medullary floor is ventrally vaulted rostral to the foramen magnum, with a short, low median ridge extending along the midline of the basisphenoid medullary floor (Extended Data Fig. 3d, 'mr'). A groove flanks either side of the braincase floor, extending from beneath the floccular region almost to the sella turcica.

The braincase is broken through the inner ear region on the left side, but the bottom half of the otic capsule is preserved on the right, featuring a large pit that likely represents the cochlear recess. The vertical anterior semicircular canal is exposed in cross-section on both sides ('scx' in Extended Data Fig. 5d) and is located just rostral to the cochlear recess on the right. A figure '8'-shaped depression for the ganglia of cranial nerves VII and VIII lies directly in front of the semicircular canal section and contains two foramina, one positioned above the other. The more dorsal foramen perforates the braincase wall, exiting laterally, and transmitted CN VII. The lower foramen, which carried one or two branches of cranial nerve VIII, appears to lead toward a bulge on the inner braincase wall directly rostral to the floccular recess. This bulge likely housed the sensory structures of the inner ear. The figure '8'-shaped depression is also present in *Shuvuuia* (IGM [Institute of Geology Mongolia]100/3619), and it also contains three distinct foramina—two for CN VIII and one for CN VII. A similar arrangement of ganglia has also been identified in the Qiupa Formation alvarezsaurid (12).

On the left lateral surface of the braincase, a wide and deep fossa representing the anterior tympanic recess is located in front of the inner ear and below the exit of the facial nerve (Extended Data Fig. 3c), as also seen in *Shuvuuia* (IGM 100/3916). The fossa is shallow but broad, with a trapezoidal outline bordered by thin, low laminae.

The lateral surface of the braincase exhibits a prominent ridge or swelling extending rostrally from the anterior tympanic recess (ATR) and passing below the level of the facial nerve (CN VII) exit ('lr' in Extended Data Fig. 3c). This lateral ridge is roughly parallel to an internal ridge ('mr' in Extended Data Fig. 3d) that overhangs and delineates the dorsal margin of the ventral grooves described previously. As the bulge on the left clearly connects to the anterior tympanic recess (Extended Data Fig. 3c) and appears pneumatic, it likely represents an expanded, tubular ala alisphenoidales, similar to structures observed in some troodontids (e.g. 71). A comparable external swelling is also present in a specimen referred to *Shuvuuia* (IGM 100/ 3619), where it represents a dorsal extension of the ATR just below the CN VII exit. This structure in *Alnashetri* likely housed the internal carotids, as in *Shuvuuia,* where the internal carotids pass through ventrally merged ATRs, each within its own osseous tube. No exit for the carotids is visible adjacent to the sella turcica in MPCA Pv 377, although this region is currently unprepared and will benefit from μCT- scanning in the near future.

On the left lateral wall of the braincase, a series of three small, matrix-filled pockets is visible (Extended Data Fig. 3c). Two blind depressions are just rostral to the CN VII exit above the lateral ridge, while the third lies caudodorsal to the facial nerve exit and may represent a break exposing part of the inner ear. The presence of two small fossae anterior to the facial nerve exit is unusual and probably represents an autapomorphy of *Alnashetri,* as these structures are absent in *Shuvuuia*.

The dorsal surface of the sella turcica is abraded along the midline at the rostral end of the preserved portion of the braincase floor, and a small pit just rostral to this region represents the floor of the hypophysial fossa. No internal carotid openings are visible within the hypophyseal fossa, although this region is incomplete. Just ventral to the caudal wall of the hypophyseal fossa, a small depression likely represents the parasphenoid recess. This recess is flanked by two small pneumatic fossae, which likely correspond to the dorsal regions of the basipterygoid recesses, as the basipterygoid processes would have projected from this region of the braincase. This triad of pneumatic depressions is also observed in *Shuvuuia* (IGM 100/3619) and *Xiyunykus* (IVPP [Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, P. R. China] V 22783). Caudal to the parasphenoid recess, the rostral outline of the basisphenoid recess is visible, although much of it is obscured by matrix securing other bone fragments. The basisphenoid recess is clearly wider than long, opens caudoventrally rather than ventrally, and is notably shallow, consistent with the morphology seen in *Shuvuuia* and *Xiyunykus*.

The dentary is triangular in shape, expanding evenly in depth along its length toward the caudal end. In ventral view, the dentaries are straight and lack symphyseal flexure. Numerous irregularly spaced mental foramina are scattered across the symphyseal region, but posterior to the 10-11th alveolus these mental foramina align into two rows extending along the length of the jaw. The upper foramina are more slit-like in appearance and set within a horizontal groove, which is more distinct on the left dentary and much subtler on the right. This groove extends to the caudal end of the tooth row on the left side but is shallower and does not reach as far posteriorly on the right, suggesting that the more pronounced groove on the left may result from taphonomic distortion. The lower row of foramina exhibits a looser linear arrangement and is not inset within a groove. The rostral margin of the external mandibular fenestra is preserved on the right side, where it is incised into the caudal end of the dentary. This fenestra appears to be quite deep dorsoventrally, as seen in *Shuvuuia* (IGM 100/977).

The complete tooth row is not fully exposed in either jaw, but 21 teeth or alveoli are visible on the left side along the rostral half of the upper jaw tooth row. It remains uncertain whether the dentary tooth row terminates rostral to the maxillary tooth row (further preparation or μCT scans might clarify this point). In contrast to the maxillary teeth, the dentary teeth are small and uniform in size and shape along the exposed tooth row, closely resembling the rostral maxillary teeth in both dimensions and morphology. The dentary teeth are only slightly recurved and are closely spaced throughout the row, but are set in individual alveoli, and not a continuous groove as in *Shuvuuia.*

The ventral edge of the left splenial is exposed in ventral view. It tapers rostrally and appears to terminate well short of the symphysis. A small, fully enclosed hhhyoid foramen is present approximately halfway along the length of the bone. It is unlikely that there was a lateral exposure of the splenial below the external mandibular fenestra (EMF), though this remains uncertain.

5.2. VERTEBRAL COLUMN

Cervical vertebrae: Nine cervicals are preserved representing the axis to the tenth cervical like in *Haplocheirus* (71). The cervical series thus appears to be shorter than in parviscursorines, which are reported to have 12 cervicals (13). All of the *Alnashetri* cervicals exhibit full neurocentral fusion with obliterated sutures. The axis appears to have a roughened concave rostral intercentral face indicating that both the odontoid and intercentrum were lost. Its neural spine is taller than those of the following cervicals, and is convex and long as in parvicursorines. The postzygapophses flare widely giving the neural arch a triangular outline in dorsal view. They are connected by a thin web of bone overhanging the neural canal and that is slightly indented on the midline. Mound-shaped and rugose epipophyses sit atop the postzygapophyses but do not overhang their caudal edges. The centrum is apneumatic and lacks either a ventral groove or a ridge.

Cervical 3 also lacks a pneumatic foramen on the centrum. The caudal intercentral face is gently concave, the rostral one is not exposed. The neural arch has widely diverging zygapophyses and is constricted between them in dorsal view. The neural spine is low and short and the epipophyses are far more subtle than on the axis. The diapophysis is located low on the side of the arch, is modest in size, and does not connect to either the pre- or postzygapophyses with ridges or laminae, unlike in other coelurosaurs but similar to parvicursorines (13,67).

Cervicals 4 - 6 are represented by arches only. They are similar to C3 in most respects but with even subtler epipophyses. All exhibit a broad web of bone connecting the postzygapophyses that deeply overhangs the neural canal.

Cervical 7 is shown in Extended Data Fig. 4a. The rostral intercentral articulation is wider than tall and flat, while the caudal face is weakly concave, and the vertebra is most accurately considered platycoelous as compared to other truly opisthocoelous alavarezsauroids like *Xiyunykus* (Extended Data Fig. 4d). The rostral end of the centrum bears a wide groove between the parapophyses, which project below the ventral edge of the centrum. The cervical rib on the right side is fused to the parapophysis and diapophysis (Extended Data Fig. 4a). The neural canal is wider than the centrum in rostral view. The rostral edge of the arch is straight between the bases of the prezygapophyses and there is no anterior ligament groove. The neural spine is very low and pinched. The arch is strongly constricted at midlength and does not overhang the centrum strongly apart from a small infrapostzygapophyseal fossa.

Cervicals 8-10 (Fig. 1b) have short prezygapophyses and long, divergent postzygapophyses. On cervical 8, the prezygapophyses are projected laterally and the web between them bears a small anterior projection on the midline. The postzygapophyses diverge caudolaterally, but are not connected by a bony web. There are no epipophyses. The neural spine is just a low pinched ridge centered on the neural arch. Cervicals 9-10 appear similar but the prezygapophyses are not well exposed, though 9 appears to have the small convexity on the midline in front of the neural spine as well. In contrast to the preceding elements, the diapophyses on these three vertebrae are well developed and projected laterally below the prezygapophyses. On cervicals 9 and 10 they appear to reach as far laterally as the postzygapophyses in dorsal view.

All 13 dorsals are preserved in articulation except for D1, which is slightly displaced from D2 (Fig. 1b). D1 is very short with a concave posterior intercentral articulation, but is otherwise poorly preserved. In both D1 and D2, the transverse processes are overhung by the prezygapophyses, but on the remaining dorsals, which are proportionately much longer, the transverse processes are situated well behind the prezygapophyses. The lateral faces of the D4-5 centra are exposed and devoid of pneumatic openings. The centra are narrow in ventral view and that of D4 appears to pinch to a ridge rostrally, although the surface is broken there, so it is impossible to ascertain whether a hypapophysis was present.

The centra of D9-D13 are ventrally exposed. They get broader and more cylindrical posteriorly and also exhibit a greater degree of midlength constriction. Although there is no sign of central pneumatic foramina on the sides of the verts, the ninth and the last two dorsal vertebrae each bear a diminutive foramen on the ventral midline near the anterior intercentral articulation. It is unclear if this is pneumatic or not.

Neural spines are broken on D1-4, but from 5 on backwards they increase in height. They are lobate, expanding axially toward their tips, and with slightly convex dorsal margins in D5-8, but a straight dorsal margin in D11 and possibly 13. From the third dorsal posteriorly, the zygapophyses are closely spaced and point straight fore and aft. The transverse processes become more slender in dorsal view and more backswept in the direction of the sacrum, but are generally short throughout the dorsal series. In the penultimate dorsal, the transverse processes point laterally and in the last dorsal they are oriented anterolaterally. The parapophyses migrate onto the arch by D5, and are nearly level with the diapophyses by D7. In these posterior dorsals, the parapophyses project laterally as small ridges or alae connected to the lower edges of their adjacent prezygapophyses, a trait also observed in other alvarezsaurids. In contrast to parvicursorines, however, the transverse processes of the dorsal vertebrae are relatively short, not exceeding the length of the neural spine. In parvicursorine taxa, the transverse processes borne on anterior trunk vertebrae are remarkably wide, and the length of each exceeds the height of the neural spine on the same vertebra.

The sacrum is composed of five co-ossified vertebrae with fused centra although the sutures are still discernible (Fig 1, Extended Data Fig. 4b). The centra are apneumatic, distinctly wider than long and dorsoventrally compressed. The second sacral is the widest element. Sacrals 1 and 2 have expanded intercentral ends and the zone of fusion between sacrals 1 and 2 and between sacrals 2 and 3 are raised. The intercentral fusion zones between the more caudal elements (3-5) are less prominent, and a narrow groove extends from sacral 3 onto sacral 4 cutting through the intercentral suture. Sacral 5 is the shortest and narrowest of the elements. Its ventral surface is pinched to form a small midline ridge or tubercle flanked by a small depression on either side (Extended Data Fig. 4b), presaging the much deeper keel on more derived alvarezsauroids (Extended Data Fig. 4e). The posterior intercentral articulation for the first caudal is gently convex in MPCA Pv 377, but not as strongly rounded as in *Patagonykus* (Extended Data Fig. 4e) or in parvicursorines.

The zygapophyses are fully fused with each other to such a degree that their sutures are completely absent. The transverse processes of the first sacral are short and constricted between their bases and tips, and slightly swept forward in dorsal view. A small but distinct infradiapophyseal fossa is present beneath each one. The transverse processes of the second sacral are wide and triangular in dorsal view, being wider rostrally than caudally. Their diapopophyses form a small ridge that connects to the transverse process from below near its rostral end. The transverse processes of the third sacral are short and laterally directed, and marked by two ridges on the ventral surface that define small infraprezygapophyseal and infradiapophyseal fossae between them. The transverse process on the fourth sacral is transversely expanded at its distal end, and connects with the anteriorly swept process of the fifth sacral to enclose an elliptical fenestra a feature that also seems to have been present in *Patagonykus* (Extended Data Fig. 4b). Only the first two sacrals preserve their neural spines. Both are roughly rectangular and terminate in a straight dorsal edge. The first is slightly rostrally inclined while that of the second is vertical. They are separated by a thin line of matrix indicating they were not fused.

Caudals: Only four caudals are preserved (Fig 1d-i), of which two are proximal (i.e. anterior to transition point), and two are distal. The anteriormost element has a boxy, amphiplatyan centrum, but lacks a ventral groove except at the ends between the chevron facets. The anterior intercentral articulation is gently concave mirroring the modest convex articulation of the last sacral, and indicating it represents the first caudal. The posterior intercentral articulation is flat to gently concave, unlike the convex ball and socket articulation of parvicursorines, *Patagonykus* (23), *Achillesaurus* (26) and *Bannykus* (11). The prezygapophyses are short and anterodorsally directed overhanging the anterior intercentral face. The postzygapophyses are level with the posterior intercentral face. The neural spine is broken but was clearly narrow and erect. The transverse processes have wide bases, but are broken so their length and shape are indeterminate.

A second proximal caudal is similar to the first in most respects, but has amphiplatyan articulations and has a slightly longer centrum. Although the transverse processes are broken, their rostral edges indicate they were backswept.

The third proximal caudal has a lower, more elongate centrum with a ventral midline groove that extends across the full length of the centrum. The transverse processes appear short and laterally directed, and the prezygapophyses are short and more dorsally than anteriorly projected.

The last two caudals were articulated (Fig 1i-h). Both have elongate, low, amphiplatyan centra with ventral grooves. The prezygapophyses are short and dorsally projected, barely overhanging the anterior intercentral face. The neural spine is represented by a low midline ridge in each, spanning the length of the neural canal. The transverse processes are reduced to diminutive nubbins at midlength. The lateral faces of the centra lack the intersecting ridges seen in *Buitreraptor* (72).

A full set of dorsal ribs is preserved on the left side (Fig 1B). They are bicapitate, but not do not appear to have the deeply separated capitula and hyperelongate tubercula like in *Shuvuuia* (IGM 100/3640). Uncinate processes are absent.

The only clearly identifiable pair of gastral elements forms an arch at the front of the cuirass, underlying and in contact with the caudal ends of the sternal plates (Fig 1b, Extended Data Fig. 4c). Those gastral segments are quite massive and comparable in girth to the rib shafts, whereas more posterior elements are considerably more slender. Gastralia are present in *Bannykus* (11), but have not been reported in alvarezsaurids including in articulated specimens (e.g. 13). They are absent in several well preserved and articulated parvicursorine skeletons collected by the MAS-AMNH expeditions observed by one of us (PJM), and were likely evolutionarily lost in that clade.

The left scapula is better preserved than the right. The scapular blade is long and slender with a modest distal expansion as in *Mononykus*. The lateral face of the blade is strongly convex. The proximal end bears a strongly everted acromion process that projects at a low angle from the blade as in paravians. The scapula forms about 2/3 of the glenoid, which faces caudally and bears a small dorsal lip (Extended Data Fig. 4g). A small muscle tuber is present along the caudal edge of the blade just above the glenoid and level with the base of the acromion process.

The coracoids appear to be co-ossified with the scapulae though the suture is evident on both sides. The right coracoid is the more complete of the two (Extended Data Fig. 4g). It is longer than tall, but the caudal postglenoid process is not as elongate as in more derived alvarezsaurids. Unlike in alvarezsaurids, there is low but discrete coracoid tuber preserved on the right side ventrolateral to the coracoid foramen ('ct' in Extended Data Fig. 4g), and it connects to a low ridge extending along the caudal process of the coracoid defining a subtle subglenoid fossa. This ridge may be homologous to the horizontal ridge observed in patagonykines (15, 19), in which extends for the full length of the coracoid. The coracoid surface is smooth in MPCA Pv 377 and lacks the vermiform sculpturing seen in *Bonapartenykus* (19).

There is no evidence of either a furcula or clavicles, just as in articulated parvicursorine skeletons (10, 13). MPCA Pv 377 preserves large paired sternal plates similar to those of maniraptorans with the left one well exposed (Extended Data Fig. 4c). The rostral edge is posterolaterally obliquely directed and forms the widest point of the plate, which tapers to a point laterally. The plate is very thin along this edge and the presence of coracoidal sulci is therefore unlikely. Coracoidal sulci are absent on the coossified sternum of parvicursorines, and the coracoids broadly overlap the lateral surfaces of the sternum from below. The lateral margin bears at least two intercostal indentations and a third may have been present near the anterolateral corner where the border is not fully preserved. This suggests three sternal rib attachments on each side, though ossified ribs were not observed on the skeleton. This paired, platelike morphology of the sternum contrasts with the boat-shaped, midline sternum of parvicursorines such as *Mononykus* (Extended Data Fig. 4f), *Shuvuuia* (10), and *Jaculinykus* (13).

5.3. <u>FORELIMB</u>

Both humeri are preserved though the right one is more complete. The humerus is long and gracile, exceeding the length of the scapula (Extended Data Fig. 4g-h), in contrast to alvarezsaurids, in which the humerus is shorter than the scapula and stoutly built. The proximal end is strongly angled relative to the shaft so that the humeral head is positioned far posterior to the shaft when the latter is held vertical (Extended Data Fig. 4h). The internal tuberosity is mound-like and has a rounded outline projecting posteriorly unlike proximally directed tab-shaped one in *Patagonykus* (15) and parvicursorines like *Mononykus* (Extended Data Fig. 4i). The deltopectoral crest is proximally positioned just below the level of the internal tuberosity. It is relatively short and lobate with a rounded outline, and it curves slightly medially in proximal view. This plesiomorphic morphology contrasts with the prominent, tab-shaped deltopectoral crest of parvicursorine taxa like *Mononykus* (Extended Data Fig. 4i), but is more similar to the condition in non-alvarezsaurid alvarezsauroids like *Bannykus* (Extended Data Fig. 4j).

There is a small ridge or tuber along the ventral half of its base on the lateral surface of the humerus with faint muscle scarring on either side of it. Just distal to the deltopectoral crest, the lateral surface of the shaft bears a small depression as in a number of other maniraptorans. It lies at the end of the more posterior tract of muscle scars emanating from the small ridge on the external surface of the deltopectoral crest.

The humeral shaft is long and slender (Fig 1j; Extended Data Fig. 4g-h) in contrast to parvicursorines (Extended Data Fig. 4i). It is straight along its proximal half, but curves anteriorly and expands mediolaterally toward the distal articulation as is typical of many coelurosaurs. The distal articulation is almost as wide as the proximal one. The condyles are indistinct and separated by a small convexity rather than by a sulcus as in other theropods. Like in alvarezsaurids, *Bannykus*, and *Xiyunykus*, a distinct, rimmed brachial fossa is absent, but the posterior face of the distal humerus is marked by a wide extensor sulcus. Unlike *Bannykus* (Extended Data Fig. 4k), *Patagonykus*, and parvicursorines, the distal humerus of *Alnashetri* lacks a large ectepicondylar tuber.

The radius and ulna are long and slender as in maniraptorans ancestrally and unlike the short and stout forearm elements of parvicursorines (Fig. 1k). They are articulated and widely separated on both arms in contrast to the tightly bound elements in *Mononykus* and other parvicursorines. This separation is due in part to the plesiomorphic posterior curvature of the ulnar shaft, which is absent in *Bannykus* (11) and early diverging alvarezsaurids like *Patagonykus* (15). The olecranon is modestly developed and does not project far above the elbow in contrast to *Bannykus*, *Patagonykus*, and parvicursorines. A sharp ridge runs from the olecranon along the posterior edge of the shaft. The distal end of the ulna is flat rather than rounded as in *Patagonykus* and *Mononykus*. The radius is straight and slender and terminates in a more flattened than rounded end with a small medial ridge above the articulation as in e.g. *Deinonychus*. There are two free carpals (Extended Data Fig. 4l), the medial of which is larger and corresponds to the semilunate distal carpal and the smaller, more proximal element is the scapholunare.

The manus is tridactyl with a robust Digit I and very slender MCs II and III (Figs. 1k, Extended Data Fig. 4l). Mc I is about half the length of II, but more than twice as wide. The proximal end is very expanded and proximally convex. The shaft is dorsoventrally flattened as in other alvarezsaurids and is constricted between the proximal and distal ends at 2/3 of its length. The distal condyles are separated by a wide sulcus and are slightly asymmetrically developed with the medial one projecting farther ventrally than the lateral one.

Phalanx I-1 is longer than MCII and has a dorsally convex curvature to its shaft (Fig. 1k). The proximal articulation has a deep intercotylar ridge and is asymmetric in end view with the lateral ginglymus wider and more distally canted than the medial side. The ventral surface bears a distinct ventral sulcus bounded by low, but sharp ridges on either side ('vs' in Extended Data Fig. 4l) similar to phalanx I-1 of *Bannykus* (11). The shaft is strongly pinched in medial view adjacent to the distal articulation, due to the continuation of the distal articular intercondylar groove on to the top of the shaft where it meets a deep extensor fossa. Ligament pits are well developed on both sides. The lateral is more dorsally positioned than the medial one.

The proximal half of the digit I ungual is preserved (Fig. 1k; Extended Data Fig. 4l). It is very similar to *Alvarezsaurus* in having a small and ridge-like flexor tubercle positioned a small distance from the proximal articulation. The claw grooves curl ventrally at their proximal ends as in *Patagonykus* and *Alvarezsaurus*, and the medial one terminates in a canal that opens ventrally as a small foramen near the flexor tubercle as in many, though not all, other alvarezsaurids. The dorsal end of the proximal articulation is wide and convex as in alvarezsaurids.

Metacarpal II is about twice as long as MC I though very slender by comparison (Fig. 1k, Extended Data Fig. 4l). Its proportions are unlike the abbreviated minor metacarpals of alvarezsaurids (21, 13), which are much shorter than MC I, or altogether absent (20). MC II is quadrangular in cross section proximally, but becomes rounded in the distal half where it is also thinner. The shaft looks slightly laterally bowed in dorsal view, but this could be due to displacement along a slight break near the midshaft. The distal articulation is developed indicating presence of phalanges, and the proximal end of a phalanx that likely represents II-1 is preserved in the matrix covering the distal end of MCII.

MC III is more slender than MC II, though both are comparable in girth near their distal ends. Both are comparable in length unlike the reduced MCIII of *Haplocheirus* and other putative Jurassic alvarezsauroids (68, 73). MC III is slightly displaced distally relative to II as in many theropods and the shaft is laterally curved like in many paravians. The distal articulation is non-ginglymous, but slightly expanded and there is lateral ligament pit exposed dorsally again indicating presence of Digit III phalanges. There is a slender non-terminal phalanx crossing underneath MCs II and III, but it is uncertain to which of the two it belongs. Its length and proximity to the end of MTIII suggest it may be III-1. The distal end is not well preserved, but the ventral border of the proximal articulation projects as two tubers well below the ventral surface of the phalangeal shaft.

A small and mediolaterally compressed manual ungual derives from either II or digit III. It is narrow, slightly curved and bears an unusually large flexor tuber with distinct peaks. The tip is missing but would not descend much below the ventral edge of the proximal articulation in lateral view. The claw grooves appear to terminate distal to the level of the flexor tuber.

5.4. PELVIC GIRDLE

None of the pelvic elements are complete. The right ilium is preserved in two sections that do not fit together (Extended Data Fig. 4m-n), but comparison to the preserved left acetabular region shows that relatively little is missing, allowing for an estimated length of 45 mm. The ilium is quite plesiomorphic relative to alvarezsaurids. The preacetabular blade is distinctly longer than the postacetabular one and is also deeper (Extended Data Fig. 4m-n). The preacatebular blade is lobate like in many paravians though the exact outline is uncertain due to breakage (Extended Data Fig. 4m). The lower edge of the preacetabular blade forms a ridge above the expanded pubic peduncle that defines a well-developed cuppedicus fossa (‘cf’ in Extended Data Fig. 4m), a structure that is reduced in *Bannykus* and lost in parvicursorines. The postacetabular blade is dolichoiliac and its dorsal edge curves down to meet the ventral edges a short distance behind the ischiadic peduncle. The dorsal edge of the postacetabular blade is laterally everted as coelurosaurs ancestrally but unlike in alvarezsaurids, where the dorsal edges of the near-horizontal ilia meet along the midline roofing over the sacrum. The brevis shelf is narrow and rounded rather than sharply defined as in many other maniraptorans. A brevis shelf is not defined in parvicursorines, though it is still weakly present in early diverging alvarezsaurids like *Achillesaurus* (25).

Unlike in alvarezsaurids, the acetabulum is marked by a pubic peduncle that is distinctly wider than the ischial one in lateral view as in coelurosaurs ancestrally (Extended Data Fig. 4m-n). The acetabulum bears a small supraacetabular shelf above its anterior half, as in *Mononykus* and *Patagonykus*, and the shelf terminates rostral to the ischial peduncle forming a small notch along the acetabular rim (Extended Data Fig. 4n). The antitrochanter of the ischiadic peduncle is slightly laterally projected as in other alvarezsaurids, while the articulation itself is crescentic in end view and wider than long.

The proximal ends of the pubes are not preserved, but parts of both shafts and their pubic boots are preserved (Extended Data Fig. 4o). The shafts are slender and cylindrical in cross section, and curve posteriorly toward their distal ends as in *Patagonykus* and also many paravians. Like in alvarezsaurids, there is no pubic apron in *Alnashetri* (Extended Data Fig. 4o). Each pubis expands into a modest triangular boot distally. The boot projects posteriorly but not anteriorly and is medially flat but laterally convex. Although the boots of both pubes meet, they are not fused (Extended Data Fig. 4o). The boot exhibits a moderate degree of mediolateral expansion rendering it more club-shaped than classically boot-shaped like in e.g. *Haplocheirus*.

The proximal parts of both ischia are preserved (Extended Data Fig. 4m). The pubic peduncle is deeper than the iliac peduncle is wide as in *Patagonykus* (15), but the peduncles are much flatter mediolaterally. There are no obturator or posterior processes. The ischial shafts are mediolaterally compressed and strap-like and exhibit an anteriorly convex curvature along their length (Extended Data Fig. 4m). The medial face of the shaft is flat whereas the lateral face is convex. A faint groove marks the rostral edge of the lateral surface of the left ischium, but terminates before it reaches the distal end of the preserved section.

5.5. <u>HINDLIMB</u>

The femoral head is not set on a distinct neck as in most theropods, and instead arises as a rounded moiety from the medial surface of the proximal femoral shaft as in *Mononykus*. Both proximal ends of the femora are abraded, but it appears there was no saddle or sulcus between the head and lesser trochanter. The tip of the anterior trochanter is lost on the right side, but on the left its anatomy is very reminiscent of *Patagonykus* with a small cleft between its tip and the greater trochanter, and a long groove that extends from the cleft and down the lateral face of the femur for a long distance (Extended Data Fig. 2a). There is no accessory trochanter on the rostral edge of the anterior trochanter. The femoral shaft is mediolaterally narrow and subtriangular in cross section just below the trochanteric region, but becomes more circular in its distal half, which is not preserved in the holotype. A distinct intramuscular line arises from the base of the lesser trochanter and extends down the rostral face of the proximal half of the femoral shaft, defining the tip of the triangular cross section, and then curves medially along the distal half of the shaft to connect to the medial condyle (Fig. 1l). A distinct fourth trochanter is absent and the m. caudofemoralis brevis insertion is marked by a subtle, elongate tubercle on the posterior face of the femur located just below the level of the base of the anterior trochanter. The femoral shaft is rostrally convex in lateral view, and very subtly sigmoid in rostral view.

The femoral shaft expands toward the distal articulation, which is roughly square in end view. Medially, the distal end of the femoral shaft bears a shallow depression right above the medial condyle. This depression is defined posteriorly by a low thin ridge emanating from the proximal end of the condyle, and rostrally by a subtle ridge that is part of the intramuscular line described above. Both femora have abraded distal condyles so it cannot be determined if the medial was more conically formed as in other alvarezsaurids. The lateral condyle bears a proximal extension of the articular surface that forms a small tuberosity adjacent to the crista tibiofibularis. A similar structure appears to be present in *Patagonykus*. The notch between this tuberosity and the crista tibiofibularis is shallow and forms an obtuse angle in end view.

The cnemial crest of the tibia is low and wide in end view with a shallow crescentic notch between the lateral condyle and cnemial crest as in *Patagonykus* (Fig. 1l). The fibular crest is low and sharp, rising gradually from the tibial shaft surface, and reaches the proximal end of the tibia as a low sharp ridge. There is no evidence of a tuber projecting into the incisura tibialis as seen in *Patagonykus*. The tibial shaft is long, slender and elliptical in cross section and is very gently laterally bowed in anterior view. The distal end is slightly expanded and anteroposteriorly flattened (Extended Data Fig. 2c-d). The lateral malleolus extends further than the medial one but is narrower in end view. The medial malleolus is flanked medially by a tall rounded ridge that would buttress the astragalus medially. Two small ridges arising from the malleoli on the posterior surface of the distal end of the tibia form a wide shallow sulcus between them as in the holotype. In medial view, the anterior and posterior ridges meet to imbue the end of the tibia with a rounded profile, whereas the lateral profile is much narrower and its surface is gently concave. In rostral view, the distal end of the tibia is marked by a groove for reception of the ascending process of the astragalus (green arrows in Extended Data Fig. 2c-e). This groove appears to house two parallel sulci distally as described above under the referral section.

Only the right fibula is preserved but poorly. The proximal end narrows very quickly so that 4/5 of the fibula is thin and splint-like. The section of the bone where a iliofibularis tubercle should be observed is missing. The fibula reaches the ankle but none of the tarsal elements are preserved even though the foot bones are articulated.

The three metatarsals match the holotype in every detail of shape and curvature as previously noted in the taxonomic referral section (Extended Data Fig. 2h-j). Metatarsal III is rectangular and pinched in end view like in *Patagonykus* (15), with the other two metatarsals having larger and rounded outer edges on their proximal ends. Metatarsal IV is broadest proximally, in both anterior and posterior views, whereas Metatarsal II is very narrow proximally in posterior view, but not anteriorly. The shafts are closely appressed and there is a shallow sulcus along both the anterior and posterior faces of the foot because Metatarsal III is more slender than the other elements proximally, though not to the degree in troodontids or unenlagiine dromaeosaurids. There are no muscle tubers or scars on the shafts. The distal articulations of the left foot are exposed though poorly preserved. All are non-ginglymous and rounded and about as wide as long. Metatarsal III projects further than the other major metatarsals, which terminate at roughly the same level.

Digit I is not preserved in articulation with the rest of the feet in either the holotype or MPCA Pv 377, but a small phalanx was recovered with the latter specimen and likely represents pedal phalanx I-1 indicating that pedal digit I was present like in other alvarezsauroids. The preserved phalanges are all proportionately elongate. Phalanx II-1 is the longest and slightly longer than III-1, and it is likely that the phalanges we referred to digit III in the holotype (7) are actually from digit II. Phalanx II-1 has a smooth rounded shaft in ventral view but lacks the notches identified in the holotype, and it is possible those are preparation or preservational artifacts, as they are not seen on the other phalanges either. Phalanx II-2 is only slightly shorter than II-1 and lacks a proximoventral keel as seen in deinonychosaurians. The distal articulation appears to be projected ventrally relative to the shaft but this could be an artifact. The distal ginglymoid articulation of II-2 is the narrowest and also has the deepest intercondylar sulcus of all the phalanges. Digit II terminates in a large and moderately recurved claw, which is trenchant to rounded along its ventral edge and bears a robust flexor tuber. The degree of curvature and sharp edge of this ungual in *Alnashetri* differs notably from the less curved, ventrally rounded pedal claws with reduced to absent flexor tubercles seen parvicursorines and *Patagonykus*.

The digit III phalanges are flat ventrally near their proximal articulation (Extended Data Fig. 2j). Phalanx III-3 is not preserved, but the ungual III-4 is found slightly anteriorly displaced between the dorsal ribs. It is curved, with a flat ventral surface adjacent to the prominent flexor tubercle. It is identical to the claw erroneously referred to digit II in the holotype description (7).

Only the first three phalanges of digit IV are preserved (Extended Data Fig. 2j). They are elongate and slender (length: width ≥ 2) unlike the extremely stubby elements in parvicursorines (e.g. 67) and *Alvarezsaurus* (Extended Data Fig. 4k). In this respect they resemble the pedal elements of paravians more. All have deeply concave ventral profiles in side view, so it is certain that the phalanges preserved with the holotype are not digit IV.

6. Remarks on Late Jurassic and Early Cretaceous theropods reidentified here as alvarezsauroids

Following initial study and preliminary phylogenetic hypotheses based on the holotype and new specimens of *Alnashetri*, we identified a series of synapomorphies that are characteristic of Alvarezsauroidea and its constituent subclades. A review of literature and personal reexamination of several relevant Late Jurassic and Early Cretaceous theropods allowed us to identify two previously unrecognized alvarezsaurids. One of these is a taxon identified from two cervical vertebrae (Yale Peabody Museum 1996, 1997; Extended Data Fig. 5) and an astragalus (YPM 963) recovered from Quarry 9 in the Morrison Formation at Como Bluff, WY, famous for its fossil mammal fauna. This material has a complicated taxonomic history, and was originally identified as part of the hypodigm of *Coelurus fragilis.* However, as shown by Makovicky (27) the two cervical vertebrae overlap in position with those of the *Coelurus* holotype, but differ significantly in their morphology. These vertebrae were described and figured previously (27), and readers are referred to that contribution, for general anatomical considerations. Here we will focus on the alvarezsaurid synapomorphies that are here recognized for the first time in this taxon.

Unlike the majority of coelurosaurs, but like in alvarezsaurids, the cervicals are opisthocoelous, with a deeply concave posterior intercentral articulation and a more gently convex anterior intercentral articulation (Extended Data Fig. 5). The degree of convexity of the anterior articulation in these vertebrae is comparable to *Xiyunykus* (IVVP V 22783), *Bannykus* (IVPP V 25026), and *Calamosaurus* (NHM UK 901), but is not as convex as seen in *Shuvuuia* or *Mononykus*. A low collar or rim borders the convex anterior articulation along its lateral and ventral edges likely marking the extent to which it projected into the opisthocoelous posterior articulation of the preceding cervical vertebra. A similar rim is observed in *Xiyunykus* (IVPP V 22783), *Shuvuuia* (IGM 100/3619), and *Mononykus* (IGM 107/6).

This rim forms a sharp transverse ridge at the anterior end of the ventral surface of the centrum, and rostrally bounds a shallow depression that is flanked by the parapophyses laterally. This depression is also present in *Bannykus* (IVPP V 25026), *Xiyunykus* (IVVP V 22783), *Shuvuuia*, and *Calamosaurus.* In the Morrison taxon, as well as in *Bannykus*, *Xiyunykus*, and *Shuvuuia*, the depression continues as a broad sulcus extending posteriorly along the ventral midline flanked by paired ventrolateral ridges that extend posteriorly from the parapophyses. A ventral sulcus is also present in a variety of other coelurosaurs including *Chirostenotes* (74) and *Falcarius* (75), and some ornithomimids (see character 787 definition and discussion in the character list). However, these taxa differ in lacking the depression at the anterior end of the sulcus bordered by a ridge or rim anteriorly.

The parapophyses are proportionately broad in anterior and posterior views in the Morrison alvarezsaurid vertebrae, and are excavated on their posterior face by a conical fossa or foramen on both sides of each of the preserved vertebrae (Extended Data Fig. 5b, f), an autapomorphy of this taxon (27). The articular surface of the parapophyses are flexed so that the dorsal part faces laterally while the ventral part faces more ventrally. Similarly broad parapophyses with flexed articular surfaces are observed in *Xiyunykus*, and in one of the more posterior cervicals the posterior face of each parapophysis bears a shallow triangular depression, though it is not as pronounced as in the Morrison taxon.

Arches generally agree with those of other alvarezsauroids especially in not having interpostzygapophyseal lamina. Both exhibit anterior and posterior peduncular foramina as in *Xiyunykus* and a variety of other theropods, but the central pneumatic foramina are unpaired unlike the more anterior cervical of the *Xiyunykus* holotype, but similar to *Bannykus*, *Shuvvuia*, and most other coelurosaurs.

An isolated astragalus from Quarry 9 at Como Bluff (YPM 9163), has been referred to *Coelurus fragilis* (76, 77), but as noted by Makovicky (27) with regard to the cervicals, the holotype of *Coelurus* derives from Quarry 13 and, furthermore, does not preserve an astragalus. The Quarry 9 astragalus (YPM 9163) shares a number of synapomorphies with the astragali of alvarezsauroids, including a laterally restricted ascending process and a groove transecting the front of the condyles. A tall lamina connects the lateral condyle also connects the astragalar lateral condyle with the edge of the ascending process in *Alnashetri* (*contra* 7), but it is not as broad as in the other two Argentinian taxa. In the Quarry 9 astragalus, as in *Patagonykus*, the lateral face of the buttress forms a concave surface for receipt of the distal end of the fibula.

The ascending process is incomplete distally, but is complete along its base and reveals that the process was restricted to the lateral half of the astragalus like in alvarezsauroids broadly (11, 15, 67). A deeply incised fossa excavates the juncture between the astragalar body and ascending process and has a sharp anterior rim. The fossa is truncated laterally. A 'craniolateral buttress' (15) connecting the lateral condyle with the base of the ascending process as seen in *Patagonykus* by Novas (15), and subsequently recognized in *Achillesaurus* (26), is not present in the Morrison taxon. The astragalar condyles are separated by a moderately developed sulcus ventrally. The condylar portion of the astragalus wraps posteriorly around the tibial malleoli terminating in an obtusely angled process in proximal view, which differs from the straight posterior edge observed in other taxa including *Alnashetri*. In anterior view the astragalar condylar body is asymmetrical with a taller lateral condyle that has a vertical lateral margin, while the lower medial condyle forms a lobate medial process. A horizontal groove extends across the anterior face of the astragalar body like in some alvarezsauroids such as *Mononykus* (67), *Patagonykus* (15), and *Bannykus* (IVPP V 25026), though the astragalus is poorly preserved in the latter. This groove reaches the medial edge of the astragalus in the Morrison Formation astragalus and *Bannykus*, but does not extend through the lateral condyle.

Based on the presence of two clear alvarezsauroid synapomorphies, namely a laterally restricted ascending process, and a groove cutting across the rostral face of the condyles, we assign YPM 9163 to Alvarezsauroidea. The astragalus is also of the right size to come from the same individual as the two vertebrae; in *Xiyunykus* the more anterior cervical is 39 mm long, while the width of the distal end of the tibia, which is a good proxy for width of the astragalus, is 35 mm. The Quarry 9 astragalus is 32 mm wide according to Carpenter et al. (77), while the more anterior of the two cervicals is 46.8 mm in length. Carpenter and coauthors (77) proposed that several other elements from Quarry 9 might also derive from this taxon, but he neither figured nor described these finds. A thorough review of all the Quarry 9 small theropod material and its possible alvarezsauroid affinities is beyond the scope of this present study.

Calamosaurus foxi is another taxon based on two cervical vertebrae, in this case from the Early Cretaceous Wealden of the Isle of Wight (Extended Data Fig. 6). Originally described by Lydekker (78), these two vertebrae have been alternatively interpreted as a possible compsognathid (28), or as possibly belonging to a tyrannosauroid, though not *Eotyrannus lengi* (79, 80) based on their modestly opisthocoelous intercentral articulations. Here we provide a more expanded description of these two vertebrae.

The more rostral of the two elements (Extended Data Fig. 6a-c,f) is likely Cervical 5, or less likely C4. The centrum is opisthocoelous with slightly angled intercentral articulations. The anterior one is gently and relatively evenly convex and slightly wider than tall (17mm wide vs 13 mm in dorsoventral height). The periphery of the anterior articulation is abraded revealing a cammelate interior. A small groove seems to have been present ventrally, off-setting the anterior intercentral articulation from the body of the centrum, forming a shallow 'lip' below the articulation in anterior view. The parapophyses project ventrolaterally below the convex anterior intercentral articulation and bear a shallow groove between them, which extends for slightly less than half the length of the centrum in ventral view. This groove terminates anteriorly at the ‘lip’ mentioned above. A small foramen in the middle of the groove is an artifact of crushing. The parapophyseal articulations are away but likely faced more laterally than ventrally and may have reach the midheight of the centrum. The centrum is hourglass shaped in ventral view, expanding rostrally due to the large ridges buttressing the parapophyses, and also caudally. At its narrowest, the centrum is about half the width of the caudal articulation. The centrum is also constricted in lateral view between its articular ends, and exhibits a prominent swelling along its caudal half. The central pneumatic foramina are large and situated caudodorsal to the parapophyses, but rostral to the narrowest part of the centrum. The caudal articulation is deeply concave and elliptical in outline. The neurocentral suture is still visible for its full length on the right side, but not as well on the left.

The arch is similar to alvarezsaurids in having very widely spaced, slender prezygapophyses with elongate, kidney shaped articulations, and slender diapophyses that project well lateral to the arch in dorsal view, in contrast to the diapophyses of many pennaraptorans which lie at the edges of the laterally expanded neural arch table. As noted by Naish et al. (28) the diapophysis is blocky and rectangular in end view unlike the flatter and more anteroposteriorly expanded diapophyses seen in ornithomimids The neural spine is moderately elongate and displaced toward the back of the arch. A deep, round ligament pit is present anterior to the spine in dorsal view, but the posterior ligament pit is hidden beneath the neural spine in dorsal view. The postzygapophyses are shorter than the prezygapophyses and are not connected by a web of bone above the neural canal as in ornithomimids or dromaeosaurids. A low ridge on the top of each postzygapophysis is the only trace of an epipophysis. All three lateral arch fossae are present with the infrapostzygapophyseal fossa largest and infradiapophyeal fossa the smallest. There is a shallow depression at the root of each prezygapophysis above the neural canal as a peduncular fossa. The caudal edge of the neural canal roof is broken, but two caudal peduncular fossae appear to have been present beneath the posterior ligament groove.

The other element (Extended Data Fig. 6d-e) was probably the preceding rather than following element judging by the size of the intercentral articulation. This vertebra is missing most of the arch except for the left peduncle. The anterior intercentral articulation is well rounded and is not as well separated from the parapophyses ventrally as in the other vertebra. Likewise it has a less developed ventral groove, though the area is slightly abraded. The parapophyses are tall ellipses that face laterally and create small dimples in the outline of the intercentral articulation in rostral view. The midlength constriction is also less developed in this vertebra likely as a result of its shorter length. The centrum bears a pair of well-developed central pneumatic foramina. Neither vertebra has small grooves or pits on the posterior face of the parapophyses unlike in the Morrison Formation alvarezsauroid.

<u>Measurements</u>
Anterior centrum length: 44.7 mm
Posterior centrum length: Centrum length 40.9 mm
Anterior centrum width: 18.3 mm; anterior centrum height 15.9 mm

Posterior centrum height: 17.4 mm; width: 20. 3 mm
Anterior vertebra, prezygapophyseal span: 34.9 mm; postzygapophyseal span: 30.8 mm
Anterior neural spine length: 16.8 mm

7. Extended discussion of phylogenetic results

Our results identified all major coelurosaurian clades (Extended Data Fig. 7a) including compsognathids, tyrannosaurs, ornithomimosaurians, alvarezsauroids, therizinosauroids, pennaraptorans, Paraves, and its three main constituent clades including Dromaeosauridae, Troodontidae, and Avialae. Internal relationships between major clades are weakly supported due to unstable taxa (81) although monophyly of those clades is more strongly supported with Bremer Support values ranging from 2 to 5+. Our results are similar to most other recent phylogenies in finding alvarezsauroids as a basal clade within Maniraptora, but differ in ways from other recent studies (e.g. 3,11), especially as concerns the identity of some putative early alvarezsauroids from the Jurassic of China, including *Shishugounykus* (73) and *Haplocheirus* (68), which we did not recover as alvarezsauroids, although we did recover *Aorun* (82) as a member of the group. *Haplocheirus* is recovered as a basal member of Maniraptora diverging earlier than alvarezsauroids in our analysis though patristically removed from them by only two nodes. Other studies have also recovered it outside of Maniraptora as an ornithomimosaur (e.g. 34). Some studies also disagree regarding whether the more fragmentary Jurassic theropods *Aorun* and *Shishugounykus* are alvarezsauroids, or not (34, 75). Our analysis recovers the small South African theropod *Nqwebasaurus* as the earliest diverging ornithomimosaur as found by some other studies (22,68), rather than as a possible alvarezsauroid (34).

Most relevant with respect to this study are comparisons to the other analyses that included *Alnashetri* (3, 7). In the description of the holotype (7), *Alnashetri* was recovered as an early branching alvarezsaurid more derived than *Alvarezsaurus* and in a polytomy that also included the patagonykine species *Patagonykus* and *Bonapartenykus*. That admittedly preliminary analysis was conducted prior to the description of a number of Jurassic and Early Cretaceous alvarezsauroids from Asia (e.g. 11, 68, 73, 82), however. Meso et al. (3) is the only other phylogenetic analysis to address the relationships of *Alnashetri*, and recovered it as the sister taxon to Alvarezsauridae. Meso et al. transcribed scorings for MPCA Pv 377 from (42) to a different cladistic matrix based on (11), although they did not include the full range of observations from the skeleton as we have done here.

We recover *Alnashetri* in an earlier diverging position here as one of the older alvaresauroid lineages (Figs. 2, S11). This position is mainly driven by its possession numerous relatively plesiomorphic traits compared to alvarezsaurids and their immediate sister taxa including *Bannykus* and *Xiyunykus*, a well-supported result that persists across all the different consensus trees we recovered . The traits in question are distributed throughout the skeleton rendering it unlikely that our phylogenetic signal is being misled by homoplasy within one anatomical region. Unlike parvicursorines, *Alnashetri* has proportionately large teeth seated in distinct alveoli. Unlike *Bannykus*, *Xiyunykus* and virtually all alvarezsaurids, *Alnashetri* lacks opisthocoelous articulations throughout its presacral vertebral column. It also retains a proportionately long forelimb, with a humerus that lacks an expanded distal end with a large ectepicondyle, a cylindrical ulna without a long olecranon process, and a hand in which metacarpals II and III exhibit ancestral maniraptoran proportions in length (though not in width). *Alnashetri* is thus important for understanding forelimb evolution in alvarezsauroids, a topic to be explored further in a future study. Alvarezsaurid synapomorphies including a proximomedial tab on metacarpal I, a ventral sulcus on phlanx I-1, and a fully enclosed ungual claw groove opening on I-2 stand in contrast to the plesiomorphic traits mentioned above, providing evidence of mosaic evolution. *Alnashetri* is also plesiomorphic in aspects of its pelvic anatomy including in having an asymmetry in the sizes of the preacetabular and postacetabular alae of the ilium, and a well-developed cuppedicus fossa.

All of our analyses recover the remaining South American alvarezsaurids as a paraphyletic grade with patagonykines as sister to a monophyletic Parvicorsorinae in keeping with most previous studies (e.g. 3, 11, 20). All relationships within Parvicursorinae are unstable due to the alternate possible positions for *Kol* and *Albertonykus* (Fig. 2A, Extended Data Fig. 7a), there is a core group of Mongolian taxa including *Shuvuuia* and *Mononykus* that these two wildcard taxa never group with.

Support for alvarezsauroid interrelationships is generally low (Fig. 2a, Extended Data Fig. 7a) with nodes present in the reduced consensus tree only having Bremer support values of between 1 and 2, and bootstrap values exceeding a 50 % threshold at many but not all ingroup nodes. Most of this low support can be attributed to the fragmentary nature of most alvarezsauroids and the resultant missing phylogenetic data. The taxa excluded from the reduced consensus trees have >90% missing data (*Kol, Albertonykus, Calamosaurus* in both EW and IW analyses, also Morrison taxon in EW analyses). Our analyses combining *Alvarezsaurus* with *Achillesaurus* and *Ceratonykus* with *Parvicursor* reduced the number of MPTs but did not alter relationships recovered in the consensus trees (Extended Data Fig. 7b)

8. Extended discussion of biogeographic analysis results

Our RASP results (Extended Data Fig. 8a-c) provide broad evidence of a widespread ancestral range for the early part of alvarezsauroid evolutionary history, unlike previous studies that quantitatively examined alvarezsauroid biogeography, which tended to restrict their ancestral range to Asia (11,19). Although the relative frequency of each ancestral area differs between analyses, all our RASP results indicate that widespread ancestral areas including at least three of the four continents are reconstructed as the most likely states for the earliest three to five nodes in the timescaled trees using S-DEC, though only the two oldest nodes when analyzed using S-DIVA. In contrast to most previous studies (11, 19) that invoke long range dispersal as the only mechanism underlying alvarezsauroid distribution, the majority of our results support vicariance as an important mechanism contributing to the early biogeographic history of Alvarezsauroidea (Fig. 2B; Extended Data Fig. 8a-c), with vicariance reconstructed between 3 (S-DEC) and 5 (S-DIVA) times. Previous studies have consistently explained the predominantly Asian and South American distribution of Late Cretaceous alvarezsaurids as resulting from a series of dispersal events (11,19), despite the fact that these two continents had lost land connections much earlier, with only one prior analysis finding support for a vicariant event between South American and Asian taxa (30). Our novel results are consistent whether we enforce constraints precluding dispersal between Gondwana and Laurasia during the Cretaceous, or not, and there is little difference between the time stratified and unconstrained S-DEC analyses (Extended Data Fig. 8a-b).

Our BioGeoBEARS results differ between unstratified and time-stratified (Extended Data Fig. 8d) analyses. The DIVALike+J model is favored in all unstratified analyses, which treat probabilities of dispersal/ range expansion between any continents as equal throughout the Jurassic and Cretaceous. On the other hand, all time-stratified analyses that accommodate tectonic history by imposing different dispersal costs between continents favor either the DEC or DEC+J models. The time stratified analyses reconstruct more nodes and internodes (5-9) as having widespread ancestral ranges (defined as including 3 or more areas) than do alternate models (1-3, see Table S1 in SI.). These widespread ancestral areas are recovered at the root and earliest divergences in the tree consistent with our RASP results (Fig S12). The predominance of widespread ancestral areas at the root and early divergences of the time-stratified results are again indicative of vicariance as an important mechanism in the early biogeographic history of alvarezsauroids, in keeping with our RASP analyses, and also proposed for other coelurosaurs (30), but in contrast to the dispersalist regime recently reported for tyrannosauroids, including Megaraptora, by Morrison et al (83).

The difference between unstratified analyses favoring DIVALIKE+J model and time-stratified models favoring DEC or DEC+J is similar to results reported by (30) for all coelurosaurs. While we find that AICc scores are slightly lower in unstratified analyses than in the corresponding time-stratified runs (Table S1), we concur with Ding et al (30) that the unconstrained analyses are more liable to inaccurately reconstruct biogeographic history by ignoring relevant paleogeographic constraints on the probability and directionality of potential dispersal events, and therefore favor the results of the time-stratified analyses.

Tree #	**Stratified**	**Best model**	**AICc**	**# of widespread ancestral areas**	**d**	**e**	**j**
24023	No	DIVALIKE+J	43.92	1	0	0	0.0577
24023	Yes	DEC	46.44	9	0.0098	0	0
24024	No	DIVALIKE+J	43.92	1	0	0	0.0577
24024	Yes	DEC	46.89	9	0.0073	1.0e-12	0
18556	No	DIVALIKE+J	41.94	3	1.0e-12	1.0e-12	0.048
18556	Yes	DEC+J	45.96	5	1.0e-12	1.0e-12	0.048
27840	No	DIVALIKE+J	43.66	1	1.0e-12	1.0e-12	0.058
27840	Yes	DEC+J	47.2	9	1.0e-12	1.0e-12	0.052

31560	No	DIVALIKE+J	43.92	1	1.0e-12	1.0e-12	0.052
31560	Yes	DEC	46.08	9	0.0097	1.0e-12	0
2023	No	DIVALIKE+J	41.94	3	1.0e-12	1.0e-12	0.048
2023	Yes	DEC+J	45.81	5	1.0e-12	1.0e-12	0.051
40307	No	DIVALIKE+J	43.66	1	1.0e-12	1.0e-12	0.057
40307	Yes	DEC+J	46.94	7	1.0e-12	1.0e-12	0.057
18370	No	DIVALIKE+J	44.02	1	1.0e-12	1.0e-12	0.057
18370	Yes	DEC+J	48.25	9	1.0e-12	1.0e-12	0.058
2091	No	DIVALIKE+J	41.94	3	1.0e-12	1.0e-12	0.048
2091	Yes	DEC+J	45.96	5	1.0e-12	1.0e-12	0.048
21319	No	DIVALIKE+J	41.94	3	1.0e-12	1.0e-12	0.048
21319	Yes	DEC+J	45.90	5	1.0e-12	1.0e-12	0.049

Table S1. Results of BioGeoBEARS analyses on 10 trees with best stratigraphic fit. Tree # refers to number of the tree among 41200 time-scaled trees. The second column informs whether or not time constraints were applied, the third column identifies which of the 6 standard models in BioGeoBEARS had the best fit as measured with AICc, the fourth provides the AICc score. The fifth column enumerates how many of the basal nodes and internodes are reconstructed as having widespread ancestral ranges (either 3 or 4 of 4 possible areas), with 4 areas being taken as evidence of a Pangean distribution. The last three columns tabulate the dispersal (d), extinction (e), and jump dispersal (j) rates for each analysis. Note that for all +j models, all dispersal via range expansion is reinterpreted as jump dispersal, likely as a consequence of nearly all taxa being represented by a single specimen and long ghost lineages.

9. Extended discussion of macroevolutionary analyses results

Our results (Fig. 2b; Extended Data Fig. 9) stand in contrast to the hypothesis that alvarezsaurids exhibit directional miniaturization, from larger sized, early diverging species to predominantly smaller sized parvicursorines (2,25). Specifically, the latter hypothesis was partly predicated on lower taxonomic sampling, including the exclusion of the large taxon *Kol* from some analyses, and also on methodological issues related to log-transforming mass data and setting of branch lengths in fossil calibration of phylogenies (84). Meso et al.(3) also found evidence for repeated rather than unidirectional evolution of small body mass among alvarezsauroids.

Here, using a more complete taxon sample including addition of the two newly recognized non-alvarezsaurid alvarezsauroids, we further expand upon previous studies of body mass evolution. Unlike previous studies that favored either active models like Ohrnstein-Uhlenbeck (2) or a directional trend (3), or a passive Brownian model (84), our analysis found that the majority of our time-stratified trees fit a white noise (= stasis) model, which describes ramdom changes around an invariant mean. Notably, the aggregate of models that favor evolution at the tips of trees (OU, WN, Lambda) fits far more trees than does the model that incorporates a stronger historic phylogenetic signal (BM), and we find very little evidence for directionality in alvarezsauroid body size evolution. In particular, the early branching position of *Alnashetri* and the Morrison taxon, coupled with the wide range of possible relationships for *Calamosaurus* with a correspondingly wide set of varying branch lengths, contributes to the lack of evidence for an active selective regime acting on alvarezsaurian body mass evolution. Although methodological concerns and small sample size may contribute to this novel result, visual examination of the distribution of body sizes in phylomorphospace underscores the lack of a clear pattern (Extended Data Fig. 9b) with branches crossing each other frequently and multiple instances of miniaturization as well as evolutionary size increases.

10. Expanded Histological Analysis and Description

In order to infer the ontogenetic growth stage of MPCA Pv 377, histological thin sections were produced from the left humerus of the specimen. Additionally, the bone microstructure of two appendicular bones (left femur and tibia) of the holotype specimen, MPCA Pv 477, were also analyzed. Transverse sections were obtained from the midshaft (or near it) of each element. Histological thin sections were prepared at the Laboratorio de Paleohistología of the Museo Provincial Carlos Ameghino (Cipolletti, Argentina), using standard methods outlined by Cerda et al. (85), and analyzed using a petrographic polarizing microscope (Leica DM750P). The nomenclature and definitions of structures used in this study follow (85, 86).

9.1 Histological descriptions

MPCA Pv 477: The transverse sections of both the femur and the tibia are each composed of a well-differentiated central medullary cavity surrounded by a compact cortex. In the femur, the primary bone tissue is mostly formed by parallel fibered bone (Extended Data Fig. 10a). The degree of spatial organization of the intrinsic fibers, nevertheless, is not homogenous, being more disorganized in some areas (Extended Data Fig. 10b). The density of the osteocyte lacunae is distinctly high in the lateral region of the cortex (Extended Data Fig. 10c). These lacunae are flattened and well organized in the sites where parallel fibered bone predominates, and are more rounded and disorganized in those areas in which intrinsic fibers are more disorganized. Vascular canals are mainly longitudinally oriented (Extended Data Fig. 10a-c). Nevertheless, radial, circumferential and even oblique anastomoses are recorded in different parts of the compacta. The density of the vascular canals strongly decreases at the antero-medial region, where parallel fibered bone predominates. Two lines of arrested growth (LAGs) are recorded in the compacta, one in the mid cortex and other near the subperiosteal margin (Extended Data Fig. 10a). The perimedullary region is lined by a thin layer of endosteally deposited, avascular lamellar bone (the inner circumferential layer, ICL) (Extended Data Fig. 10a-c).

The preservation of the tibia is poor in comparison with the femur. Intrinsic fibers appear to be mostly circumferentially arranged, although in some areas they appear to be more disorganized (Extended Data Fig. 10d-f). A patch of bone tissue with irregular appearance is observed in the inner cortex of the lateral region. It consists of compacted coarse cancellous bone, which is separated from the periosteal bone by a distinct resorption line (Extended Data Fig. 10f). The compacta is interrupted by two LAGs, one in the mid cortex and the other close to the subperiosteal margin (Extended Data Fig. 10g). Vascularization is reduced in comparison with the femur. Longitudinally oriented vascular canals predominate. As recorded in the femur, a thin ICL is formed around the medullary cavity (Extended Data Fig. 10g), but it has been partially eroded by medullary cavity expansion.

MPCA Pv 377: The midshaft of the humerus presents a compact cortex surrounding a large, open medullary cavity. The inner half of the cortex is formed by vascularized woven-fibered bone, which grades to a less vascularized parallel-fibered bone in the outer cortex (Extended Data Fig. 10h). Intrinsic fiber arrangement is mainly inferred from the density and spatial orientation of the osteocyte lacunae (i.e., abundant and haphazardly arranged in the woven matrix, less abundant and more ordered in the parallel fibered matrix) than the optical properties of the matrix, which is mostly monorefringent. Vascular canals are mostly longitudinally oriented (Extended Data Fig. 10h-j). Short radial and less common circumferential and oblique canals are also scattered throughout the compacta (Extended Data Fig. 10h-j). The primary bone tissue is interrupted by at least four LAGs (Extended Data Fig. 10h, j). From the inner to the outer cortex, the first two LAGs are closely spaced. The outermost formed LAG is observed immediately below the subperiosteal margin. Another possible LAG appears to be present between the two innermost LAGs. Due to imperfect preservation, LAGs cannot be traced around their full circumference.

A distinct area formed by secondary bone tissue is observed in the posterior quadrant of the inner cortex. This feature exhibits a semilunar appearance and contains some secondary osteons, clearly differentiated by the presence of cementing lines (Extended Data Fig. 10h, I, k). The interstitial bone tissue in the non-remodeled areas appears to be formed by compacted coarse cancellous bone tissue. The ICL is well formed around the medullary cavity, and is larger than the ICL in the femur and tibia of MPCA-Pv 477 (Extended Data Fig. 10h-l) in both absolute and relative terms. The ICL exhibits at least two generations of secondarily deposited lamellar bone tissue. A distinct endosteal tissue surrounds the medullary cavity and lines the ICL (Extended Data Fig. 10h-m). The best preserved portions of this tissue are formed by a matrix of woven-fibered bone containing large, simple vascular canals (Extended Data Fig. 10l, m). Unlike the ICL, in which osteocyte lacunae are uniformly flattened and highly organized in parallel arrangement, these lacunae are plump and do not exhibit a particular orientation in the woven matrix. A distinct cementing line delimits this endosteal tissue from the ICL.

9.2. Discussion

Ontogenetic stage and minimum age: The bone microstructure preserves records of significant events in the life history of vertebrates (86-87). In this regard, discrete microstructural changes occur when individuals reach both somatic (i.e. asymptotic growth) and sexual maturity (88-91). Somatic maturity is usually inferred on the basis of the presence of an external fundamental system (EFS) in the subperiosteal cortex (89-90). An EFS is a particular bone tissue which can be formed in the subperiosteal cortex and is commonly recorded in long bones. This structure consists of a distinct layer of parallel-fibered or lamellar tissue, which is poorly vascularized (or avascular) (90-91). Different lines of evidence suggest that sexual maturity was attained well before somatic maturity in non-avian dinosaurs (e.g. 92- 94). The onset of sexual maturity is usually inferred on the basis of a noticeable change in the spatial organization of intrinsic collagen fibers (from poorly to well-organized) and/or a evident reduction in the spacing between successive cyclical growth marks (95-96). These changes usually also occur along with a clear reduction in the vascular density of primary bone.

The clear absence of a distinct EFS in all the examined elements reveals that both individuals died before the onset of the somatic maturity. Regarding sexual maturity, the humerus of MPCA Pv 377 exhibits a clear decrease in vascular density in the outer third of the compacta, which is also accompanied by an increase in the intrinsic fiber spatial arrangement and the presence of at least four LAGs, indicating that sexual maturity had been attained by this individual. In the case of MPCA Pv 477, a noticeable reduction in the vascular density (and increase in the intrinsic fiber arrangement) is only observed in the anteromedial region of the femoral cortex. Furthermore, the two LAGs recorded in this individual are widely spaced in both sampled elements. This set of histological features suggests that MPCA Pv477 had not yet attained sexual maturity. This variation in the ontogenetic stages between the two known individuals of *Alnashetri* concurs with both their respective body sizes (MPCA Pv 377 is larger than MPCA Pv 477), and with their estimated minimum ages inferred from LAG counts (four and two in MPCA Pv 377 and MPCA Pv 477 respectively).

Discussion regarding the unusual endosteally-formed woven bone tissue:
A distinct layer of woven bone tissue of endosteal origin was identified surrounding the medullary cavity of the MPCA Pv 477 humerus. At first glance, this bone tissue could be interpreted as homologous to avian medullary bone. Medullary bone consists of highly vascularized, mostly woven, and endosteally-derived tissue that is deposited along the endosteal surfaces of (and sometimes completely filling) the medullary cavity and intertrabecular spaces in ovulating female birds, to be later resorbed apace with the progress of oogenesis (97-98). Endosteally deposited bone tissues described in the medullary cavity of a non-avian dinosaur and interpreted as homologous to avian medullary bone was first reported by Schweitzer et al. (99) for an individual of *Tyrannosaurus rex*. Other similar reports in other non-avian theropods and even in ornithopod dinosaurs were later published (99-100). The evidence for a tissue homologous to avian medullary bone allows for recognition of sexually mature and gravid females, and also permits inferences regarding sexual dimorphism and sexual maturity in extinct forms (100). However, since the avian-like medullary bone reported in fossil taxa shares many features with pathological bone, the homology of this tissue with

reproductive medullary bone has been challenged (e.g. 101-102). Several authors have discussed the diagnostic features of avian medullary bone that allow for an unambiguous identification of this tissue in fossil forms (e.g. 97-98,101-105). Among these, the most recent and complete review of the criteria for medullary bone identification was provided by Canoville et al. (98), who concluded that the morphological and chemical diversity of medullary bone, its taxonomically variable skeletal distribution, ephemeral nature and poor characterization among extant birds create complications for defining consistent and unique characteristics that allow for its unambiguous identification in extinct taxa. Hence, although the endosteally formed woven bone tissue found in MPCA-Pv 477 fits with most of the criteria proposed for avian medullary bone, such an identification is still tentative.

11. Tables of measurements

Bone	Length	L-M width (shaft)	L-M width (proximal end)	L-M width (distal end)	A-P width (shaft)	A-P width (proximal end)	A-P width (distal end)	D-V length (shaft)	D-V length (proximal end)	D-V length (distal end)	D-V height
Humerus	45.7	3.8			3.8		9.8				
Femur	74.46	5.8	16.47	11.12	5.87	9.74	8.25	-	-	-	
Tibia	97.48*	6.08	-	10.22	4.1	-	5.92	-	-	-	
Fibula	96.2*	-	-	-	-	-	-	-	-	-	
MT II	54.67	-	-	-	-	-	-	-	-	-	
MT III	57.6*	-	-	-	-	-	-	-	-	-	
MT IV	55.55	-	-	-	-	-	-	-	-	-	
Pp II-1	13.79	-	-	-	-	-	-	-	-	-	
Pp II-2	11.25	-	-	-	-	-	-	-	-	-	
Pp II-3	8.78	-	-	-	-	-	-	-	-	-	
Pp III-1	14.03	-	-	-	-	-	-	-	-	-	
Pp III-2	10.76	-	-	-	-	-	-	-	-	-	
Pp IV-1	10.04	-	-	-	-	-	-	-	-	-	
Pp IV-2	8.3	-	-	-	-	-	-	-	-	-	
Pp IV-3	7.43	-	-	-	-	-	-	-	-	-	
Radius	39.64	2.28	4.31	4.39	-	-	-	2.7	3.42	3.21	
Ulna	40.9	2.32	7.8*	3.3	-	-	-	2.56	4.34	4.47	
MC I	11.96	3.26	6.32	5.53	-	-	-	1.6	2.6	3.3	
MC II	22.15	2.12	3.02	2.9	-	-	-	1.7	2.33	3.04	
MC III	18.22*	1.83	-	2.07	-	-	-	1.26	-	2.26	
Mp I-1	17.78	2.96	4.8	3.8				2.98	5.05	4.84	
Mp I-2	8.37*	-	3.12	-	-	-	-	-	6.15	-	
Mp II-1	5.65*	-	3.3	-	-	-	-	-	3.02	-	
Mp III-1	8.86	1.64	2.28	-	-	-	-	1.66	1.9	2.26	
Scapula	37.2	2.06	-	-	2.68	6.1	10.2	-	-	-	
Coracoid	12.95*	-	-	-	-	-	-	-	-	-	8.8*
Pubis	44.7	-	-	-	-	-	-	-	-	-	-

Table S2. Select measurements of limb and girdle bones of *Alnashetri cerropoliciensis* MPCA Pv 377. Measurements are in millimeters. Abbreviations: A-P, anteroposterior; L-M, lateromedial.

Bone	Length anteroposterior (centrum)	High dorsoventrally anterior (centrum)	High dorsoventrally posterior (centrum)	Length anteroposterior (arch)	Width arch	High dorsoventrally arch
Cervical A	-	-	-	-	-	-
Cervical B	8.9	2.34	3.98	12.45	-	-
Cervical C	6.68	3.2	-	7.6*	8.66*	4.8
Cervical D	-	-	-	10.68	9.65	-
Cervical E	-	-	-	12.16	10.44	-
Cervical F	-	-	-	9.5*	10.46*	-
Cervical G	-	-	-	11.4*	9.92	-
Cervical H	-	-	-	10.42	9.56	-
Cervical I	7.2	-	-	9.6	7.37*	5.47*
Dorsal A	6.35	4.5	3.1	4.83*	8.54*	4.85*
Dorsal B	6.76	4.8	4.37	8.07*	11.92	4.8
Dorsal C	7.46	3.94	3.2	8.48*	7.33*	4.8*
Dorsal D	8.84	3.83*	4.2	10.38*	9.36*	4.44
Dorsal E	7.5	3.5	4	10.55	11.25	6.12
Dorsal F	7.58	5.18	4.98*	10.86*	11.67	6.64
Dorsal G	?	?	?	10.8	?	7.3*
Dorsal H	?	?	?	11.88	10.9*	7.74
Dorsal I	8.4	?	?	12.54	10.6*	6.08
Dorsal J	9.5	?	4.5	12.72	10.5*	6.1
Caudal C	9.72	3.8	3.87	10.3*	8.98*	?
Dorsal K	9.1	5.9	?	13.07	11.4*	9.04
Dorsal L	8.62	4.5	4.1	12.8	10.85*	7.98*
Dorsal M	8.08	3.72	3.2	13.5	10.18*	9.4
Sacra A	7.17	?	?	11.3	?	?

Sacra B	6.76	?	?		10.15	?	?	
Sacra C	6.75	?	?		?	?	?	
Sacra D	6.45	?	?		?	?	?	
Sacra E	7.62	?	?		?	?	?	
Caudal A	7.54	3.86	4.8		8.96	10.06*		5.84
Caudal B	8.43	4.24	3.82	8.16*		9*		6.22
Caudal D	13.05	4.17	4.64	11.8*		4.76*	2.7*	
Caudal E	13.97	4.04	3.92	13.54*		4.4	3.76*	

Table S3. Select measurements of vertebral elements of *Alnashetri cerropoliciensis* MPCA Pv 377. Measurements are in millimeters.

12. LIST OF CHARACTERS

This list is modified from the character list in Gianechini et al. (42), which in turn is mainly an expansion of Brusatte et al. (43), and we refer the reader to that paper for full references of literature cited in the character descriptions. Through review we found that several characters are duplicated or overlap with previous ones and these have been deactivated during analyses, but are maintained in the character list below to allow for review and to maintain consistent numbering with previous TWiG versions. These characters are:

241 304 463 604 611 742 747 749 754 757 820 857 859 861 862 863 865 870 871 872 874 875

Numerous characters are ordered here: 3 16 17 18 19 24 25 27 38 39 40 45 63 66 72 74 84 103 108 111 114 117 119 121 123 130 146 148 152 154 161 163 166 168 169 171 175 178 179 181 195 197 200 217 222 232 234 235 238 242 250 252 255 256 261 262 265 268 270 279 287 292 299 309 316 319 321 326 328 347 351 359 364 379 384 385 387 393 401 409 413 415 417 420 425 426 427 428 433 434 443 445 446 459 462 475 482 485 488 494 499 520 540 545 556 557 560 578 579 605 613 622 628 631 632 635 642 648 651 665 669 670 684 694 698 702 711 712 715 727 728 763 780 805 806 807 818 823 842 843 885 888 890 891 893 907 908 910 911

Character 1: Feathers, vaned feathers on forelimb, form:
- 0: symmetric
- 1: asymmetric

Character 2: Orbit, shape

0: circular in lateral or dorsolateral view
1: dorsoventrally elongate
Note: A “dorsoventrally elongate” orbit was not explicitly defined by Turner et al. (2012) or previous versions of the TWiG dataset, but is here held to be any orbit that is greater than 1.5 times deeper dorsoventrally than long anterposteriorly at its midpoint. This character state is only present in some adult tyrannosauroid specimens among coelurosaurs. The presence of a circular orbit in *Alioramus* may be a consequence of the juvenile status of the one quality specimen of this taxon (IGM 100/1844), or alternatively, it could be a product of the dorsoventrally shallow and anteroposteriorly elongated snout of this taxon.

Character 3: Postorbital, ventral ramus, projection into orbit: (ORDERED)
0: does not project into orbit, suborbital process absent
1: projects into orbit, suborbital process present and large in adults and small and unpronounced in
sub-adults
2: projects into orbit, suborbital process present and large in sub-adults and adults
Note: Turner et al. (2012) and previous TWiG datasets utilized a binary character relating to the presence/absence of an anterior process projecting into the orbit. We here modify this character by splitting the “presence” state into two states, relating to the varying degree of postorbital projection in tyrannosauroids (to distinguish the hypertrophied condition in *Tyrannosaurus* and *Tarbosaurus* in which the postorbital projects strongly into the orbit in both sub-adults and adults). We have also reversed the 0 and 1/2 designation relative to Turner et al. (2012) so that “0” now refers to the lack of postorbital projection and “1” and “2” refer to the two conditions of postorbital projection, following Brusatte et al. (2010a). We have changed the score of *Haplocheirus* from present to absent based on Choiniere et al. (2010a).

Character 4: Postorbital, shape of anterior (frontal) process in lateral view:
0: straight
1: curving anterodorsally, such that dorsal border of temporal bar is dorsally concave

Character 5: Postorbital, ventral ramus, orientation: (UNORDERED)
0: parallels quadrate, lower temporal fenestra rectangular in shape
1: oriented strongly obliquely relative to quadrate, jugal and postorbital approach or contact quadratojugal to constrict lower temporal fenestra
2: oriented anteroventrally relative to the long axes of the quadrate and lacrimal, angle of postorbital ventral ramus long axis with the lacrimal long axis (if lacrimal is approximately vertical) greater than 30 degrees
Note: This is a modified version of the original TWiG character, which adds a third state denoting the anteroventrally oriented postorbital ventral rami of some basal coelurosaurs (e.g., tyrannosauroids).

Character 6: Braincase, otosphenoidal crest, form and position:
0: vertical on basisphenoid and prootic, and does not border an enlarged pneumatic recess
1: well developed, crescent shaped, thin crest forms anterior edge of enlarged pneumatic recess

Character 7: Braincase, crista interfenestralis, location:
0: confluent with lateral surface of prootic and opisthotic
1: distinctly depressed within middle ear opening

Character 8: Braincase, subotic recess (pneumatic fossa ventral to fenestra ovalis):
0: absent
1: present

Note: Carr et al. (2011) described a “subotic fossa and recesses” in *Teratophoneus*, but these are not similar to the large, invasive subotic recess of ornithomimosaurs and troodontids.

Character 9: Basisphenoid recess: (UNORDERED)
0: present between basisphenoid and basioccipital
1: entirely within basisphenoid
2: absent

Note: This multistate character is not considered ordered because there is not a clear nested set of primary homologies. The basisphenoid recess is primitive for coelurosaurs, so it is not clear whether the reduced and absent conditions form a transformational sequence. Therefore, the character is left unordered. The reduction of the basisphenoid recess to lie entirely within the basisphenoid in *Tyrannosaurus* and *Tarbosaurus* is most likely due to the extreme anterposterior foreshortening of the recess in these taxa (character 158 in Brusatte et al. 2010a).

Character 10: Basisphenoid recess, posterior opening, form:
0: single opening
1: divided into two small, circular foramina by a thin bar of bone

Character 11: Parasphenoid, base of cultriform process (parasphenoid rostrum), pneumatization:
0: not highly pneumatized
1: expanded and pneumatic (parasphenoid bulla present)

Character 12: Braincase, basipterygoid processes, direction of projection: (UNORDERED)
0: ventral or anteroventrally projecting
1: lateroventrally projecting
2: laterally projecting

Character 13: Braincase, basipterygoid processes, form:
0: well developed, extending as a distinct process from the base of the basisphenoid
1: processes abbreviated or absent

Character 14: Braincase, basipterygoid processes, pneumatization:
0: absent or very subtle, process solid
1: processes hollow, invaded by pneumatic recess (anterior tympanic recess and/or basisphenoid recess)

Note: Turner et al. (2012) scored hollow basipterygoid processes as absent in several tyrannosauroids. However, these are indeed present in taxa that have been CT scanned, including *Alioramus* (Bever et al. 2011), *Gorgosaurus* (Witmer and Ridgely 2009), and *Tyrannosaurus* (Witmer and Ridgely 2009). Therefore, we have scored the character as present in these tyrannosauroids and considered it questionable “?” in all tyrannosauroids (and other basal coelurosaurs) that have not been studied using CT. We anticipate that this character state will eventually be identified in many taxa once they have been the subject of CT study. We also suggest that there may be a difference between the extensively hollow basipterygoid processes of ornithomimosaurs and troodontids (which have long been noted without CT) and more subtle, less invasive recesses in other taxa (such as tyrannosauroids). For the time being, however, we consider these conditions homologous because it is difficult to differentiate them in a discrete manner.

Character 15: Basisphenoid, basipterygoid recesses on dorsolateral surfaces of basipterygoid processes:

0: absent

1: present

Note: This character refers only to the presence of discrete external pneumatic foramina or fenestrae on the lateral surface of the basipterygoid processes (or immediately above). Brusatte et al. (2010a, character 157) utilized a different character relevant to the ingroup relationships of tyrannosauroids, concerning the presence or absence of a single large, window-like fenestra in this region, which is present in juveniles of *Bistahieversor*, *Alioramus*, and *Daspletosaurus* (but not adults of *Bistahieversor* and *Daspletosaurus*). Because of its ontogenetically variable nature, we do not use the Brusatte et al. (2010a) character here, although we incorporate it into a character relating to the anterior tympanic recess below. Rather, we retain the original character of the TWiG dataset which refers to the simple presence or absence of pneumatic foramina on the basipterygoid processes.

Character 16: Prootic, depression for pneumatic recess (Dorsal Tympanic Recess): (**ORDERED)**

0: absent

1: present as dorsally open fossa on prootic/opisthotic

2: present as deep, posterolaterally directed concavity

Note: Brusatte et al. (2010a, character 163) utilized a similar character for tyrannosauroids, and we use those character scores here. Most notably, *Dilong* is scored as uncertain (not as possessing a dorsally open recess as in Turner et al. [2012]). *Guanlong*, however, does possess a dorsal tympanic recess.

Character 17: Braincase, accessory tympanic recess dorsal to crista interfenestralis: (**ORDERED)**

0: absent

1: small pocket present

2: extensive with indirect pneumatization

Character 18: Braincase, caudal (posterior) tympanic recess: (ORDERED)

0: absent

1: present as opening on anterior surface of paroccipital process

2: extends into opisthotic posterodorsal to fenestra ovalis, confluent with this fenestra

Note: Derived tyrannosauroids possess state “2”, as can be seen by their inflated and heavily pneumatized paraoccipital processes (Witmer and Ridgely 2009; Bever et al. 2011, 2013). *Guanlong* clearly does not possess such extensively inflated paroccipital processes, but in the absence of CT data it is uncertain whether it possesses state 0 or state 1. Because of this uncertainty we conservatively score it as "[01]".

Character 19: Braincase, exits of cranial nerves X-XII, location and form: (ORDERED)

0: flush with surface of exoccipital

1: located together in a shallow bowl-like depression

2: located together in a deep, funnel-like depression

Note: We have modified the original binary character of Turner et al. (2012) and previous TWiG versions into an ordered multistate, to differentiate between two conditions of the "bowl-like depression". The first condition, a shallow depression, is commonly seen in coelurosaurs. The second, an extremely deep funnel-like morphology, is present in some derived tyrannosauroids (Brusatte et al. 2010a, character 153). *Bistahieversor* and *Teratophoneus*, which were scored as "?" in Brusatte et al. (2010a), are now scored as possessing the funnel-like morphology based on recent reexaminations of both specimens by Thomas Carr (as noted in Bever et al. 2013).

Character 20: Premaxilla, maxillary process, extent and articulation: (UNORDERED)

0: contacts nasal to form posterior border of nares

1: reduced so that maxilla participates broadly in external naris

2: extends posteriorly to separate maxilla from nasal posterior to nares

Character 21: Premaxilla and nasal, internarial bar, morphology of external surface:

0: rounded

1: flat

Character 22: Premaxilla, crenulated margin on buccal edge of bone:

0: absent

1: present

Character 23: External naris, position of posterior margin:

0: farther anterior than antorbital fossa

1: nearly reaching or overlapping the anterior border of the antorbital fossa

Character 24: Premaxilla, shape of conjoined left and right bones in ventral view: (ORDERED)

0: acute, V-shaped

1: rounded, U-shaped, first two teeth oriented mediolaterally and third and fourth teeth oriented parasagitally

2: rounded, U-shaped, entire tooth row oriented mediolaterally

Note: We have expanded this character into consider this character into an ordered multistate to take into account variation in the "rounded" condition in tyrannosauroids, as denoted by Brusatte et al. (2010a, character 10). All non-tyrannosauroids with rounded snouts are scored for state 1, as are basal tyrannosauroids. Derived tyrannosauroids in which the entire premaxillary tooth row is oriented mediolaterally are scored for state 2.

Character 25: Maxilla, anteromedial process (= "secondary palate"): (ORDERED)

0: short

1: long, with extensive palatal shelves on maxilla

2: extremely elongated, extending back at least to the level of alveolus 4

Note: We have added a second derived state to the character of Turner et al. (2012) and previous TWiG analyses, to differentiate the extremely elongated anteromedial processes of tyrannosauroids, which extend back to at least the level of alveolus 4. The second derived state is present in all score-able tyrannosauroids, as well as ornithomimosaurs (e.g., *Struthiomimus*, *Pelecanimimus*, *Nqwebasaurus*) and the long-snouted dromaeosaurid *Austroraptor*). It is possible that this character may eventually diagnose a more inclusive clade of basal coelurosaurs, given that elongate anteromedial processes are present in nearly all coelurosaurs. However, it is currently difficult to distinguish between the long and extremely long processes of many coelurosaurs, because many specimens are preserved on slabs and therefore fine details of the medial maxilla are not visible. It is clear, however, that derived paravians such as *Dromaeosaurus* and *Deinonychus*, while possessing long anteromedial processes, do not possess the extremely elongate morphology of tyrannosauroids (e.g.., Currie 1995). This is also true of basal coelurosaurs such as *Zuolong* (Choiniere et al. 2010b). Whether compsognathids may have possessed the tyrannosauroid condition is somewhat unclear, because most preserved specimens are either preserved on slabs or are not preserved in disarticulation (precluding observation of the medial surface of the maxilla). However, high resolution photographs of *Compsognathus* published by Göhlich et al. (2006) indicate that this taxon had a somewhat elongate palatal process, and definitely did not possess the extremely elongated condition of tyrannosauroids (therefore, we score it for state 1).

Character 26: Maxilla, palatal shelf, midline ventral "tooth-like" projection:

0: absent, palatal shelf flat

1: present

Character 27: Maxilla, maxillary fenestra: (ORDERED)

0: absent

1: present, fenestra occupies less than half of the depressed area between the anterior margins of the antorbital fossa and antorbital fenestra

2: present, fenestra large and takes up most of the space between the anterior margins of the antorbital fenestra and fossa

Note: the second derived state refers only to the huge fenestrae of some troodontids, which are so large that they take up nearly the entire antorbital fossa region anterior to the antorbital fenestra, with only a thin strut of bone separating the two openings. Other characters referring to nuances of the size and position of the fenestrae are given below.

Character 28: Maxilla, maxillary fenestra, location:

0: situated at anterior border of antorbital fossa

1: situated posterior to anterior border of fossa

Note: This is equivalent to character 17 in Brusatte et al. (2010a). Among tyrannosauroids, *Daspletosaurus*, *Tarbosaurus*, *Tyrannosaurus*, and *Sinotyrannus* have state 0. We here score *Dilong* for state 1, contra Turner et al. (2012). In *Dilong* the maxillary fenestra approaches the anterior border of the antorbital fossa, but it doesn't reach the border.

Character 29: Maxilla, promaxillary fenestra:

0: absent

1: present

Note: We score *Eotyrannus* as possessing the fenestra, based on personal observation of the holotype (MIWG 1997.550)

Character 30: Nasal, pneumatization: (UNORDERED)

0: apneumatic or poorly pneumatized

1: 1: with 1-3 large pneumatic openings, set into a fossa, on the lateral surface above the antorbital fenestra, leading into an extensive internal pneumatic cavity

2: with extensive pneumatic fossae, especially along posterodorsal rim of naris

NOTE: Turner et al. (2012) utilized a binary character, and Brusatte et al (2014) added a new state based on Brusatte et al. (2010a, character 43). They not consider the two pneumatic states to be directly homologous or form a nested series of homology, because of distinct differences in the region of the external pneumatopores (posterodorsal rim of naris vs. midpoint of bone) and the form of the pneumatopores (several pneumatopores posterodorsal to the rim of the naris and close/towithin the narial fossa vs. 2-3 discrete pneumatic openings centered in a fossa. The oviraptorosaur state may be derived from that observed in other taxa through shorterning of the rostrum and nasals, however, as *Incisivosaurus* has a pneumatic fossa that is both directly above the antorbital fossa as in the outgroups and some basal tyrannosauroids and the dromaeosaurids *Deinonychus* and *Tianyuraptor* but also close to the naris given the shortened rostral region. We have therefore changed the orer of states so that 1 refers to the outgroup condition, while state refers to the specialized condition seen in oviraptorosaurs, and we have made this an ordered character.

Character 31: Jugal and postorbital, contribution to postorbital bar:

0: contribute equally to postorbital bar

1: ascending process of jugal reduced and descending process of postorbital ventrally elongate

Character 32: Jugal, dorsoventral height beneath lower temporal fenestra:

0: tall, twice or more as tall dorsoventrally as it is wide transversely

1: very short, jugal rod-like

Character 33: Jugal, pneumatic recess in posteroventral corner of antorbital fossa:

0: present

1: absent

Note: This character refers to an internal pneumatic recess of the jugal, which hollows out some or all of the bone internally. As shown by Tahara and Larsson (2011), the presence of a discrete jugal diverticulum (located in the jugal portion of the antorbital fossa) does not always equate to the presence of an internal recess hollowing the jugal. The presence of an internal recess can be confidently assessed by the presence of a discrete pneumatopore externally, which leads into the recess. *Pelecanimimus* possesses this pneumatopore (LH 7777) and is here scored for state 0, whereas all other ornithomimosaurs are scored for state 1 because they lack the external pneumatopore, and in the case of *Ornithomimus* are known to lack the internal recess based on CT scans (Tahara and Larsson 2011).

Character 34: Jugal, medial jugal foramen:

0: present on medial surface ventral to postorbital bar

1: absent

Note: Turner et al. (2012) scored the foramen as absent in *Dilong*, but the medial surface of the jugal is obscured in the holotype specimen, which has not yet been the subject of CT study. Therefore, we have changed the score to "?".

Character 35: Quadratojugal, shape:

0: without horizontal process posterior to ascending process (reversed "L" shape)

1: with horiziontal posterior process (i.e., inverted 'T' or 'Y' shape)

Character 36: Jugal and quadratojugal, fusion:

0: absent

1: present, the two bones are not distinguishable from one another

Character 37: Lacrimal, supraorbital crests in adult individuals: (UNORDERED)

0: absent

1: dorsal crest above orbit

2: lateral expansion anterior and dorsal to orbit

Note: Following Turner et al. (2012), we consider this an unordered character because we do not hypothesize primary homology between state 1 (discrete crests or tubercles along the dorsal margin of the lacrimal, as present in outgroups and tyrannosauroids) and state 2 (a lamina-like triangular sheet that expands laterally above the orbit, as present in troodontids). Turner et al. (2012) scored *Shuvuuia* for state 1, but we have rescored this as state 0 because this taxon does not possess the discrete crest/tubercle along the dorsal margin of the lacrimal as in outgroups and tyrannosauroids.

Character 38: Lacrimal, pneumatic foramina opening laterally at the junction of the anterior and ventral processes above the antorbital fenestra: (ORDERED)

0: absent

1: present, extent of pneumaticity limited to partially hollowing the bone in the region where the anterior and ventral rami meet

2: present and extensive, completely hollowing the bone where the anterior and ventral rami meet

Note: Turner et al. (2012) used a binary character to distinguish between the presence/absence of lacrimal pneumaticity, and we add a third state to distinguish the greatly extensive pneumatic recess of some tyrannosauroids. Therefore, this is now an ordered character. Turner et al. (2012) scored *Eotyrannus* as lacking lacrimal pneumaticiy, but observation of the type specimen shows that it has a shallow pneumatic recess with external pneumatopores, as in *Guanlong*, *Dilong*, and other basal tyrannosauroids.

Character 39: Lacrimal, posterodorsal process: (ORDERED)

0: absent, lacrimal is inverted 'L' shaped or '7' shaped in lateral view

1: present, lacrimal 'T' shaped in lateral view

2: present but reduced, anterodorsal process much longer than posterodorsal process

Note: Turner et al. (2012) and previous TWiG datasets have referred to the presence of an "anterodorsal process", which creates a T-shaped lacrimal, in this character. This T-shaped condition contrasts with the "inverted L" shape of most theropod lacrimals. However, the inverted L shape is due to a pronounced anterior process along the dorsal margin of the bone (the anterodorsal process) and the lack of any posterior process along the dorsal margin (the posterodorsal process). Therefore, we have reworded the character to refer specifically to the posterodorsal process. We also consider this an ordered character, because state 2 (the presence of a posterodorsal process that is much shorter than the anterodorsal process) is a sub-condition of state 1, meaning that there is a nested primary homology hypothesis. Brusatte et al. (2010a, character 48) utilized a character distinguishing the T-shaped and 7-shaped lacrimals of tyrannosauroids. We utilize this as a separate character below. *Zulong*, which possesses a small posterodorsal process that appears large because of the presence of an autapomorphic notch ventral to it, is scored for state 0.

Character 40: Prefrontal, exposure in dorsal view: (ORDERED)

0: large, dorsal exposure similar to that of lacrimal, forms much of orbital rim and usually separates or nearly separates frontal and lacrimal

1: greatly reduced in size, not exposed widely along the orbital rim and allows for wide contact between frontal and lacrimal

2: absent

Note: We have slightly reworded this character based on language in Brusatte et al. (2010a, character 111). Turner et al. (2012) scored *Dilong* for a reduced frontal, based on the description in Xu et al. (2004). However, personal observation of the holotype (IVPP V14243) reveals that it is difficult to distinguish the prefrontal from surrounding bones, so we conservatively score this taxon as "?" following Brusatte et al. (2010a).

Character 41: Frontals, shape of conjoined left and right elements in dorsal view:

0: triangular, narrowing anteriorly as a wedge between nasals

1: rectangular, end abruptly anteriorly, suture with nasal transversely oriented

Note: Brusatte et al. (2010a, character 113) distinguished between the broad triangular shape of most tyrannosauroid frontals and the anteroposteriorly foreshortened shape of derived tyrannosaurid frontals. However, the frontals of all tyrannosauroids are triangular, so we retain the current character and add a new character below to distinguish between the tyrannosauroid morphologies.

Character 42: Frontal, outline of anterior emargination of supratemporal fossa:

0: straight or slightly curved

1: strongly sinusoidal and reaching onto postorbital process

Character 43: Frontal, form of articulation between postorbital process and frontal orbital margin in dorsal view:

0: smooth transition from orbital margin

1: sharply demarcated from orbital margin

Note: Turner et al. (2012) scored some derived tyrannosaurids for state "1", but we here rescore these as state "0," because they do not possess the strongly demarcated and discrete postorbital processes that are seen in some dromaeosaurids (which state "1" refers to).

Character 44: Frontal, form of lateral margin of lacrimal (or prefrontal) suture:

0: smooth

1: with discrete notch

Character 45: Parietals, form of dorsal surface and presence of sagittal crest(s): (ORDERED)

0: flat, lateral ridge borders supratemporal fenestra, sagittal crest (or crests) absent

1: convex with very low sagittal crest (or crests) along midline

2: convex with well developed sagittal crest (or crests)

Note: This character was unordered in Turner et al. (2012), but we here make it an ordered character because states 1 and 2 are a nested series of homologies defining progressively more prominent sagittal crests, whereas state 0 refers to the absence of a crest. This character subsumes character 122 in Brusatte et al. (2010a), which referred to the presence/absence of sagittal crests in tyrannosauroids.

Character 46: Parietals, fusion of left and right elements:

0: unfused

1: fused on the midline in sub-adults and adults (when known)

Note: This character is equivalent to character 127 in Brusatte et al. (2010a).

Character 47: Squamosal, quadratojugal (descending) process, orientation of long axis:

0: dorsoventral or slightly oblique, essentially parallels quadrate shaft

1: anteroposterior, nearly perpendicular to quadrate shaft

Note: This character is equivalent to character 92 of Brusatte et al. (2010a). Brusatte et al. (2010a) scored *Bistahieversor* for state 0, but we here change this to state 1. This miscoding was an error in the Brusatte et al. (2010a) analysis.

Character 48: Squamosal, contact of descending (ventral) process with quadratojugal:

0: present

1: absent, squamosal does not contact quadratojugal

Character 49: Squamosal, posterolateral shelf overhanging quadrate head:

0: absent

1: present

Character 50: Quadrate, orientation of shaft when in articulation:

0: vertical

1: strongly inclined anteroventrally so that ventral end lies far forward of dorsal end

Character 51: Quadrate shaft, form of lateral surface:

0: straight, without any prominent processes projecting laterally; quadrate foramen not visible in lateral view

1: with broad, triangular process along lateral edge of shaft contacting squamosal and quadratojugal above an enlarged quadrate foramen, which is often partially or largely visible in lateral view

Note: We have slightly reworded the character to explain it more clearly.

Character 52: Foramen magnum, shape:

0: subcircular, slightly wider than tall

1: oval, taller than wide

Character 53: Occipital condyle, mediolateral width and dorsoventral height of neck linking condyle to remainder of braincase:

0: approximately the same width and height as the condyle

1: constricted in width and height relative to the condyle

Note: We have reworded this character to make it clearer here, so that it refers specifically to a discrete neck that is constricted in width and height relative to the width of the condyle.

Character 54: Paroccipital processes, shape:

0: elongate mediolaterally and slender dorsoventrally compared to mediolateral length, with dorsal and ventral edges nearly parallel

1: process short mediolaterally, deep dorsoventrally compared to mediolateral length, with convex distal end

Character 55: Paroccipital processes, orientation in posterior view:

0: straight, projects laterally or slightly posterolaterally

1: downturned, distal end curves ventrally and is pendant

Note: This character is not equivalent to character 150 in Brusatte et al. (2010a), which refers to a distinct ventral flange at the distal end of the paroccipital processes of some tyrannosauroids. This character is utilized below.

Character 56: Paroccipital process, orientation of dorsal edge:

0: straight

1: twisted anterolaterally at distal end

Character 57: Ectopterygoid, form of the opening into the pneumatic fossa on the ventral surface:

0: constricted opening relative to fossa

1: widely opened fossa

Note: Turner et al. (2012) scored *Albertosaurus* and *Gorgosaurus* for state “0”, which is unusual among coelurosaurs. Our observations of tyrannosauroids do not reveal any discrete differences between these taxa and other tyrannosauroids, both basal (e.g., *Guanlong*, *Xiongguanlong*) and derived (e.g., *Alioramus*, *Tarbosaurus*, *Tyrannosaurus*) forms. Therefore, all tyrannosauroids are scored “1” here.

Character 58: Ectopterygoid: dorsal recess:

0: absent

1: present

Note: This character does not refer to the principal pneumatic recess of the ectopterygoid, which hollows out much of the bone and opens via a large pneumatopore on the ventral surface. Rather, it refers to a separate dorsal recess present in some dromaeosaurids.

Character 59: Pterygoid, morphology of the posterior flange for articulation with quadrate and epipterygoid:

0: well developed

1: reduced in size or absent

Note: This character has been reworded here for clarity. See Balanoff et al. (2009) for a good description of state 1, which is present in oviraptorosaurs and a handful of other coelurosaurs.

Character 60: Palatine and ectopterygoid, articulation between the two bones:

0: absent, the two bones separated from each other by the pterygoid

1: present, the two bones contact each other

Character 61: Palatine, jugal process:

0: present, palatine tetraradiate in shape

1: absent, palatine triradiate in shape

Character 62: Skull, suborbital fenestra, size:

0: large, similar in anteroposterior length to the anteroposterior length of the orbit

1: reduced in size (less than one quarter orbital length) or absent

Character 63: Dentary, form of symphyseal region in dorsal or ventral view: (ORDERED)

0: approximately straight anteroposteriorly, paralleling lateral margin of the remainder of bone; conjoined dentaries narrow

1: recurved slightly medially relative to remainder of bone, conjoined dentaries U-shaped

2: recurved strongly medially relative to remainder of bone, conjoined dentaries forming broad U-shaped muzzle

Note: This character has been reworded for clarity.

Character 64: Dentary, orientation of dorsal margin of symphyseal region in lateral view:

0: in line with the remainder of the dorsal (alveolar) margin of the dentary

1: downturned relative to the remainder of the dorsal margin

Character 65: Lower Jaw, coronoid prominence (usually located on surangular):

0: absent

1: present

Character 66: Dentary, contribution to the dorsal margin of the external mandibular fenestra: (ORDERED)

0: absent or slight, without discrete posterodorsal process

1: present, with discrete posterodorsal process above anterior end of fenestra

2: present and extensive, with elongate posterodorsal process extending over most of fenestra

Character 67: Dentary, morphology of lateral surface:

0: flat, tooth row approximately in line with the remainder of the lateral surface

1: bearing lateral ridge, tooth row inset from remainder of lateral surface

Character 68: Dentary, shape:

0: subtriangular in lateral view, with dorsoventral depth expanding posteriorly

1: strap-like in lateral view, with subparallel dorsal and ventral edges and a consistent dorsoventral depth across its length

Note: Turner et al. (2012) scored some derived tyrannosauroids (*Eotyrannus*, *Gorgosaurus*, *Tyrannosaurus*, *Daspletosaurus*) for state “1”, whereas the basal tyrannosauroids *Dilong* and *Proceratosaurus* were scored for state “0”. This character was introduced to the TWiG matrix based on the descriptions of Currie (1995), who noted that some dromaeosaurids (and other coelurosaurs) had dentaries that maintained an approximately even depth across their entire lengths, unlike the dentaries of most theropods that funnel out in depth posteriorly (so-called “subtriangular” dentaries). The subtriangular condition is indeed present in basal tyrannosauroids, but also in more derived tyrannosauroids, contra Turner et al. (2012) (e.g., Brochu 2003; Currie 2003; Carr et al. 2011; Brusatte et al. 2012a). We here score all tyrannosauroids for state “0”. Turner et al. (2012) scored *Eotyrannus* for state “1”, seemingly because the preserved portions of the left and right dentaries of the holotype (MIWG 1997.550) are gracile and do not expand posteriorly. However, neither of these dentaries are complete posteriorly, so the degree of expansion cannot be assessed. Therefore, we here score *Eotyrannus* as “?”.

Character 69: Dentary, primary neurovascular foramina on lateral surface, arrangement:

0: distinct but superficial foramina

1: distinct foramina lie within a deep and sharp groove across the middle and posterior regions of the dentary

Note: This character is equivalent to character 176 in Brusatte et al. (2010a). It has long been utilized in the TWiG matrix, with state 1 scored for a handful of coelurosaurs. Brusatte et al. (2010a) recognized that a distinct and sharp groove is also present in the basal tyrannosauroids *Guanlong*, *Proceratosaurus*, and *Sinotyrannus*.

Character 70: Lower jaw, external mandibular fenestra, shape

0: oval

1: subdivided by a spinous anterior process of the surangular

Character 71: Lower jaw, internal mandibular fenestra (opening between splenial and prearticular on medial surface of mandible), size and shape:

0: small and slit-like

1: large and rounded

Note: This character was introduced into the TWiG dataset based on Currie (1995), who describe an unusual morphology of the internal mandibular fenestra in some dromaeosaurids, in which this opening is large and circular. This contrasts with the smaller and more ovoid opening of most theropods, which is often reduced to a small slit. Turner et al. (2012) scored *Tyrannosaurus* for a large and rounded fenestra, but as shown by Brochu (2003) this opening, although absolutely large due to the large size of Tyrannosaurus, is not circular and is smaller in relation to the size of the dentary than in dromaeosaurids. Therefore, *Tyrannosaurus* and all other tyrannosauroids with known splenials are here scored for state 0. This state can be inferred in isolated splenials by the size and shape of the notch along the posterior margin, which forms the anterior margin of the internal mandibular fenestra.

Character 72: Surangular, foramen in lateral surface of surangular anterior to the mandibular articulation: (ORDERED)

0: absent

1: present but small

2) present and large, approximately 30% of the dorsoventral depth of the posterior surangular

Note: This multistate ordered character combines two characters in the Turner et al. (2012) dataset: character 74 that scores the presence or absence of the surangular foramen and character 258 that scores variability in size of the foramen. The latter character is also used by Brusatte et al. (2010a, character 179) to distinguish between the small and extremely large foramina of some tyrannosauroids. This ordered multistate better encapsulates the full range of variation among not only coelurosaurs, but also tyrannosauroids (basal taxa such as *Guanlong* lack the foramen all together, whereas intermediate taxa such as *Eotyrannus* have a small foramen and derived tyrannosauroids have a derived enlarged foramen). Turner et al. (2012) scored *Eotyrannus* as “?”, but the recent realization that the holotype (MIWG 1997.550) includes surangular material shows that *Eotyrannus* has a small foramen.

Character 73: Splenial, exposure in lateral view:

0: not widely exposed on lateral surface of mandible

1: exposed as a broad triangle between dentary and angular on lateral surface of mandible

Character 74: Lower jaw, coronoid ossification, presence and shape: (ORDERED)

0: present as a large, triangular bone (fused with the supradentary)

1: present but reduced to a thin splint

2: absent

Character 75: Articular, elongate and slender medial process emanating from retroarticular process (can project medially, posteromedially, or dorsomedially):

0: absent

1: present

Note: Turner et al. (2012) scored *Dilong* and *Daspletosaurus* as lacking the process, and *Gorgosaurus* and *Tyrannosaurus* as possessing it. We could not confirm any observation of the articular medial process on *Dilong*, so we score this taxon as "?". *Daspletosaurus* has the same general morphology of *Tyrannosaurus* and *Gorgosaurus*, which a pronounced dorsally and medially extending process at the posteromedial corner of the retroarticular process (Currie 2003). Therefore, we score it for state 1. We also have identified this process in *Tarbosaurus* and *Proceratosaurus*.

Character 76: Articular, retroarticular process, presence and shape: (UNORDERED)

0: present, short and stout, with a distinct region between the glenoid and the portion of the retroarticular process to which the jaw depressors attached

1: present, elongate and slender

2: present but extremely reduced, with no (or only a very short) margin between the glenoid and the muscle attachment region

Note: We have modified this character to include an additional state signifying the extremely reduced retroarticular processes of tyrannosauroids. In tyrannosauroids, including basal taxa such as *Guanlong* and *Dilong*, the retroarticular process is so short that there is essentially no separation between the mandibular glenoid and the attachment site (on the retroarticular process) for the jaw depressor muscles. This is not the case in *Tanycolagreus*, which has a longer retroarticular process and a wider margin between the glenoid and muscle attachment site (Carpenter et al. 2005a, fig. 2.4). In tyrannosauroids lacking an articular, the short retroarticular process can be inferred with a high degree of confidence by the short retroarticular region of the surangular, which articulates with the angular. This inferral is based on the one-to-one correspondence of the short surangular process and short articular retroarticular process in all known tyrannosauroids.

Character 77: Lower jaw, glenoid articular surface for mandible, anteroposterior length:

0: approximately as long as distal quadrate condyles

1: twice or more as long as distal quadrate condyles, allowing anteroposterior movement of mandible

Note: This character can usually be confidently inferred from the shape of all or part of the glenoid articular surface on the surangular and articular. Oviraptorosaurs, which possess state 1, have a radically different morphology compared to other theropods. In oviraptorosaurs, the quadrate condyles do not tightly articulate with the mandibular glenoid, and the lack of a clear, corresponding fit can be seen by observing the surangular and articular.

Character 78: Premaxilla, teeth:

0: present

1: absent

Character 79: Premaxillary dentition, size of second premaxillary tooth:

0: approximately equivalent in size to other premaxillary teeth

1: markedly larger than third and fourth premaxillary teeth

Character 80: Maxilla, teeth:

0: present

1: absent

Character 81: Maxillary and dentary teeth, serrations: (UNORDERED)

0: present on all known teeth

1: some teeth without serrations on mesial (anterior) carina (except at base in *S. mongoliensis*)

2: all known teeth without serrations on both mesial and distal carinae

Note: This character is considered unordered, because we do not hypothesize a nested sequence of primary homology. In other words, we do not hypothesize that there is a clear transformational sequence from serrations to only distal serrations to no serrations, although we recognize that this is a possibility that needs testing without assuming that the character is ordered. We score *Zuolong* for state 1. Choiniere et al. (2010b) described the mesial carina of an isolated lateral tooth as lacking serrations, but considered it difficult to rule out the absence of serrations across the entire carina because of the missing apical tip of the tooth. We feel that enough of the tooth is preserved to show that serrations certainly weren't present across most of the length of the carina, and if were present, were restricted to the very apical tip of the tooth. We consider this equivalent to state 1.

Character 82: Maxillary and dentary teeth, size [Ordered]:

0: large

1: small (>25>30 teeth in dentary when complete series is observable; each crown is small relative to skull length)

2: Diminutive (describes the condition in e.g. *Shuvuuia* and *Halszkaraptor*)

Note: The "large" condition is the normal condition for theropods in which 10-20 distinct maxillary teeth and 10-20 distinct dentary teeth are present. The "small" condition refers to the higher number of tightly packed teeth in the maxillae and dentaries of some coelurosaurs. Although a complete or near-complete maxilla and/or dentary are needed to score this character confidently, usually the size of individual teeth can be used to predict the state of this character.

Character 83: Dentary teeth, implantation:

0: in separate alveoli

1: set in open groove

Character 84: Maxillary and dentary teeth, serrations (denticles):

0: large

1: small

Note: Turner et al. (2012) and previous versions of the TWiG matrix have followed Farlow et al. (1991) in quantifying this difference. In the current dataset, along with previous TWiG matrices, the "large" condition refers only to the pronounced, coarse denticles of therizinosauroids and troodontids (~1-5 serrations per millimeter), whereas other coelurosaurs are scored for the “small” condition (~more than 5 serrations per millimeter).

Character 85: Maxillary and dentary teeth, serrations, form:

0: simple, convex, and approximately perpendicular to the long axis of the tooth

1: large, hooked and pointing toward the tip of the crown on the distal and often mesial carinae

Character 86: Maxillary and dentary teeth, constriction between root and crown:

0: present

1: absent, root and crown confluent

Character 87: Dentary teeth, spacing between teeth:

0: evenly spaced across tooth row

1: anterior dentary teeth smaller, more numerous, and more closely appressed than those in middle of tooth row

Character 88: Dentary, interdental plates, form:

0: distinct internal plates absent (although a homologue to the plates is probably present)

1: distinct, clearly demarcated interdental plates medially between teeth

Note: As reviewed by Turner et al. (2012), state 0 refers to the condition in dromaeosaurids and troodontids in which clear, distinct, unambiguously demarcated interdental plates are absent. It is likely, however, that bony tissue homologous to the interdental plates is present in this region but has been morphologically transformed.

Character 89: Premaxillary tooth crowns, position of mesial carina: (ORDERED)

0: along mesial margin of tooth, tooth cross section sub-oval to sub-circular

1: rotated distally on premaxillary teeth 1 and 2, such that anterior teeth have an asymmetrical cross section (D-shaped, with highly convex labial surface and flat lingual surface, with narrow spacing between mesial and distal carinae)

2: rotated distally on all premaxillary teeth, such that all teeth are D-shaped in cross section.

Note: Turner et al. (2012) and previous TWiG matrices have utilized a binary character relating to tooth cross sectional shape, differentiating “sub-oval” and “sub-circular” teeth, which are present in the outgroups and most coelurosaurs, from “D-shaped” teeth, which are present in tyrannosauroids and a few other coelurosaurs. We note that some outgroups (allosauroids) and many coelurosaurs do possess premaxillary teeth that are roughly D-shaped in cross section, due to a labial margin that is somewhat convex and a lingual margin that is somewhat flat (and always flatter than the labial margin). For this character, however, we define D-shaped teeth based on the morphology of the mesial carina. A “D-shaped” tooth is held to be a tooth in which the mesial carina is rotated strongly distally, such that it is present on the lingual surface of the tooth. This condition is seen almost exclusively in tyrannosauroids, and roughly follows the definition of D-shaped teeth by Currie et al. (1990), Choiniere et al. (2010b), and previous authors. This condition is always associated with a highly convex labial surface and a flat lingual surface, on which the two carinae are only very narrowly separated. In contrast, the somewhat D-shaped teeth of allosauroids and other coelurosaurs exhibit wider separation between both carinae on the lingual surface and a less convex labial surface. Therefore, these morphologies are not considered homologous to the “D-shaped” condition as defined here, although we recognize that there may be some homology shared between these taxa and coelurosaurs with true D-shaped teeth that is not present in more basal theropods such as coelophysoids, ceratosaurs, and some basal tetanurans (assessing this hypothesis awaits further study of theropod teeth more generally). Furthermore, following Brusatte et al. (2010a, character 196), we divide the “D-shaped” condition into two character states, which we consider to be nested homologies. Although these characters refer to the presence “D-shaped” morphology of either some (state 1) or all (state 2) of the tooth row, we here score all taxa lacking any sign of “D-shaped” teeth with rotated mesial carinae for state 0. It is possible that some of these taxa that do not preserve entire premaxillary tooth rows may eventually be scored for state 1, but we conservatively score them 0 here to minimize missing data.

Character 90: Cervical vertebrae, number:

0: ≤10

1: 12 or more

Character 91: Axis, epipophyses, form:

0: absent or poorly developed as a small pyramidal mound, not extending past posterior edge of postzygapophyses

1: large, rugose, and posteriorly directed flange, extending far beyond postzygapophyses

Note: This character is equivalent to Brusatte et al. (2010a, character 210). The form of the axial epipophyses in tyrannosauroids conforms to the form of the epipophyses in the anterior-middle postaxial cervicals, so if these cervicals are well preserved they can be used as a confident proxy for scoring this character. Because this correspondence is not necessarily clear for coelurosaurs as a whole, we only use anterior-middle cervicals as a proxy for tyrannosauroids.

Character 92: Axis, neural spine, form of dorsal portion:

0: flared transversely

1: compressed mediolaterally

Character 93: Cervical vertebrae, epipophyses, position:

0: placed distally on postzygapophyses, above postzygapophyseal facets

1: placed proximally, anterior to postzygapophyseal facets

Character 94: Cervical vertebrae, position of centrum in anterior cervical vertebrae:

0: terminates level with or anterior to the posterior extent of the neural arch

1: extending beyond the posterior limit of the neural arch

Character 95: Cervical vertebrae, carotid process on posterior cervical vertebrae:

0: absent

1: present

Character 96: Cervical vertebrae, shape of anterior articular surface of anterior cervical centra:

0: subcircular or square in anterior view

1: distinctly wider than high, kidney shaped

Character 97: Cervical vertebrae, neural spines, shape in dorsal view:

0: anteroposteriorly long

1: short and centered on neural arch, giving arch an “X” shape in dorsal view

Note: This is equivalent to character 211 in Brusatte et al. (2010a).

Character 98: Cervical vertebrae, number of pneumatic foramina on lateral surface of centra:

0: one on each side

1: two on each side

2: no pneumatic formina (the interior can still be pneumatized via the arch or other access point)

Character 99: Cervical and anterior trunk vertebrae, form: (UNORDERED)

0: amphiplatyan or weakly amphiocoelous (anterior surface flat or weakly concave, posterior surface is flat or weakly concave)

1: opisthocoelous (anterior surface is convex and posterior surface concave forming a proper ball and socket joint) – although some authors have described opsithocoely as present in taxa such as *Alioramus* (Brusatte et al., 2012) these do not exhibit true ball and socket joint, and are scored as 0 here.

2: at least partially heterocoelous

Note: Although the cervicals of tyrannosauroids and some other coelurosaurs are often referred to as "opisthocoelous," this character distinguishes between very weak opisthocoely in which the anterior surface is only very slightly convex (state 0, considered homologous to the amphiplatyan condition) and strong opisthocoely in which the anterior face is strongly convex and forms a proper 'ball-an-socket' joint with the preceding vertebra (state 1). This latter condition is present in *Dilong* and *Eotyrannus* among tyrannoauroids, *Compsognathus*, some alvarezsaurids, and rarely among other coelurosaurs.

Character 100: Dorsal vertebrae, hypapophyses in anterior trunk vertebrae:

0: absent or very small

1: large and pronounced

Character 101: Dorsal vertebrae, parapophyses in posterior trunk vertebrae, form:

0: flush with neural arch

1: distinctly projected on pedicels

Character 102: Dorsal vertebrae, hyposphene-hypantrum articulations:

0: absent

1: present

Character 103: Dorsal vertebrae, opposing zygapophyses on the same vertebra: (ORDERED)

0: abutting or nearly abutting one another above neural canal, opposite hyposphenes (if present) meet to form a single structure (lamina or rectangular projection)

1: zygapophyses placed distinctly lateral to neural canal and hyposphenes (if present) separated as two widely-spaced laminae, which are joined medially by an inset web of bone

2: zygapophyses placed distinctly lateral to neural canal and hyposphenes (if present) separated as two widely-spaced lamina, which are separated medially by a deep groove (the inset web of bone in state 1 is absent)

Note: We have modified this character by dividing state 1 of Turner et al. (2012), which scores for the absence/presence of abutting postzygapophyses, into two states. Both of these states are applicable to taxa with widely separated postzygapophyses and hyposphenes on the midline. Most coelurosaurs have this condition, in which separate left and right hyposphenes take the form of vertical sheets, which are distinctly separated from each other. However, the region between the separated hyposphenes can either house a web of bone, which is only slightly inset from the hyposphenes (state 1), or the web of bone is lost and the hyposphenes and zygapophyses are separated by a deep groove (state 2). Some coelurosaurs have left and right hyposphenes that are appressed to each other on the midline due to closely appressed left and right zygapophyses (*Alxasaurus*, derived tyrannosauroids). This is also the condition in outgroups (e.g., *Allosaurus*), and these taxa and the outgroups are scored for state 0. This character is ordered because the states describe a progressive sequence of conjoined-separation-loss of separating web.

Character 104: Cervical vertebrae, pneumatic foramina on side of centrum:

0: absent

1: present

Character 105: Dorsal vertebrae, transverse processes of anterior dorsals, form:

0: long (in mediolateral direction) and thin (in anteroposterior direction)

1: short (in mediolateral direction), wide (in anteroposterior direction), and only slightly inclined

Character 106: Dorsal vertebrae, neural spines, mediolateral expansion of dorsal end:

0: absent

1: present, expanded to form 'spine table'

Character 107: Dorsal vertebrae, scars for interspinous ligaments, position:

0: terminate at apex of neural spines

1: terminate below apex of neural spine

Character 108:   vertebrae, number: (ORDERED)

0: 5 or less

1: 6

2: 7

3: 8

4: 9

5: 10

6: 11 or more

7: 15 or more

Character 109: Sacral vertebrae, fusion of zygapophyses:

0: absent, or zygapophyses partially fused to each other but still retaining the morphology of the original discrete structures

1: present, completely fused zygapophyses forming a sinuous ridge in dorsal view

Character 110: Sacral centra, ventral surface of posterior sacrals, form: (UNORDERED)

0: gently rounded, convex

1: ventrally flattened, sometimes with shallow sulcus

2: centrum constricted transversely, last sacral with keel or tuber on ventral surface

Character 111: Sacral vertebrae, pneumatic foramina on lateral surfaces of centra: (ORDERED)

0: absent on sacral vertebrae
1: present on anterior sacrals only
2: present on all sacrals

Character 112: Sacral vertebrae, morphology of the posterior articular face of the last sacral centrum:

0: flat or slightly concave
1: convex

Character 113: Caudal vertebrae, change in morphology of free caudals along the tail:

0: present, with distinct transition point from shorter centra with long transverse processes proximally to longer centra with small or no transverse processes distally
1: absent, vertebrae homogeneous in shape, without transition point

Character 114: Caudal vertebrae, location of transition point along the tail: (ORDERED)

0: begins distal to the 10th caudal vertebra
1: between the 7th and 10th caudal vertebra
2: or proximal to the 7th caudal vertebra

Character 115: Caudal vertebrae, morphology of anterior caudal centra: (UNORDERED)

0: tall, oval in cross section
1: with box-like centra in caudals I-V
2: anterior caudal centra laterally compressed with ventral keel

Character 116: Caudal vertebrae, neural spines, form:

0: simple, undivided
1: separated into anterior and posterior alae throughout much of caudal sequence

Character 117: Caudal vertebrae, neural spines on distal caudals (distal to ~caudal 15), form: (ORDERED)

0: present as a low ridge
1: absent
2: absent and location of spine replaced by midline sulcus in center of neural arch

Note: Turner et al. (2012) scored *Dilong* for state 1, but we conservatively rescore this taxon as "?" because we have been unable to observe the caudal vertebrae directly, and also based on the illustrations in Xu et al. (2004), which seem to indicate that there may indeed be remnants of the neural spines on caudals in the vicinity of caudal 15 (state 0). Turner et al. (2012) may have scored this taxon as state 1 based on Xu et al.'s (2004) illustrations of extreme distal caudal vertebrae, which do lack neural spines. However, this is also the case in the extreme distal caudals of tyrannosaurids (e.g., *Tyrannosaurus*) and outgroups (*Allosaurus*), both of which Turner et al. (2012) scored for state 0. What we recognize as state 1 here is the condition in taxa such as *Compsognathus* (Peyer 2006), in which neural spines cease to be recognizable as discrete structures around ca. caudal 15 (in *Tyrannosaurus* and *Allosaurus* this happens much more posteriorly in the tail, ca. caudal 30: Brochu 2003).

Character 118: Caudal vertebrae, length of prezygapophyses of distal caudals: (UNORDERED)

0: between 1/3 and whole centrum length

1: extremely long (up to 10 vertebral segments long in some taxa)

2: strongly reduced or absent, terminate at approximately the anterior level of the centrum

3: prezygapophyses present but negligible in size, clasping the posterior surface of neural arch of preceding vertebrae, postzygapophyses negligible (this is an autapomorphy of *Ichthyornis dispar*)

Note: Turner et al. (2012) scored *Dilong* for state 2, but personal observation of the holotype and the figures of Xu et al. (2004) show that state 0 is the correct score.

Character 119: Caudal vertebrae, number: (ORDERED)

0: more than 40

1: 35-40

2: 25-35

3: 8-25

4: less than 8 free caudal vertebrae, tail very short

Note: We have modified this character by breaking down what was previously a single state (25-40 caudals) into two states, which better allows this character to differentiate the moderately elongate tails of ornithomimosaurs and alvarezsauroids (which have approximately 35 vertebrae) from the shortened tails of therizinosauroids, ornithomimosaurs, and many paravians (which have approximately 25 vertebrae).

Character 120: Chevrons, form of chevrons from proximal part of tail:

0: long and slender, proximal end short anteroposteriorly and shaft cylindrical

1: short and stout, proximal end elongate anteroposteriorly and shaft flattened and plate-like

Note: Turner et al. (2012) scored various compsognathids for state 1, but we have rescored these taxa for state 0, as their proximal chevrons are elongate bones (with anteroposteriorly short proximal ends) that are proportionally similar to other taxa with state 0, such as outgroups (*Allosaurus*) and tyrannosauroids (e.g., *Tyrannosaurus*), and distinct from the short and stout proximal chevrons of other taxa scored for state 1 (such as dromaeosaurids).

Character 121: Chevrons, form of chevrons from distal part of tail: (ORDERED)

0: simple

1: anteriorly bifurcate

2: bifurcate at both ends

Character 122: Cervical ribs, shaft: (UNORDERED)

0: slender and longer than vertebra to which they articulate

1: broad and shorter than vertebra

2: extremely thin and slender, hair-like

Note: We have modified this character to include a third state designating the extremely thin and hair-like cervical ribs of compsognathid-grade theropods, as recognized by Göhlich and Chiappe (2006). This character is unordered because there is no clear set of nested homologies or no clear character transformation sequence.

Character 123: Ossified uncinate processes: (ORDERED)

0: absent

1: present and unfused to ribs

2: present and fused to ribs

Character 124: Ossified ventral (sternal) rib segments:

0: absent

1: present

Character 125: Gastralia, lateral gastral segment, size:

0: shorter than medial one in each lateral-medial gastralium set

1: longer than the medial one

Note: We have modified this character following Claessens (2004). Claessens showed that in outgroups (*Allosaurus*) and tyrannosaurids (*Gorgosaurus*, *Tyrannosaurus*) the medial gastral segment is longer than the lateral gastral segment (state 0), contra the scores in Turner et al. (2012) and previous TWiG matrices. Furthermore, Norell and Makovicky (1997) showed that in *Velociraptor* the lateral segment is longer than the medial segment (state 1), which was affirmed by Claessens (2004) but contra the score in Turner et al. (2012). We suspect that scores 0 and 1 may have been swapped for some or all taxa accidentally in the TWiG matrix. Because of the confusion of scores in the original TWiG matrix, we conservatively take all character scores from Claessens (2004) and leave all other taxa as "?", unless observed personally by S. Brusatte or specifically reported in the literature.

Character 126: Sternum, ossified sternal plates, fusion:

0: absent, left and right plates separate in adults

1: present, left and right plates fused

Character 127: Sternum, lateral xiphoid process posterior to costal margin:

0: absent

1: present

Character 128: Sternum, groove on anterior edge for reception of coracoid:

0: present

1: absent

Character 129: Sternum, position of articular facet for coracoid (conditions may be determined by the position of the the articular facet on coracoid in taxa without ossified sternum):

0: anterolateral or more lateral than anterior

1: almost anterior

Character 130: Furcula, hypocledium: (**ORDERED)**

0: absent

1: present as tubercle

2: present as an elongate process

Character 131: Scapula, orientation of acromion margin:

0: continuous with blade

1: anterior edge laterally everted relative to blade

Character 132: Coracoid, expansion of posterolateral surface ventral to glenoid fossa:

0: unexpanded

1: posterolateral edge of coracoid expanded to form triangular subglenoid fossa bounded laterally by enlarged coracoid tuber

Character 133: Scapula and coracoid, fusion:

0: absent, two bones separate

1: present, two bones fused into scapulacoracoid

Character 134: Coracoid, shape in lateral view: (UNORDERED)
0: subcircular, with shallow ventral blade
1: subquadrangular with extensive ventral blade
2: shallow ventral blade with elongate posteroventral process
3: height more than twice width, coracoid strut-like
Character 135: Scapula and coracoid, form of their articulation:
0: form a continuous arc in posterior and anterior views
1: coracoid inflected medially relative to scapula, scapulocoracoid 'L' shaped in lateral view
Character 136: Scapula and coracoid, glenoid fossa, orientation of articular surface:
0: faces posteriorly or posterolaterally
1: faces laterally
Character 137: Scapula, length compared to length of humerus:
0: longer
1: approximately same length or shorter
Note: In *Guanlong*, the scapula and humerus are approximately the same length (Xu et al. 2006), so this taxon is scored for state 1. The same scoring is used for all ornithomimosaurs, which have humeri that are slightly longer than the scapula (Osmólska et al. 1972) or have humeri and scapulae of approximately the same length (e.g., Nicholls and Russell 1985; Kobayashi and Lü 2003; Kobayashi and Barsbold 2005; Makovicky et al. 2010).
Character 138: Humerus, deltopectoral crest, extent and morphology: (UNORDERED)
0: large and distinct, proximal end of humerus quadrangular or triangular in anterior view
1: deltopectoral crest less pronounced, forming an arc rather th an being quadrangular
2: deltopectoral crest very weakly developed, proximal end of humerus with rounded edges
3: deltopectoral crest extremely long and rectangular
Character 139: Humerus, deltopectoral crest, form of anterior surface:
0: smooth
1: with distinct muscle scar near lateral edge along distal end of crest for insertion of biceps muscle
Character 140: Ulna, olecranon process, size [Ordered]:
0: weakly developed
1: distinct and large
2: Very expanded, more than 30% length of ulna (state 2 added for later diverging alvarezsauroids with a hypertrophied olecranon). This character has been ordered here to reflect the intermediate condition of state 1.
Character 141: Ulna, morphology of distal articular surface (dorsal condyle and dorsal trochlea in birds):
0: flat
1: convex, semilunate surface
Character 142: Ulna, morphology of proximal surface:

0: a single continuous articular facet

1: divided into two distinct fossae (one convex, the other concave) separated by a median ridge

Character 143: Lateral proximal carpal (ulnare?), shape in proximal view:

0: quadrangular

1: triangular

Character 144: Distal carpals in contact with metacarpals, number:

0: two separate carpals, one covering the base of metacarpal I (and perhaps contacting metacarpal II) the other covering the base of metacarpal II

1: a single distal carpal capping metacarpals I and II

Character 145: Semilunate distal carpal, size: (UNORDERED)

0: well developed, covering all of proximal ends of metacarpals I and II

1: small, covers about half of base of metacarpals I and II

2: covers bases of all metacarpals

3: covers MC II and MC III

Character 146: Metacarpal I, length: (ORDERED)

0: less than half the length of metacarpal II

1: approximately half of the length (~50-70%) of metacarpal II

2: subequal in length to metacarpal II

Note: We have modified the character of Turner et al. (2012) to include a new state, signifying the condition in some tyrannosauroids (and outgroups and other coelurosaurs) in which metacarpal I is approximately half of the length of metacarpal II. In essence, we have divided the original “half or less of the length of metacarpal II” character into two distinct states. This follows the character of Brusatte et al. (2010a, character 252). We have also removed the state in Turner et al.’s (2012) character that refers to the autapomorphically short and robust metacarpals I of alvarezsaurids, which are wider transversely than long proximodistally. We now provide a separate character denoting the presence or absence of this peculiar morphology below.

Character 147: Third manual digit, size:

0: present and large, phalanges present

1: reduced to no more than metacarpal splint

Note: This character is equivalent to Brusatte et al. (2010a, character 249).

Character 148: Manual unguals, curvature: (ORDERED)

0: strongly curved, flexor margin deeply concave

1: weakly curved, flexor margin shallowly concave (third ungual may be straight)

2: all manual unguals straight

Note: We have divided the original character of Turner et al. (2012) and previous TWiG matrices, which related to both the curvature and size of the flexor tubercle, into two separate characters. This character now refers to the degree of curvature, whereas a separate character has been added below for the size of the flexor tubercle. Furthermore, a separate character has also been added to simply denote the presence and absence of manual unguals (to distinguish the condition of derived avialans in which unguals are absent, which was originally one of several unordered character states in Turner et al.’s character). As constructed, this current character on manual ungual curvature subsumes c haracter 255 of Brusatte et al. (2010a). We here score *Dryptosaurus* for state 0 (strongly curved manual unguals) based on the recent redescription of this taxon by Brusatte et al. (2011c), contra the “weak curvature” score in Brusatte et al. (2010a). Many ornithomimosaurs have a straight manual ungual 3 but more curved manual unguals 1 and 2. These taxa are here scored for state 1, whereas those ornithomimosaurs with straight manual digits 1-3 are scored as state 2. We do not differentiate state 1 into multiple states for “weak curvature in all unguals” vs. “weak curvature in unguals 1 and 2 and a straight ungual 3,” because derived tyrannosauroids do not possess a manual ungual 3, which would make it impossible to score them for this character as currently constructed. Therefore, we conservatively lump together these two conditions into state 1, but recognize that future authors may advocate subdividing this character (but this would necessitate scoring derived tyrannosaurids as inapplicable, or dividing this character into multiple characters).

Character 149: Manual unguals, size of ungual on digit I compared to the other manual unguals in the hand:

0: generally similar in size

1: distinctly larger

Character 150: Manual unguals, a transverse ridge immediately dorsal to the articulating surface (“proximodorsal lip”):

0: absent

1: present

Character 151: Ilium, preacetabular process, anteroventral corner, form: (UNORDERED)

0: subtriangular, ventral margin of preacetabular process is shallowly concave

1: subquadrate with recurved anterior margin, ventral margin of preacetabular process is deeply concave such that the open region between the pubic peduncle and anteroventral region of the preacetabular process defines much of a circle

2: process strongly hooked

Note: This character subsumes Brusatte et al. (2010a, character 259). State 1 is seen in some derived tyrannosauroids and ornithomimosaurs (and a few other coelurosaurs), and specifically refers to an anteroventral corner of the preacetabular process that is so recurved and ventrally projecting that the notch between it and the pubic peduncle is wide and essentially circular. Turner et al. (2012) and previous TWiG matrices scored the ougroups (*Allosaurus* and *Sinraptor*) as possessing state 1. However, although these taxa do have somewhat of a hooked anterior margin of the preactabular process (as do some compsognathids such as *Sinocalliopteryx*), they do not have the extremely pronounced condition of derived tyrannosauroids.

Character 152: Ilium, preacetabular process, length: (ORDERED)

0: roughly as long as postacetabular process

1: markedly longer (more than 2/3 of total ilium length) than postacetabular process

2: postacetabular blade much longer than postacetabular process

Character 153: Ilium, morphology of anterior margin of preacetabular process: (UNORDERED)

0: gently rounded or straight

1: anterior end strongly convex, lobate

2: pointed at anterodorsal corner with concave anteroventral edge

3: distinctly concave dorsally

Note: Turner et al. (2012) scored *Dilong* for state 0, which is unexpected if it is a tyrannosauroid (as all known tyrannosauroids possess state 3). However, based on personal observation of the specimen (IVPP V14243) the anterodorsal margin of the ilium is broken, so we here score this taxon as "?". *Sinocallipteryx* is described as possessing a "slightly concave" anterodorsal margin of the preacetabular process, and this is clearly shown in an accompanying figure (Ji et al. 2007). Although we would prefer to confirm this score based on the original specimen, in order to determine whether it is genuine or a potential artifact of breakage, we here score *Sinocallipteryx* for state 3. Li et al. (2010) noted that *Mirischia* may possess an anterodorsal concavity, but personal observation of the specimen (SMNK 2349 PAL) shows that this region is broken, and therefore we score this taxon as "?".

Character 154: Ilium, supraacetabular crest on ilium, form: (ORDERED)

0: present as a separate process from the antitrochanter, and forming a "hood" over the femoral head

1: reduced but still separate from the antitrochanter, not forming "hood"

2: absent

Character 155: Ilium, postacetabular process, shape of distal end: (UNORDERED)

0: squared

1: acuminate

2: squared, with nearly vertical posterior margin that is nearly equivalent in depth to the anterior margin of the preacetabular process

Note: We have expanded this character into an unordered multistate, by adding a third state referring to the extremely deep and squared-off postacetabular processes of some derived tyrannosauroids such as *Alioramus* and *Tyrannosaurus*, as noted by Brusatte et al. (2010a, character 267). This condition differs from the shallower postacetabular processes of more basal tyrannosauroids such as *Guanlong*, *Dilong*, and *Juratyrant*. In these taxa the postacetabular process is squared off posteriorly, but is much shallower than the preacetabular process.

Character 156: Ilium, opposing postacetabular blades, orientation in dorsal view:

0: subparallel to each other

1: diverge posteriorly from each other

Note: The "subparallel" condition includes those iliac blades which are oriented medially to contact each other (or nearly contact) above the sacrum (these blades are parallel to each other, but instead of their lateral surfaces being oriented straight laterally they are instead oriented dorsolaterally, hence the convergence above the midline). In some of these taxa, such as the ornithomimosaurs *Gallimimus* and *Garudimimus*, the postacetabular blades diverge from each other when seen in dorsal view, but this is a result of the reorientation of the lateral surface to face dorsolaterally, due to the medial orientation of the two blades to contact each other (or nearly contact) above the acetabulum. Without this medial rotation the postacetabular processes would be parallel or nearly parallel to each other. State 1 refers to the condition in some maniraptorans in which the two iliac blades clearly diverge from each other posteriorly when seen in dorsal view.

Character 157: Ilium, tuber along dorsal edge of ilium dorsal or slightly posterior to acetabulum:

0: absent

1: present

Character 158: Ilium, brevis fossa, form: Unordered

0: shallowly inset into bone, brevis shelf projects strongly medially

1: deeply inset into bone, with both lateral lamina and medial brevis shelf curving ventrally to demarcate the deeply concave fossa

2: Medial brevis shalf low but situated high on medial face of postacaetabular blade (seen in alavarezsaurids)

Character 159: Ilium, antitrochanter, form:

0: absent or poorly developed

1: prominent

Note: This character is equivalent to Brusatte et al. (2010a, character 261). In scoring this character, we hold that the large antitrochanters of derived tyrannosauroids, which are extensive flanges that are deeply inset from the remainder of the ischial peduncle, are primarily homologous to the prominent antitrochanters of most other coelurosaurs. Therefore, tyrannosauroids with flange-like antitrochanters and other coelurosaurs with prominent antitrochanters are both scored for state 1.

Character 160: Ilium, ridge bounding cuppedicus fossa, extension:

0: terminates anterior to acetabulum or curves ventrally onto anterior end of pubic peduncle

1: extends far posteriorly and to become confluent or almost confluent with acetabular rim

Character 161: Ilium, cuppedicus fossa, form: (ORDERED)

0: deeply inset into the anterior and lateral surfaces of the pubic peduncle, with a pronounced dorsal rim

1: reduced, fossa shallow or flat, with little or no overhanging dorsal rim

2: absent

Character 162: Ischium, prominent median posterior process along posterior edge of bone:

0: absent, posterior edge of bone straight

1: present

Character 163: Ischium, morphology of shaft distal to the acetabular (obturator) region: (ORDERED)

0: extremely rod-like, midshaft diameter 30-50% midshaft diameter of pubis

1: rod-like, midshaft diameter 60-100% midshaft diameter of pubis

2: wide, flat, and plate-like, midshaft diameter greater than midshaft diameter of pubis

Note: This is a modified character that subsumes character 280 in Brusatte et al. (2010a). In essence, we here separate the “rod-like” character into two characters: extremely rod-like (in which the ischial shaft is less than 50% of the width of the pubic shaft, seen in some derived tyrannosauroids) and somewhat rod-like (in which the ischial shaft and pubic shaft are approximately the same diameter, seen in many coelurosaurs). We have rescored *Ornitholestes* for state 1 (somewhat rod-like), from Turner et al.’s (2012) polymorphic score for both a rod-like and a plate-like shaft in this taxon. We also score the tyrannosauroids *Dryptosaurus* and *Alioramus* as polymorphic for states 0 and 1. This is a conservative score, because it is clear that the ischium of these taxa is rod-like but it is unclear how the midshaft diameter compares to the pubic midshaft diameter.

Character 164: Ischium, orientation of shaft: (UNORDERED)

0: straight

1: curved anteriorly at the ventral end

2: hooked posteriorly at the ventral end

Character 165: Ischium, surface morphology of lateral face of ischiadic blade: (UNORDERED)

0: flat or gently rounded

1: concave

2: with longitudinal ridge subdividing lateral surface into anterior (including obturator process) and posterior parts

Character 166: Ischium, obturator process of ischium: (ORDERED)

0: absent

1: proximal in position (midpoint of process positioned at less than 30% of the total length of the ischium)

2: located near middle of ischiadic shaft (midpoint of process positioned at approximately 40-50% of the total length of the ischium)

3: located at distal end of ischium (midpoint of process positioned distal to the midpoint of the ischium)

Note: The language in this character has been modified following the quantitative character description of Brusatte et al. (2010a, character 281).

Character 167: Ischium, obturator process, contact with pubis:

0: absent

1: present

Character 168: Ischium, obturator foramen or notch in proximal portion of obturator process: (ORDERED)

0: enclosed foramen present

1: open notch present (i.e., a foramen that is no longer completely enclosed)

2: notch or foramen absent

Note: This character has been modified to take into account the closed obturator foramen of *Guanlong* and *Mirischia*, which although unusual among coelurosaurs and proximal outgroups (allosauroids) is also seen in more distal basal theropod outgroups. Although Naish et al. (2004) described the left and right obturator foramina in *Mirischia* as asymmetrical (one open as a notch, one enclosed), we interpret the supposedly open notch as a closed foramen that has been broken, based on personal observation of the specimen (SMNK 2349 PAL). Turner et al. (2012) scored derived tyrannosauroids for “notch or foramen absent,” whereas *Dilong*, compsognathids, and ornithomimosaurs were scored for “open notch present.” However, all tyrannosauroids have an open obturator notch that is essentially identical in morphology to those of ornithomimosaurs and compsognathids. Therefore, these taxa are here scored for state 1.

Character 169: Ischium, ischial tubercle (“semicircular scar”) ventral to iliac peduncle on the posterior margin of the proximal end of ischium: (ORDERED)

0: absent or potentially homologous structure present as a groove

1: present as a convex bulge on the posterior surface of the ischium

2: present as a rugose, ovoid or triangular flange whose lateral surface is depressed relative to the remainder of the ischium

Note: This character has been modified, and an additional state added, based on Brusatte et al. (2010a, character 278). We consider the condition in ornithomimosaurs to be equivalent to the "convex bulge" condition of the tyrannosauroid *Juratyrant*, and score more derived tyrannosauroids for a hierarchically nested condition of an especially rugose, flange-like tubercle. We also consider the "groove-like" morphology of this region of the ischium to be homologous, at some level, to the ischial tubercle itself (see Hutchinson 2001). Because it is difficult to distinguish the groove-like condition from true absence of any muscular attachment in this region, we lump together both conditions as state 0 but recognize that future work may be able to subdivide these conditions into separate character states.

Character 170: Ischium, length of bone:

0: greater than two-thirds of pubis length

1: two-thirds or less of pubis length

2: greater than length of pubis (added to reflect condition in scansoriopterygidae)

Character 171: Ischium, morphology of distal ends of opposing ischia: (ORDERED)

0: form symphysis

1: approach one another but do not form symphysis

2: widely separated

Note: We here score all tyrannosauroids for state 0, contra Turner et al. (2012) who score derived taxa for state 1. As discussed by Brusatte et al. (2012a), the distal ischia of tyrannosauroids do make contact with each other, although this contact is unfused. This is equivalent to the condition in ornithomimosaurs and compsognathids, and we here score all of these taxa for state 0.

Character 172: Ischium, distal end, expansion relative to midshaft:

0: present, resulting in an ischial "boot"

1: absent, ischial "boot" absent

Note: This character is equivalent to Brusatte et al. (2010a, character 279).

Character 173: Ischium, tubercle on anterior edge of bone:

0: absent

1: present

Character 174: Pubis, orientation of shaft when in articulation: (UNORDERED)

0: projecting anteroventrally (propubic)

1: vertical

2: projecting posteroventrally (opisthopubic)

3: appressed to ischium

Note: This character subsumes Brusatte et al. (2010a, character 275). We consider this character unordered because there is not a clear transformation sequence or nested set of homologies, although it is possible that future authors may argue for an anteroventral-vertical-posteroventral trend in theropod pelvic evolution.

Character 175: Pubis, pubic boot, anterior projection of boot relative to posterior projection: (ORDERED)

0: equal in size or anterior process larger than posterior process

1: anterior process small, approximately 10-40%

2: anterior process completely absent, posterior process large

3: both anterior and posterior processes absent (i.e., boot present but without distinct anterior and posterior projections)

Note: This character subsumes Brusatte et al. (2010a, character 273). We have added an additional state here, to distinguish between taxa in which the anterior and posterior projections are equal in size (some derived tyrannosaurids) and those taxa in which anterior projections are present but are approximately 10-40% of the length of the posterior projection (many other coelurosaurs). Using our character scoring scheme, compsognathids and various paravians are scored for state 2, which refers to the complete lack of an anterior process and a pubic boot that is often "hook-like" in its morphology.

Character 176: Pubis, shelf on shaft proximal to symphysis ('pubic apron'): (UNORDERED)

0: extends medially from middle of shaft

1: shelf extends medially from anterior edge of shaft

2: strongly reduced (restricted to distal end of pubis) or absent

Note: Turner et al. (2012) scored tyrannosauroids (including *Dilong* and tyrannosaurids) for state 0, but we here rescore all score-able tyrannosauroids for state 1, based on personal observation of specimens. In all known tyrannosauroid pubes the pubic apron arises from the anterior margin of the shaft, not the middle of the shaft as in outgroups like *Allosaurus* (Madsen 1976). We have also removed the language in the original TWiG character relating to the cylindrical or anteroposteriorly flattened nature of the shafts, as these conditions do not correspond 1-to-1 with the location of the apron. Future authors may wish to reintroduce a character relating to the morphology of the shaft (cylindrical vs. flattened), but we could not identify clear, distinct categories of variation among taxa and hence do not utilize such a character here.

Character 177: Pubis, curvature of shaft: (UNORDERED)

0: absent, shaft straight

1: distal end curves anteriorly, anterior surface of shaft concave

2: distal end curves posteriorly, anterior surface of shaft convex

Note: This character subsumes character 269 of Brusatte et al. (2010a). Derived tyrannosauroids are here scored for state 1, a concave anterior margin of the pubic shaft, based on Brusatte et al. (2010a).

Character 178: Pubis, length of pubic apron: (ORDERED)

0: about half of pubic shaft length

1: less than 1/3 of shaft length

2: greatly reduced, restricted to far distal end of pubis

3: absent

Note: We modified this character to make it into an additive multistate referring to the presence/absence and size of the pubic apron. For all other pubic apron characters, those taxa without an apron are scored as inapplicable ("?").

Character 179: Pubic apron, form of contact between opposing pubes distally: (ORDERED)

0: both pubes meet extensively

1: contact between pubes disrupted by a slit (pubic foramen)

2: no contact between pubes distally, pubic apron absent in this part of pubis but present further proximally

Note: The pubic fenestra is usually considered a synapomorphy of Tetanurae (Rauhut 2003; Benson et al. 2009). Turner et al. (2012) scored *Dilong* for state 0, but personal observation of the specimen indicates that the distal portion of the conjoined pubes is too damaged (and not complete enough) to permit observation of the fenestra. Therefore, it is here scored "?". Turner et al. (2012) also scored *Haplocheirus* for state 0, which would be unexpected, but because we cannot confirm this with a personal observation we conservatively score it as "?".

Character 180: Femur, head, fovea capitalis for attachment of capital ligament:

0: absent or subtle

1: present as a distinct circular fovea located in center of the medial surface of the head

Character 181: Femur, interaction of lesser and greater trochanters: (ORDERED)

0: separated from each other by deep cleft

1: separated from each other by small groove

2: completely fused to each other (absent as distinct structures), forming a trochanteric crest

Character 182: Femur, lesser trochanter, shape in lateral view:

0: alariform, projects anteriorly as a broad flange that is anteroposteriorly wider than the greater trochanter

1: reduced to approximately the same anteroposterior width as the greater trochanter, cylindrical in cross section

Character 183: Femur, ridge on lateral surface distal to lesser and greater trochanters (homologous to the trochanteric shelf):

0: absent or represented only by faint rugosity or bulge

1: distinctly raised from shaft as a pronounced, mound-like ridge

Character 184: Femur, fourth trochanter:

0: present

1: absent (or reduced to a subtle and barely distinguishable margin)

Character 185: Femur, accessory trochanteric crest distal to lesser trochanter:

0: absent

1: present

Note: We consider the "accessory trochanteric crest" (identified by Makovicky and Sues [1998] in *Microvenator*) as equivalent to the accessory trochanter that is present in some tetanurans (including some coelurosaurs: e.g., Brusatte et al. 2008c), as both structures are accessory flanges or ridges along the anterior margin of the distal portion of the lesser trochanter. Therefore, this character is equivalent to Brusatte et al. (2010a, character 287). Accessory trochanters are large and prominent in basal tyrannosauroids (*Guanlong*, *Xiongguanlong*) but are lost in more derived tyrannosauroids. They are also large and prominent in several basal coelurosaurs (e.g., ornithomimosaurs, *Mirischia*, *Zuolong*, *Coelurus*, *Tanycolagreus*).

Character 186: Femur, mesiodistal crest, form:

0: absent or present as a subtle structure

1: present as a pronounced longitudinal crest extending proximally from medial condyle, which is seen to strongly overhang the remainder of the medial margin of the femur in posterior view (i.e., is visible as a broad flange in posterior view

Note: We have reworded this character to make it refer specifically to the pronounced mesiodistal crest of some coelurosaurs. This crest is either located on the anterior surface of the femur (as described in the original TWiG character) or along the anteromedial corner of the femur, but in all cases extends proximally from the medial condyle.

Character 187: Femur, flexor groove, morphology of distal end:

0: open distally, smoothly confluent with distal articular surface

1: closed off distally by contact between distal condyles, separated from distal articular surface

Character 188: Fibula, distal extent:

0: reaches proximal tarsals

1: short, tapering distally, and not in contact with proximal tarsals

Character 189: Fibula, medial margin of proximal end in proximal view:

0: concave

1: flat

Character 190: Fibula, deep oval fossa, with well defined margins, on medial surface near proximal end:

0: absent

1: present

Note: This character refers specifically to the discrete, ovoid fossa of some tyrannosauroids and ornithomimosaurs, as well as outgroup taxa. Some other basal coelurosaurs such as *Coelurus* and *Zuolong* have a depressed groove excavating much of the medial surface of the proximal fibula, but this is not present as a discrete, indented fossa with well defined margins (instead, the groove has a well defined anterior margin but opens posteriorly). The outgroups are scored for state 0, because they possess an open fossa (without a distinct posterior margin) as in most coelurosaurs.

Character 191: Astragalus and calcaneum, morphology of distal condyles:

0: condyles separated by shallow, indefinite sulcus

1: condyles separated by prominent tendinal groove on anterior surface

Character 192: Tibia, number of cnemial crests:

0: single pronounced crest

1: two crests (main crest with accessory anterior crest)

Character 193: Astragalus, ascending process, form: (UNORDERED)

0: tall and broad, covering most of anterior surface of distal end of tibia (70% or more of mediolateral width of surface) and dorsoventral height greater than twice the height of the main body of the astragalus

1: process short and slender, covering only lateral half of anterior surface of tibia and dorsoventral height less than twice the height of the main body of the astragalus

2: ascending process tall, but with medial notch that restricts it to lateral side of anterior face of distal tibia

3: Process medially restricted but long and bearing a lateral extension that contacts the fibula.

Note: This character includes information on both the dorsoventral height and mediolateral width of the ascending process. Sometimes these measurements are given separate characters, but we here hold that they are generally correlated, in the sense that taxa with a very tall ascending process always have a mediolaterally broad process as well, and taxa such as *Guanlong* and *Falcarius* with a short ascending process also have a mediolaterally restricted process. We recognize, however, that future authors may want to break this character into separate characters referring to length and width, but we hesitate to do so because we do not wish to introduce a second character that is likely correlated with the first.

The ascending processes of compsognathids have been described as somewhat reduced, in that they only cover approximately 70% of the anterior surface of the tibia (Ostrom 1978; Currie and Chen 2001; Hwang et al. 2004). We consider this condition equivalent to state 0 here, but recognize that future authors may want to subdivide state 0 into separate characters for a broad ascending process that covers most of the anterior surface of the tibia and a reduced process that covers approximately 70% of the surface. These could be associated with state 1 here (a process covering half the tibial surface) to create an ordered multistate, and state 2 here (which is unique to some alvarezsaurids) could be made into its own character. We do not do this, however, because we hesitate to divide state 0 into additional states because the “reduced” ascending processes of compsognathids are all based on slab specimens, which are difficult to measure and often prone to misinterpretation. It is clear, however, that these compsognathids do not possess the reduced and laterally restricted ascending processes of some basal coelurosaurs (e.g., *Guanlong*, *Coelurus*, *Tugulusaurus*) and the ougroups (*Allosaurus*, *Sinraptor*), which are denoted by state 1. This character is an equivalent, but expanded, version of Brusatte et al. (2010a, character 297).

Character 194: Astragalus, ascending process, articulation with condyles distally:

0: confluent with condylar region of astragalus

1: separated from condylar region by transverse groove or fossa across base

Character 195: Astragalus and calcaneum, fusion: (ORDERED)

0: absent, astragalus and calcaneum unfused to each other or to tibia in adults

1: present, astragalus and calcaneum fused to each other, unfused to tibia

2: present, astragalus and calcaneum completely fused to each other and to tibia

Character 196: Distal tarsals, fusion with metatarsals:

0: absent, distal tarsals and metatarsals separate

1: present, distal tarsals and metatarsals fused into tarsometatarsus

Character 197: Metatarsals, fusion: (ORDERED)

0: absent, metatarsals not co-ossified

1: present, metatarsals co-ossified proximally

2: present, metatarsals co-ossified proximally and distally

3: present, metatarsals co-ossified proximally and distally, with distal fusion extreme and distal vascular foramen closed

Character 198: Metatarsal II, morphology of distal end:

0: smooth, not ginglymoid

1: with developed ginglymus that extends onto extensor surface, giving the distal end a strongly concave profile in extensor (anterior) view

Character 199: Metatarsal III, morphology of distal end:

0: smooth, not ginglymoid

1: with developed ginglymus: smooth articular region extends proximally onto extensor surface and is broadly exposed

Note: We here consider the condition in some basal coelurosaurs (*Zuolong*, *Tugulusaurus*, *Dilong*, *Guanlong*) to represent a well developed ginglymus, as defined for character state 1. Xu et al. (2004) recognized that *Dilong* was unusual among tyrannosauroids in possessing a gingylmus on metatarsal III (although it is absent on metatarsal II), a character score that was followed by Turner et al. (2012). Later discoveries showed that this character state is also present in some other basal coelurosaurs: Rauhut and Xu (2005) later noted that one was present on *Tugulusaurus* and Choiniere et al. (2010b) described and figured it for *Zuolong*. Our personal observations of *Guanlong* show that it is present in this taxon as well. *Bicentenaria* is described by Novas et al. (2012) as lacking a ginglymoid distal end of metatarsal III, but we score this taxon here as "?" because we have not been able to observe it, and therefore cannot assess if it has the basal coelurosaur-style ginglymoid condition of *Guanlong*, *Tugulusaurus*, and *Zuolong*.

Character 200: Metatarsal III, exposure of proximal shaft in extensor view: (ORDERED)

0: prominently exposed between MT II and MT IV along entire metapodium

1: MT III proximal shaft constricted and much narrower than either II or IV, but still exposed along most of metapodium, subarctometatarsal

2: very pinched, not exposed along proximal section of metapodium, arctometatarsal

3: proximal part of MT III lost entirely

Note: We here consider this character ordered, because we hypothesize nested homology between the subarctometatarsal-arctometatarsal-mt III lost states (i.e., these form an ordered, progressive sequence of metatarsal III pinching and eventual loss). This character is equivalent to Brusatte et al. (2010a, Character 299).

Character 201: Pedal digit II, ungual and penultimate phalanx, morphology:

0: similar to those of III

1: penultimate phalanx highly modified for extreme hyper-extension, ungual more strongly curved and significantly larger than that of digit III

Character 202: Metatarsal II, site of articular surface for metatarsal I: (UNORDERED)

0: the middle of the medial surface of metatarsal II

1: the posterior surface of distal quarter

2: the medial surface near the proximal end

3: the medial surface at or near the distal end

Character 203: Metatarsal I, form of proximal end:

0: attenuates proximally, articular surface for metatarsal II is a simple butt joint lying against the shaft of metatarsal II

1: large and robust, similar to those of metatarsals II-IV

Note: Although character states could probably be inferred by the form and position of the metatarsal I articular scar on metatarsal II, we conservatively score taxa for an affirmative score only if we can observe metatarsal I itself.

Character 204: Metatarsal IV, shaft thickness:

0: round or thicker dorsoventrally (extensor-flexor direction) than wide mediolaterally in cross section

1: mediolaterally widened and flat in cross section

Character 205: Foot, symmetry:

0: symmetrical

1: asymmetrical with slender MTII and very robust MT IV, excluding flange

2: asymmetrical with slender MTIV terminating in triangular distal articulation that is much longer than wide and a more robust MT II. State 2 was defined by Motta et al. (in press) to distinguish unenlagiines like *Neuquenraptor*, *Pamparaptor*, and *Austroraptor*

Character 206: Dorsal vertebrae, neural spines on posterior dorsals, shape in lateral view:

0: rectangular or square

1: fan-shaped, anteroposterior length of spine expanding dorsally

Note: State 1 refers specifically to the fan-shaped neural spines of compsognathids and *Pelecanimimus*, whose dorsal extremity is substantially longer anteroposteriorly than is the base of the spine. This is due to a "funneling outwards) in anteroposterior length dorsally across the length of the spine. Some theropods (e.g., *Tanycolagreus*, some ornithomimosaurs in intermediate phylogenetic position between *Pelecanimimus* and derived taxa with rectangular neural spines) have some dorsal vertebrae with neural spines that are moderately expanded at their dorsal tips, but these do not exhibit the striking fan shape of compsognathids, and are thus scored for state 0.

Character 207: Manual phalanx I-1, shaft diameter:

0: less than or approximately equal to the shaft diameter of radius.

1: greater than the shaft diameter of radius.

Note: State 1 of this character refers to a phalanx that is substantially thicker in diameter than the radius. Several coelurosaurs (e.g., *Tanycolagreus*, tyrannosauroids, ornithomimosaurs) have a phalanx I-1 that is approximately the same diameter of the radius, and sometimes is slightly larger (~10%). These taxa are scored for state 0, however, because this condition differs from the condition in compsognathids in which the phalanx is dramatically larger than the radius (state 1).

Character 208: Angular, extent in lateral view:

0: widely exposed, suture between surangular and angular reaches or nearly reaches posterior end of mandible

1: reduced in exposure, suture between surangular and angular does not reach posterior end of the mandible

Character 209: Surangular, laterally inclined flange along dorsal edge of bone for articulation with the lateral process of lateral quadrate condyle:

0: absent

1: present

Character 210: Distal articular ends of metacarpals I + II: (UNORDERED)

0: ginglymoid

1: rounded, smooth

2: II ginglymoid and MC I shelf

Character 211: Radius and ulna, articulation with each other:

0: well separated

1: with distinct adherence or syndesmosis distally

Character 212: Upper and lower jaws, occlusion:

0: occlude for their full length

1: diverge anteriorly due to kink and downward deflection of the dentary (pronounced downward deflection of dentary buccal margin anteriorly)

Character 213: Quadrate, exposure of head in lateral view:

0: absent, covered by squamosal laterally

1: present, exposed because quadrate cotyle of squamosal opens laterally due to a wide notch between the ventral and posterior processes

Character 214: Ilium, brevis fossa, orientation and exposure in lateral view:

0: faces primarily ventrally, but it is widely visible in lateral view (especially anteriorly)

1: faces primarily ventrally and medially, and it is obscured in lateral view across its entire length by a well developed lateral lamina of the postacetabular process of the ilium

Note: This character is equivalent to character 310 in the revised version of the Brusatte et al. (2010a) analysis published by Brusatte and Benson (2013). We have altered the wording here to reflect the character language of Brusatte and Benson (2013), which focuses specifically on whether the fossa is visible or obscured in lateral view.

Character 215: Lesser trochanter, vertical ridge on lateral surface:

0: present

1: absent

Character 216: Supratemporal fossa, extension onto the squamosal:

0: absent, fenestra bounded laterally and posteriorly by the squamosal, with no distinct fossa present on the dorsal surface of the squamosal

1: present, distinct fossa extends onto the dorsal surface of the squamosal

Character 217: Dentary, teeth: (ORDERED)

0: present across much of bone, dentary fully toothed

1: present but only at the far anterior tip

2: absent, dentary edentulous

Character 218: Coracoid, ventral (=anterior) margin of bone anterior (=ventral) to glenoid, form:

0: straight or shallowly indented by a notch

1: deeply indented by a pronounced notch separating the glenoid and postglenoid process, glenoid lip everted

Note: State 1 refers to the deep notch of ornithomimosaurs, which separates the glenoid from a pronounced and hook-shaped postglenoid process anteriorly. Many other coelurosaurs have a shallow notch in this region, but only ornithomimosaurs have a discrete, deep notch, which helps to define the characteristic hook-like postglenoid process in these taxa.

Character 219: Articular, retroarticular process, orientation:

0: points posteriorly

1: curves gently posterodorsally

Character 220: Scapula, flange on supraglenoid buttress:

0: absent

1: present

Character 221: Laterosphenoid, depression (possibly pneumatic) on ventral surface of postorbital process of bone:

0: absent

1: present

Character 222: Braincase, basal tubera, mediolateral width of conjoined tubera relative to occipital condyle: (ORDERED)

0: as wide as or wider than the occipital condyle

1: narrower than occipital condyle, reduced to a set of small processes directly below the condyle and separated by a narrow notch

2: tubera absent

Note: This character is not equivalent to characters 154 and 155 in Brusatte et al. (2010a), which refer to the dorsoventral depth of the basal tubera and the depth of the notch between the tubera, respectively. This character refers solely to the mediolateral width of the tubera, and is considered an ordered character because we hypothesize a nested set of homologies (large-small-absent). The highly modified basal tubera of derived therizinosauroids are here regarded as possessing state 0 and not state 2 (absent), as remnants of the tubera are still present despite their incorporation into the basisphenoidal bulla.

Character 223: Ilium, postacetabular process, morphology of dorsal edge:

0: convex or straight

1: deeply concave, ventral portion of postacetabular process (housing brevis shelf medially) extending posterior to dorsal portion of the postacetabular process as a tab-like structure

Note: State 1 refers to the condition in some dromaeosaurids (e.g., *Unenlagia*), in which the dorsal margin of the postacetabular process is deeply concave, due to the extension of the ventral portion of the postacetabular process posteriorly as a discrete, rectangular, tab-like structure. This tab-like structure is ornamented by the brevis shelf medially, and therefore houses an extension of the brevis fossa itself. Some ornithomimosaurs have a subtly concave dorsal border of the postacetabular process, but this is not considered equivalent to the marked condition of some dromaeosaurids.

Character 224: Ilium, posterior end of postacetabular process, morphology in dorsal view:

0: terminating in rounded or square end, due to a brevis shelf that extends no farther than the posterior margin of the lateral lamina (lateral surface) of the postacetabular process

1: with lobate brevis shelf projecting beyond posterior end of lateral lamina of postacetabular process

Character 225: Pedal phalanx II-2, flexor heel, form:

0: small and asymmetrically developed only on medial side of vertical ridge subdividing proximal articulation

1: heel long and lobate, with extension of midline ridge extending onto its dorsal surface

Note: Taxa without a discrete flexor heel are scored as inapplicable (“?”).

Character 226: Metatarsal IV, large, longitudinal flange along posterior or lateral surface of bone:

0: absent
1: present

Character 227: Ischium, proximodorsal process, form:
0: small, tab-like or pointed process along posterior edge of ischium
1: large, proximodorsally hooked, and separated from iliac peduncle of the ischium by a notch
Note: Taxa without a discrete proximodorsal process are scored as inapplicable (“?”).

Character 228: Pubis, prominent tubercle on lateral surface of shaft, at approximately the midpoint of the shaft:
0: absent, shaft smooth
1: present

Character 229: Ischium, distally placed dorsal process along posterior edge of shaft:
0: absent
1: present

Character 230: Ischium, obturator process, shape:
0: tab-like, with distal end separated from shaft by a discrete notch
1: triangular, with distal end confluent with shaft

Character 231: Ischium, morphology of triangular obturator process (only in those taxa with a triangular process as defined in character 233):
0: longer proximodistally than wide anteroposteriorly at the center of the process
1: shorter proximodistally than wide anteroposteriorly at the center of the process, resembles an elongate triangle extending anteriorly

Character 232: Metatarsal II, tuber along extensor surface (associated with the insertion of the tendon of the m. tibialis cranialis in Aves): (ORDERED)
0: absent
1: present, on approximately the center of the proximodorsal surface of metatarsal II
2: present, developed on lateral surface of metatarsal II, at contact with metatarsal III or on lateral edge of metatarsal III

Character 233: Ulna: femur length ratio:
0: substantially less than one
1: equal to or greater than one

Character 234: Maxilla, position of maxillary fenestra relative to ventral margin of antorbital fossa: (ORDERED)
0: abuts ventral margin
1: dorsal to ventral margin, at approximately the dorsoventral midpoint of the antorbital fossa
2: far dorsal to the ventral margin, dorsal to the dorsoventral midpoint of the antorbital fossa
Note: This character has been modified to take into account variation in the position of the maxillary fenestra in tyrannosauroids, as noted by Brusatte et al. (2010a, character 18). State 0 here refers to the condition in *Daspletosaurus*, *Tarbosaurus*, and *Tyrannosaurus*, in which the maxillary fenestra abuts the ventral margin of the antorbital fossa.

Character 235: Maxilla, dorsoventral depth of main body of bone (=jugal process) at the midpoint of the antorbital fenestra compared to the depth of the entire skull at this measuring point: (ORDERED)

0: shallow, less than 16% of the depth of the entire skull

1: between 16-22% of skull depth

2: deep, greater than 22% of skull depth

Note: This character has been modified into an ordered multistate to take into account additional variation noted by Brusatte et al. (2010a, character 23).

Character 236: Maxilla, maxillary fenestra, recessed within a shallow, posteriorly or posterodorsally open fossa, which is itself located within the maxillary antorbital fossa:

0: absent

1: present

Character 237: Maxilla, ascending process (=dorsal ramus or nasal process), form:

0: prominent, exposed medially and laterally

1: absent or reduced to a process with slight medial and no lateral exposure

Character 238: Maxilla, participation of the ventral ramus of the nasal process (=ascending process) in the anterior margin of the antorbital fenestra (as seen in lateral view): (ORDERED)

0: present extensively

1: small dorsal projection of the maxilla participates in the anterior margin

2: no dorsal projection of maxilla participates in the anterior margin

Character 239: Antorbital fenestra, composition of the dorsal border (as seen in lateral view):

0: lacrimal and maxilla

1: lacrimal and nasal

Character 240: Antorbital fossa, composition of the dorsal border (as seen in lateral view): (UNORDERED)

0: lacrimal and maxilla

1: lacrimal and nasal

2: maxilla, premaxilla, and lacrimal

Character 241: Maxilla, lateral lamina of the ascending ramus:

0: present and broadly exposed in lateral view

1: present but reduced to small triangular exposure in lateral view

Character 242: Frontal, supratemporal fossa, anteroposterior length compared to overall length of exposed portion of frontal on skull roof: (ORDERED)

0: less than 30%

1: between 30-60%

2: greater than 60%

Note: This character has been modified and transformed into an ordered multistate using the quantitative character descriptions of Brusatte et al. (2010a, character 115). As worded here, this character now refers solely to the extent of the supratemporal fossa onto the frontal, unlike the previous TWiG character that referred to the qualitative extent (minor, extensive) of the fossa onto the frontal and postorbital.

We note, however, that taxa with an extensive fossa on the frontal usually also have an extensive fossa on the dorsal surface of the postorbital.

Character 243: Jugal, contribution to antorbital fenestra margin (in lateral view):

0: absent

1: present

Character 244: Maxillary and dentary teeth, size of mesial (=anterior) and distal (=posterior) denticles:

0: not substantially different in size

1: mesial denticles, when present, substantially smaller than distal denticles

Character 245: Maxillary teeth, orientation relative to the long axis of the lower jaw:

0: almost perpendicular to jaw margin

1: inclined strongly posteroventrally

0Character 246: Maxillary teeth, apicobasal height of teeth along tooth row:

0: highly variable with gaps evident for replacement

1: almost isodont with no replacement gaps

Character 247: Splenial, posterior margin (anterior margin of internal mandibular fenestra):

0: smooth

1: with distinct notch

Character 248: Premaxillary teeth, cross sectional size of first tooth crown compared with crowns of premaxillary teeth 2 and 3: (UNORDERED)

0: slightly smaller or same size

1: much smaller

2: much larger

Character 249: Maxilla, promaxillary fenestra in adults, visibility in lateral view:

0: visible (either as complete fenestra or portion of the fenestra)

1: completely obscured by ascending ramus of maxilla

Note: This character is equivalent to character 15 in Brusatte et al. (2010).

Character 250: Nasal, shape of dorsal surface: (ORDERED)

0: flat or slightly convex

1: convex (vaulted) anteriorly, above and immediately posterior to the external naris

2: vaulted across most of their length

Note: This character has been modified following Brusatte et al. (2010, character 38). Tyrannosauroids with a midline nasal crest are scored as inapplicable (“?”).

Character 251: Nasal, fusion between left and right nasals:

0: absent

1: present

Character 252: Quadratojugal and squamosal, constriction of lateral temporal fenestra: (ORDERED)

0: absent, anterior margins of both bones are approximately vertical

1: present, convex kink along the suture between the two bones that projects into the fenestra, constricting it to approximately one half or less of its maximum anteroposterior length

2: present, dorsal region of quadratojugal moderately expanded anteroposteriorly relative to the remainder of the bone, constricting fenestra to approximately one half of its maximum anteroposterior length

3: present, dorsal region of quadratojugal expanded anteroposteriorly by at least twice the minimum anteroposterior dimension of the bone, forming a flange that meets the ventral ramus of the squamosal to nearly divide the fenestra

Note: This character is expanded into an ordered multistate using the character state definitions of Brusatte et al. (2010a, character 98).

Character 253: Supraoccipital, pronounced and strongly demarcated median ridge on posterior (occipital) surface:

0: absent

1: present

Character 254: Surangular, anteroventral extension divides external mandibular fenestra by contacting angular anteriorly

0: absent

1: present

Character 255: Ilium, vertical ridge on lateral surface of iliac blade above acetabulum: (ORDERED)

0: absent or poorly developed

1: present as a well-developed, linear structure extending vertically or anterodorsally

2: present as a well-developed, linear structure extending posterodorsally

Note: This character is modified into an ordered multistate to take into account variation within tyrannosauroids as noted by Brusatte et al. (2010a, character 258).

Character 256: Premaxilla, main body, dorsoventral depth compared to anteroposterior length: (ORDERED)

0: less than or equal to

1: between 1.0-1.9 times larger

2: greater than 2 times larger

Note: This character is modified into an ordered multistate to take into account variation within tyrannosauroids as noted by Brusatte et al. (2010a, character 8).

Character 257: Nasal, external texture of mid section of bone:

0: smooth to slightly rugose

1: pronounced rugosities and accessory vascular foramina present

Note: This character is equivalent to Brusatte et al. (2010a, character 40).

Character 258: Jugal, shape of anterior process underneath the lacrimal: (UNORDERED)

0: tapering

1: bluntly squared anteriorly

2: expanded

3: bifurcated

Character 259: Axis, neural spine, morphology in lateral view:

0: extensive and anteroposteriorly elongate, sheet-like

1: anteroposteriorly reduced, rod-like

Character 260: Cervical vertebrae, prezygapophyses in anterior postaxial cervicals, orientation:

0: straight across their lengths

1: anteroposteriorly convex, flexed ventrally anteriorly

Character 261: Dorsal vertebrae, extent of pneumaticity (pneumatic foramina on lateral surfaces): (ORDERED)

0: foramina absent

1: foramina present in anterior dorsals

2: present in all dorsals

Note: This character is equivalent to Brusatte et al. (2010, character 218).

Character 262: Femur/humerus length ratio: (ORDERED)

0: more than 3.3

1: between 3.3-2.5

2: between 1.2 and 2.5

3: less than 1

Note: This character has been modified to include additional variation within tyrannosauroids, following Brusatte et al. (2010a, character 239).

Character 263: Humerus, shape in lateral view:

0: sigmoidal

1: straight

Note: We consider this character to be equivalent to character 242 in Brusatte et al. (2010a), which scores for the presence/absence of humeral shaft rotation (quantified by the angle between the long axes of the proximal and distal ends). Brusatte et al. (2010a) scored *Dryptosaurus* for such rotation, but this taxon has a straight humerus in lateral view and is thus scored for state 1 here. It is possible that there is a subtle amount of variation within this character, such that taxa like *Dryptosaurus* have a straight humerus in lateral view but still retain some degree of rotation (a 30-45 degree angle between the long axes of the proximal and distal ends). However, we do not want to subdivide this character too finely, because it makes recognizing homologies across a wide swath of taxa more difficult. Therefore, we retain a simple binary character here.

Character 264: Radius, length compared to that of humerus:

0: more than half the length of humerus

1: less than half the length of humerus

Character 265: Premaxilla, fusion of opposing premaxillae at the symphysis: (ORDERED)

0: unfused in adults

1: fused anteriorly in adults, posterior nasal [frontal] processes not fused to each other

2: fused anteriorly and opposing frontal processes completely fused

Character 266: Dentary, form of articulation between opposing dentaries at the symphysis:

0: joined proximally by ligaments

1: joined by bone

Character 267: Dentary, symphysis region, two strong grooves forming an anteriorly opening ‘v’ in ventral view:

0: absent

1: present

Character 268: Cranium, facial margin, composition: (ORDERED)

0: primarily formed by the maxilla, with the maxillary process of the premaxilla restricted to the anterior tip

1: maxillary process of the premaxilla extending along half of facial margin

2: maxillary process of the premaxilla extending more than half of facial margin

Character 269: Premaxilla, nasal (frontal) process, length:

0: short

1: long, closely approaching frontal

Character 270: External naris, size compared to the antorbital fenestra: (ORDERED)

0: considerably smaller

1: long axis approximately same length as long axis of antorbital fenestra

2: larger

Note: This character has been expanded into an ordered multistate to take into account variation within tyrannosauroids noted by Brusatte et al. (2010a, character 4). *Sinotyrannus* is here scored for state 1; although the antorbital fenestra is not preserved in this taxon, state 1 is hypothesized because the external naris long axis is as long as the first seven teeth of the maxillary tooth row, similar to the proportions in *Guanlong* and *Proceratosaurus*, which are scored for state 1, but differing from the state in other tyrannosauroids (and most other coelurosaurs) in which the naris is no longer than the first 4-5 teeth.

Character 271: Ectopterygoid:

0: present

1: absent

Character 272: Vomer and pterygoid, form of articulation between bones: (UNORDERED)

0: present, well developed

1: reduced, narrow process of pterygoid passes dorsally over palatine to contact vomer

2: absent, pterygoid and vomer do not contact

Note: This character is left unordered because it is unclear if states 1 and 2 form a nested set of homologies.

Character 273: Palatine and pterygoid, form of articulation between bones:

0: long, anteroposteriorly overlapping contact

1: short, primarily dorsoventral contact

Character 274: Palatine, contacts with bones of the facial region:

0: contacts maxillae only

1: contacts premaxillae and maxillae

Character 275: Vomer, contact with premaxilla:

0: present

1: absent

Character 276: Basisphenoid, projecting articulation with pterygoid via discrete basipterygoid processes:

0: present

1: absent

Character 277: Basisphenoid, location of pterygoid articular surface:

0: located basal on basisphenoid

1: located markedly anterior on basisphenoid (parasphenoid rostrum) such that the articulations are subadjacent on the narrow rostrum

Character 278: Basisphenoid and pterygoid articulation, orientation of contact: (UNORDERED)

0: anteroventral

1: mediolateral

2: entirely dorsoventral

Character 279: Pterygoid, articular surface for basisphenoid, morphology: (ORDERED)

0: concave ‘socket’ or short groove enclosed by dorsal and ventral flanges

1: flat to convex

2: flat to convex facet, stalked, variably projected

Character 280: Pterygoid, shape of bone:

0: kinked, surface for basisphenoid articulation at high angle to axis of palatal process of pterygoid

1: straight, basisphenoid articulation in line with axis of palatal process

Character 281: Ossified interorbital septum, sphenethmoid:

0: absent

1: present

Note: This character is equivalent to Brusatte et al. (2010a, character 167), which recognizes the presence of an ossified mesethmoid and sphenethmoid in derived tyrannosauroids. In the absence of developmental data, it is not clear if the ossification referred to as the sphenethmoid in tyrannosauroids is homologous to that in birds. However, we retain a single character scoring for the presence/absence of an ossified sphenethmoid for simplicity. The Brusatte et al. (2010a) character refers to both an ossified sphenethmoid and mesethmoid, but here we consider only the sphenethmoid in defining this character, so that it is equivalent to the original character in Turner et al. (2012). All known tyrannosauroids with an ossisfied sphenethmoid also possess an ossified mesethmoid, so their presence is probably correlated.

Character 282: Ossified interorbital septum, mesethmoid:

0: unossified or small, restricted to the ventral surface of the frontal or marginally extends anteriorly past the premaxillae/frontal contact but does not surpass posterior edge of external nares

1: large, extends anterior to the posterior extent of the frontal processes of premaxillae and anterior to the posterior edge of the external nares

Character 283: Eustachian tubes, morphology: (UNORDERED)

0: paired and lateral

1: paired, close to cranial midline

2: paired and adjacent on midline or single anterior opening

Character 284: Eustachian tubes, ossification:

0: absent

1: present

Character 285: Squamosal, ventral (=zygomatic) process, morphology:

0: large and elongate, dorsally encloses otic process of the quadrate and extends anteroventrally along shaft of quadrate, dorsal head of quadrate not visible in lateral view

1: short, head of quadrate exposed in lateral view

Note: This character is not redundant with Turner et al. (2012, character 216), because this character refers specifically to the size of the ventral process. A reduced ventral process is one means of exposing the quadrate head in lateral view, as is a wide notch between the ventral and posterior processes (which is what is scored in character 216).

Character 286: Quadrate, orbital process (=pterygoid flange) of quadrate, form of articulation with pterygoid:

0: pterygoid broadly overlapping medial surface of orbital process (i.e., ‘pterygoid ramus’ present)

1: pterygoid contact restricted to anteromedial edge of orbital process

Character 287: Quadrate, form of pterygoid articulation with orbital process in those taxa where the contact is restricted to the anteromedial edge of the process: (ORDERED)

0: pterygoid articulates with anterior-most tip

1: pterygoid articulation does not reach tip

2: pterygoid articulation with no extent up orbital process, restricted to quadrate corpus

Note: All taxa scored for state 0 in the previous character are here scored as inapplicable (“?”).

Character 288: Quadrate/pterygoid contact, morphology in those taxa where the contact is restricted to the anteromedial edge of the orbital process:

0: as a facet, variably with slight anteromedial projection cradling base

1: condylar, with a well-projected tubercle on the quadrate

Note: All taxa scored for state 0 for character 286 are here scored as inapplicable (“?”).

Character 289: Quadrate, well-developed tubercle on anterior surface of dorsal process:

0: absent

1: present

Character 290: Quadrate, form of articulation with quadratojugal:

0: overlapping

1: peg and socket articulation

Character 291: Quadrate, dorsal process, articulation with other bones:

0: with squamosal only

1: with squamosal and prootic

Character 292: Quadrate, dorsal process, development of intercotylar incisure between prootic and squamosal cotylae: (ORDERED)

0: absent, articular surfaces not differentiated (usually meaning prootic contact was absent)

1: two distinct articular facets, incisure not developed

2: incisure present, ‘double headed’

Character 293: Quadrate, mandibular articulation, form:

0: divided into two condyles

1: divided into three condyles, due to additional posterior condyle or broad surface

Character 294: Quadrate, pneumaticity:

0: absent

1: present

Note: This character scores specifically for the presence or absence of an internal pneumatic recess in the quadrate. Many coelurosaurs have an internally pneumatic quadrate, but this recess communicates with the external surface of the bone in two distinct ways (Tahara and Larsson 2011). Most coeluorsaurs have a small foramen, usually on the posterior surface of the quadrate, that leads into the recess. Derived tyrannosauroids, on the other hand, possess a large, deep, funnel-like pneumatic opening on the anterior surface of the quadrate where the pterygoid wing and mandibular condyles meet. Both conditions are considered homologous at the level of absence/presence of quadrate pneumaticity here, but we utilize separate characters below for the absence/presence of the posterior foramen and the absence/presence of the anterior funnel. The homologous nature of both conditions is supported by the morphology of *Dilong*, which clearly has an anterior funnel and also a posterior foramen (IVPP V14243; Xu et al. 2004).

Character 295: Quadrate, cluster of pneumatic foramina on the posterior surface of the tip of the dorsal process:

0: absent

1: present

Note: Because we are uncertain whether this condition may be homologous to the broader condition of quadrate pneumaticity, we score taxa lacking this character for state 0, even if they are also scored for state 0 (absence) for the general character of quadrate pneumaticity.

Character 296: Quadrate, form of pneumatization, large single pneumatic foramen on the posterior or posteromedial surface of the shaft:

0: absent

1: present

Note: See discussion regarding quadrate pneumaticity above. All taxa without quadrate pneumaticity are scored as inapplicable (“?”) for this character.

Character 297: Articular, pneumaticity:

0: absent

1: present

Character 298: Dentary, morphology of posterior end:

0: approximately straight or with a weakly developed separation into dorsal and ventral forks (i.e., small dorsal ramus)

1: strongly forked with the dorsal and ventral rami approximately equal in posterior extent

Character 299: Splenial, anterior extent: (ORDERED)

0: limited, stops well posterior to mandibular symphysis

1: elongate, extends to mandibular symphysis but does not participate in symphysis

2: elongate, extends to anterior tip of mandible to contacting on midline and participate in symphysis

Character 300: Mandibular symphysis, anteroposteriorly extensive, flat to convex, dorsal-facing surface:

0: absent, symphysis concave
1: present

Character 301: Mandibular symphysis, symphyseal foramina:
0: absent
1: present

Character 302: Mandibular symphysis, symphyseal foramina, number:
0: single
1: paired

Character 303: Mandibular symphysis, symphyseal foramina, location:
0: opening on posterior edge of symphysis
1: opening on dorsal surface of symphysis

Character 304: Dentary, Meckelian groove, exposure in medial view:
0: exposed as deep and conspicuous groove, not completely covered by splenial
1: not exposed, covered by splenial
(this overlaps logically with char.299)

Character 305: Lower jaw, anterior external mandibular fenestra:
0: absent
1: present

Character 306: Jugal, contact with postorbital:
0: present
1: absent

Character 307: Frontal/parietal suture
0: open
1: fused

Character 308: Thoracic vertebrae (with ribs articulating with the sternum, or in the middle-posterior dorsal series of theropods without preserved sterna), one or more with prominent hypapophyses:
0: absent
1: present

Character 309: Thoracic vertebrae, number: (ORDERED)
0: 12 or more
1: 11
2: 10 or fewer

Character 310: Thoracic vertebrae, form of articular surfaces:
0: at least part of series with round or ovoid articular surfaces (e.g. amphicoelous/ opisthocoelous) that lack the dorsoventral compression seen in heterocoelous vertebrae
1: series completely heterocoelous

Character 311: Thoracic vertebrae, parapophysis, position:
0: anterior to transverse process
1: directly ventral to transverse process (close to midpoint of vertebra)

Character 312: Thoracic vertebrae, centrum, proportions:
0: approximately equal in anteroposterior length and midpoint mediolateral width
1: length markedly greater than midpoint width

Character 313: Thoracic vertebrae, morphology of lateral surfaces of centra: (UNORDERED)

0: flat to slightly depressed

1: deep, emarginated fossae

2: central ovoid foramina

Note: Turner et al. (2012) scored some taxa with large pneumatic foramina in the dorsals for character state 2 (e.g., *Balaur*). Because the size and shape of pneumatic foramina are variable, and because dorsal pneumaticity is already scored in other characters, we restrict state 2 to representing the large, ovoid, central foramina of some avialans (and also *Linhenykus*). Turner et al. (2012) also scored *Tyrannosaurus* for state 1, possibly because of the pneumatic foramen and surrounding fossa on the dorsal centra. We do not consider this homologous to the deeply emarginated fossae on the lateral surfaces of some avialan and oviraptorosaur vertebrae, and therefore consider *Tyrannosaurus* (as well as all other tyrannosauroids and non-maniraptoran coelurosaurs) to be scored for state 0.

Character 314: Thoracic vertebrae with ossified connective tissue bridging transverse processes:

0: absent

1: present

Character 315: Notarium:

0: absent

1: present

Character 316: Sacral vertebrae, series of short vertebrae, with dorsally directed parapophyses just anterior to the acetabulum: (ORDERED)

0: absent

1: present, three such vertebrae

2: present, four such vertebrae

Character 317: Caudal vertebrae, anterior free caudals prior to transition point, length of transverse processes:

0: subequal to width of centrum

1: substantially shorter than centrum width

This is scored as 0&1 in most non avian taxa, but the ‘free’ caudals are just the proximal ones which bear long transverse processes in most non-avian theropods. This fact may justify a wholesale rescoring of the trait in the future.

Character 318: Caudal vertebrae, fusion of distal caudals:

0: unfused to each other

1: fused to each other

Character 319: Caudal vertebrae, extent of fused distal caudals: (ORDERED)

0: fused element length equal or greater than 4 free caudal vertebrae

1: length less than 4 caudal vertebrae

2: less than 2 caudal vertebrae in length

Character 320: Gastralia:

0: present

1: absent

Character 321: Sternum, carina or midline ridge, morphology: (ORDERED)

0: absent

1: slightly raised

2: distinctly projected

Character 322: Sternum, position of carina or midline ridge: (UNORDERED)
0: restricted to posterior half of sternum
1: approaches anterior limit of sternum
2: restricted to the anterior half of the sternum
Character 323: Sternum, dorsal surface, pneumatic foramen (or foramina):
0: absent
1: present
Character 324: Sternum, pneumatic foramina in the depressions (loculi costalis) between rib articulations (processi articularis sternocostalis):
0: absent
1: present
Character 325: Sternum, coracoidal sulci spacing on anterior edge: (UNORDERED)
0: widely separated mediolaterally
1: adjacent
2: crossed on midline
Character 326: Sternum, number of processes for articulation with the sternal ribs: (ORDERED)
0: three
1: four
2: five
3: six
4: seven or more
Character 327: Sternum, raised, paired intermuscular ridges (linea intermuscularis) parallel to sternal midline:
0: absent
1: present
Character 328: Sternum, posterior margin, distinct posteriorly projected medial and/or lateral processes, morphology: (**ORDERED)**
0: absent
1: with distinct posterior processes
2: midpoint of posterior sternal margin connected to medial posterior processes to enclose paired fenestrae
Character 329: Clavicles, fusion:
0: left and right bones fused together
1: left and right bones unfused
Note: We here score *Juravenator* as polymorphic "[01]". Chiappe and Göhlich (2010) described an unfused furcula in *Juravenator*, but because this specimen is such a young individual we cannot rule out that the two clavicles may have later fused in adults. Therefore, we conservatively score it as polymorphic for both conditions.
Character 330: Clavicles, interclavicular angle between left and right clavicles:
0: greater than, or equal, to 90 degrees
1: less than 90 degrees
Character 331: Furcula, lateral excavation:
0: absent
1: present

Character 332: Furcula, dorsal (omal) tip, form:
0: flat or blunt
1: with a pronounced posteriorly pointed tip
Character 333: Furcula, ventral margin of apophysis, form:
0: curved, angling
1: with a truncated or squared base
Character 334: Scapula and coracoid, form of articulation: (UNORDERED)
0: pit-shaped scapular cotyla developed on the coracoid, and coracoidal tubercle developed on the scapula ('ball and socket' articulation)
1: scapular articular surface of coracoid convex
2: flat
Character 335: Coracoid, procoracoid process: Distinct from coracoid (bicpes) tuber
0: absent
1: present
Character 336: Coracoid, lateral margin, form:
0: straight to slightly concave
1: convex
Character 337: Coracoid, dorsal surface (= posterior surface of taxa less derived than Paraves), form:
0: strongly concave
1: flat to convex
Note: This character can be scored by examining the trace of the scapula-coracoid suture in lateral view. Those taxa with state 0 have a strong concavity on the coracoid, whereas those scored for state 1 have either a flat suture or one with a convexity on the coracoid.
Character 338: Coracoid, pneumaticity:
0: absent
1: present
Character 339: Coracoid, position of pneumatic foramen:
0: proximal
1: distal
Character 340: Coracoid, lateral process:
0: absent
1: present
Character 341: Coracoid, ventral surface (=anterior surface of taxa less derived than Paraves), lateral intermuscular line or ridge:
0: absent
1: present
Character 342: Coracoid, position of glenoid facet:
0: dorsal to, or at approximately same level as, acrocoracoid process/'uberubercle' (or estimated position of biceps tubercle is a discrete tubercle is absent)
1: far ventral to acrocoracoid process
Character 343: Coracoid, acrocoracoid process, shape:
0: straight

1: hooked medially

Character 344: Coracoid, n. supracoracoideus passes through coracoid (usually via coracoid foramen):

0: present

1: absent

Note: This character is not equivalent to the presence or absence of a large, discrete coracoid foramen (Turner et al. 2012, character 440). Although a noticeable foramen is sometimes absent in non-avialan coelurosaurs, the overall morphology of the coracoid (and pectoral region in general) suggests that the n. supracoracoideus still passes through the coracoid, unlike the condition in some derived avialans. In the absence of soft tissue information in fossil taxa, we consider all non-paravian theropods with a traditional plate-like coracoid to possess state 0.

Character 345: Coracoid, medial surface, area of the foramen n. supracoracoideus (when developed)

0: strongly depressed

1: flat to convex

Note: Turner et al. (2012) scored the outgroup *Allosaurus* and derived tyrannosauroids for state 1, but in these taxa this surface of the coracoid is indeed depressed (the condition in these taxa is basically identical to the ornithomimosaur *Gallimimus*, for instance, which was scored for state 0). Therefore, we score these taxa for state 0. State 1 is now scored only in some avialans, some alvarezsaurids, and *Microvenator*.

Character 346: Coracoid and scapula, angle between bones at glenoid:

0: greater than 90 degrees

1: 90 degrees or less

Character 347: Scapula, ratio of dorsoventral depth of distal end to minimum dorsoventral depth of blade: (ORDERED)

0: greater than 2.5

1: slightly taller or approximately the same depth as proximal dorsoventral shaft width, ratio between 1.0 and 2.5

2: tapering distally, ratio less than 1.0

Note: This character has been modified into an ordered multistate to take into account variation within tyrannosauroids noted by Brusatte et al. (2010a, character 235).

Character 348: Scapula, curvature in lateral view:

0: absent, bone straight

1: present, bone dorsoventrally curved

Note: Turner et al. (2012) scored some basal coelurosaurs (*Haplocheirus*, *Mononykus*, *Archaeornithomimus*, *Gallimimus*) for the curved condition, but these taxa have straight scapular blades that are extremely similar in overall shape to closely related taxa that were scored for the straight condition. We score them for the straight condition here, meaning that the curved condition is restricted to some derived maniraptorans.

Character 349: Scapula, position of acromion process:

0: extends anteriorly to surpass the articular surface for coracoid (facies articularis coracoidea)

1: does not extend further anteriorly than the articular surface for coracoid

Character 350: Scapula, orientation of acromion process:

0: straight

1: laterally hooked tip

Note: Turner et al. (2012) scored tyrannosauroids for state 1, which is otherwise present only in some derived avialans. We do not recognize any discrete difference in the orientation of the acromion process of derived tyrannosauroids relative to other basal coelurosaurs, and therefore score all tyrannosauroids with well-preserved scapulae for state 0.

Character 351: Humerus and ulna, length comparison: (ORDERED)

0: humerus longer than ulna

1: ulna and humerus approximately the same length (within ~10% of each other)

2: ulna substantially longer than humerus

Character 352: Humerus, head, shape in anterior or posterior view

0: strap-like, articular surface flat or weakly convex, no proximal midline convexity

1: prominent and highly convex (domed) proximally

Note: We consider this character equivalent to character 240 in Brusatte et al. (2010a), which scores for the absence/presence of an enlarged head that occupies the majority of the proximal end, is bulbous in –

proximal view, and overhangs both anterior and posterior surfaces. This feature, which is seen in some derived tyrannosauroids, is here considered equivalent to state 1.

Character 353: Humerus, proximal end, shape of proximal projection:

0: dorsal edge projected farthest

1: midline projected farthest

Character 354: Humerus, ventral tubercle and capital incisure:

0: absent

1: present

Character 355: Humerus, capital incisure, morphology:

0: an open groove

1: closed by tubercle associated with a muscle insertion just distal to humeral head

Character 356: Humerus, anterior surface, well-developed fossa on midline making proximal articular surface appear v-shaped in proximal view:

0: absent

1: present

Character 357: Humerus, 'transverse groove':

0: absent

1: present, developed as a discrete, depressed scar on the proximal surface of the bicipital crest or as a slight transverse groove

Character 358: Humerus, deltopectoral crest, orientation:

0: projected laterally or dorsally, such that it is in line with the long axis of humeral head

1: projected anteriorly, such that it is approximately perpendicular to the long axis of the head

Character 359: Humerus, deltopectoral crest, thickness compared with thickness of shaft: (ORDERED)
0: less
1: same width
2: dorsoventral thickness greater than shaft thickness

Character 360: Humerus, deltopectoral crest, proximoposterior surface (=proximolateral surface in most non-avialan theropods), form:
0: flat to convex
1: concave

Character 361: Humerus, deltopectoral crest, large fenestra:
0: absent, crest not perforate
1: present, crest perforate

Character 362: Humerus, bicipital crest, pit-shaped scar/fossa for muscular attachment on anterodistal, distal, or posterodistal surface of crest:
0: absent
1: present

Character 363: Humerus, bicipital crest, position of pit-shaped fossa for muscular attachment: (UNORDERED)
0: anterodistal on bicipital crest
1: directly ventrodistal at tip of bicipital crest
2: posterodistal, variably developed as a fossa

Character 364: Humerus, bicipital crest, anterior projection: (ORDERED)
0: absent or subtle
1: present, developed as an anterior projection relative to shaft surface in ventral view
2: present as a hypertrophied, rounded tumescence

Character 365: Humerus, proximal end, one or more pneumatic foramina:
0: absent
1: present

Character 366: Humerus, distal articular condyles, position:
0: on distal surface of bone
1: on anterior surface of bone

Character 367: Humerus, long axis of dorsal (lateral) distal condyle, orientation:
0: at low angle to humeral axis, proximodistally orientated
1: at high angle to humeral axis, almost transversely orientated

Character 368: Humerus, distal condyles, form:
0: prominent, subround and bulbous
1: weakly defined, ‘strap-like’

Character 369: Humerus, distal margin, orientation:
0: approximately perpendicular to long axis of humeral shaft
1: oblique (angling strongly ventrally) to long axis of humeral shaft, ventrodistal margin projected significantly distal to dorsodistal margin (sometimes described as a well-projected flexor process)

Character 370: Humerus, distal end, compressed anteroposteriorly and flared dorsoventrally:
0: absent

1: present

Character 371: Humerus, brachial fossa:

0: absent

1: present, developed as a flat scar or as a scar-impressed fossa

Character 372: Humerus, ventral (medial) distal condyle, length of long axis:

0: less than the long axis of the dorsal (lateral) condyle

1: the same or greater than the long axis of the dorsal (lateral) condyle

Character 373: Humerus, demarcation of muscle origins (e.g. m. extensor metacarpi radialis in Aves) on the dorsal (=lateral in non-avialan theropods) edge of the distal humerus:

0: no indication of origin as a scar, a pit, or a tubercle

1: indication as a pit-shaped scar or as a variably projected scar-bearing tubercle or facet

Character 374: Humerus, groove for passage of m. scapulotriceps on distal end of posterior surface:

0: absent

1: present

Character 375: Humerus, m. humerotricipitalis groove:

0: absent

1: present as a ventral depression contiguous with the olecranon fossa

Character 376: Ulna, cotylae, orientation of dorsal (lateral) and ventral (medial) cotylae:

0: dorsoventrally adjacent

1: widely separated by a deep groove

Character 377: Ulna, dorsal cotyla, form: convex

0: flat or non-distinct

1: convex

Character 378: Ulna, distal end, dorsal (lateral) condyle, dorsal trochlear surface, extent along posterior margin:

0: less than transverse measure of dorsal trochlear surface

1: approximately equal in extent

Character 379: Ulna, bicipital scar: (ORDERED)

0: absent

1: present, developed as a slightly raised scar

2: present, developed as a conspicuous tubercle

Character 380: Ulna, brachial scar

0: absent

1: present

Character 381: Radius, posteroventral surface (=posteromedial surface of non-avialans), texture: (UNORDERED)

0: smooth

1: with muscle impression along most of surface

2: deep longitudinal groove

Character 382: Ulnare:

0: absent

1: present

Character 383: Ulnare, shape:
0: circular, triangular, or ‘heart-shaped’, with no or minimal differentiation into short dorsal and ventral rami
1: V-shaped, well- developed dorsal and ventral rami
Character 384: Ulnare, ventral ramus (crus longus), length: (ORDERED)
0: shorter than dorsal ramus (crus brevis)
1: same length as dorsal ramus
2: longer than dorsal ramus
Character 385: Semilunate carpal and metacarpals, fusion: (ORDERED)
0: separate from each other, no fusion
1: incomplete proximal fusion
2: complete proximal fusion
3: complete proximal and distal fusion
Character 386: Metacarpal III, anteroposterior (extensor-flexor) diameter at midshaft compared to anteroposterior diameter of metacarpal II:
0: approximately equal or greater than 50%
1: less than 50%
Character 387: Metacarpal I, anteroproximally projected muscular process, form: (ORDERED)
0: absent, no distinct process visible
1: present as small knob at anteroproximal tip of metacarpal
2: present, tip of process marginally surpasses the distal articular facet for phalanx 1 in anterior extent
3: present, tip of process conspicuously surpasses articular facet by approximately half the width of the facet, producing a pronounced knob
4: present, tip of process conspicuously surpasses articular facet by approximately the entire width of the facet, producing a pronounced knob
Character 388: Metacarpal I, shaft, anterior (extensor) surface, shape:
0: roughly hourglass-shaped proximally, at least moderately expanded anteroposteriorly, and constricted just before flare of articulation for phalanx 1
1: anterior surface broadly convex
Character 389: Carpometacarpus, pisiform process:
0: absent
1: present
Character 390: Carpometacarpus, ventral surface, supratrochlear fossa deeply excavating proximal surface of pisiform process or adjacent region:
0: absent
1: present
Character 391: Carpometacarpus, intermetacarpal space (between metacarpals II and III):
0: reaches proximally as far as the distal end of metacarpal I
1: terminates distal to end of metacarpal I
Note: All taxa without a carpometacarpus are scored as inapplicable (“?”).
Character 392: Metacarpals II and III, distal ends, position of articular surfaces for digits:

0: articular surface on metacarpal II located at same distal level as, or surpasses distally, articular surface on metacarpal III

1: articular surface on metacarpal III extends further distally than articular surface on metacarpal II

Character 393: Metacarpals, intermetacarpal process or tubercle: (ORDERED)

0: absent

1: present as scar

2: present as tubercle or flange

Character 394: Manual digit II, phalanx 1, shape:

0: subcylindrical to subtriangular in cross section

1: strongly dorsoventrally compressed, flat posterior surface

Character 395: Manual digit II, length of phalanx II-1 compared to that of II-2:

0: less than or equal to

1: longer

Character 396: Manual digit II, phalanx 2, internal index process on posterodistal edge:

0: absent

1: present

Character 397: Pelvis, ilium, ischium, and pubis, proximal contact between bones in adult individuals: (ORDERED)

0: unfused to each other

1: partially fused to each other (pubis not ankylosed)

2: completely fused to each other

Note: State 0 includes the condition in derived therizinosauroids in which the pubis and obturator process of the ischium meet and fuse ventral to the acetabulum, which does not include fusion between the ilium and other pelvic bones.

Character 398: Ilium/ischium, distal co-ossification to completely enclose the ilioischiadic fenestra:

0: absent

1: present

Character 399: Ischium, dorsal process

0: does not contact ilium

1: contacts ilium

Note: All taxa without a dosrsal process are scored as inapplicable (“?”).

Character 400: Ilium, antitrochanter, position:

0: directly posterior to acetabulum

1: posterodorsal to acetabulum

Character 401: Ilium, preacetabular pectineal process: (ORDERED)

0: absent

1: present as a small flange

2: present as a well-projected flange

Character 402: Ilium, preacetabular processes, orientation of left and right processes:

0: approach on midline but do not contact (open space between them, possibly a cartilaginous connection)

1: make contact with each other on midline and fuse, dorsal closure of 'iliosynsacral canals'

Character 403: Ilium, preacetabular process, morphology of process as it extends anterior to first sacral vertebra:

0: no free ribs overlapped

1: one or more ribs overlapped

Character 404: Ilium, postacetabular process, orientation:

0: dorsoventrally orientated, such that broad external surface faces laterally

1: mediolaterally orientated, such that broad external surface faces dorsally

Character 405: Ilium, postacetabular process, ventral surface, renal fossa:

0: absent

1: present

Character 406: Ilium, cuppedicus fossa, form:

0: broad, mediolaterally oriented surface directly anteroventral to acetabulum

1: small and entirely laterally facing fossa anterior to the acetabulum

Note: All taxa without a cuppedicus fossa (scored as absent for the character denoting the absence/presence of the fossa above) are scored here as inapplicable ("?").

Character 407: Pubis, cross section:

0: suboval

1: compressed mediolaterally

Character 408: Pubes, contact of distal ends of left and right pubes:

0: present, variably co-ossified into symphysis

1: absent, pubes noncontacting

Character 409: Femur, posterior trochanter: (ORDERED)

0: present, developed as a slightly projected tubercle or flange

1: present, hypertrophied into a 'shelf-like' conformation (in combination with development of the trochanteric shelf)

2: absent

Character 410: Femur, patellar groove

0: absent

1: present

Note: Turner et al. (2012) scored derived tyrannosauroids for possessing a patellar groove, probably because these taxa have a deep extensor groove for muscle attachment (a feature that is variably developed in tetanurans). We do not consider this feature homologous to the distinct patellar groove of birds, which houses a patella ossification (which is not known for tyrannosauroids or any other non-avialan theropod). Instead, we utilize a separate character (below) to refer to the extensor groove.

Character 411: Femur, ectocondylar tubercle (crista tibiofibularis) and lateral condyle, separation:

0: present, separated by deep notch

1: absent, form single trochlear surface

Character 412: Femur, posterior projection of the lateral border of the distal end, continuous with lateral condyle:

0: absent

1: present

Character 413: Femur, laterally projected fibular trochlea: (ORDERED)
0: absent
1: present, developed as small notch
2: present, developed as a shelf-like projection
Character 414: Tibia/tarsals, condyles, extent of medial and lateral condyles:
0: medial condyle projecting further anteriorly than lateral
1: equal in anterior projection
Character 415: Tibia/tarsals, condyles, extensor canal: (ORDERED)
0: absent
1: present as an emarginated groove
2: present as a groove bridged by an ossified supratendoneal bridge
Character 416: Tibia/tarsals, condyles, tuberositas retinaculi extensoris indicated by short medial ridge or tubercle proximal to the condyles close to the midline and a more proximal second ridge on the medial edge:
0: absent
1: present
Character 417: Tibia/tarsals, condyles, mediolateral widths of lateral and medial condyles: (ORDERED)
0: medial condyle wider
1: approximately equal
2: lateral condyle wider
Character 418: Tibia/tarsals, condyles, medial constriction of lateral and medial condyles:
0: present, gradual sloping medial constriction of condyles
1: absent, no medial tapering of either condyle
Character 419: Tibia/tarsals, condyles, intercondylar groove, mediolateral width:
0: broad, approximately 1/3 width of anterior surface
1: narrow, less than 1/3 width of total anterior surface
Character 420: Tibia/tarsals, position of articular surface for distal tarsals/tarsometatarsus: (ORDERED)
0: on distal surface or restricted to distal-most edge of posterior surface, no broad extension of trochlear surface onto posterior surface of bone
1: well-developed articular surface extending up the posterior surface of the tibiotarsus (sulcus cartilaginis tibialis of Aves)
2: well-developed articular surface extending up the posterior surface of the tibiotarsus, with well-developed and posteriorly projecting medial and lateral crests
Character 421: Tibia, mediolateral width of distal end:
0: wider than midpoint of shaft, giving distal profile a weakly developed triangular form
1: approximately equal to midshaft width, no distal expansion of whole shaft (although condyles may be variably splayed mediolaterally)
Character 422: Metatarsal V:
0: present
1: absent
Character 423: Metatarsal III, position of proximal end:
0: proximally in same plane with II and IV

1: proximally displaced plantarly (to the extensor surface), relative to metatarsals II and IV

Character 424: Tarsometatarsus or metatarsals, intercotylar eminence:

0: absent

1: well developed, globose

Character 425: Tarsometatarsus or metatarsals, projected surface or grooves on proximoposterior surface (associated with the passage of tendons of the pes flexors in Aves; hypotarsus): (ORDERED)

0: absent

1: developed as posterior projection with flat posterior surface

2: developed as a posterior projection, with distinct crests and grooves

3: developed as a posterior project with distinct crests and grooves, at least one groove enclosed by bone posteriorly

Character 426: Tarsometatarsus or metatarsals, proximal vascular foramina: (ORDERED)

0: absent

1: single foramen present, between metatarsals III and IV

2: two foramina present

Character 427: Metatarsal I, shape: (ORDERED)

0: straight

1: curved or distally deflected but not twisted, ventral surface convex ('J shaped')

2: distally deflected and twisted, such that the ventromedial surface is concave proximal to trochlear surface for phalanx I

Character 428: Metatarsal II, distal extensor surface, fossa for metatarsal I: (ORDERED)

0: absent

1: present as a shallow notch

2: present as a conspicuous ovoid fossa

Character 429: Metatarsal IV, mediolateral width at midshaft: (UNORDERED)

0: metatarsal IV approximately the same width as metatarsals II and III

1: metatarsal IV narrower than MII and MIII

2: metatarsal IV greater in width than either metatarsal II or III

Character 430: Metatarsals, comparative trochlear width (UNORDERED):

0: II approximately the same size as III and/or IV (this includes taxa in which metatarsal III is slightly wider than the other metatarsals disally)

1: II markedly wider than III and/or IV

2: II markedly narrower than III and/or IV

3: IV markedly narrowest.

Character 431: Metatarsus, distal vascular foramen, form:

0: simple, with one exit

1: forked, two exits (plantar and distal) between metatarsals III and IV.

Character 432: Metatarsal III, distal trochlea in extensor view, proximal extent of lateral and medial edges:

0: equally extended proximally

1: lateral edge extends further proximally

Character 433: Metatarsal II, distal extent of metatarsal II relative to metatarsal IV: (ORDERED)

0: approximately equal in distal extent

1: metatarsal II shorter than metatarsal IV, but reaching distally further than base of metatarsal IV trochlea

2: metatarsal II shorter than metatarsal IV, reaching distally only as far as base of metatarsal IV trochlea

Character 434: Caudal vertebrae, middle to posterior caudals, anteroposterior length: (ORDERED)

0: shortened, less than 1.5x length of dorsal vertebrae (where known) and anteroposterior length of centrum less than twice its maximum mediolateral width

1: 1.5x-2x or less the length of dorsal vertebrae

2: 3x-4x length of dorsal vertebrae

Note: This is a modified version of the original Turner et al. (2012) character, which takes into account an additional state (denoted as state 0) noted by Zanno et al. (2009).

Character 435: Coracoid, coracoid fenestra:

0: absent

1: present

Character 436: Metatarsal V, elongated and bowed

0: absent

1: present

Character 437: Chevrons, degree of posterior extension of posterior chevrons:

0: not substantially elongated

1: very elongated

Character 438: Radius, width at midshaft:

0: roughly half or greater than width of ulna

1: less than half width of ulna

Character 439: Manus, combined length of metacarpal I and phalanx I-1:

0: greater than length of MC II

1: equal to or less than length of MC II

Character 440: Metacarpal III, shape:

0: straight

1: bowed

Character 441: Metatarsal I, position of distal trochlea:

0: proximally placed relative to trochleae of other metatarsals

1: inline distally with others

Character 442: Metatarsal I:

0: present

1: absent

Character 443: Braincase, preotic pendant, form: (ORDERED)

0: absent

1: present but small

2: present and robust

Character 444: Braincase, metotic strut, shape:

0: short and robust

1: long and narrow

Character 445: Prootic, pneumatic excavation on lateral surface leading into anterior tympanic recess: (ORDERED)

0: absent

1: present and shallow

2: present and deep

Note: Witmer (1997), Makovicky and Norell (1998), Bever et al. (2013) and others have described lateral pneumatic excavations on the prootic, which are present in some coelurosaurs, to be associated with the anterior tympanic recess, which is present in most theropods. The character here does not code for the absence/presence of the recess, but rather for the absence/presence of discrete external pneumatic openings on the lateral surface of the prootic that lead into the recess. Contra Turner et al. (2012), tyrannosauroids are scored for state 1, as they possess a distinct fossa on the lateral surface of the prootic that includes the external foramina of the trigeminal and facial nerves, along with pneumatic openings that lead into the anterior tympanic recess (Bever et al. 2013). This fossa itself is a distinct tyrannosauroid character, which is listed as a separate character below.

Character 446: Braincase, anterior tympanic recess (ATR), manifestation on external surface of basisphenoid: (ORDERED)

0: subtle, external fossa not deeply impressed into the lateral surface of the basisphenoid

1: deeply impressed into the lateral surface of the basisphenoid in juveniles but not adults

2: deeply impressed into the lateral surface of the basisphenoid in adults

Note: Turner et al. (2012) originally scored for the absence/presence of an anterior tympanic recess. Witmer (1997), Bever et al. (2013), and others have shown that this recess is present in most theropods, so we have modified this character to refer specifically to the external manifestation of the recess on the basisphenoid. This character scores for a shallow/deep lateral fossa or fossae on the basisphenoid. We have also subdivided the "deeply impressed" condition into two states, to take into account the recognized loss of a deeply impressed recess during ontogeny in some tyrannosauroids (Bever et al. 2013). This character is therefore equivalent to Brusatte et al. (2010a, character 157).

Character 447: Braincase, anterior tympanic recess and anterior tympanic crista (crest marking the posterior and dorsal border of the ATR), location:

0: below the exit foramen of cranial nerve VII exit and just proximal to the otic recess

1: anteriorly, with little or no development of the recess posterior to the basipterygoid processes

Character 448: Braincase, anterior tympanic recess confluent with the subotic recess:

0: absent

1: present, forming the Lateral Depression

Note: All taxa without a subotic recess are scored as inapplicable ("?").

Character 449: Braincase, V-shaped opening between basal tubera (or remnants of tubera):

0: absent
1: present

Character 450: Braincase, small tubera medial to basal tubera (or remnants of basal tubera) and ventral to occipital condyle:

0: absent
1: present

Character 451: Pedal phalanx II-2, size of distal articular surface relative to proximal articular surface:

0: approximately equal in size or distal surface slightly smaller than proximal surface
1: distal surface less than half the size of proximal surface

Character 452: Sternum, ossification of sternal plates:

0: absent, plates unossified
1: present, plates ossified

Character 453: Ulna, size of proximal cotylae:

0: unequal in size, lateral (=dorsal in avialans) condyle smaller
1: equal in size

Character 454: Braincase, middle ear resides within the Lateral Depression (formed by merged anterior tympanic recess and subotic recess):

0: absent
1: present

Character 455: Feathers, filamentous integumentary structures (Stage 1 feathers):

0: absent
1: present

Character 456: Feathers, vaned feathers (Stage 4 feathers):

0: absent
1: present

Character 457: Quadratojugal, size:

0: large
1: greatly reduced

Character 458: Frontal, notch for postorbital contact on postorbital process of frontal:

0: absent, process smooth or facet small
1: large notch present

Character 459: Frontal and parietal, position of fronto-parietal suture relative to postorbital processes of frontal: (ORDERED)

0: well posterior to the postorbital processes
1: at the level of the postorbital processes
2: anterior to postorbital processes

Character 460: Cervical vertebrae, orientation of articular surfaces between cervical vertebrae:

0: surfaces vertical to subvertical
1: strongly slanted anteroventrally

Character 461: Skull roof, accessory depression in supratemporal fossa:

0: absent
1: present

Character 462: Ilium, relative ventral extension of pubic and ischiadic peduncles: (ORDERED)

0: equal

1: pubic peduncle extends farther ventrally

2: pubic peduncle hyperelongate, approximately 2.5-3 times the proximodistal length of the ischial peduncle

Note: This is a modified version of the original Turner et al. (2012) character, which incorporates a second derived state referred to the hyperelongate condition of some derived therizinosauroids (see Zanno et al. 2009: character ZCD 311). We also consider this character to be equivalent to Zanno et al. (2009: character ZCD 309).

Character 463: Parasphenoid, ala parasphenoidalis:

0: absent

1: present, well-developed and crest-shaped forming anterior edge of enlarged pneumatic recess with the ala continuous with the anterior tympanic crista

This trait needs to be better reconciled with lateral depression and other ATR traits already employed

Character 464: Furcula, cross-section:

0: nearly circular

1: anteroposteriorly compressed near the symphysis

Character 465: Furcula, shape:

0: V-shaped

1: U-shaped

Character 466: Furcula, epicledial processes, form:

0: unexpanded

1: expanded

Character 467: Furcula, lateral expansion of the rami between the hypocledium and the epicledial process:

0: absent

1: present

Character 468: Furcula, hypocledium, shape:

0: rounded

1: keeled

Character 469: Furcula, symmetry:

0: asymmetrical

1: nearly symmetrical

Character 470: Furcula, thickness of rami:

0: thin

1: thick

Character 471: Metatarsal III, extensor (=anterior or dorsal) surface, shape:

0: relatively narrow and flat

1: transversely expanded and slightly concave

Character 472: Metatarsal IV, accessory longitudinal ridge on anterolateral side of the distal end of the bone:

0: absent

1: present

NEW CHARACTERS ADDED TO THE TWiG DATASET HERE:

***Expansions of Turner et al. (2012) Characters:**

Character 473: Metacarpal I, width of proximal articular surface compared to proximodistal length of entire metacarpal:

0: shorter

1: wider

Note: This character is a new character, originally part of Turner et al. (2012, character 149), which distinguishes the extremely short and wide metacarpals I of some alvarezsaurids.

Character 474: Manual unguals:

0: present

1: absent

Note: This character is a new character, originally part of Turner et al. (2012, character 151), which distinguishes the absent manual unguals of derived avialans.

Character 475: Manual unguals, size of flexor tubercle: (ORDERED)

0: large, robust, rugose, structure

1: reduced to a small convexity

2: absent

Note: This character is a new character, originally part of Turner et al. (2012, character 151), which distinguishes the large flexor tubercles of most coelurosaurs from the small flexor tubercles of some tyrannosauroids, ornithomimosaurs, and other taxa. Some alvarezsauroids have completely absent flexor tubercles, which is denoted by state 2. This character is equivalent to Brusatte et al. (2010a, character 255).

***Characters Relevant to Tyrannosauroidea (from Brusatte et al. 2010a):**

Character 476: Skull, occipital region, orientation:

0: posteriorly

1: posteroventrally

Character 477: Skull, general shape:

0: long and low, length: height ratio greater than 3.2

1: deep, length: height ratio less than 3.2

Note: Length is premaxilla-quadrate cotyle length; height is maximum height of the upper jaw, not counting any cranial crests.

Character 478: Skull, anteroposterior length:

0: less than 40% trunk length

1: greater than 40% trunk length

Note: Trunk length is the anterior extremity of the pectoral girdle to the posterior extremity of the pelvic girdle, as defined by Sereno et al. (2009).

Character 479: Lateral temporal fenestra, orientation of long axis relative to long axis of orbit:

0: posterodorsal

1: approximately parallel

Character 480: Premaxilla, nasal process of opposing premaxillae, orientation:

0: divergent from each other, with small process of nasals fitting in between them

1: closely appressed to each other

Character 481: Premaxilla, deep foramen or fossa on the lateral surface of the base of the nasal process, within the anteroventral corner of the narial fossa:

0: absent

1: present

Character 482: Premaxilla, maxillary process orientation: (ORDERED)

0: mostly laterally (and resultantly widely visible in lateral view)

1: dorsolaterally (facing almost equally dorsally and laterally)

2: dorsally (and resultantly mostly hidden in lateral view)

Character 483: Premaxilla, form of narial fossa ventral to external naris:

0: shallowly excavated

1: deeply excavated, anterior margin invaginated as a deep groove

Character 484: Premaxilla, extent of narial fossa:

0: limited to region immediately ventral to external naris

1: extensive, covers most of main body of premaxilla

Character 485: Premaxilla, orientation and shape of anterior margin: (ORDERED)

0: smoothly curved and projecting posterodorsally, angle between ventral margin of premaxilla and anterior margin is less than 90 degrees;

1: smoothly curved and projecting vertically or slightly anterodorsally, angle between ventral margin of premaxilla and anterior margin is equal to or greater than 90 degrees

2: projecting vertically or slightly anterodorsally, with a discrete inflection point between a more vertical ventral portion and a more horizontal dorsal portion

Note: We have transformed the original character of Brusatte et al. (2010a: character 13) into an ordered multistate by adding a new intermediate state referring to an approximately vertical (or slightly anterodorsally inclined) anterior margin of the ventral portion of the premaxilla. State 2 now refers to a special condition of this state, in which the anterior margin is vertical (or anterodorsally inclined) and there is also a discrete inflection point between the more vertical ventral portion of the anterior margin and the more horizontal dorsal portion of the margin. Taxa with this condition, therefore, do not possess a smoothly curved anterior margin of the premaxilla. Tyrannosauroids are characterized by either state 1 or state 2, with state 2 referring to a subset of basal tyrannosauroids (*Dilong*, *Guanlong*, *Kileskus*, *Proceratosaurus*, *Sinotyrannus*).

Character 486: Premaxilla, position of palatal process:

0: immediately above interdental plates

1: separated from interdental plates by deep lingual surface of premaxilla

Character 487: Maxilla, promaxillary fenestra, position:

0: anterior margin of antorbital fossa

1: extreme anteroventral corner of antorbital fossa

Character 488: Maxilla, maxillary fenestra, anteroposterior length compared to the distance between the anterior margins of the antorbital fossa and fenestra: (ORDERED)

0: less than half
1: greater than half
2: greater than half and also greater than half of the length of the eyeball-bearing portion of the orbit

Character 489: Maxilla, maxillary fenestra, position within maxillary antrum:
0: does not abut dorsal border of the antrum in medial view
1: abuts dorsal border of the antrum in medial view

Character 490: Maxilla, antorbital fossa, extent:
0: reaches nasal suture
1: does not reach nasal suture

Character 491: Maxilla, interfenestral strut, anteroposterior length:
0: greater than 50% of long axis of maxillary fenestra
1: less than 50% of long axis of maxillary fenestra
Note: In oviraptorosaurs, the size of the interfenestral strut is measured relative to the “accessory antorbital fenestra,” whose homology with the maxillary and/or premaxillary fenestrae of other theropods is not clear (e.g., Balanoff et al. 2009).

Character 492: Maxilla, antorbital fossa, trend of dorsoventral depth across main body:
0: uniform
1: diminishes

Character 493: Maxilla, subcutaneous flange bordering the antorbital fossa laterally on the posterior end of the main body, resulting in the fossa forming a channel between the flange and the main body:
0: absent
1: present

Character 494: Maxilla, dorsolateral process, coverage by antorbital fossa: (ORDERED)
0: process absent
1: process covered by subcutaneous surface only
2: ventral half of process covered by antorbital fossa
3: antorbital fossa completely excluded

Character 495: Maxilla, narrow region of smooth surface texture between anterior margin of antorbital fossa and the subcutaneous surface:
0: absent
1: present

Character 496: Maxilla, ventral margin of the anterior region of the bone, profile:
0: straight
1: convex

Character 497: Maxilla, joint surface for palatine, depth:
0: shallow, does not obscure the tooth root bulges from view
1: deep, obscures tooth root bulges from view

Character 498: Maxilla, anterior ramus (demarcated by concave step in anterior margin of maxilla):
0: absent
1: present

Character 499: Maxilla, form of contact with nasal in subadult to adult specimens: (ORDERED)
0: smooth
1: weakly scalloped
2: deeply scalloped with interlocking transverse ridges on both elements
Character 500: Maxilla, form of external subcutaneous surface texturing:
0: random foramina and shallow grooves and ridges
1: deep, prominent, dorsoventrally trending grooves and ridges
Character 501: Maxilla, swollen rim separating antorbital fossa and subcutaneous surface:
0: present
1: absent
Character 502: Maxilla, size of ascending ramus, anteroposterior chord directly above maxillary fenestra compared to dorsoventral depth of maxilla below anterior edge of antorbital fenestra:
0: greater than 1.75 times (ascending ramus large)
1: less than 1.60 times (ascending ramus small)
Character 503: Maxilla, posterior region of the main body (portion including the final 3-5 teeth and anterior to the jugal process), shape:
0: maintains a relatively constant dorsoventral depth
1: tapers in depth posteriorly
Character 504: Maxilla, primary row of neurovascular foramina, form:
0: continues as a row posteriorly
1: transitions posteriorly into a sharp groove, paralleling the antorbital fossa rim
Character 505: Maxilla, antorbital fossa, extent on main body:
0: covers more than half of the depth of the main body beneath the anterior margion of the antorbital fenestra
1: covers less than half of this depth
Character 506: Nasals, midline crest on dorsal surface:
0: absent
1: present
Character 507: Nasal, shape in dorsal view: (UNORDERED)
0: expands in width posteriorly
1: relatively constant width across the length of the bone, due to subparallel lateral sides
2: tapers in width posteriorly
Character 508: Nasal, frontal process, mediolateral width:
0: unconstricted
1: constricted, less than ½ width of widest point of nasal
Character 509: Nasal, posterolateral process that overlaps the lateral surface of the lacrimal:
0: absent
1: present
Character 510: Nasal, extent of narial fossa on premaxillary process:
0: limited to ventral margin of process
1: covers entire process, and thus meets opposite fossa on dorsal midline

Character 511: Nasal, medial processes of frontal articulation, shape: (UNORDERED)

0: processes absent or very subtle

1: lanceolate

2: tapered

Character 512: Nasal, thin, low, and laterally projecting crest at the corner where lateral and dorsal surfaces meet:

0: absent

1: present

Character 513: Lacrimal, angle between anterior and ventral rami

0: 90 degrees (=inverted L shaped) or greater

1: approximately 70-80 degrees (=7 shaped)

Character 514: Lacrimal, cornual process on dorsal surface, form: (UNORDERED)

0: barely perceptible ridge across entire length of anterior ramus (equivalent to the state "cornual process absent" in tyrannosauroid-specific datasets)

1: broad, shallow, dorsally convex, laterally overhanging swelling across most of the length of the anterior ramus

2: discrete conical projection

3: small, conical, smooth projection that rises 2-3 millimeters from skull roof

Note: All taxa without a cornual process (those scored as absent for character 37) are here scored as inapplicable ("?").

Character 515: Lacrimal, cornual process, form:

0: smoothly rounded

1: discrete apex present

Note: All taxa without a discrete cornual process (those scored as absent for character 37 and those scored as 0 for character 514) are here scored as inapplicable ("?").

Character 516: Lacrimal, cornual process, position of apex:

0: dorsal to ventral ramus

1: anterior to ventral ramus

Note: All taxa without a discrete cornual process (those scored as absent for character 37 and those scored as 0 for character 514 and 515) are here scored as inapplicable ("?").

Character 517: Lacrimal, anterior ramus, pneumaticity:

0: not inflated

1: inflated by pneumatic recess

Character 518: Lacrimal, size of primary external opening for lacrimal recess:

0: small, anterior end located approximately at the same level as the anterior end of the ventral ramus

1: large, anterior end located far anterior to the ventral ramus

Character 519: Lacrimal, interaction of primary external opening for lacrimal recess and antorbital fossa:

0: separate

1: blend

Character 520: Lacrimal, accessory external openings for lacrimal recess on the anterior ramus: (ORDERED)

0: absent
1: present and proximally located (i.e., near to primary recess)
2: present and distally located

Character 521: Lacrimal, pneumatic recess opening internally onto medial surface of bone as a discrete pneumatic fenestra (pneumatopore):
0: absent
1: present

Character 522: Lacrimal, dorsal prong of anterior ramus for articulation with maxilla ("anterodorsal process"), size:
0: absent or small
1: present and elongate
Note: We have combined "absent" and "small" into a single character statement, because the subtle process can easily be mistaken for absent if it is broken or poorly preserved.

Character 523: Lacrimal, ventral ramus, extent of medial lamina:
0: greater than half of the dorsoventral depth of the ramus
1: half or less of the dorsoventral depth of the ramus

Character 524: Lacrimal, orbitonasal ridge on medial surface, position:
0: anterior to posterior margin of ventral ramus
1: adjacent to or contacting posterior margin of ventral ramus

Character 525: Lacrimal, articulation with frontal, form:
0: squamous
1: conical lacrimal process set into deep pit in frontal

Character 526: Lacrimal, posterior process for articulation with frontal, inflated by pneumatic recess:
0: no
1: yes

Character 527: Lacrimal, extent of antorbital fossa on ventral ramus:
0: covers greater than 60% of anteroposterior length along the contact with the jugal
1: covers less than this measure

Character 528: Lacrimal, maxillary process of anterior ramus, visibility in lateral view:
0: both dorsal and ventral margins visible
1: dorsal margin concealed by subcutaneous surface abouve antorbital fossa and only ventral margin visible
Note: Those taxa without a maxillary process ("dorsal prong" in character 522) are here scored as inapplicable ("?").

Character 529: Jugal, maxillary ramus, depth:
0: shallow, not expanded relative to subortibal portion of bone
1: deep, expanded relative to suborbital portion of bone

Character 530: Jugal, antorbital fossa, extent on maxillary ramus:
0: edge of fossa undercut and continues posterodorsal to jugal recess
1: fossa edge does not extend past the jugal recess
Note: Those taxa without a jugal recess (e.g., most ornithomimosaurs) are here scored as inapplicable ("?") for this character.

Character 531: Jugal, pneumatic recess, location relative to ventral ramus of lacrimal:

0: ventral

1: anterior

Note: Those taxa without a jugal recess (e.g., most ornithomimosaurs) are here scored as inapplicable (“?”) for this character.

Character 532: Jugal, pneumatic recess, orientation of long axis:

0: approximately horizontal

1: inclined at approximately 45 degrees relative to the ventral skull margin

Note: Those taxa without a jugal recess (e.g., most ornithomimosaurs) are here scored as inapplicable (“?”) for this character.

Character 533: Jugal, secondary fossa for pneumatic recess, position relative to recess:

0: ventral

1: dorsal

Note: Those taxa without a jugal recess (e.g., most ornithomimosaurs) are here scored as inapplicable (“?”) for this character.

Character 534: Jugal, suture with lacrimal, angle of the posterior half of the contact

0: low

1: steep

Character 535: Jugal, fossa on lateral surface of postorbital ramus, depth inset into bone:

0: shallow

1: deep

Character 536: Jugal, articulation with postorbital, form of ventral extremity of suture:

0: tapering scarf joint

1: interlocking notch for postorbital

Character 537: Jugal, articulation with postorbital, extent of scarf joint on lateral surface of postorbital ramus:

0: limited, occupies less than 50% of anteroposterior length of the process

1: extensive, occupies approximately 50-75% of the anteroposterior length of the process

Character 538: Jugal, articulation with postorbital, braced by a pronounced ridge on the lateral surface of the postorbital ramus, which borders the postorbital posteriorly:

0: no

1: yes

Character 539: Jugal, postorbital ramus, orientation relative to ventral margin of jugal:

0: approximately perpendicular

1: posterodorsal (obtuse angle between the long axis of the process and the ventral margin)

Character 540: Jugal, cornual process: (ORDERED)

0: absent

1: present
2: present and distinctive (mediolaterally wide and heavily rugose)

Character 541: Jugal, dorsal prong of quadratojugal ramus, slope in lateral view:
0: horizontal
1: posterodorsal

Character 542: Jugal, ventral prong of quadratojugal ramus, slope of joint surface in lateral view:
0: approximately anteroposteriorly oriented, angled less than 45 degrees from horizontal
1: angled anterodorsally at greater than 45 degrees from horizontal

Character 543: Jugal, shape of orbital margin:
0: weakly concave, approximately level with lacrimal-jugal suture
1: U-shaped, extends ventral to lacrimal-jugal suture

Character 544: Jugal, raised rim on the lateral surface, paralleling the ventral margin of the bone and anteriorly confluent with the antorbital fossa rim of the maxilla:
0: absent
1: present

Character 545: Postorbital, cornual process: (ORDERED)
0: absent
1: limited to rugose rim at posterodorsal corner of orbit
2: present as a rugose, convex boss

Character 546: Postorbital, cornual process, position:
0: separated from dorsal margin of postorbital by a smooth, convex region
1: approaches or extends past dorsal margin of bone
Note: Those taxa without a cornual process are scored as inapplicable ("?").

Character 547: Postorbital, cornual process, position:
0: located at orbital margin
1: located posterodorsal to orbital margin
Note: Those taxa without a cornual process are scored as inapplicable ("?").

Character 548: Postorbital, squamosal ramus, form of posterodorsal margin:
0: uninterrupted convex arc
1: emarginated by squamosal (discrete concave notch within the margin)

Character 549: Postorbital, squamosal ramus, extent relative to posterior margin of lateral temporal fenestra:
0: reaches or extends posterior to
1: terminates anterior to

Character 550: Postorbital, suborbital process, position:
0: at ventral end of ventral process
1: flange-like, separated from ventral tip of the ventral process by a notch
Note: Taxa without a suborbital process are here scored as inapplicable ("?").

Character 551: Postorbital, anterior ramus, form:
0: short and stout, long axis is approximately half the length of the ventral ramus and the thickness at the base is approximately the same as the thickness of the midpoint of the ventral ramus

1: long and slender, long axis is greater than 60% of the length of the ventral ramus and the thickness at the base is approximately half that of the midpoint of the ventral ramus

Character 552: Postorbital, ventral ramus, anteroposterior width at midpoint: (UNORDERED)

0: approximately the same width as ventral ramus of the lacrimal
1: substantially wider than ventral ramus of lacrimal
2: substantially narrower than ventral ramus of lacrimal

Character 553: Squamosal, lateral ridge delimiting supratemporal fossa, form:

0: ridge unpronounced or undivided
1: divided

Character 554: Squamosal, supratemporal fossa, surface morphology:

0: flat or concave
1: convex

Character 555: Squamosal, quadratojugal process, morphology of anterior tip in those taxa with horizontal processes:

0: tapered point
1: squared off

Character 556: Squamosal, quadratojugal process, flange that is covered laterally by the quadratojugal, dorsoventral depth of entire process compared to portion of process that is exposed in lateral view when in articulation with quadratojugal: (ORDERED)

0: flange absent
1: thinner
2: substantially thicker

Character 557: Squamosal, pneumaticity: posterior process, inflated by squamosal recess: (ORDERED)

0: absent
1: present as a deep, concave depression on the ventral surface of the main body
2: present as a deep, concave depression on the ventral surface of the main body, and extending posteriorly to inflate the squamosal posterior process

Note: This is a modified version of the original character in Brusatte et al. (2010a, character 95) which includes a second derived state referring to squamosal pneumaticity in general. This character is ordered, as state 2 is a special condition of state 1 in which the pneumatic recess that invades the ventral surface of the main body of the squamosal also extends posteriorly into the posterior process of the squamosal.

Character 558: Squamosal, posterior process, length of the long axis:

0: long, approximately 1/3-1/2 length of quadratojugal process
1: short, approximately 1/6 length of quadratojugal process

Character 559: Squamosal, anterior process, flange that extends dorsal to the postorbital posterior process:

0: absent
1: present

Character 560: Quadratojugal, dorsal process, ridge along anterior margin of lateral surface: (ORDERED)

0: absent
1: present, subtle and fades in strength dorsally
2: present, robust and extends to the dorsal margin of the bone

Character 561: Quadratojugal, form of jugal articulation, dorsal prong of posterior process of jugal approaching the base of the quadratojugal (the corner where the anterior and dorsal processes of the quadratojugal meet):
0: absent
1: present

Character 562: Quadratojugal, anterior process for articulation with jugal, form of anterior region: (UNORDERED)
0: tapered
1: rounded
2: squared off or double pronged

Character 563: Quadratojugal, anterior process, extent related to anterior margin of lateral temporal fenestra:
0: terminates posterior to fenestra margin
1: level with or anterior to fenestra margin

Character 564: Quadratojugal, curvature of bone:
0: mediolaterally compressed and flat
1: posterior region flexed so that it curves posteriorly, thus delimiting the lateral edge of a deep pocket that borders the quadrate foramen laterally in posterior view

Character 565: Quadratojugal, posterior process, length and orientation:
0: short, oriented mostly laterally
1: elongate, wraps onto the posterior surface of the quadrate cotyles

Character 566: Quadrate foramen, size:
0: small, long axis approximately 10% of the dorsoventral depth of the quadrate shaft
1: large, long axis greater than 20% of the dorsoventral depth of the quadrate shaft

Character 567: Quadrate, form of pneumatization, deep recess on the anterior surface where the psterygoid wing and condyles meet:
0: absent
1: present

Character 568: Quadrate, condyles, position relative to occipital condyle when skull is in articulation:
0: aligned (i.e., quadrate condyles approximately ventral to occipital condyle, or slightly anterior to condyle)
1: completely posterior

Character 569: Quadrate, quadratojugal articulation, extent on lateral surface of lateral condyle:
0: limited, occupies only part of the surface
1: extensive, covers entire lateral surface and extends dorsally to partially enclose quadrate foramen laterally

Character 570: Quadrate, articular surface for quadratojugal on quadrate lateral condyle, orientation of medial margin as seen in posterior view where quadratojugal wraps around quadrate:

0: vertical or dorsomedial
1: dorsolateral

Character 571: Prefrontal, contacts nasal:
0: yes
1: no, excluded by frontal-lacrimal contact

Character 572: Prefrontal, ventral process, extent:
0: large, extends 1/2-1/4 of the way down the ventral ramus of the lacrimal to make an extensive contribution to the preorbital bar
1: reduced or absent, ventral process is a thin flange that is continuous with the crista cranii of the frontal, and does not extend more than approximately ¼ of the length of the preorbital bar

Character 573: Frontal, shape (in those taxa with frontals that narrow anteriorly as a wedge between the nasals):
0: triangular
1: posterior end expanded into a rectangular shape, with a small anterior triangle
Note: Taxa with frontals that do not narrow anteriorly between the nasals (scored in character 41) are scored here as inapplicable (“?”).

Character 574: Frontal, size of single frontal, ratio of anteroposterior length of exposed portion on skull roof to mediolateral width at midpoint:
0: greater than 2.0 (usually greater than 2.5)
1: less than 2.0

Character 575: Frontal, supratemporal fossa, medial extension:
0: fossa restricted to posterolateral corner of frontal
1: meets opposing fossa at the midline

Character 576: Frontal, sagittal crest: (UNORDERED)
0: absent or subtle, only discernable as a slight midline bulge
1: present and pronounced (dorsoventrally tall), single structure
2: present and pronounced (dorsoventrally tall), paired structure
Note: This charater is not equivalent to a parietal sagittal crest. Rather, it refers specifically to raised crests on the dorsal surface of the frontal, which may or may not be continuous with a sagittal crest on the parietal.

Character 577: Frontal, sagittal crest, anteroposterior length:
0: short, less than 15% length of the frontal
1: extensive, approximately 25% of the length of the frontal
Note: Those taxa without a frontal sagittal crest are scored as inapplicable (“?”).

Character 578: Frontal, postorbital suture: (ORDERED)
0: dorsoventrally shallow and undifferentiated
1: dorsoventrally shallow (approximately 6 times longer than deep) and differentiated into a vertical region anteriorly and a horizontal region posteriorly
2: dorsoventraly deep (approximately twice as long as deep) and subtly differentiated into vertical and horizontal regions

Character 579: Frontal, contribution to orbital rim: (ORDERED)
0: extensive
1: present but limited to a small notch
2: excluded by postorbital-lacrimal contact in large specimens
3: exclueed by postorbital-lacrimal articulation and oval “palpebral” ossification

Character 580: Parietal-frontal suture, form:
0: transversely smooth
1: tab-like wedge from parietal extends anteriorly to overlie frontal on mindline
Character 581: Parietal, sagittal crest, form:
0: comprised of two parallel crests
1: comprised of a single midline crest
Note: Those taxa without a parietal sagittal crest are here scored as inapplicable (“?”).
Character 582: Parietal, skull table between supratemporal fossae, width:
0: broad, more than 10% of the mediolateral width of the fossa
1: extremely reduced, sagittal crest or crests (if present) pinched between opposing fossae
Character 583: Parietal, sagittal crest, dorsoventral depth:
0: consistent across length of crest
1: peaked anteriorly at frontal-parietal suture
Note: Those taxa without a parietal sagittal crest are here scored as inapplicable (“?”).
Character 584: Parietal, nuchal crest, dorsoventral depth:
0: as low as or lower than dorsal surface of the interorbital region
1: extends higher than the dorsal surface of the interorbital region
Character 585: Vomer, shape of anterior end:
0: lanceolate (lateral margins parallel-sided)
1: expanded into a diamond
Character 586: Ectopterygoid, extent of internal recess:
0: does not inflate body of the bone and the pterygoid process
1: inflates body of the bone and the pterygoid process
Character 587: Ectopterygoid, jugal process, external pneumatic foramina leading into ectopterygoid recess:
0: absent
1: present
Character 588: Ectopterygoid, jugal process, pneumaticity:
0: is not inflated by the internal recess
1: is visibly inflated by the internal recess
Character 589: Ectopterygoid, external opening of pneumatic recess, shape:
0: thin ovoid slot
1: large, round or triangular
Character 590: Ectopterygoid, surface posteriorly adjacent to external opening of pneumatic recess, form:
0: flat, recess grade smoothly into the floor of the lateral temporal fenestra (=subtemporal fenestra)
1: lip, recess separated from lateral temporal fenestra (=subtemporal fenestra)
Character 591: Palatine, vomeropterygoid process, ratio of anteroposterior length of dorsal margin to length of greatest constriction of process neck:
0: greater than 2.0
1: less than 2.0
Character 592: Palatine, vomeropterygoid process, orientation of neck:

0: inclined anterodorsally
1: vertical

Character 593: Palatine, pneumaticity:
0: absent
1: present

Character 594: Palatine, pneumatic recess, number of external pneumatic openings:
0: one
1: two

Character 595: Palatine, primary external opening of palatine recess, location of posterior margin:
0: level with or extends posterior to posterior margin of the vomeropterygoid process neck
1: located far anterior to posterior margin of the vomeropterygoid process neck

Character 596: Palatine, primary opening of palatine recess, location of anterior margin:
0: level with or extends posterior to anterior margin of the vomeropterygoid process neck
1: located far anterior to anterior margin of the vomeropterygoid process neck

Character 597: Palatine, jugal process, location of contact surface for lacrimal:
0: posterior (“distal”), separated from opening of palatine recess by wide margin
1: anterior (“proximal’), closely approaches opening of palatine recess

Character 598: Palatine, maxillary process, form of maxillary articulation:
0: flat
1: deeply excavated as a slot, demarcated dorsally by a pronounced lip of bone

Character 599: Palatine, extension of pneumatic recess into jugal process:
0: no
1: yes, process visibly inflated

Character 600: Palatine, maxillary articulation, form:
0: maxilla abuts lateral surface of maxillary process and anterior region of jugal process
1: contact reinforced by a “brace” at the anteroventral corner of the jugal process, which sits within internal antorbital fossa

Character 601: Palatine, morphology of maxillary articulation brace:
0: projects ventrally due to a jugal process that extends further ventrally than the maxillary process, such that there is a discrete corner between the two processes in lateral view
1: projects laterally, with no discrete corner between the smoothly confluent jugal and maxillary processes in lateral view

Character 602: Internal choana, shape:
0: anteroposteriorly elongate oval
1: nearly circular

Character 603: Suborbital fenestra, shape:
0: anteroposteriorly elongate oval
1: nearly circular

Character 604: Braincase, orientation of occipital surface:

0: faces posteriorly
1: faces posteroventrally
This is a duplication of character 476

Character 605: Supraoccipital, contribution to dorsal rim of foramen magnum (ORDERED)

0: forms entire rim
1: makes limited contribution to rim via triangular ventral process
2: completely excluded from rim

Character 606: Supraoccipital, form of dorsal margin

0: smoothly convex and undivided
1: divided into two processes (“forked”)

Character 607: Exoccipital-opisthotic, paroccipital process, ventral flange at distal end:

0: absent
1: present

Character 608: Exoccipital-opisthotic, paroccipital processes, deep fossa on posterior surface dorsolateral to the foramen magnum:

0: present
1: absent

Character 609: Exoccipital-opisthotic, crista tuberalis (=metotic strut), extent in posterior view:

0: 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

1: extensive, width greater than one half braincase depth

Character 610: Basioccipital, basal tubera, dorsoventral depth:

0: less than depth of occipital condyle
1: greater than depth of occipital condyle

Character 611: Basioccipital, basal tubera, concave notch ventrally between opposing tubera, dorsoventral depth:

0: shallow, less than 40% depth of tubera
1: deep, approximately 50% depth of tubera
A duplicate of character 449

Character 612: Basioccipital, subcondylar recess, depth of pneumatic fossae on posterior surface of basal tubera:

0: absent or shallow
1: deep

Character 613: Basisphenoid, basisphenoid recess, orientation of central axis: (ORDERED)

0: vertical, recess obscured in posterior view
1: posteroventral, recess partially visible in posterior view
2: extremely posteroventral, recess compressed anteroposteirorly and widely visible in posterior view, and basipterygoid processes located beneath the basal tubera

Character 614: Basisphenoid, basisphenoid recess, inflation of the ceiling of the recess:

0: absent

1: present

Character 615: Basisphenoid, basisphenoid recess, shape in ventral view:

0: funnel-like, expands in mediolateral width posteriorly

1: ovoid or circular, no posterior expansion

Character 616: Basisphenoid, shape of basicranium (rectangle defined by positions of both basal tubera and both basipterygoid processes):

0: anteroposteriorly longer than mediolaterally wide

1: wider than long

Character 617: Parasphenoid, shape of rostrum:

0: anteroposteriorly expanded, ventral margin is a smooth concave arch

1: dorsoventrally expanded, ventral margin is nearly vertical posteriorly and then abruptly transitions to horizontal trend anteriorly

Character 618: Laterosphenoid, antotic crest separating lateral wall of braincase from orbital and temporal spaces:

0: absent or indistinct

1: present, robust and rugose

Character 619: Laterosphenoid, antotic crest, form:

0: single structure

1: bifurcates ventrally

Character 620: Laterosphenoid, fossa on lateral surface that houses head of epipterygoid:

0: absent or shallow

1: present, deep and rugose

Character 621: Mandibular ramus, dorsoventral depth of dentary at level of dentary-surangular contact on the dorsal margin of the lower jaw:

0: less than 18% of the total anteroposterior length of the lower jaw

1: greater than 18% of the total anteroposterior length of the lower jaw

Character 622: External mandibular fenestra, dorsoventral depth relative to depth of mandible at midpoint of fenestra: (ORDERED)

0: greater than 25% depth of mandible

1: less than 25% depth of mandible

2: absent

Character 623: Lower jaw, articulation, glenoid position relative to level of alveolar margin of dentary: (UNORDERED)

0: approximately level with

1: dorsal to

2: strongly ventral to

Character 624: Dentary, position of the transition point between the ventral and anterior margins of the bone in lateral view:

0: below alveoli 1-3, anterior margin of bone rounded (or in some cases nearly straight)

1: below alveolus 4 (or more posteriorly), anterior margin nearly straight and projects posteroventrally

Character 625: Dentary, ventrally projecting rugose process (“chin”) where the anterior and ventral margins of the dentary meet:

0: absent

1: present, visible as a pointed projection in lateral view and convex in medial view, braces dentary symphysis

Character 626: Dentary, symphysis, texture:

0: generally smooth

1: strongly rugose and beveled, with interlocking ridges and convexities for articulation with the opposing symphysis

Character 627: Dentary, articular surface for splenial along ventral region of dentary ramus below the Meckelian fossa, form:

0: dorsoventrally shallow and smooth

1: dorsoventrally deep (nearly as deep as anterior depth of fossa) and rugose

Character 628: Dentary, anterior alveoli, size in comparison to alveoli in middle of tooth row: (ORDERED)

0: approximately same size

1: first two alveoli substantially smaller

2: first alveolus substantially smaller

Note: This character is ordered here, because we hypothesize that state 2 (which is seen only in a small subset of derived tyrannosaurids: *Tarbosaurus* and *Tyrannosaurus*) is a special condition of state 1 (which is present in all score-able tyrannosauroids except for the derived subset).

Character 629: Dentary, dorsal margin of bone in lateral view, profile: (UNORDERED)

0: straight

1: strongly concave

2: strongly convex

Character 630: Dentary, Meckelian groove, form:

0: dorsoventrally deep and shallowly inset into medial surface of bone

1: dorsoventrally shallow and deeply inset into bone, groove appears as a thin, sharp structure

Character 631: Surangular, surangular shelf on lateral surface, form: (ORDERED)

0: low ridge or absent

1: prominent ridge that is offset laterally from the bone but dorsoventrally thin

2: prominent shelf that is dorsoventrally deep

Note: The “low ridge” and “absent” conditions are considered primarily homologous here, because a very low ridge may appear absent on a specimen due to poor preservation. Taxa that genuinely appear to lack a ridge (e.g., *Shuvuuia*) are scored as inapplicable (“?”) for the following characters related to the form and the position of the ridge.

Character 632: Surangular, surangular shelf on lateral surface, position and form: (ORDERED)

0: placed far dorsal to posterior surangular foramen

1: foramen abuts shelf but shelf projects laterally and does not overhang foramen

2: shelf projects ventrolaterally to overhang foramen

Character 633: Surangular, surangular shelf on lateral surface, orientation relative to the long axis of the lower jaw: (UNORDERED)

0: anterodorsal

1: anteroventral

2: straight anteroposteriorly

Character 634: Surangular, pneumatic fossa posterodorsal to posterior surangular foramen:

0: absent

1: present

Character 635: Surangular, adductor muscle attachment site dorsal to surangular shelf, orientation: (ORDERED)

0: faces primarily dorsally

1: faces almost equally dorsally and laterally

2: faces primarily laterally

Character 636: Surangular, triangular fossa on the lateral surface of the surangular shelf immediately anteroventral to glenoid:

0: absent

1: present

Character 637: Surangular, fossa on the lateral surface of the bone immediately ventral to, and separated from, the glenoid:

0: absent

1: present

Character 638: Surangular, anteroposterior length of anterior flange (region anterior to anterior margin of external mandibular fenestra) compared to overall length of surangular:

0: less than 30%

1: greater than 30%

Character 639: Angular, ventral margin, form:

0: smoothly convex

1: anterior region “flexed” relative to posterior region, such that there is a discrete step between them

Character 640: Articular, mediolateral width of jaw muscle attachment site:

0: less than width of glenoid for articulation with quadrate

1: approximateily equal to width of glenoid

Character 641: Articular, smooth non-articular region between glenoid and attachment site for depressor mandibular muscles:

0: present

1: absent

Character 642: Splenial, anterior mylohoid foramen, shape and size: (ORDERED)

0: small circular or ovoid opening, or absent

1: large, anteroposteriorly ovoid shape

2: extremely large, approximately as deep dorsoventrally as the anterior process of the splenial

Note: The small and absent conditions are here treated as a single character state, because poor preservation often makes a very small foramen appear absent.

Character 643: Splenial, dorsal region overlapped medially by prearticular:

0: absent

1: present

Character 644: Prearticular, ventral bar, series of ridges on lateral surface to strengthen articulation with angular:

0: absent
1: present

Character 645: Supradentary ossification, shape:
0: elongate, shallow strip
1: deep, crescentic shape

Character 646: Supradentary and coronoid ossifications, form of contat at their zone of fusion:
0: ossifications smoothly confluent
1: ossifications offset by a concave notch

Character 647: Premaxillary tooth crown 4, apicobasal height relative to largest maxillary crown:
0: subequal
1: approximately 50%

Character 648: Premaxillary teeth, median vertical ridge on lingual surface: (ORDERED)
0: absent
1: present as a subtle structure in anterior (mesial) premaxillary teeth
2: present as pronounced structure in all premaxillary teeth

Character 649: Premaxillary teeth, curvature of distal (posterior) teeth:
0: recurved
1: straight

Character 650: Maxillary teeth, number:
0: 13 or more
1: less than 13 (in the largest adult specimens when growth series are known)

Character 651: Maxillary and dentary teeth, form: (ORDERED)
0: ziphodont, transverse width of base less than 60% of mesiodistal length
1: incrassate, width greater than 60% of length
2: incrassate, width nearly equal to length
Note: Those taxa with conical or leaf-like teeth are scored as inapplicable (“?”) for this character (e.g., therizinosauroids, most alvarezsauroids).

Character 652: Axis and postaxial cervicals, anteroposterior length of centrum compared to dorsoventral height of posterior centrum face:
0: greater
1: less than or equal to

Character 653: Axis, pneumatic foramen (pleurocoel), position:
0: near midheight of entrum
1: dorsally located, directly underneath neurocentral suture and directly posterior to diapophysis

Character 654: Axis, pneumatic foramen (pleurocoel), extent of surrounding fossa:
0: limited to margins of foramen
1: extensive, occupies most of lateral surface of centrum

Character 655: Axis, ridge on ventral surface of centrum:
0: absent
1: present

Character 656: Axis, pneumatic foramina and fossae on each side of the anterior ridge on the neural spine:

0: absent

1: present

Character 657: Axis, neural spine, texture of dorsal region of anterior surface:

0: generally smooth or with subtle texture

1: highly rugose, with series of grooves, ridges, and eminences

Character 658: Axis, dorsal region of neural spine, number of projections on "crown" region:

0: two lateral projections, dorsal surface of spine smoothly concave

1: two lateral projections and one dorsal projection on the midline

Note: Only those taxa scored for a mediolaterally broad ("transversely flared") neural spine for character 92 are relevant to this charater. All taxa with a mediolaterally compressed neural spine are scored as inapplicable ("?").

Character 659: Axis, supradiapophyseal fossa (fossa posterodorsal to diapophysis), form:

0: absent or shallow

1: deeply excavated and funnel-like

Character 660: Cervical vertebrae, neural spines in middle-posterior cervicals, dorsoventral height:

0: substantially shorter than height of posterior centrum face

1: approximately same length as or longer than height of posterior centrum face

Character 661: Cervical vertebrae, morphology of posterior centrodiapophyseal laminae in anterior-middle cervicals:

0: absent or present as a weak ridge

1: present as a thick, laterally offset lamina that demarcates a deep infradiapophyseal fossa anteriorly

Character 662: Cervical vertebrae, hypapophysis on anterior region of ventral surface:

0: absent

1: present

Character 663: Cervical vertebrae, position of prezygapophysis in middle cervicals:

0: slightly overhangs centrum laterally

1: strongly overhangs centrum laterally, entire prezygapophyseal facet placed lateral to centrum

Character 664: Cervical vertebrae, orientation of posterior centrodiapophyseal lamina in anterior-middle cervicals:

0: projects posteroventrally, infrapostzygapophyseal fossa located primarily posterior to lamina

1: nearly horizontal, fossa located primarily dorsal to lamina

Character 665: Cervical and dorsal vertebrae, rugose ligament attachment scars in pre- and postspinal fossae: (ORDERED)

0: absent or weakly developed

1: present as prominent, rectangular flanges that extend outside of the fossae and are visible in posterior view, but on the dorsal vertebrae only

2: prominent in dorsals and cervicals

Character 666: Dorsal vertebrae, neural spine, level of posterior termination:

0: at approximately the same level as the posterior centrum face

1: far posterior to the posterior centrum face

Character 667: Dorsal vertebrae, anteroposterior length of middle-posterior dorsal centra compared to dorsoventral height of posterior centrum face:

0: greater

1: less than or equal

Character 668: Dorsal vertebrae, middle-posterior dorsals, position of postzygapophysis relative to prezygapophysis:

0: at same level

1: elevated dorsally

Character 669: Dorsal vertebrae, middle-posterior dorsals, form of anterior and posterior centrodiapophyseal laminae: (ORDERED)

0: discrete laminae absent, or laminae present but do not demarcate a deep infradiapophyseal fossa between them

1: present and make contact on ventral surface of transverse process, demarcating a triangular infradiapophyseal fossa

2: present and do not make contact but roughly parallel each other, infraprezygapophyseal and infradiapophyseal fossa merged into a single fossa

Character 670: Sacral vertebrae, fenestrae between fused neural spines: (ORDERED)

0: neural spines unfused

1: spines fused but fenestrae absent

2: spines fused and fenestrae present

Character 671: Sacral ribs, position of central ribs on sacrum:

0: span two sacrals

1: limited to a single sacral

Character 672: Sacral ribs, position of rib attachment for central ribs on individual sacrals:

0: span centrum and neural arch

1: limited to neural arch only

Character 673: Sacral vertebra five, position of ventral margin of posterior articular face in lateral view:

0: at same level as ventral margin of anterior articular face

1: positioned ventral to ventral margin of anterior articular face

Character 674: Sacral vertebrae, form of hyposphene in posteriormost sacral:

0: absent or present as a single midline structure

1: present and comprised of two parallel-sided sheets

Character 675: Caudal vertebrae, anterior caudals, position of base of neural spine:

0: anterior to posterior surface of centrum

1: level with or posterior to posterior surface of centrum

Character 676: Caudal vertebrae, anterior caudals, shape of transverse processes in dorsal view:

0: rectangular, with parallel anterior and posterior sides, or slightly ovoid with a gradual expansion in width distally

1: distal end expanded into a spatulate bulb

Character 677: Caudal vertebrae, anterior caudals, two laminae linking prezygapophysis and transverse process, between which is a deep, triangular fossa:

0: absent

1: present

Character 678: Scapula, angle between posterior margin of glenoid and dorsal margin of blade:

0: greater than 90 degrees

1: approximately 90 degrees

Character 679: Scapula, acromion, dorsoventral depth:

0: less than 3.0 times minimum dorsoventral depth of blade

1: greater than 3.0 times minimum dorsoventral depth of blade

Character 680: Scapula, ratio of anteroposterior length of bone to minimum dorsoventral depth of blade:

0: less than 10.0

1: greater than 10.0

Character 681: Scapula and coracoid, glenoid, position relative to posteroventral margin of blade:

0: offset posteroventrally (by a distance equivalent to the width of the neck of the blade to ½ of the width of neck of the blade)

1: offset only slightly posteroventrally (less than 50% the width of the neck of the blade)

Character 682: Coracoid, anteroposterior length at midpoint:

0: approximately 100-150% of the length of the scapular acromion at midheight

1: 200% or greater than the length of the scapular acromion at midheight

Character 683: Coracoid, coracoid foramen:

0: present

1: absent or extremely small

Character 684: Humerus, apex of deltopectoral crest, location from proximal end: (ORDERED)

0: 35-50% of the length of the humerus

1: 25-35% of the length of the humerus

2: less than 25% of the length of the humerus

Character 685: Humerus, additional muscle attachment tubera at the corner of the anterior and lateral surfaces distal to the deltopectoral crest:

0: absent

1: present

Character 686: Humerus, concave notch between external tuberosity and deltopectoral crest:

0: present, two structures clearly separated

1: absent, two structures smoothly confluent

Character 687: Humerus, form of distal condyles:

0: lateral and medial condyles expanded equally (offset from shaft in anterior or posterior view is approximately equal)

1: medial condyle expanded further medially than the lateral condyle is laterally

Character 688: Ulna, shaft axis, form:

0: bowed

1: straight

Character 689: Principal distal carpal, shape:

0: semilunate in lateral view with trochlear proximal surface

1: discoid with flat proximal surface

Character 690: Metacarpal I, medial distal condyle, form:

0: well formed and large

1: rudimentary

Character 691: Metacarpal I, medial margin, shape in proximal view:

0: concave

1: smoothly convex or straight

2: Expanded into a ridge-like medial process extending beyond the margin of the proximal articulation. This state is principally observed in alavarezsauroids and in *Nqwebasaurus.* Alvarezsauroids possess an elongate tab.

Character 692: Metacarpals, metacarpal II, mediolateral width at midpoint compared to midpoint width of metacarpal I:

0: equal to or narrower than

1: more robust than

Character 693: Manual phalanx II-1, length compared to that of metacarpal 1:

0: longer

1: subequal to

Character 694: Ilium, anteroposterior length compared to length of femur: (ORDERED)

0: 70-85%

1: 95-105%

2: 105-115% (or greater, in some birds)

Character 695: Ilium, dorsal margin of blade, position relative to sacral neural spines: (UNORDERED)

0: separated by a gap

1: lies against neural spines and opposing iliac blaces may make contact above neural spines in some individuals

2: separated by a wide gap

Note: This is a modified version of the Brusatte et al. (2010a) character, which adds a second derived state ("separated by a wide gap") to refer to the condition of some derived therizinosauroids, as used by Zanno et al. (2009, character ZCD 306).

Character 696: Ilium, supraacetabular crest, maximum lateral projection relative to ischial peduncle:

0: significantly greater

1: subequal

Character 697: Ilium, supraacetabular crest, extent on pubic peduncle:

0: extensive, extends along most or all of the edge of the peduncle

1: limited, discretely offset from acetabular edge of pubic peduncle

Character 698: Ilium, pubic and ischial peduncles, anteroposterior lengths at dorsal base: (ORDERED)

0: pubic peduncle substantially longer than ischial peduncle
1: both peduncles approximately the same length
2: ischial peduncle longer than pubic peduncle

Character 699: Ilium, ventral margin of postacetabular process, shape:

0: straight to slightly convex
1: hightly convex, forming a discrete “lobe”-like flange

Character 700: Ilium, dorsal margin, shape:

0: smoothly convex or straight across entire length
1: convex anteriorly and straightens out posteriorly

Note: In dromaeosaurids such as *Unenlagia*, which possess a separate posterior tab-like process of the postacetabular process, this character refers to the shape of the remainder of the ilium (i.e., the entirety of the bone except the tab-like process). Therefore, these taxa are scored for state 0.

Character 701: Ilium, ratio of anteroposterior length to dorsoventral depth above acetabulum:

0: greater than 3.0, ilium is long and low
1: less than 2.8, ilium is subovoid in shape

Character 702: Pubis, pubic tubercle: (ORDERED)

0: absent
1: present as a convexity on the anterior margin of the pubis
2: present as a rugose flange that is discretely offset from the anterior margin of the pubis and is bordered posteriorly by heavy rugosities on the lateral surface on the obturator region of the pubis

Character 703: Pubis, pubic tubercle, position:

0: distally positioned, located ventral to the level of the obturator notch
1: proximally positioned, located level with or dorsal to the obturator notch

Note: All taxa without a pubic tubercle are here scored as inapplicable (“?”).

Character 704: Pubis, pubic boot, anteroposterior length relative to total long axis length of pubis:

0: less than 60%
1: greater than 60%

Character 705: Pubis, pubic boot, position of anterior process relative to posterior process:

0: displaced dorsally, resulting in a highly convex ventral margin of the boot
1: placed at the same level, ventral margin of the boot essentially straight

Note: Taxa without a discrete anterior process (e.g., compsognathids) are here scored as inapplicable (“?”).

Character 706: Pubis, anteroposterior expansion of proximal obturator plate region relative to the anterior edge of the pubis shaft at its midpoint:

0: less than twice the anteroposterior thickness of the shaft at its midpoint
1: greater than twice the anteroposterior thickness of the shaft at its midpoint

Character 707: Pubis, obturator notch, form:

0: discrete structure, demarcated ventrally by extensive obturator flange
1: essentially absent, no ventral flange

Note: The enclosed obturator foramen of *Mirischia* is here scored as equivalent to state 0. The presence of a completely enclosed foramen is autapomorphic of *Mirischia* among coelurosaurs.

Character 708: Ischium, position of medial apron:

0: along posterior margin of shaft

1: along anterior margin of shaft

Character 709: Femur, circular scar on posterior surface of shaft distal to fourth trochanter, position:

0: absent, low, or positioned approximately centrally on the shaft

1: abuts medial edge of shaft

Character 710: Femur, lesser trochanter, height relative to greater trochanter:

0: shorter, terminates further distally

1: subequal or slightly taller, the two structures extend to approximately the same level proximally

Note: This is equivalent to Zanno et al. (2009: character ZCD 325).

Character 711: Femur, proximal margin in anterior view: (ORDERED)

0: approximately straight and perpendicular to the long axis of the shaft

1: approximately straight and oriented at an obtuse angle to the long axis of the shaft (=dorsally or proximally inclined head)

2: concave and oriented at an obtuse angle to the long axis of the shaft, due to head that is proximally inclined and a greater trochanter that is elevated substantially relative to the central portion of the proximal surface of the femur

Note: Characters relating to the inclination of the femoral head are often used in theropod phylogenetic datasets, but it is often difficult to develop a standard system of measurement for quantifying the orientation of the head. We use the character as defined here, which concerns the angle between the long axis of the shaft and the long axis of the proximal end, as measured in anterior view (note that many taxa with obtuse angles between the head and shaft in anterior view, such as *Tyrannosaurus*, appear to have perpendicular angles when measured in posterior view). Usually, taxa with an obtuse angle between head and shaft (i.e., a dorsally inclined femoral head) have a proximomedially projecting proximal surface of the femur when seen in anterior view, and this may indicate the presence of an inclined head in specimens that do not preserve the shaft. Furthermore, taxa with an obtuse angle between head and shaft (a dorsally inclined femoral head) possess a head that is elevated proximally relative to the greater trochanter, which is another means for recognizing the inclined condition in specimens that do not preserve the shaft. We also recognize a second derived state, encoded by Zanno et al. (2009: character oZCD 339) and Brusatte et al. (2010a: character 285), referring to the deeply concave proximal margins of the derived tyrannosaurids *Tyrannosaurus* and *Tarbosaurus* and some derived therizinosauroids, which have dorsally inclined heads but also greater trochanters that are raised substantially relative to the remainder of the proximal femur (except for the head), giving the proximal margin a deeply concave profile in posterior view. This character is equivalent to Zanno et al. (2009, character oZCD 320), which refers to the distinction between a medially ("perpendicular to shaft") and dorsally inclined femoral head. Brusatte et al. (2012a) stated that *Tanycolagreus* possesses a dorsally inclined (elevated) femoral head, but we here note that this is not correct and that this taxon possesses a head that is perpendicular to the shaft (state 0).

Character 712: Femur, trochanteric fossa on the posterior surface of the head, lateral to the ligament sulcus (for the capital ligament), form: (ORDERED)

0: absent or shallow

1: deep fossa

2: deep, extensive triangular depression that covers most of the posterior surface of the femur proximally and is demarcated medially and ventrally by a pronounced, curving, swollen ridge

Character 713: Femur, fourth trochanter, position, measurement from proximal margin of head to distal termination of trochanter relative to total length of the femur:

0: 40% or less

1: greater than 40%

Character 714: Femur, lateral condyle, shape in distal view:

0: circular or ovoid

1: ovoid, but with an anterior bulge that is slightly separated from the remainder of the condyle

Character 715: Femur, extensor groove on anterior surface of distal end, form: (ORDERED)

0: absent or extremely shallow, anterior surface flat between the condyles in distal view (extensor groove may be present but does not manifest itself as a groove on the anterior margin in distal view)

1: groove present but shallow, expressed as a broad concave margin in distal view but present as an extensive depression on the anterior surface of the femur

2: groove present and deep, expressed as a deep, U-shaped cleft in distal view and present as an extensive depression on the anterior surface of the femur

Character 716: Femur, mesiodistal crest, form:

0: single structure

1: bifurcates distally to enclose fossa on the medial surface of the medial condyle

Character 717: Tibia, length relative to the femur:

0: 1.05 or greater

1: less than 1.00

Character 718: Tibia, lateral condyle of proximal end, anterior process:

0: absent

1: present

Character 719: Tibia, lateral malleolus, lateral extent:

0: limited, mediolateral measure is less than 40% of mediolateral width of adjacent shaft

1: extensive, mediolateral measure greater than 40% of mediolateral width of adjacent shaft

Character 720: Tibia, lateral malleolus, position relative to medial malleolus:

0: extent to approximately the same level distally

1: lateral malleolus extends substantially further distally than medial malleolus

Character 721: Fibula, iliofibularis tubercle, form:

0: single crest

1: large, rugose, and formed by two crests separated by a depressed fossa ("bipartite" condition)

Character 722: Astragalus, fossa on anterior surface of ascending process, form:

0: shallow concavity that covers most of the ventral region of the ascending process

1: 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

Character 723: Pes, metatarsal III, form of medial surface in anterior or posterior view:

0: straight or subtly convex

1: with medial convex expansion forming a bulge along the distal part of the shaft

Note: This character is equivalent to L. Xu et al. (2011: character 48), who utilized it as a character relevant to ornithomimosaurs. It was first used as a character by Kobayashi (2005).

Character 724: Pes, metatarsal III, ventral nonarticular surface (on the flexor surface) immediately proximal to the distal condyles, form:

0: concave

1: raised subtriangular platform

Character 725: Pes, metatarsals II-IV, distal separation when in articulation:

0: metatarsals closely appressed and distance between II-III and III-IV is approximately equal

1: distal ends of II and IV diverge from III, and distance between III-IV greater than that between II-III

Character 726: Pes, metatarsal II, articular scar for metatarsal III on distal portion of lateral surface of shaft, form:

0: subtle or absent

1: enlarged as a rugose fossa that occupies more than half of the proximodistal length of the shaft and expands in anteroposterior width distally

Character 727: Pes, metatarsal II, lateral surface in proximal view, shape: (ORDERED)

0: flat or weakly concave

1: moderately concave

2: strongly concave (deep concave notch is present)

Note: This is an expanded version of the original Brusatte et al. (2010a, character 304) character, which adds a new derived state to take into account the subtly concave condition in some ornithomimosaurs, which differs from the flat condition in outgroups and many basal coelurosaurs (e.g., *Ornitholestes*) and the deeply concave notched condition of derived tyrannosaurids.

Character 728: Pes, metatarsal IV, distal end, ratio between anteroposterior long axis (measured from midpoint of condyles posteriorly to anterior surface of bone) and mediolateral width (measured at midpoint: (ORDERED)

0: greater than 1.40, distal surface is elongate anteroposteriorly

1: between 1.40 and 1.20

2: less than 1.20, distal surface nearly square shaped with nearly flat anterior surface

Character 729: Pes, proximal pedal phalanges of digits II and III, ratio of length to midshaft width:
0: greater than 3.0
1: less than 3.0
Character 730: Pes, pedal unguals, lip overhanging proximal articular surface dorsally (on extensor surface):
0: present
1: absent or reduced to a subtle tuber

***Characters Relevant to Ornithomimosauria (from L. Xu et al. 2011):**

Character 731: Maxilla, series of discrete foramina along ventral edge of lateral surface:
0: present
1: absent
Character 732: Lacrimal, prominence on lateral surface of bone:
0: absent
1: present
Character 733: Dentary, morphology of dorsal border in transverse cross section:
0: rounded and lacks “cutting edge”
1: sharp with a “cutting edge”
Character 734: Surangular, foramen on dorsal edge of bone dorsal to mandibular fenestra (anterior surangular foramen):
0: present
1: absent
Character 735: Neck, length compared to that of skull:
0: less than twice skull length
1: greater than twice skull length
Character 736: Coracoid, coracoid tubercle, position:
0: positioned close to base of posterior process (closer to coracoid-scapula suture than to anterior edge of coracoid)
1: positioned more anterior than the base of the posterior process (closer to anterior edge of coracoid than to coracoid-scapula suture)
Character 737: Coracoid, position of infraglenoid buttress relative to that of posterior process when bone is seen in dorsal view:
0: two structures extend to same level laterally
1: buttress offset laterally from posterior process
Character 738: Metacarpal II, length compared to metacarpal III:
0: shorter
1: equal to or longer
Character 739: Manual digit I, length of phalanx I-1 compared to metacarpal II:
0: shorter
1: longer
Character 740: Manual unguals, flexor tubercles, position:
0: near proximal end
1: distal to proximal end

Note: Those alvarezsauroids without discrete flexor tubercles are scored as inapplicable ("?").

Character 741: Pubis, shape of ventral margin of pubic boot:

0: straight or slightly convex

1: strongly convex with ventral expansion

Character 742: Pes, pedal digit I:

0: present

1: absent

Character 743: Pes, phalanx II-2, length:

0: more than 60% of length of pedal phalanx II-1

1: less than 60% of length of pedal phalanx II-1

Character 744: Pubis, angle between anterior process of pubic boot and shaft:

0: greater than 90 degrees

1: approximately 90 degrees

Character 745: Pubis, position of anterior edge of anterior process of pubic boot:

0: approximately same level as anterior margin of pubic shaft

1: markedly anterior to the anterior margin of pubic shaft

Character 746: Pes, pedal unguals, shape:

0: curved in lateral view

1: straight

***Characters Relevant to Basal Coelurosauria (from Li et al. 2010):**

Character 747: Premaxillary teeth, size compared to mesial (anterior) maxillary teeth:

0: approximately same size, slightly smaller, or larger

1: considerably smaller

This is another duplicated character

Character 748: Ischium, form of articulation with ilium on proximal surface of iliac peduncle:

0: approximately flat or slightly concave

1: deeply concave as a deep socket to receive a peg-like ischial peduncle of the ilium

Note: Some tyrannosauroids and ornithomimosaurs have been described as possessing an accessory peg-like structure on the distal edge of the ischial peduncle of the ilium, which fits into a deep socket on the ischium (e.g.., *Alioramus*, *Gallimimus*: Brusatte et al. 2012a). Because it is often difficult to determine the presence or absence of this subtle peg-like process, we here consider the peg-like process and a peg-like ischial peduncle itself as primarily homologous. The presence of either of these processes can be clearly determined by the presence of a funnel-like socket on the iliac peduncle of the ischium. Because both structures leave a similar mark on the ischium, this supports the hypothesis of their primary homology (at least at some level). This character was included in versions of the TWiG matrix published in *The Dinosauria* 2nd Ed, but were not include din some subsequent versions that derived from the Hwang et al. (2002) version.

Character 749: Scapula, acromion process, shape:

0: much deeper dorsoventrally than long anteroposteriorly, generally tapering or triangular in shape

1: approximately as long as or longer anteroposteriorly than deep dorsoventrally, with short reach beyond scapular blade and squared-off profile

This character appears above where it is defined as acromion length to height ratio using factor of 3 to distinguish between states.

Character 750: Basisphenoid, pronounced muscle scars flanking basisphenoid recess:

0: absent

1: present

Character 751: Ilium, form of distal articular surface of pubic peduncle:

0: convex

1: flat or concave (notched)

***Characters Relevant to Alvarezsauroidea (from Choiniere et al. 2010a,b, 2012 and Choiniere, pers. comm.):**

Character 752: Lacrimal, orientation of ventral ramus relative to the long axis of the alveolar margin of the upper jaw when the articulated skull is seen in lateral view

0: approximately vertical or inclinded slightly anteroventrally

1: inclined strongly posteroventrally

Character 753: Exoccipital-opisthotic, position of ventral edge of the base of the paroccipital process:

0: level with or dorsal to the dorsal border of the occipital condyle

1: situated at mid-height of occipital condyle or further ventrally

Character 754: Maxillary teeth, shape: (UNORDERED)

0: mediolaterally thin and recurved

1: lanceolate (as in therizinosauroids)

2: conical (as in alvarezsauroids)

Character 755: Dorsal vertebrae, form of opisthocoely in taxa with opisthocoelous dorsals:

0: some dorsal vertebrae opisthocoelous

1: most or all dorsal vertebrae opisthocoelous

Note: Only those taxa with strongly opisthocoelous dorsal vertebrae (character 99) are scored for an affirmative score here. All other taxa are scored as inapplicable (“?”).

Character 756: Dorsal vertebrae, shape of neural spine in posterior dorsals:

0: approximately square-shaped or slightly rectangular, with a dorsoventral height that is equal to or slightly greater than the anteroposterior length at the base

1: rectangular, much higher dorsoventrally than long anteroposteriorly at the base

Character 757: Dorsal vertebrae, position of parapophysis in posterior dorsals:

0: distinctly ventral to transverse process

1: at approximately same dorsoventral level as transverse process

Character 758: Caudal vertebrae, morphology of intercentral articulations [ORDERED]:

0: amphiplatyan
1: only anterior caudals procoelous
2: anterior and distal caudals procoelous

We modified this character by a adding a thrd state to capture the variation in alvarezsauroids, where some taxa (*Alnashetri*, *Xiyunykus*) have procoelous artivulations in only one or a few proximal caudals, whereas later-diverging taxa such s *Bonpartenykus* and *Shuvuuia* exhibit procoelous articulations throughout most of the caudal series.

Character 759: Caudal vertebrae, position of transverse process on anterior caudals:
0: approximately centered (in the anteroposterior dimension) on the centrum
1: anteriorly displaced

Character 760: Coracoid, biceps tubercle:
0: absent
1: present as a discrete, mound-like structure

Character 761: Coracoid, strong lateral ridge on lateral surface, extending posteriorly from biceps tubercle along posteroventral process:
0: absent
1: present

Character 762: Scapula, tubercle on posterior surface of bone dorsal to glenoid:
0: absent
1: present

Character 763: Humerus, shape of internal tuberosity in anterior view: (ORDERED)
0: triangular or rounded, not discretely separated from remainder of humerus
1: rectangular, separated from the humeral head by a small but distinct notch
2: rectangular and hypertrophied, separated from the humeral head by a large notch

Note: This character is modified into an ordered multistate with the addition of a second derived state, to distinguish between the condition in some therizinosauroids in which the internal tuberosity is rectangular and offset by a small notch (*Falcarius*, *Erliansaurus*) and that in which the internal tuberosity is rectangular but also proportionally hypertrophied and set off by a larger notch (*Segnosaurus*, *Erlikosaurus*, *Neimongosaurus*, *Suzhousaurus*, *Nothronychus*). This distinction follows Zanno et al. (2009, character ZCD 285).

Character 764: Ulna, shape of olecranon process:
0: transversely broad
1: mediolaterally thin and blade-like

Character 765: Ulna, position of distal articular surface:
0: limited to distal end
1: trochlear articular surface extends onto dorsal surface of ulna, bulbous in shape

Character 766: Metacarpal III, form of proximal articular surface:
0: flat or slightly convex
1: deeply concave and cup-like

Character 767: Metacarpal III, length:

0: considerably longer than length of metacarpal I

1: approximately same length as, or slightly longer than, metacarpal I

Character 768: Manual digits, paired flexor processes on proximal portion of ventral surfaces of proximal-most phalanges:

0: absent

1: present

Character 769: Manus, shape of proximal articular surface of ungual of first digit:

0: ovoid, dorsoventrally taller than mediolaterally wide

1: approximately square shaped, as mediolaterally wide as dorsoventrally tall

Character 770: Manus, form of lateral groove on ungual of first digit:

0: broad, open groove

1: groove terminates in a notch or tunnel, and is either partially or fully covered in external view

Character 771: Femur, interaction of head and greater trochanter:

0: confluent

1: separated by a cleft

Character 772: Femur, shape of lateral distal condyle:

0: distally rounded

1: distally conical, projecting substantially further distally than medial condyle

Character 773: Tibia, shape of medial posterior condyle of proximal end in proximal view:

0: posteriorly rounded

1: posteriorly conical, projecting substantially further posteriorly than lateral condyle

Character 774: Fibula, orientation of proximal margin (as seen in lateral view):

0: horizontal or nearly horizontal

1: anterior portion of proximal margin extends substantially further proximally than posterior portion

Note: This character is equivalent to Zanno et al. (2009: character ZCD 329).

Character 775: Fibula, shape of proximal surface in proximal view:

0: anterior and posterior portions of surface with nearly equal mediolateral widths

1: anterior portion markedly wider mediolaterally than posterior portion

Note: This character is equivalent to Zanno et al. (2009: character ZCD 331).

Character 776: Astragalus, fossa on anterior surface of lateral portion of base of ascending process, sometimes bearing accessory fenestrations:

0: absent

1: present

Character 777: Astragalus, main body: horizontal groove across anterior surface of condyles:

0: present

1: absent

This character refers to a groove that runs across the articular condyles in outgroups and many early diverging coelurosaur clades. It is not the same groove referred to in character 194, which refers to the depression at the base of the ascending process.

Character 778: Pes, phalanges of pedal digit IV, shape:

0: anteroposteriorly long, proximal and distal articular surfaces well separated

1: anteroposteriorly short, with proximal and distal articular surfaces very close together essentially eliminating a cylindrical shaft section, particularly in distal elements

***Characters Relevant to Therizinosauroidea (from Zanno et al. 2009 and Zanno 2010):**

Character 779: Basisphenoid, inflated basisphenoidal bulla:

0: absent

1: present

Character 780: Braincase, foramen magnum, size (area): (ORDERED)

0: smaller than size of occipital condyle

1: approximately equal in size with occipital condyle

2: larger than size of occipital condyle

Character 781: Ectopterygoid, position:

0: posterior to palatine

1: lateral to palatine

Character 782: Dentary, mediolateral width of symphyseal region of conjoined dentaries:

0: narrower than width of post-symphyseal region

1: broader than width of post-symphyseal region

Character 783: Premaxillary teeth, serrations:

0: present

1: absent

Note: It has been shown that unserrated premaxillary teeth are present in some juvenile tyrannosaurids, but serrations are gained during ontogeny (Carr and Williamson 2004). Taxa in which this ontogenetic shift occurs are scored for the present condition (state 0). Any taxa with any trace of serrations on any premaxillary tooth (whether all teeth are serrated or not) are also scored for the present condition. Only those taxa in which all known premaxillary teeth are lacking serrations are scored for the absent condition (state 1). It is likely that there is positional variation in serration presence/absence along the premaxillary tooth row, but this is difficult to parse out because complete dentitions are not known for most taxa. We recognize that future authors may wish to divide this character into additional states referring to serration presence/absence on individual premaxillary teeth or regions of the premaxillary dentition.

Character 784: Dentary teeth, shape of mesial (anterior) teeth:

0: not conical (i.e., ziphodont or lanceolate)

1: conical

Note: Although the first one or two dentary teeth of derived tyrannosauroids such as *Alioramus* and *Tyrannosaurus* are small and somewhat conical (in comparison to the remainder of the dentary tooth row), these taxa are here scored for state 0. State 1 refers to taxa in which the first several teeth of the dentary (at least the first four, where visible) are distinctly conical compared to the more posterior (distal) dentary teeth, but are of approximately the same size as the more distal premaxillary teeth. Oftentimes this condition is referred to in the literature as “anterior dentary teeth that are similar to the premaxillary teeth in shape”.

Character 785: Dentary, extent of tooth row:

0: teeth present at anterior (mesial) tip of dentary

1: teeth absent at anterior dentary but present further posteriorly (distally)

Note: This character encapsulates Zanno et al.’s (2009) revision of the original TWiG character number 220, which is character number 217 in the current analysis. We retain character 217 in the original language of Turner et al. (2012) here, as it refers to an ordered progression of fully toothed-posteriorly edentulous-completely edentulous, and therefore the addition of a fourth state for an anteriorly edentulous dentary (which is unique to some derived therizinosauroids) would disrupt this ordered sequence. Our preference is to include the therizinosauroid condition as a separate character, with those taxa that are completely edentulous scored as inapplicable (“?”).

Character 786: Cervical vertebrae, length of anterior centra:

0: up to three times longer anteroposteriorly than the minimum transverse centrum width in ventral view (or the height of the anterior articular surface in lateral view, if the centrum cannot be viewed ventrally)

1: hyperelongate, approximately five times longer than wide

Note: Zanno et al. (2009) presented a three-state character, but we do not want to over divide a ratio character such as this, and therefore recognize the major distinction among coelurosaurs as between a centrum that is fairly anteroposteriorly short (somewhere between 1-3 times longer than wide) and the so-called “hyperelongate” condition in which the centrum is approximately five times longer than wide. Those taxa that do not preserve anterior cervical, but have middle cervical that are hyperelongate, are scored for state 1.

Character 787: Cervical vertebrae, morphology of ventral surface of centrum:

0: smoothly flat or convex

1: with distinct depression anteriorly (at the level of the parapophyses)

Character 788: Cervical vertebrae, posterolateral margins of ventral surface of centrum, form:

0: unpronounced

1: developed into prominent crests (ventrally projecting “fins”)

Note: Zanno (2010) notes that less pronounced crests, potentially homologous to state 1, are present on the cervical vertebrae of some ornithomimosaurs, but Zanno et al. (2009) scores all score-able ornithomimosaurs for state 0. We agree that ornithomimosaurs should be scored for state 0, as taxa such as *Gallimimus* (ZPAL MgD/I-94) clearly do not possess the prominent “fin-like” crests of therizinosauroids and some basal oviraptorosaurs.

Character 789: Dorsal vertebrae, anterior dorsals, dorsoventral depth of neural arch compared to that of centrum:

0: depth of region between prezygadiapophyseal lamina and base of neural spine less than or equal to depth of anterior and/or posterior articular surface of centrum

1: depth of region between prezygadiapophyseal lamina and base of neural spine greater than depth of anterior and/or posterior articular surface of centrum (neural arch hypaxially inflated relative to centrum)

Character 790: Dorsal vertebrae, size of parapophyses on anterior dorsals:

0: moderate in size, articular facet of parapophysis less than half dorsoventral depth of anterior articular surface of centrum

1: hypertrophied, articular facet greater than two thirds of the dorsoventral depth of the anterior articular surface of centrum

Character 791: Caudal vertebrae, pneumatic foramina on the centra of anterior caudals:

0: absent

1: present

Character 792: Scapula, dorsal flange on dorsal margin of scapular blade:

0: absent

1: present

Character 793: Humerus, crest on posteromedial surface of humeral shaft:

0: absent

1: present

Character 794: Humerus, tuberosity on anterior surface of distal humerus, proximal to entepicondyle:

0: absent

1: present

Character 795: Humerus, entepicondyle:

0: present and prominent as a spherical, conical, or crest-like structure in cranial view

1: extremely reduced or absent

Note: This is a modified version of Zanno et al. (2009: character ZCD 291). We find it difficult to distinguish between Zanno et al.'s discrete conditions of "spherical" and "crest-like," which are given separate states in the original analysis. Therefore, we combine these conditions into a single "present and prominent" state, and recognize the major difference between coelurosaurs as the presence or absence of a prominent entepicondyle. Taxa with a prominent entepicondyle usually, if not always, exhibit a prominent groove proximal to the entepicondyle, whereas those that have a reduced or absent condyle do not. Therefore, we do not utilize Zanno et al.'s (2009: character oZCD 292) separate character for the groove.

Character 796: Humerus, mediolateral width of distal end:

0: greater than 2x minimum width of shaft.

1: less than 2x minimum width of shaft

Note: This is a modified version of Zanno et al. (2009: character oZCD 293), which combines two of the original states ("moderately expanded" and "significantly expanded") into a single state of "greater than 2x minimum width of shaft. Therefore, the character as worded here distinguishes the aberrantly unexpanded distal humeri of ornithomimosaurs and some tyrannosauroids from the standard condition among theropods.

Character 797: Humerus, morphology of distal humerus in anterior view:

0: medial aspect of distal humerus unexpanded, entepicondyle situated proximal to ulnar condyle

1: medial aspect of distal humerus expanded and subtriangular in anterior view, entepicondyle located well medial to ulnar condyle

Character 798: Metacarpal I, rectangular buttress on ventrolateral aspect of proximal surface that underlies ventromedial surface of metacarpal II:

0: absent

1: present

Character 799: Manus, ratio of the proximodistal length of metacarpal II to that of the combined proximodistal lengths of phalanges II-1 and II-2:

0: less than or equal to 1.0

1: greater than 1.0 (i.e., metacarpal II longer than combined lengths of phalanges II-1 and II-2)

Character 800: Manus, ligament pits on manual phalanges:

0: strongly developed

1: weakly developed or absent

Character 801: Manus, manual unguals, proximodistal length:

0: shorter to, equal to, or slightly longer than length of penultimate phalanx

1: elongate, twice or more as long as penultimate phalanx

Character 802: Ilium, orientation of ventral portion of preacetabular process:

0: parasagittal, in line with dorsal portion of process

1: laterally deflected, extends nearly perpendicular from sagittal plane of ilium

Character 803: Ilium, size of preacetabular process:

0: moderately developed, anteroposterior length of process subequal with dorsoventral height of ilium directly dorsal to the center of the acetabulum

1: hyperelongate, length of process at least twice the height of ilium above acetabulum

Character 804: Ilium, orientation of blade:

0: parallel or gently inclined relative to dorsoventral plane passing through the pubic and ischial peduncles (the ventral portion of the ilium)

1: angled laterally relative to the ventral portion of the ilium, rising steeply at at least a 30 degree angle from the dorsoventral plane passing through the peduncles

Character 805: Ilium, morphology of dorsal surface of postacetabular process in dorsal view: (ORDERED)

0: smooth and non-rugose

1: with rugosity causing transverse expansion of the posterior dorsal margin

2: hyperrugose, with hypertrophied posterior tuberosity

Character 806: Ilium, orientation of pubic peduncle: (ORDERED)

0: straight

1: posteriorly recurved, articular face posteroventrally directed

2: posteriorly recurved, articular face posteriorly directed

Character 807: Ilium, morphology of antitrochanter: (ORDERED)

0: separated from ischial peduncle

1: merged with ischial peduncle, both structures together form enlarged ventrolaterally flattened boss

2: merged with ischial peduncle as a boss, which is hypertrophied and spherical

Character 808: Ischium, position of distally placed dorsal process along posterior edge of shaft: (UNORDERED)

0: entirely proximal to obturator process

1: opposite obturator process

2: extending distal to obturator process

Note: This character refers to the position of the dorsal process of the ischium, whose presence or absence is scored in character 226. Those taxa without a process are scored as inapplicable (“?”).

Character 809: Ischium, shape of obturator process in those taxa in which the process contacts the pubis:

0: approximately square-shaped

1: elongate anteroposteriorly, approximately twice as long as dorsoventrally deep

Note: The presence/absence of an obturator process contacting the pubis is scored in character 164. Those taxa scored for the absence of this feature in character 164 are scored as inapplicable (“?”) for the current character.

Character 810: Ischium and pubis, morphology of contact surfaces between the two bones:

0: flat

1: markedly sinuous

Character 811: Pubis, shape of shaft:

0: rod-like

1: mediolaterally flattened

Character 812: Pubis, morphology of distal shaft:

0: distal portion of shaft approximately equal (or less than) in anteroposterior length to proximal portion of shaft

1: distal portion of shaft greatly enlarged, more than twice the anteroposterior length of the proximal portion of shaft

Character 813: Femur, anteroposterior width of region bridging femoral head and greater trochanter in proximal view:

0: smoothly confluent with head and greater trochanter

1: anteroposteriorly constricted relative to head and greater trochanter

Character 814: Femur, hook-like process at distal edge of femoral head, demarcating a notch between the head and the shaft

0: present

1: absent, shaft and head smoothly confluent

Note: This is equivalent to Zanno et al. (2009: character oZCD 323), which refers to the presence or absence of a “raised ventral rim” that separates the femoral head from the femoral neck (essentially the shaft). The “ventral rim” is equivalent to the hook-like process of the femoral head, which extends further distally relative to the remainder of the head to demarcate a notch between the head and shaft in anterior and posterior views.

Character 815: Tibia, morphology of incisura tibialis (lateral fossa on the tibia in proximal view):

0: deeply inset

1: wide and shallow, nearly absent

Character 816: Tibia, shape of tibia in proximal view:

0: anteroposteriorly longer than mediolaterally wide (measurements taken through midpoint of proximal surface)

1: mediolaterally wider than anteroposteriorly long

Character 817: Tibia, length of fibular crest:

0: short and proximally positioned, extends up to approximately 1/3 of the length of the tibia

1: long and distally extensive, extends to approximately the midshaft of the tibia

Character 818: Tibia, exposure and morphology of the anteromedial region of the distal tibia: (ORDERED)

0: covered anteriorly by the astragalus

1: not covered anteriorly by the astragalus, exposed

2: exposed and developed into an anterior tuberosity

Character 819: Fibula, iliofibularis tubercle, position:

0: proximal to midshaft of fibula

1: approximately at midshaft of fibula

Note: In those alvarezsauroids with an apomorphically shortened fibula (e.g., *Shuvuuia*, *Xixianykus*, *Parvicursor*), the position of the tubercle is measured relative to the length of the shaft of the tibiotarsus. Therefore, these taxa are scored for state 0 although their tubercles are located near the distal end of the shortened fibula.

Character 820: Astragalus, ascending process position:

0: lateral edge terminates approximately at the lateral edge of the tibia, or medial to the lateral edge of the tibia

1: lateral edge extends lateral to the tibial shaft to contact and overlap the fibula

Excluded because state 1 overlaps with state 3 of char 193

Character 821: Astragalus, lateral condyle of distal end, morphology:

0: well developed

1: strongly reduced, lateral tibia exposed on distal and anterior surfaces of tibiotarsal region when tibia and astragalus are in articulation

Character 822: Metatarsus, overall shape:

0: elongate, unit comprised of metatarsals II-IV much longer proximodistally than wide mediolaterally

1: short and broad, unit comprised of metatarsals II-IV less than twice as long as wide

Character 823: Metatarsus, proximodistal length: (ORDERED)

0: greater than 45% length of tibia

1: between 44-38% length of tibia

2: less than 36% length of tibia

Note: For those taxa in which only isolated metatarsals are present (i.e., not a complete metatarsus), the length of metatarsals II, III, or IV is taken as a proxy for the length of the metatarsus as a whole.

Character 824: Metatarsus, orientation of individual metatarsals II-IV:

0: not closely appressed, divergent from each other

1: appressed throughout most of metatarsus

Note: The outgroups *Allosaurus* and *Sinraptor* are scored for state 0, as in these taxa metatarsals II and III are closely appressed but metatarsal IV is divergent. *Zuolong* has closely appressed metatarsals II and III, but because only a fragment of metatarsal IV is known it cannot be determined if IV was appressed or divergent, and therefore this taxon is scored as “?”. Within coelurosaurs, all therizinosauroids are scored for a divergent metatarsus, following Zanno et al. (2009: character ZCD 335). Taxa without a complete metatarsus can be scored based on the shape of metatarsal IV (a laterally divergent kink along the shaft is indicative of state 0, whereas a straight shaft is indicative of state 1).

Character 825: Pes, pedal unguals of digits III-IV, proximodistal length:

0: approximately the same length as the penultimate phalanx (ungual may be slightly shorter or longer than the penultimate phalanx)

1: twice as long or more than the penultimate phalanx

***New Characters Relevant to Basal Coelurosaurs Established in this Dissertation (Note that some are inspired by published literature, as described in the main text, and others may have been added to published analyses during the time this dissertation was written).**

Character 826: Premaxilla, anteroposterior length compared to that of maxilla:

0: length of ventral (alveolar) margin greater than 10% total anteroposterior length of maxilla

1: length of ventral (alveolar) margin less than 10% total anteroposterior length of maxilla

Character 827: Supraoccipital, tab-like processes on left and right sides of dorsal margin of bone:

0: absent

1: present

Note: This character has been included in previous phylogenetic analyses of tyrannosauroid interrelationships (e.g., Carr and Williamson 2010), but Brusatte et al. (2010a) combined this and the absence/presense of a dorsal bifurcation of the supraoccipital into a single character, due to a presumed equivalency between the characters. As outlined by Bever et al. (2013), however, the tabs are separate from the bifurcation, as many tyrannosauroids have tabs but only a few taxa exhibit a bifurcation. The tabs themselves are created by midline depression of supraoccipital relative to left and right sides, as explained by Bever et al. (2013).

Character 828: Nasal, premaxillary processes (=supranarial processes), extent of their apposition to each other on the midline in dorsal view:

0: apposed for nearly their entire length (may abruptly separate from each other at their tips)

1: not apposed for most of their length, and therefore do not abruptly separate from each other at their tips

Character 829: Dentary, Meckelian groove, position:

0: approximately centered at dorsoventral midheight of dentary

1: positioned ventrally, located closer to the ventral margin than the dorsal margin

Note: This character was originally used by Carr and Williamson (2010: character 211), in which state 0 was scored for all score-able tyrannosauroids. We here note that this condition is also present in outgroups, *Compsognathus*, and derived therizinosauroids (*Erlikosaurus*), whereas state 1 is present in *Ornitholestes*, ornithomimosaurs (*Harpymimus*), basal therizinosauroids (*Falcarius*, *Beipiaosaurus*, *Alxasaurus*), and paravians (e.g.., *Deinonychus*, *Zanabazar*).

Character 830: Dentary, row of foramina on lateral surface paralleling ventral margin:

0: absent or limited to a small series of foramina at the anterior end of the dentary (at the level of the first 1-4 alveoli)

1: present as a distinct row that extends along most of the lateral surface of the dentary (across the entire length of the tooth row at the very least)

Character 831: Splenial, notch along dorsal margin of anterior process, where the splenial contacts the supradentary (if present):

0: absent

1: present

Character 832: Cervical vertebrae, position of prezygapophyses in anterior-middle cervicals:

0: prezygapophyseal facet approximately level with anterior face of centrum

1: prezygapophyseal facet entirely anterior to anterior face of centrum

Character 833: Caudal vertebrae, morphology of dorsal portion of neural spines of anterior caudals:

0: unexpanded

1: expanded anteroposteriorly relative to the remainder of the neural spine (and often mediolaterally as well)

Character 834: Ulna, morphology of distal end:

0: expanded mediolaterally at least 1.5x relative to midshaft mediolateral width

1: expanded less than 1.5x midshaft mediolateral width

Note: The denoted measurements are taken in anterior (extensor) and posteror (flexor) views.

Character 835: Ilium, medial surface of preacetabular process, pronounced horizontal shelf continuing from anterior margin of pubic peduncle to demarcate the cuppedicus fossa dorsally:

0: absent

1: present

Character 836: Metatarsal III, mediolateral width of distal end compared to mediolateral widths of distal ends of metatarsals II or IV (whichever of the latter is greater):

0: less than 1.3 times as wide

1: greater than 1.3 times as wide

Character 837: Lacrimal, extent of antorbital fossa on region where anterior and ventral rami meet:

0: extensive, fossa excavates nearly entire region and nearly extends to the posterodorsal corner of the lacrimal (the lacrimal angle), leaving only a thin region of bone at the posterodorsal corner of the lacrimal

1: reduced, fossa stops well short of the posterodorsal corner of the lacrimal

Character 838: Scapula and coracoid, deep fossa on lateral surfaces of both bones in the region of their suture (covering the posterior half of the coracoid and anterior portion of the acromion plate region of the scapula):

0: present

1: absent

Character 839: Scapula and coracoid, contribution of each bone to the glenoid: (UNORDERED)

0: both bones contribute approximately equally in the anteroposterior dimension

1: scapula contribution markedly anteroposteriorly longer than coracoid contribution

2: coracoid contribution markedly anteroposteriorly longer than scapula contribution

Character 840: Femur, shape of anterior margin in proximal view:

0: strongly convex, due to a midline tubercle

1: essentially straight or slightly concave

Character 841: Femur, horizontal ridge on the anterior surface of the head and neck, demarcating a deep fossa ventrally:

0: absent

1: present

Character 842: Femur, extent of crista tibiofibularis in distal view: (ORDERED)

0: projects further posteriorly than medial condyle

1: extends to the same approximate posterior level as medial condyle

2: terminates well short of the posterior level of the medial condyle (medial condyle projects substantially further posteriorly)

Character 843: Tibia, position of medial ridge on posterior surface of distal end: (ORDERED)

0: displaced laterally, positioned lateral to the medial edge of the distal tibia by approximately 25-33% of the mediolateral width of the distal tibia

1: positioned lateral to the medial edge of the distal tibia approximately 10-20% of the mediolateral width of the distal tibia

2: positioned medially, positioned at approximately the posteromedial corner of the distal tibia in distal view

Character 844: Scapula, fossa on lateral surface of bone immediately above glenoid, which is demarcated dorsally by a convex bulge or ridge spanning the scapula-coracoid suture:

0: absent

1: present

Character 845: Humerus, deltopectoral crest, orientation relative to mediolateral long axis of proximal end of humerus in proximal view:

0: straight, approximately perpendicular to long axis of proximal end of humerus

1: curves strongly medially as it continues anteriorly, such that anterior end of crest is oblique to long axis of proximal end of humerus

Note: Those taxa scored for state 0 for character 358 (a deltopectoral crest that is projected laterally or dorsally, such that it is in line with the long axis of proximal end of the humerus) are here scored as inapplicable (“?”).

Character 846: Femur, position of fourth trochanter: (UNORDERED)

0: along posteromedial corner of shaft along its entire length

1: positioned near center of posterior surface of shaft distally and extending proximomedially to become confluent with posteromedial corner of shaft proximally

2: positioned near center of posterior surface of shaft distally and extending proximolaterally to bcome confluent with the greater trochanter

Character 847: Fibula, anteroposterior width of the minimum point of the midshaft compared to the maximum anteroposterior width of the proximal end:

0: 20% or greater

1: less than 18%, fibula shaft exceptionally gracile

Character 848: Maxillary teeth, posterior (distal) extent of tooth row:

0: extensive, extends posterior to the level of the maxillary ascending ramus and underneath the antorbital fenestra (if present)

1: limited, terminates posteriorly at the level of the maxillary ascending ramus

Character 849: Dentary, shape of ventral margin in lateral view:

0: approximately straight or slightly convex

1: broadly concave

Character 850: Maxilla, posterior extent of the ascending ramus relative to that of the main body (jugal ramus):

0: the two rami extend to approximately the same level posteriorly, distance between posterior tip of ascending ramus and posterior tip of main body no more than 1/3 of the anteroposterior length of the entire maxilla

1: main body extends considerably further posteriorly relative to the ascending ramus, distance between the posterior tips of the two rami is greater than 1/3 of the length of the maxilla

Character 851: Tibia, proximal surface, proximal extent of cnemial crest relative to the proximal extent of the posterior condyles:

0: cnemial crest extends further proximally than condyles

1: cnemial crest and condyles extend to same approximate level proximally

Character 852: Prootic, prominent fossa on the lateral surface of the bone, anterior to the otic recess and posterior to the preotic pendant, that houses the external foramina of the trigeminal and facial nerves and pneumatic openings:

0: absent

1: present

Character 853: Palatine, form of pneumaticity in those taxa with pneumatic palatines:

0: pneumatic fossa on the external surface of the bone

1: large internal chamber that opens externally via a window-like pneumatic opening

Character 854: Length of the skull

0: less than the length of the femur

1: the same or 25% greater than the length of the femur (NEW)

2: more than 25% the length of the femur

Modified from Novas et al. (2009). A new state 1 was added because some taxa, e.g., *Yanornis martini*, have a skull longer than the femur but less than 25% of the length of this bone.

Character 855: Postantral wall of the maxilla posteriorly extended (Novas et al., 2009)

0: absent

1: present

Character 856: Striations on the crowns of the teeth (Gianechini et al., 2009, 2011)

0: absent

1: present

Striations on the crowns are considered as two or more longitudinal furrows on the labial and/or lingual surface. Isolated furrows, as those observed in *Sinornithosaurus millenii*, are not considered as striations.

Characters from Hu et al. (2009)

Character 857: Dorsal centra
0: ≥ 1.2×taller than long
1: height ≤ length
Excluded as it duplicates a similar character above
Character 858: Length of manual digit II (including metacarpal)
0: less than 1.25×femoral length
1: ≥ 1.25×femoral length
Character 859: Manual phalanx I-1 (Pérez-Moreno et al., 1994)
0: longer than metacarpal II
1: shorter than metacarpal II
Excluded as it duplicates a similar character above
Character 860: Strong kink of pubis at midshaft
0: absent
1: present, displacing distal half of pubis caudally
Character 861: In adult, femur length
0: longer than tibia
1: shorter than tibia
Excluded as it duplicates character 717
Character 862: Metatarsus length
0: less than half length of femur
1: more than half femoral length
Excluded as it duplicates/ is colinear with the information in char 823
Character 863: Length of pedal phalanx II-2
0: between 0.6×and 1× length of phalanx II-1
1: ≤0.6 × length of phalanx II-1
2: ≥1× length of phalanx II-1
Character 864: Manual phalanx II-1
0: shorter than I-1
1: longer than I-1
Character 865: Pneumatopores in anterior caudal vertebrae
0: absent
1: present
Excluded as it duplicates 791
Character 866: Length of manual phalanx III-2
0: subequal to length of phalanx III-1
1: significantly shorter than phalanx III-1
2: significantly longer than phalanx III-1
Character 867: Location of the anteroventral process of ilium
0: anteriorly located, close to the anterior end of the bone
1: posteriorly located, significantly away from the anterior end
Character 868: Location of the postorbital process of the jugal
0: located significantly anterior to the posterior end of the jugal
1: close to the posterior end, and consequently the quadratojugal process is very short

New characters in Gianechini et al (2018)

Character 869: Inclination of the ventral process of the lacrimal
0: ventrally directed so the process is vertical
1: anteroventrally inclined
Character 870: Inclination of the dorsal portion of the ilium above or slightly posterior to the acetabulum
0: in the same plane as the main body of the iliac blade
1: strongly laterally deflected to overhang the acetabular region, so the lateral surface of the iliac blade is partially hidden in dorsal view.
2(NEW STATE ADDED). Iliac blade inclined medially at 45 degrees or more, dorsal rim medial to and close to level with acetabulum, and lateral surface of ilium fully visible in dorsal view.
Character 871: Extension of the supracetabular crest of the ilium
0: extended only along the dorsal border of the acetabulum
1: anteriorly extended along the lateral surface of the pubic peduncle, reaching or almost reaching the ventral end of the peduncle
Character 872: Angle between the posterior border of the pubic shaft and the dorsal border of the pubic boot
0: less than 90°
1: greater than 90°
Character 873: Dorsal surface of the acetabulum
0: perpendicular with the lateral surface of the iliac blade, so the acetabulum is totally open
1: dorsal surface of the acetabulum ventrally and medially inclined, so the acetabulum is walled off like in most Neoaves
Character 874: Anteroposterior extension of the pubic peduncle
0: less than the anteroposterior extension of the acetabulum
1: between 1 and 1.5 the anteroposterior extension of the acetabulum
2: > 1.5 the anteroposterior extension of the acetabulum
Character 875: Foramen in the ventral part of the splenial (mylohyoid foramen) (character from Rauhut, 2003):
0: absent
1: completely enclosed in the splenial
2: opened anteroventrally
Excluded as it needs to be better distinguished from char 642.
Character 876: Middle of maxillary tooth row, spacing between teeth:
0: narrow, teeth separated by less than one crown width
1: wide, adjacent teeth separated by a gap corresponding to one crown width or more.

CHARCATER ADDED FROM FOTH AND RAUHUT (2014)
Character 877:Pennaceous feathers on the body: absent (0) or present (1).
Character 878: Elongated pennaceous feathers on forelimbs: absent (0) or present and symmetric (1) or present and asymmetric (2).
Character 879: Alula: absent (0) or present (1).

Character 880: Elongated pennaceous feathers on the tibia: absent (0) or present (1).
Character 881: Elongated pennaceous feathers on the foot (Metatarsus and/or and pedal phalanges): absent (0) or present (1).
Character 882: Elongated pennaceous feathers on the tail: absent (0) or present (1)
Character 883: Pennaceous tail feathers only along distal half (0) or along the whole tail (1) or in form of a fan-shaped tail plumage (2).
Character 884. A pair of extremely elongated pennaceous feathers (e.g. PRPFs); absent (0) or present (1)

CHARACTERS ADDED FROM GRELLET-TINNER AND MAKOVICKY (2006)
Character 885: Egg geometry:symmetric(**0**);asymmetric(**1**);asymmetric with modern avian outline (**2**). ORDERED CHARACTER STATES.
Character 886: Ratio of the two egg diameters: At or around 36% (**0**); at or around 60% (**1**); at or around 85% (**2**). (convert this to elongation ratio mentioned by Varricchio and Jackson)
Character 887: Eggs in nest: no pattern (**0**); paired (**1**).
Character 888: Clutch morphology (a): none (**0**); two or more layers of eggs (**1**); one layer of eggs (**2**). ORDERED CHARACTER STATES.
Character 889: Clutch and (or) nest morphology (b): absence of empty space in the center (**0**); presence of empty space in the center (**1**).
Character 890: Spatial position of the long axis of the egg to the sub- strate: none (**0**); parallel or nearly parallel to substrate (**1**); 20° to 45° (**2**); 46° to 90° (**3**). ORDERED CHARACTER STATES.
Character 891: Nest care behavior: none (**0**); protection and (or) brooding (**1**); incubation, direct contact with brood patch or parent (**2**). ORDERED. Contact with a brood patch is considered present in *Troodon formosus*, following data presented by Varricchio and Jackson (2004*a*).
Character 892: Eggshell ornamentation: absent (**0**); present (**1**).
Character 893: Number of eggshell layers: one (**0**); two (**1**); three (**2**).ORDERED
Character 894: Nature of boundary between layers 1 and 2: aprismatic (**0**); prismatic (**1**), (see Grellet-Tinner and Norell (2002) for definition).
Character 895: Type of boundary between layers 2 and 3: aprismatic (**0**); prismatic (**1**).
Character 896: Crystal morphology in mammillae of layer 1: acicular (**0**); bladed (**1**).
Character 897: Ratio between layers 1 and 2: ratio <1 (**0**); ratio 1.5 (**1**).
Character 898: Ratio between layers 3 and 2: ratios >0.20 but <0.6 (**0**); ratios <0.1 (**1**).
(**Character 899:** Organic lines in layer 2: uniform distribution (**0**); two or more subdivisions (**1**).
Character 900: Organic line orientation in outer region of layer 2: horizontal, parallel to eggshell surface (**0**); undulating, follow- ing eggshell surface ornamentation, or even perpendicular to egg shell surface (**2**).
Character 901: Shape of pore opening: round (**0**); elliptical (**1**).
Character 902: Pore canal orientation: straight (**0**); oblique (**1**).
Character 903: Pore canal shape: simple (**0**); branched (**1**).

CHARACTERS ADDED IN THIS STUDY

Character 904: Maxilla, antorbital fossa above toothrow and in front of maxillary fenestra: smooth (0) scalloped by penumatic fossae, some extending between roots of teeth (1) (see Turner et al. 2006 Shanag; Xu et et al (2001) Sinornhosaurus).

Character 905: Largest pair of rectrices: smaller than remiges (0) or comparable to/longer than remiges (1)

Character 906: Cervical vertebrae, centrum in ventral view: rounded or flat (0); with a longitudinal groove in some or all (1), or anterior cervicals with centra constricted and forming a keel, and posterior centra grooved (2). While therizinosaurs (Zanno, 2010) and some unenlagiines (Makovicky et al, 2005) exhibit lateral fins or ridges along the caudoventral section of some cervical centra, those are directed laterally and do not enclose a ventral groove, which is specifically what this character is referring to. Ordered.

Character 907: Distal tibia, anterior surface: flat or gently concave for reception of astragalus (0), or with a marked groove borderd by a ridge laterally for articulations with the ascending process of the stragalus (1). The latter condition is seen in a number of alvarezsauroids including *Tugulusaurus* and was recognized by Xu et al 2018, *Current Biol.* It is also present in the tibia BMNH R186 referred to *Calamospondylus*

Character 908: Manual Phalanx I-1, ventral surface: rounded (0), or with groove defined by flexor ridges extending from the proximal articulation to the distal one (1); or ventral groove present and medial flexor ridge forming a deep, keel-like ridge or process (2) Ordered. State 1 is seen in early diverging alvarezsauroids, Stet 2 is present in Patagonykus and in parvicursorines.

Character 909: Anterior cervical centra, ventral surface adjacent to anterior intercentral face; ventral depression: absent (0) present between rim of intercentral articular face and parapophyses (1). This striat is distinct from the sulcus described in char. 906, because in some alvarezsaurids including the cervical of the *Patagonykus* holotype and unpublished anterior cervicals of *Bonapartenykus,* this depression is observed on elements where the ventral surface of the centrum forms an expanded keel along its posterior 2/3.

Character 910: Extent of keel on posterior sacral centra: no keel-bearing vertebrae (0) midline keel (or tuber) limited to a single vertebra (1), or midline keel extending across 2 or more vertebrae (2). Ordered. This supplements char 110 by specifying the number of keeled elements.

Character 911: Manual digit I ungual, flexor tubercle shape: moundlike (0) or mediolaterally pinched (1), or formed as an elongate ridge (2) or reduced to an arced ridge extending transversely and sometimes with a midline gap, bordering a flat to concave surface adjacent to the proximal articulation (3). This character specifically concerns tuber shape and thus differs from char 475, which expressly deals with flexor tuber size irrespective of shape.

Character 912: astragalus, craniolateral butress (see Novas 1997 for definition): absent(0), or present, connecting lateral condyle to base of the ascending process (1).

Character 913: humeral internal tuberosity, shape: round or pointed (0) or rectangular, tab shaped (1) from Novas (1997)

Character 914: humeral internal tuberosity, orientation: directed posteriorly (0) directed proximally (1)

Character 915: Sternal plates: unossified (0), or ossified sternal plates/ sternum present (1)

Character 916: Shafts of metatarsals in plantar view: shafts of MTII and MTIV separated by MTIII along distal half of metatarsus in plantar (caudal) view (0), or shafts of MTII and MTIV contact each other posterior to MTIII shaft in plantar view (1). This character distinguishes between arctometatarsal taxa in which metatarsals II and IV are separated by the shaft of MTIII for most of their length (e.g. many caenagnathids) even if MTIII is wedge-shaped to triangular in cross section, from others where metatarsals II and IV underlie the shaft of MTIII like derived troodontids and alvarezsaurids even when the latter doesn't reach the proximal end of the foot as in alvarezsaurids. Importantly, among taxa with a proximally truncated MTIII, this trait parses parvicursorines (including *Kol guva*) from *Avimimus.*

Character 917: Pubic and ischiadic shafts: separated, or only touching via enlarged obturator process of ischium (0), or adpressed to one another for most of their length (1). This trait is principally observed in parviscursorine alvarzesaurids, which also lack anobtirator process.

13. ADDITIONAL REFERENCES

14. ADDITIONAL REFERENCES

59. Candia-Halupczok, D. J., Sánchez, M. L., Veiga, G. D., Apesteguía, S. Dinosaur tracks in the Kokorkom desert, Candeleros formation (Cenomanian, Upper Cretaceous), Patagonia, Argentina: Implications for deformation structures in dune fields. *Cretaceous Res.* **83**, 194–206 (2018).
60. Apesteguía, S. & Novas, F. E. Large Cretaceous sphenodontian from Patagonia provides insight into lepidosaur evolution in Gondwana. *Nature* **425**, 609–612 (2003).
61. Garberoglio, F. F., et al.. New skulls and skeletons of the Cretaceous legged snake *Najash*, and the evolution of the modern snake body plan. *Sci. Adv.* **5**, eaax5833 (2019). https://doi.org/10.1126/sciadv.aax5833
62. Maniel, I. J., et al.. Cranial and postcranial remains of a new species of *Prochelidella* (Testudines: Pleurodira: Chelidae) from 'La Buitrera' (Cenomanian of Patagonia, Argentina), with comments on the monophyly of this extinct chelid genus from southern Gondwana. *J. Syst. Palaeontol.* **18**, 1033–1055 (2020).
63. Fernández Dumont, M. L., Pol, D., Bona, P. & Apesteguía, S. A new species of *Araripesuchus* with durophagous dentition increases the ecological disparity among uruguaysuchid crocodyliforms. *J. Syst. Palaeontol.* **22**, 2373987 (2024). https://doi.org/10.1080/14772019.2024.2373987
64. Makovicky, P. J., Apesteguía, S. & Agnolín, F. L. The earliest dromaeosaurid theropod from South America. *Nature* **437**, 1007–1011 (2005).
65. Apesteguía, S., et al. Dinosaur tracks with skin impressions in the La Buitrera Paleontological Area (Candeleros Formation, Cenomanian), Río Negro Province, Argentina. *Cretaceous Res.* **150**, 105584 (2023).
66. Leanza, H. A., Apesteguía, S., Novas, F. E. & de la Fuente, M. S. Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages. *Cretaceous Res.* **25**, 61–87 (2004).
67. Perle, A., Chiappe, L. M., Rinchen, B., Clark, J. M. & Norell, M. Skeletal morphology of *Mononykus olecranus*(Theropoda, Avialae) from the late Cretaceous of Mongolia. *Am. Mus. Novit.* **3105** (1994).
68. Choiniere, J. N., et al. A basal alvarezsauroid theropod from the early Late Jurassic of Xinjiang, China. *Science* **327**, 571–574 (2010).
69. de Valais, S., Apesteguía, S. & Garrido, A. C. Cretaceous small scavengers: feeding traces in tetrapod bones from Patagonia, Argentina. *PLoS One* **7**, e29841 (2012).
70. Gianechini, F. A. & de Valais, S. Bioerosion trace fossils on bones of the Cretaceous South American theropod *Buitreraptor gonzalezorum* Makovicky, Apesteguía and Agnolín, 2005 (Deinonychosauria). *Hist. Biol.* **28**, 533–549 (2016).

71. Currie, P. J. & Zhao, X. J. A new troodontid (Dinosauria, Theropoda) braincase from the Dinosaur Park Formation (Campanian) of Alberta. *Can. J. Earth Sci.* **30**, 2231–2247 (1993).
72. Motta, M. J., Egli, F. B., & Novas, F. E. Tail anatomy of *Buitreraptor gonzalezorum* (Theropoda, Unenlagiidae) and comparisons with other basal paravians. *Cretac. Res.* **83**, 168-181 (2018).
73. Qin, Z., Clark, J., Choiniere, J. & Xu, X. A new alvarezsaurian theropod from the Upper Jurassic Shishugou Formation of western China. *Sci. Rep.* **9**, 11727 (2019).
74. Sues, H. D. On *Chirostenotes*, a Late Cretaceous oviraptorosaur (Dinosauria: Theropoda) from western North America. *J. Vertebr. Paleontol.* **17**, 698–716 (1997).
75. Zanno, L. E. Osteology of *Falcarius utahensis* (Dinosauria: Theropoda): characterizing the anatomy of basal therizinosaurs. *Zool. J. Linnean Soc.* **158**, 196–230 (2010).
76. Welles, S. P. & Long, R. A. The tarsus of theropod dinosaurs. *Ann. S. Afr. Mus.* **64**, 191–218 (1974).
77. Carpenter, K. Redescription of the small maniraptoran theropods *Ornitholestes* and *Coelurus* from the Upper Jurassic Morrison Formation of Wyoming. in *Carnivorous Dinosaurs* 49 (2005).
78. Lydekker, R. On the remains and affinities of five genera of Mesozoic reptiles. *Q. J. Geol. Soc. London* **45**, 41–59 (1889).
79. Naish, D. & Martill, D. M. Dinosaurs of Great Britain and the role of the Geological Society of London in their discovery: basal Dinosauria and Saurischia. *J. Geol. Soc. London* **164**, 493–510 (2007).
80. Naish, D. & Cau, A. The osteology and affinities of *Eotyrannus lengi*, a tyrannosauroid theropod from the Wealden Supergroup of southern England. *PeerJ* **10**, e12727 (2022).
81. Pol, D., & Goloboff, P. A. The Impact of Unstable Taxa in Coelurosaurian Phylogeny and Resampling Support Measures for Parsimony Analyses. *Bull. Am. Mus. Nat. Hist.* **440**, 97–115 (2020).
82. Choiniere, J. N. et al. A juvenile specimen of a new coelurosaur (Dinosauria: Theropoda) from the Middle–Late Jurassic Shishugou Formation of Xinjiang, People's Republic of China. *J. Syst. Palaeontol.* **12**, 177–215 (2014).
83. Morrison, Cassius, et al. Rise of the king: Gondwanan origins and evolution of megaraptoran dinosaurs. *Royal Soc. Open Sci.* **12** 242238 (2025).
84. Qin, Z. et al. Correction to Growth and miniaturization among alvarezsauroid dinosaurs. *Curr. Biol.* **31**, 3687–3693 (2021).
85. Cerda, I. A. et al. A basic guide for sampling and preparation of extant and fossil bones for histological studies. *Publ. Electr. Assoc. Paleontol. Argentina* **20**, 15–28 (2020).
86. Francillon-Vieillot, H. et al. Skeletal biomineralization: patterns, processes and evolutionary trends. In *Microstructure and Mineralization of Vertebrate Skeletal Tissues* (ed. Carter, J. G.) 471–548 (Van Nostrand Reinhold, 1990).

87. de Buffrénil, V. & Quilhac, A. Bone tissue types: a brief account of currently used categories. In *Comparative Skeletal Histology and Palaeohistology* (eds. de Buffrénil, V., Zylberberg, L., Padian, K. & de Ricqlès, A.) 147–190 (CRC Press, 2021).
88. Chinsamy Turan, A. *The Microstructure of Dinosaur Bones: Deciphering Biology Through Fine-Scale Techniques* (The Johns Hopkins University Press, 2005).
89. Erickson, G. M. On dinosaur growth. *Annu. Rev. Earth Planet Sci.* **42**, 675–697 (2014).
90. Horner, J. R., de Ricqlès, A. & Padian, K. Variation in dinosaur skeletochronology indicators: implications for age assessment and physiology. *Paleobiology* **25**, 295–304 (1999).
91. Woodward, H. N., Horner, J. R. & Farlow, J. O. Osteohistological evidence for determinate growth in the American Alligator. *J. Herpetol.* **45**, 339–342 (2011).
92. Sander, P. M. Long bone histology of the Tendaguru sauropods: implications for growth and biology. *Paleobiology* **26**, 466–488 (2000).
93. Erickson, G. M. et al. Growth patterns in brooding dinosaurs reveals the timing of sexual maturity in non-avian dinosaurs and genesis of the avian condition. *Biol. Lett.* **3**, 558–561 (2007).
94. Lee, A. H. & Werning, S. Sexual maturity in growing dinosaurs does not fit reptilian growth models. *Proc. Natl. Acad. Sci.* **105**, 582–587 (2008).
95. Castanet, J. & Baez, M. Adaptation and evolution in *Gallotia* lizards from the Canary Islands: age, growth, maturity and longevity. *Amphibia-Reptilia* **12**, 81–102 (1991).
96. Khonsue, W., Chaiananporn, T. & Pomchote, P. Skeletochronological assessment of age in the Himalayan crocodile newt, *Tylototriton verrucosus* (Anderson, 1871) from Thailand. *Trop. Nat. Hist.* **10**, 181–188 (2010).
97. Canoville, A., Schweitzer, M. H. & Zanno, L. E. Systemic distribution of medullary bone in the avian skeleton: ground truthing criteria for the identification of reproductive tissues in extinct Avemetatarsalia. *BMC Evol. Biol.* **19**, 71 (2019).
98. Canoville, A., Schweitzer, M. H. & Zanno, L. Identifying medullary bone in extinct avemetatarsalians: challenges, implications and perspectives. *Philos. Trans. R. Soc. B* **375**, 20190133 (2020).
99. Schweitzer, M. H., Wittmeyer J. L., & Horner, J. R.. Gender-specific reproductive tissue in ratites and *Tyrannosaurus rex*. *Science* **308**, 1456-1460 (2005).
100. Hübner, T. R. Bone histology in *Dysalotosaurus lettowvorbecki* (Ornithischia: Iguanodontia) - variation, growth, and implications. *PLoS One* **7**, e29958 (2012).
101. Chinsamy, A. & Tumarkin-Deratzian, A. Pathological bone tissue in a turkey vulture and a nonavian dinosaur. *Anat. Rec.* **292**, 1478–1484 (2009).

102. Cerda, A., Chinsamy, A. & Pol, D. Unusual endosteally formed bone tissue in a Patagonian basal sauropodomorph dinosaur. *Anat. Rec.* **297**, 1385–1391 (2014).
103. Chinsamy, A., Cerda, I. & Powell, J. Vascularised endosteal bone tissue in armoured sauropod dinosaurs. *Sci. Rep.* **6**, 24858 (2016).
104. O'Connor, J. et al. Medullary bone in an Early Cretaceous enantiornithine bird and discussion regarding its identification in fossils. *Nat. Commun.* **9**, 5169 (2018).
105. Werning, S. Medullary bone is phylogenetically widespread and its skeletal distribution varies by taxon. *J. Ornithol.***159**, 527–543 (2018).