

A Complete Skeleton of a Late Triassic Saurischian and the Early Evolution of Dinosaurs

Sterling J. Nesbitt,^{1,2*}† Nathan D. Smith,^{3,4} Randall B. Irmis,^{5,6} Alan H. Turner,⁷ Alex Downs,⁸ Mark A. Norell¹

Characterizing the evolutionary history of early dinosaurs is central to understanding their rise and diversification in the Late Triassic. However, fossils from basal lineages are rare. A new theropod dinosaur from New Mexico is a representative of the early North American diversification. Known from several nearly complete skeletons, it reveals a mosaic of plesiomorphic and derived features that clarify early saurischian dinosaur evolution and provide evidence for the antiquity of novel avian character systems including skeletal pneumaticity. The taxon further reveals latitudinal differences among saurischian assemblages during the Late Triassic, demonstrates that the theropod fauna from the Late Triassic of North America was not endemic, and suggests that intercontinental dispersal was prevalent during this time.

By the Late Triassic (~230 million years ago), Dinosauria had diversified into three major lineages: Sauropodomorpha, Theropoda, and Ornithischia (1, 2). In comparison to the later Mesozoic, fossils of Triassic early dinosaurs and their closest relatives are generally rare, fragmentary, and incomplete (3, 4). Indeed, the record from the Ischigualasto Formation, which provides some of the most detailed information on early dinosaur evolution (1, 2, 5), reveals that dinosaur specimens constitute less than 6% of the tetrapod assemblage (6). This depauperate fossil record has limited our understanding of early dinosaur interrelationships, diversification, and paleobiogeography, and the origin of modern avian morphologies during a critical interval of Mesozoic climate change and faunal turnover (7–9).

Here we report on a new carnivorous dinosaur represented by two nearly complete skeletons and several other partial specimens collected in a tightly associated small grouping at a single locality. Characterization of this taxon's morphology and phylogenetic history enables us to solidify basal saurischian dinosaur relationships and bears directly on the evolution of early saurischian character systems, paleobiogeography, and diversification.

Systematic paleontology: Archosauria Cope 1869 *sensu* Gauthier and Padian 1985. Dinosauria

Owen 1842 *sensu* Padian and May 1993. Theropoda Marsh 1881 *sensu* Gauthier 1986. *Tawa hallae*, nov. taxa.

Etymology. *Tawa*, Hopi name for the Puebloan sun god; *hallae*, after Ruth Hall, who collected many of the specimens that formed the genesis of the Ghost Ranch Ruth Hall Museum of Paleontology (GR) collections. **Holotype.** GR 241. A nearly complete associated but disarticulated skull and postcranial skeleton. **Paratypes.** A nearly complete skeleton of a larger individual (GR 242) and at least six other individuals found in the same area of the quarry [see supporting

online material (SOM) (10)] including femora, pelvis, and tail (GR 155) and cervical vertebrae (GR 243). A complete right femur (GR 244) is from Hayden Quarry (HQ) site 3. **Locality and horizon.** Site 2, HQ, Ghost Ranch, Rio Arriba County, New Mexico, USA. The HQ has been dated to ~215 to 213 million years ago (11) and is in the lower portion of the Petrified Forest Member of the Upper Triassic Chinle Formation (12).

Diagnosis. A theropod diagnosed by the following combination of characters (autapomorphies are noted by an asterisk here and in Figs. 1 and 2): Prootics meet on the ventral midline of the endocranial cavity; anterior tympanic recess greatly enlarged on the anterior surface of the basioccipital and extending onto prootic and parabasisphenoid; deep recess on the postero-dorsal base of paroccipital process*; sharp ridge extending dorsoventrally on the middle of the posterior face of the basal tuber*; incomplete ligamental sulcus on the posterior side of the femoral head and semicircular muscle scar/excavation on the posterior face of the femoral head*; small semicircular excavation on the posterior margin of the medial posterior condyle of the proximal end of the tibia*; “step” on ventral surface of the astragalus*; and metatarsal I similar in length to other metatarsals. See SOM for differential diagnosis (10).

Description. The holotype material is a juvenile or subadult individual, based on comparison to the largest femur among the referred material and the open braincase and neurocranial sutures. The premaxilla (Fig. 1) is similar to that

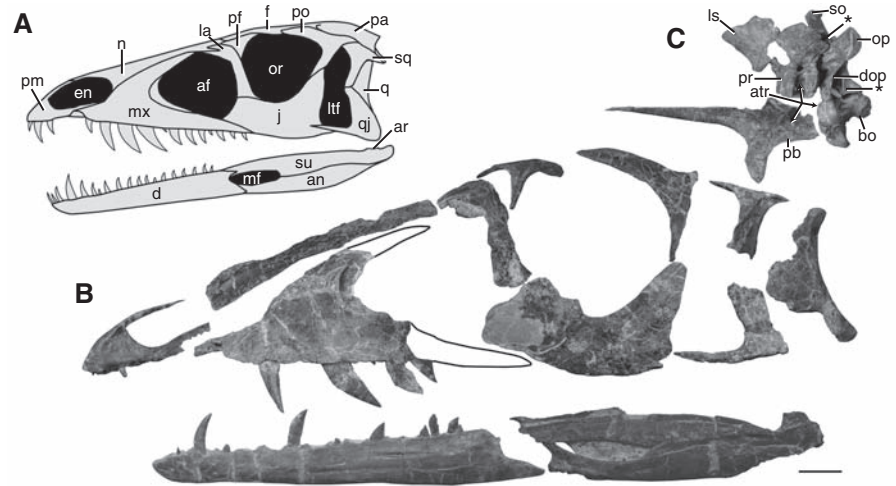


Fig. 1. The skull of *T. hallae* nov. taxa. (A) Reconstruction of the skull in lateral view. (B) The preserved skull elements of the holotype of *T. hallae* (GR 241) in left lateral view (j, qj, and the posterior portion of the mandible were reversed, and the matrix was digitally erased from the pm, mx, and n. The processes of the maxilla are present but obscured by matrix in lateral view, so they are represented here in outline). (C) Braincase of *T. hallae* in left lateral view (parabasisphenoid reversed). Abbreviations in the figure are as follows: antorbital fenestra (af), angular (an), articular (ar), anterior tympanic recess (atr), basioccipital (bo), dentary (d), descending process of the opisthotic (dop), external naris (en), frontal (f), jugal (j), lacrimal (la), laterosphenoid (ls), lower temporal fenestra (ltf), maxilla (mx), mandibular fenestra (mf), nasal (n), opisthotic (op), orbit (or), parabasisphenoid (pb), prefrontal (pf), premaxilla (pm), postorbital (po), prootic (pr), quadrate (q), quadratojugal (qj), supraoccipital (so), squamosal (sq), and surangular (su). Scale bar, 1 cm. Autapomorphies are noted by an asterisk.

¹Division of Paleontology, American Museum of Natural History, New York, NY 10024, USA. ²Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY 10964, USA. ³Committee on Evolutionary Biology, University of Chicago, Chicago, IL 60637, USA. ⁴Department of Geology, Field Museum of Natural History, Chicago, IL 60605, USA. ⁵Utah Museum of Natural History, 1390 East Presidents Circle, Salt Lake City, UT 84112–0050, USA. ⁶Department of Geology and Geophysics, University of Utah, Salt Lake City, UT 84112–0102, USA. ⁷Department of Anatomical Sciences, Stony Brook University, Health Science Center T-8 (040), Stony Brook, NY 11794, USA. ⁸Ruth Hall Museum of Paleontology, Ghost Ranch Conference Center, Abiquiu, NM 87510–9601, USA.

*To whom correspondence should be addressed. E-mail: nesbitt@jsg.utexas.edu

†Present address: Jackson School of Geosciences, University of Texas at Austin, Austin, TX 78712, USA.

of coelophysids in possessing unserrated premaxillary teeth and a narial process of the premaxilla that is elongate and forms a low angle with the alveolar margin. It differs from neotheropods by having a relatively tall maxillary process that extends dorsally beyond the posterior border of the naris as in *Herrerasaurus*. In dorsal view, the premaxilla-nasal suture is simple, lacking the W-shaped morphology present in Neotheropoda. Like basal neotheropods (such as *Coelophysis bauri* and *Dilophosaurus wetherilli*), a subnarial gap is expressed between the premaxilla and maxilla, but unlike these taxa, *Tawa* and *Herrerasaurus* lack an extensive antorbital fossa on the lateral surface of the maxilla. A concave narial fossa is located on the anterolateral surface of the nasal. A lateral ridge on the nasal forms the dorsal border to the antorbital fossa, similar to *Eoraptor lunensis* and *C. bauri*. Unlike most basal neotheropods, in *Tawa* the jugal participates in the antorbital fenestra and lacks distinct lateral ridges on the maxilla and jugal. The lacrimal is anterodorsally inclined, as in *Herrerasaurus* and more basal dinosaurs. The anterior process of the quadratojugal is elongate as in *C. bauri* but unlike that in *Herrerasaurus*.

Tawa lacks several braincase character states present in most other dinosauriforms. Absent character states include a reduced and medially

recessed descending process of the opisthotic [the crista interfenestralis (10)] and a metotic strut. A weak parabasisphenoid recess is present on the ventral surface of the braincase, similar to that in *Herrerasaurus*, *Eoraptor*, and Neotheropoda.

The vertebral column (Fig. 2) shares several apomorphic features with neotheropods. Cervical vertebrae preserve anterior pneumatic pleurocoels (as rimmed fossae) and anterior and posterior infrazygapophyseal fossae; these features are present in all basal neotheropods. The diapophyses and parapophyses of the anterior to midcervical vertebrae are close together and nearly contact. *Tawa* shares with *Herrerasaurus* pronounced ventral keels on the cervical vertebrae and elongate prezygapophyses in the distal caudal vertebrae, as in neotheropods. The dorsal vertebrae possess hyposphene-hypantra articulations and there appear to be only two sacral vertebrae.

The complete forelimb (found in articulation) and shoulder girdle share numerous apomorphic features with *Herrerasaurus* and neotheropods such as *C. bauri* and *D. wetherilli*. The elongate manus is particularly theropod-like, with metacarpals abutting each other along their shafts (without overlapping margins) and the presence of weak extensor pits (traits also present in the basal ornithischian *Heterodontosaurus*). The shaft width of metacarpal IV is reduced in *Tawa*, and

the accompanying phalanges are greatly reduced. Moreover, digit V is completely absent, as in *Herrerasaurus* and other basal theropods. The manus of *Tawa* retains a plesiomorphically small medial-most distal carpal. The hand of *Tawa* also retains nine carpals, similar to the basal ornithischian *Heterodontosaurus*, whereas *Herrerasaurus* has seven and *C. bauri* has five.

The *Tawa* pelvis is generally plesiomorphic with respect to neotheropods. The preacetabular process of the ilium (GR 241) does not extend anterior to the pubic peduncle. Additionally, the anterior end is rounded, unlike the squared-off morphology of neotheropods. The supraacetabular crest projects laterally without any ventral deflection but is distally restricted in that it does not approach the articular facet of the pubic peduncle. The supraacetabular crest is continuous with the ventrolateral edge of the postacetabular process, as in coelophysoids. In contrast, the pubis displays a well-developed pubic boot similar to that present in neotheropods, *Herrerasaurus*, and *Staurikosaurus*.

The proximal articular sulcus of the femur, common to Dinosauriformes, is asymmetrically developed in *Tawa* and neotheropods. The fourth trochanter is symmetrical and bladelike in lateral outline, in contrast to the plesiomorphic saurischian condition of a thick asymmetrical ridge. The proximal condyles of the tibia align along the posterior

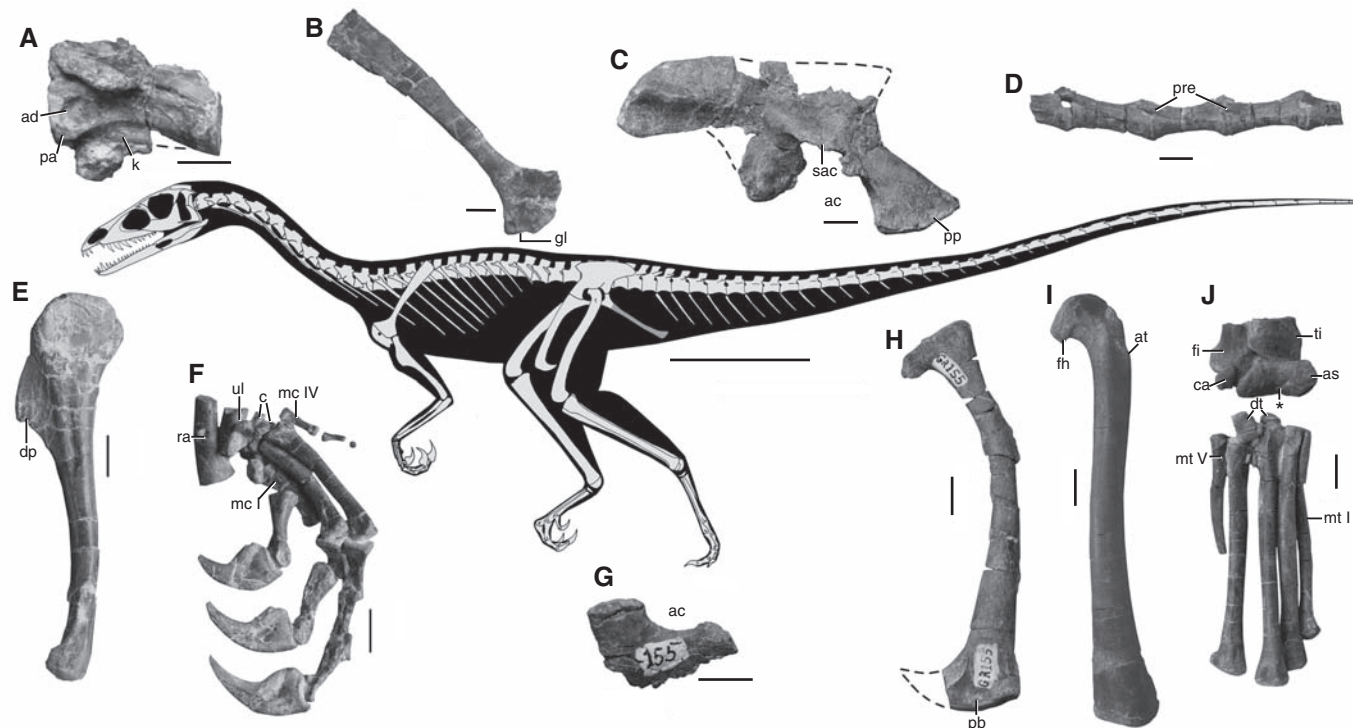


Fig. 2. Skeletal anatomy of *T. hallae* nov. taxa. (A) Anterior cervical vertebra (GR 243) in lateral view. (B) Right scapula (GR 242) in lateral view. (C) Right ilium (GR 155) in lateral view. (D) Middle caudal vertebrae (GR 155) in lateral view. (E) Left humerus (GR 242) in posterolateral view. (F) Complete right manus (GR 242) in posterior view. (G) Right proximal portion of the ischium (GR 155) in lateral view. (H) Right pubis (GR 155) in lateral view. The proximal portion of the apron is incomplete. (I) Left femur (GR 244) in anterior view. (J) Articulated right pes (GR 242) in anterior view.

Abbreviations in the figure are as follows: acetabulum (ac), anterior depression (ad), astragalus (as), anterior trochanter (at), carpals (c), calcaneum (ca), deltopectoral crest (dp), distal tarsals (dt), femoral head (fh), fibula (fi), glenoid (gl), keel (k), metacarpal (mc), metatarsal (mt), parapophysis (pa), pubic boot (pb), pubic peduncle (pp), prezygapophyses (pre), radius (ra), supraacetabular crest (sac), tibia (ti), and ulna (ul). Matrix was digitally erased from around the manus. Scale bars, 1 cm and reconstruction scale = 0.25 m. Autapomorphies are noted by an asterisk.

edge as in *Herrerasaurus* and neotheropods (such as *C. bauri*). The tibia lacks a fibular crest, and the cnemial crest is not proximally expanded above the proximal articular surface. Two neotheropod character states—an expanded medial edge and a distinct proximodistally elongate posterior ridge—are absent on the distal end of the tibia in *Tawa*. The pes of *Tawa* is plesiomorphic in having metatarsals I to IV elongated. As in other basal saurischians, the fourth tarsal lacks a rounded posterior edge and the astragalus and calcaneum are not co-ossified. The astragalus retains a rimmed basin on the proximal surface posterior to the ascending process. However, the calcaneum of *Tawa* is reduced relative to the astragalus in a manner similar to that of neotheropods. It is mediolaterally compressed and completely lacks a medial process. Metatarsal I retains contact with the ankle in *Tawa*, as in *Herrerasaurus* and *Eoraptor*.

Cladistic analysis identifies *T. hallae* as the closest taxon to Neotheropoda (Fig. 3). The transitional morphology of *Tawa* present in both the skull and the postcranium results in the recovery of *Herrerasaurus* and *Eoraptor* as definitive basal theropods. Although initially described as early theropods (1, 2), the phylogenetic affinities of these taxa have been debated, with some authors arguing for a nondinosaurian position for *Herrerasaurus* (13), a nontheropod, but basal saurischian position for *Herrerasaurus* and *Eoraptor* (14), a basal saurischian position for *Herrerasaurus* and a theropod position for *Eoraptor* (15), or a basal theropod position for both taxa (5). In our analysis, *Herrerasaurus* forms a monophyletic Herrerasauridae with *Staurikosaurus* and *Chindesaurus* at the base of Theropoda, although clade support is weak (10). It takes six steps to recover *Tawa* and *Chindesaurus* as sister taxa. *Eoraptor* and *Tawa* form successively closer sister taxa to Neotheropoda.

Despite the absence of postcranial skeletal pneumaticity in the basal saurischians *Saturnalia*, *Herrerasaurus*, and *Eoraptor*, the presence of anterior cervical pleurocoels in *Tawa* and *Chindesaurus* supports the hypothesis that the origin of cervical air sacs predates the divergence of Neotheropoda and may be ancestral for Saurischia or possibly even Ornithodira [(16) and references therein]. The disarticulated braincase of the holotype of *Tawa* also documents the earliest example of an expansive pneumatic anterior tympanic recess, and the caudal expansion of this recess into the basioccipital. The weak excavation on the ventral surface of the basisphenoid in *Tawa* relative to neotheropods also suggests that development of the cavities associated with the middle ear sac (such as the anterior tympanic recess) preceded the elaboration of the median pharyngeal system into an expansive basisphenoid sinus in neotheropods. Despite the extensive nature of the anterior tympanic recess of *Tawa*, an antero-medial border to the recess is still provided by the basisphenoid and prootic. This reinforces the hypothesis that contralateral connections of the tympanic diverticula are not homologous in crocodiles

and birds, and that the “interaural passage” used in sound localization by modern avians, and possibly some basal coelurosaurs (17), had not evolved by the time of the divergence of *Tawa* from Neotheropoda.

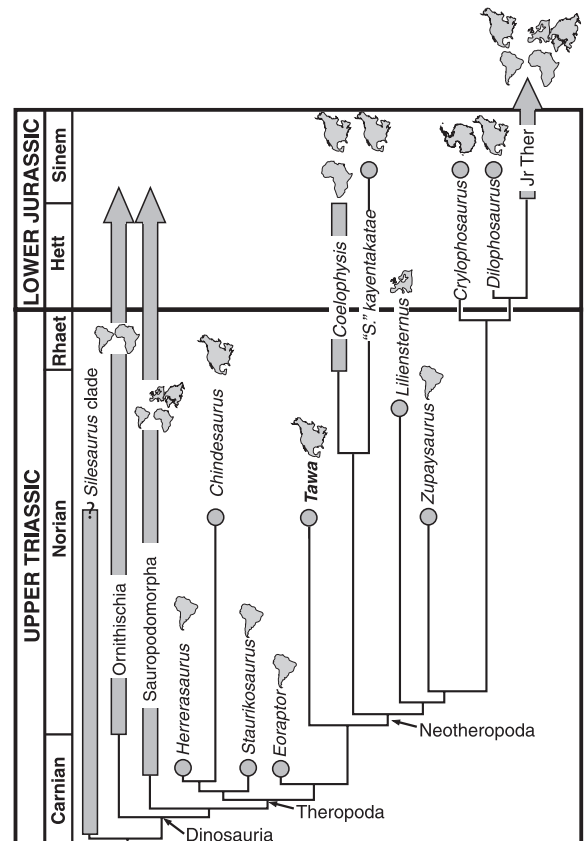
Coelophysoid monophyly is unsupported in our analysis. Without *Tawa* and *Eoraptor*, phylogenetic analyses support a variety of characters as synapomorphies of a clade of “coelophysoid” taxa (*Coelophysis*, “*Syntarsus*” *kayentakatae*, *Liliensternus*, *Zupaysaurus*, *Cryolophosaurus*, and *Dilophosaurus*), because they are absent in both tetanurans and neotheropod outgroups (10). With *Tawa*, these characters are more clearly inferred to have been primitive for Neotheropoda and later lost in the lineage leading to Tetanurae (10). Previous work (18) suggested that resolution of an inclusive Coelophysoidea may be artificial for two reasons: (i) the failure to sample Early Jurassic taxa that possess a mosaic of coelophysoid and more-derived neotheropod features, and (ii) the failure to recognize a broader distribution among basal dinosaurs of many coelophysoid synapomorphies. *Tawa* confirms these hypotheses because it possesses both coelophysoid traits (such as the low angle of the narial process to the premaxillary alveolar margin, the presence of a subnarial gap, and a strong ridge connecting the supraacetabular shelf and brevis shelf) and neotheropod plesiomorphies that collapse Coelophysoidea in our analysis (10). We suggest that the traditional basal theropod clade Coelophysoidea has acted as a phylogenetic vacuum cleaner, with deep thermo-

pod synapomorphies and ceratosaur/tetanuran reversals being “sucked up” and optimized as coelophysoid synapomorphies, because critical taxa were absent across the basal theropod tree. This result reiterates the centrality of new discoveries and increased taxon sampling to providing increased phylogenetic accuracy by breaking long branches [see references in (19)], is critically important for polarizing character evolution in more-derived theropod lineages, and bears directly on the magnitude of turnover in theropod faunas at the Triassic-Jurassic and Early-to-Middle Jurassic boundaries (7, 20).

The presence of multiple carnivorous theropod lineages (*Chindesaurus*, a coelophysoid-grade theropod, and *Tawa*) and an absence or rarity of sauropodomorphs suggest that the HQ saurischian assemblage was qualitatively more like that of the older Ischigualasto Formation (21), where only a single sauropodomorph specimen has been reported, than that of the overlying Los Colorados Formation, which is closer in age to the Hayden assemblage (21). In contrast, the Los Colorados saurischian assemblage contains diverse and abundant sauropodomorphs but only a single reported theropod. These patterns support the hypothesis that the evolution of Triassic dinosaur faunas was diachronous across Pangea (12).

The HQ taxa are spread throughout the stem of theropod phylogeny, and none are each other’s closest relative. This demonstrates that they do not represent a monophyletic Norian radiation endemic to the North American protocontinent. Instead, the

Fig. 3. Phylogenetic relationships of *T. hallae* among dinosaurs and the paleobiogeographic distribution of early dinosaur taxa [see SOM (10) for details of the analysis]. Relative temporal relationships for the early Mesozoic are indicated, with minimum ghost lineage extensions implied by phylogeny. The length of the gray bars indicates stratigraphic imprecision, and those with arrows continue through the Sinemurian. Abbreviations are as follows: Hett, Hettangian; Jr Ther, other Jurassic theropods; Rhaet, Rhaetian; and Sinem, Sinemurian.



HQ theropods are separated from each other by branches subtending taxa from other continental faunas, indicating that dispersal between these geographical regions probably occurred during the Camian-Norian. Other contemporaneous theropod assemblages from Europe (22) and South America contain only members of Neotheropoda and do not match the diversity of theropods at the HQ.

Both parsimony (23) and likelihood-based (24) biogeographic methods for ancestral range reconstruction reject scenarios of an endemic North American theropod radiation (10). Analyses differ slightly in support for range reconstructions at individual nodes, but provide high relative support for inferring the South American protocontinent as the ancestral range through the spine of the basal dinosaur tree (10). In most analyses, the distributions of the three HQ theropods are explained by either dispersal to North America from South America or allopatric and/or vicariant speciation from an ancestral widespread range encompassing North and South America (10). This pattern is apparent in many other clades during the Late Triassic, including actosaurs (25), crocodylomorphs (26), shuvosaurids (27), and “traversodont” cynodonts (28). The ubiquity of this phylogenetic pattern in clades encompassing markedly different ecomorphotypes argues against the presence of physiographic barriers isolating the Norian faunas of North America. Thus, the conspicuous absence of saurpodomorphs in the Norian of North America (3, 12) cannot be attributed to their inability to disperse to these areas but rather to their inability to become established in areas sampled by Late Triassic terrestrial sedimentary outcrops. Latitudinal differentiation of Norian faunas attributable to climatic

differences and climatic tolerances remains an intriguing explanation for the global ubiquity of basal theropod taxa such as *Tawa* and the North American absence of saurpodomorphs. Indeed, recent paleoclimate models and proxy data for the Late Triassic reveal a marked dichotomy between low and high paleolatitudes (29). Alternative explanations, including smaller-scale ecological differences, community-level interactions, or facies-dependent sampling biases, cannot be ruled out, nor are these explanations mutually exclusive (12). Explaining these patterns remains an outstanding problem in early dinosaur evolution at the nexus of phylogenetic, geologic, and paleoclimatic studies of the Late Triassic.

References and Notes

- P. C. Sereno, F. E. Novas, *Science* **258**, 1137 (1992).
- P. C. Sereno, *Science* **284**, 2137 (1999).
- S. J. Nesbitt, R. B. Irmis, W. G. Parker, *J. Syst. Palaeontol.* **5**, 209 (2007).
- R. B. Irmis, W. G. Parker, S. J. Nesbitt, J. Liu, *Hist. Biol.* **19**, 3 (2007).
- F. E. Novas, *J. Vertebr. Paleontol.* **16**, 723 (1996).
- R. R. Rogers, C. C. Swisher III, P. C. Sereno, C. A. Forster, A. M. Monetta, *Science* **260**, 794 (1993).
- S. P. Hesselbo, S. A. Robinson, F. Surlyk, S. Piasecki, *Geology* **30**, 251 (2002).
- P. E. Olsen *et al.*, *Science* **296**, 1305 (2002).
- J. C. McElwain, D. J. Beerling, F. I. Woodward, *Science* **285**, 1386 (1999).
- See supporting material on Science Online.
- R. Mundil, G. Gehrels, A. L. Deino, R. B. Irmis, *Eos* **89**, abstract V13A-2108 (2008).
- R. B. Irmis *et al.*, *Science* **317**, 358 (2007).
- N. C. Fraser, K. Padian, G. M. Walkden, A. L. M. Davis, *Palaeontology* **45**, 79 (2002).
- M. C. Langer, M. J. Benton, *J. Syst. Palaeontol.* **4**, 309 (2006).
- M. D. Ezcurra, *Geodiversitas* **28**, 649 (2006).
- R. J. Butler, P. M. Barrett, D. J. Gower, *Biol. Lett.* **5**, 557 (2009).

- M. Kundrát, J. Janáček, *Naturwissenschaften* **94**, 769 (2007).
- N. D. Smith, P. J. Makovicky, W. R. Hammer, P. J. Currie, *Zool. J. Linn. Soc.* **151**, 377 (2007).
- N. D. Smith, A. H. Turner, *Syst. Biol.* **54**, 166 (2005).
- G. T. Lloyd *et al.*, *Proc. R. Soc. London Ser. B* **275**, 2483 (2008).
- R. Irmis, R. Mundil, *J. Vertebr. Paleontol.* **28**, 95A (2008).
- O. W. M. Rauhut, A. Hungerbühler, *Gaia* **15**, 75 (2000).
- F. Ronquist, *Syst. Biol.* **46**, 195 (1997).
- R. H. Ree, S. A. Smith, *Syst. Biol.* **57**, 4 (2008).
- W. G. Parker, *J. Syst. Palaeontol.* **5**, 41 (2007).
- J. M. Clark, X. Xu, C. A. Forster, Y. Wang, *Nature* **430**, 1021 (2004).
- S. J. Nesbitt, *Bull. Am. Mus. Nat. Hist.* **302**, 1 (2007).
- J. A. Hopson, H.-D. Sues, *Paläontol. Z.* **80**, 124 (2006).
- B. W. Sellwood, P. J. Valdes, *Sediment. Geol.* **190**, 269 (2006).
- Fieldwork and research were funded by the National Geographic Society (grant no. 8014-06 to K. Padian), David Clark Inc., the Jean Butz Memorial Fund, the Theodore Roosevelt Memorial Fund (to R.B.I.), the Jurassic Foundation (to S.J.N.), an Explorers Club Exploration Grant (to S.J.N.), an NSF Graduate Fellowship (to S.J.N. and R.B.I.), the Samuel & Doris Welles Research Fund (to R.B.I. and K. Padian), a Bryan Patterson Memorial Grant (to R.B.I.), the University of California–Berkeley Department of Integrative Biology (to R.B.I.), the University of Utah (to R.B.I.), and the Systematics Research Fund (to N.D.S.). We thank the reviewers, R. Ree, and the Field Museum (Chicago) VertMorph discussion group; and the staff, volunteers, and paleontology seminar participants at Ghost Ranch for assistance with fieldwork. Ghost Ranch, the American Museum of Natural History, the Field Museum of Natural History, and the University of California Museum of Paleontology all facilitated the preparation of specimens.

Supporting Online Material

www.sciencemag.org/cgi/content/full/326/5959/1530/DC1
SOM Text
Figs. S1 to S8
Tables S1 to S5
References

10 August 2009; accepted 2 October 2009
10.1126/science.1180350

An Analytical Solution to the Kinetics of Breakable Filament Assembly

Tuomas P. J. Knowles,^{1,2} Christopher A. Waudby,³ Glyn L. Devlin,³ Samuel I. A. Cohen,³ Adriano Aguzzi,⁴ Michele Vendruscolo,³ Eugene M. Terentjev,¹ Mark E. Welland,^{2*} Christopher M. Dobson^{3*}

We present an analytical treatment of a set of coupled kinetic equations that governs the self-assembly of filamentous molecular structures. Application to the case of protein aggregation demonstrates that the kinetics of amyloid growth can often be dominated by secondary rather than by primary nucleation events. Our results further reveal a range of general features of the growth kinetics of fragmenting filamentous structures, including the existence of generic scaling laws that provide mechanistic information in contexts ranging from in vitro amyloid growth to the in vivo development of mammalian prion diseases.

Molecular self-assembly is the basis of phenomena ranging from the construction of materials for nanotechnology (1) to the formation of molecular machineries within living cells (2). The assembly of these frequently complex and highly intricate structures typically depends on a series of individual steps that are inherently simple and are therefore amenable in principle to a quantitative analysis

based on physical principles. An important class of molecular structures that emerges from the self-assembly of simpler components is that of filamentous assemblies of biological macromolecules. Many proteinaceous aggregates of this type, which are increasingly linked with normal and aberrant biological processes (2), form through a nucleation mechanism followed by a self-templated growth where the ends of exist-

ing filaments recruit soluble molecules into aggregates that can themselves multiply through secondary nucleation processes such as fragmentation (Fig. 1A).

One of the key questions in molecular self-assembly phenomena is to determine the relative importance of different microscopic processes and their contribution to the overall reaction (3, 4). Master equation approaches are particularly powerful in this context as they enable the explicit description of microscopic processes and have thus offered a series of insights (5–10) into phenomena including the formation of amyloid fibrils, species that are of increasing interest particularly because of their association with clinical disorders ranging from Alzheimer’s disease to type II diabetes (2). The lack of analytical

¹Cavendish Laboratory, University of Cambridge, J. J. Thomson Avenue, Cambridge CB3 0HE, UK. ²Nanoscience Centre, University of Cambridge, J. J. Thomson Avenue, Cambridge CB3 0FF, UK. ³Department of Chemistry, University of Cambridge, Lensfield Road, Cambridge CB2 1EW, UK. ⁴Institute of Neuro-pathology, University Hospital Zurich, Schmelzbergstrasse, 8091 Zurich, Switzerland.

*To whom correspondence should be addressed. E-mail: mew10@cam.ac.uk (M.E.W.); cmd44@cam.ac.uk (C.M.D.)



Supporting Online Material for

A Complete Skeleton of a Late Triassic Saurischian and the Early Evolution of Dinosaurs

Sterling J. Nesbitt,* Nathan D. Smith, Randall B. Irmis, Alan H. Turner, Alex Downs,
Mark A. Norell

*To whom correspondence should be addressed. E-mail: nesbitt@jsg.utexas.edu

Published 11 December 2009, *Science* **326**, 1530 (2009)
DOI: 10.1126/science.1180350

This PDF file includes:

SOM Text
Figs. S1 to S8
Tables S1 to S5
References

Supporting Online Material for:

A COMPLETE SKELETON OF A LATE TRIASSIC SAURISCHIAN AND THE
EARLY EVOLUTION OF DINOSAURS

Sterling J. Nesbitt^{1,2}, Nathan D. Smith^{3,4}, Randall B. Irmis^{5,6}, Alan H. Turner⁷, Alex
Downs⁸, and Mark A. Norell¹

¹Division of Paleontology, American Museum of Natural History, New York, NY 10024, USA.

²Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY 10964, USA.

³Committee on Evolutionary Biology, University of Chicago, Chicago, IL 60637, USA.

⁴Department of Geology, Field Museum of Natural History, Chicago, IL 60605, USA.

⁵Utah Museum of Natural History, 1390 E. Presidents Circle, Salt Lake City, UT 84112-0050, USA.

⁶Department of Geology & Geophysics, University of Utah, Salt Lake City, UT 84112, USA.

⁷Department of Anatomical Sciences, Stony Brook University, Health Science Center T-8 (040), Stony
Brook, NY 11794, USA.

⁸Ruth Hall Museum of Paleontology, Ghost Ranch Conference Center, Abiquiu, NM 87510-9601, USA.

* Correspondence and requests for materials about the characters list and matrix presented below should be
addressed to S.N. (sjn2104@gmail.com)

This file includes:

1. Extended differential diagnosis of *Tawa hallae*.
2. Paratypes and referred material of *Tawa hallae*.
3. Details of the biogeographic analysis.
4. Details of the phylogenetic analysis.

5. Further implications of *Tawa* for the relationships of theropods.
6. Supporting Online Material references.

1. Extended differential diagnosis of *Tawa hallae*.

In addition to the long list of autapomorphies described in the main text, *Tawa* can be differentiated from other theropods using a unique combination of character states. *Tawa* differs from *Herrerasaurus* in that the premaxilla of *Tawa* is dorsoventrally short, the nasal process of the premaxilla forms an angle with the alveolar margin that is less than 70 degrees, and the absence of a ridge on the lateral side of the jugal. *Tawa* differs from *Staurikosaurus* in the presence of a proportionally larger lateral flange of the distal end of the tibia, a proportionally longer postacetabular blade of the ilium, and a symmetrical fourth trochanter. *Tawa* differs from *Eoraptor* in lacking a distinct ridge on the lateral surface of the maxilla, the possession of a strap-like scapula, and the presence of a rimmed fossa (pneumatic “pleurocoel”) medial to the parapophysis in the cervical vertebrae. *Tawa* differs from all neotheropods in the presence of a long metatarsal I that contacts the proximal end of metatarsal II, the absence of a proximally expanded cnemial crest, and the absence of a fibular crest on the lateral side of the tibia. *Tawa* differs from TTU-P 10072 in that the posterior margin of the ilium is rounded, the ilium lacks a rugosity on the posterodorsal portion, and the incomplete ligamental sulcus on posterior side of femoral head.

Tawa and *Chindesaurus bryansmalli* differ morphologically in a number of respects, even though both taxa are present in the Hayden Quarry. The preserved material of the holotype of *Chindesaurus* (Petrified Forest National Park [PEFO] 10396) and referred femur from the Hayden Quarry (Ghost Ranch Ruth Hall Museum of Paleontology [GR] 226) lack all of the autapomorphies listed for *Tawa*. Furthermore, the two posterior condyles of the proximal portion of the tibia of *Tawa* are about equal in size, whereas the lateral condyle of the proximal portion of the tibia of *Chindesaurus* is significantly larger than the medial condyle, an autapomorphy of the taxon (Long and Murry 1995; Nesbitt et al. 2007). Additionally, the lateral margin of the lateral condyle of the tibia forms an acute angle in *Chindesaurus* whereas the same margin is squared-off in *Tawa*. In *Chindesaurus*, there is a strong lip on the lateral side of the posterior face of the distal end of the tibia for articulation with posterolateral corner of astragalus, whereas this feature is absent in *Tawa*. The only preserved cervical of *Chindesaurus* lacks a prominent ventral keel; this feature is present in the cervical vertebrae of *Tawa*. The pneumatic pleurocoel on the anterior half of the cervical vertebra of *Chindesaurus* is a distinct foramen whereas the pleurocoel in the cervical vertebrae of *Tawa* is a large rimmed fossa medial to the parapophysis, a feature that it shares with coelophysids (Rauhut 2003). Lastly, the supra-acetabular crest (=rim) of the ilium extends distally to the articular surface of the pubic peduncle in *Chindesaurus* whereas the supra-acetabular crest terminates well short of the articular surface of the pubic peduncle in *Tawa*. On the femur, the fourth trochanter of *Chindesaurus* is asymmetrical and rugose whereas the fourth trochanter of *Tawa* is blade-like and symmetrical. All known femora of *Chindesaurus* possess a distinct trochanteric shelf, even in specimens (GR 226) that are significantly smaller than *Tawa* femora that lack a trochanteric shelf (GR 240). The previous list of differences between *Tawa* and *Chindesaurus* illustrates that the two taxa are not the same. Indeed, some of the differences between *Tawa* and *Chindesaurus* are phylogenetic informative (e.g., fourth trochanter shape) and indicate that although the

two taxa are both basal theropods, they are not particularly closely related (Fig. 3 of main text).

2. Paratype and referred material of *Tawa hallae*.

All of the material known for *Tawa* originates from the Hayden Quarry, Petrified Forest Member of the Chinle Formation in northern New Mexico. The Hayden Quarry contains temnospondyl amphibians, phytosaurs, aetosaurs, and other suchians, as well as a dinosauriform assemblage including the non-dinosauriform dinosauriform *Dromomeron romeri*, a *Silesaurus*-like taxon, *Chindesaurus bryansmalli*, and at least one member of the Coelophysoidea (Irmis et al. 2007). Most of the remains of vertebrates are disarticulated or loosely associated over a small area. In contrast, nearly all of the *Tawa* specimens were found as partially articulated or closely associated skeletons in a small pocket (6 m² area) within Site 2 of the Hayden Quarry. To date, at least six individuals were found in this pocket, but it is unclear how many *Tawa* specimens were originally in the accumulation because the pocket was exposed on the surface prior to excavation. These specimens comprise the paratypes of *Tawa hallae*. Remains of *Tawa*, although rare, are present as isolated elements in sites 3 and 4 of the Hayden Quarry. Nearly all of the isolated elements are from larger individuals, thus it is clear that the holotype and paratypes are immature individuals. Further preparation of collected material and continued excavation of the Hayden Quarry will no doubt add to the referred material list.

Paratypes: GR 155, ilium, pubes, proximal ischium, femora, sacral vertebra, and caudal vertebrae; GR 242, nearly complete individual (largest of the group); GR 243, cervical vertebrae; GR 244, complete right femur.

Referred material: GR 240, nearly complete femur.

Association

GR 241 – Disarticulated skull, disarticulated forelimb and pectoral girdle, partially articulated presacral column, articulated hindlimbs and disarticulated pelvic girdle, associated ribs and gastralia. Found mixed among the remains of GR 242.

GR 242 – Largely articulated skull, articulated cervical series, articulated anterior caudal series, articulated pectoral girdle, forelimb and manus, disarticulated pelvic girdle, articulated hindlimbs (not fully prepared).

GR 155 – Articulated caudal vertebrae, associated and loosely articulated hindlimb and pelvic girdle.

GR 243 – Disarticulated cervical vertebrae associated with a largely complete, associated but disarticulated skeleton (unprepared).

GR 244 – Isolated femur found among the remains of phytosaurs, aetosaurs, rauisuchians, amphibians, and other dinosauriforms.

Diagnostic Characters Present in Each Specimen

GR 241 – prootics meet on the ventral midline of the endocranial cavity; anterior tympanic recess greatly enlarged on the anterior surface of the basioccipital and extending onto prootic and parabasisphenoid; deep recess on the posterodorsal base of paroccipital process; sharp ridge extending dorsoventrally on middle of the posterior face

of the basal tuber; incomplete ligamental sulcus on posterior side of femoral head and semicircular muscle scar/excavation on the posterior face of the femoral head; small semicircular excavation on posterior margin of the medial posterior condyle of the proximal end of the tibia; ‘step’ on ventral surface of the astragalus; and MT I similar in length to other metatarsals.

GR242 – incomplete ligamental sulcus on posterior side of femoral head and semicircular muscle scar/excavation on the posterior face of the femoral head; small semicircular excavation on posterior margin of the medial posterior condyle of the proximal end of the tibia; ‘step’ on ventral surface of the astragalus; and MT I similar in length to other metatarsals.

GR 155 – incomplete ligamental sulcus on posterior side of femoral head and semicircular muscle scar/excavation on the posterior face of the femoral head; and small semicircular excavation on posterior margin of the medial posterior condyle of the proximal end of the tibia.

GR 244 – incomplete ligamental sulcus on posterior side of femoral head and semicircular muscle scar/excavation on the posterior face of the femoral head.

3. Details of the biogeographic analysis.

The purpose of this biogeographic analysis was primarily to infer the ancestral ranges of lineages at the base of the dinosaur tree. We were particularly interested in the lineage leading to Neotheropoda, as it subtends the three distinct theropod taxa from the Hayden Quarry (HQ hereafter) (see main text; Irmis et al. 2007). These include *Chindesaurus*, *Tawa*, and a ‘coelophysoid’ taxon that is closely related to *Coelophysis bauri* (Irmis et al. 2007; unpubl. data). We chose to utilize two biogeographic methods developed for the explicit reconstruction of ancestral ranges: Dispersal Vicariance Analysis (DIVA), a parsimony-based method that does not incorporate temporal information (Ronquist 1997); and the Dispersal-Extinction-Cladogenesis (DEC) model, a likelihood method that can explicitly incorporate temporal information (Ree et al. 2005; Ree & Smith 2008a).

Taxon Sampling

Given our primary interest of reconstructing the ancestral ranges of nodes at the base of the dinosaur tree, and subtending the HQ theropods, we modified the taxon sampling from our phylogenetic dataset accordingly. Only Dinosauriformes were included in the analyses. Notably, our taxon-sampling for Sauropodomorpha is incomplete, though we do include several undisputed basal members (Yates, 2007). Sauropodomorph phylogeny is currently undergoing intense revision, with multiple different hypotheses of relationships recently proposed (e.g., Upchurch et al., 2007; Yates, 2007). However, most analyses (e.g., Upchurch et al., 2007; Yates, 2007) agree that *Saturnalia* is the basal-most member of Sauropodomorpha, or that the recently described *Panphagia*, also from South America, is the basal-most sauropodomorph, and sister-taxon to a clade of (*Saturnalia* + all other sauropodomorphs) (Martinez and Alcozar, 2009). Thus, we expect the impact of this lack of sampling on reconstructions outside of the node Sauropodomorpha to be minor, caution should be exercised in interpreting reconstructions for nodes at and within the Sauropodomorpha.

Taxa younger than the Triassic were pruned from the MPT. The rationale for pruning taxa that significantly post-date the temporal period of interest for a biogeographic analysis has been discussed in detail (Grande 1985; Upchurch et al. 2002; Donoghue and Moore 2003; Turner 2004). In addition to these concerns, we would cite both the poor quality of the terrestrial fossil record for the Early Jurassic, and the occurrence of the fifth largest mass extinction in earth history as potential confounding factors that warrant exclusion of taxa younger than the Triassic.

Taxon Ages

For the analyses incorporating temporal information, point estimates of ages of the included taxa were required. However, absolute dating in the terrestrial Triassic is nearly non-existent (Mundil 2007; Irmis and Mundil 2008), and nearly all taxa are either reported as a range (e.g., Carnian) or confined to a certain portion of the Stage (e.g., mid-Norian). Thus we attempted to set taxon ages at the midpoint of their reported ages. We chose to set the age of all taxa from the Santa Maria and Ischigualasto Formations at 230 Ma, with the exception of *Pisanosaurus* (age set at 228 Ma), which is known to occur higher up in the stratigraphic section of the Ischigualasto Formation than the other taxa. The age of *Silesaurus* was set at 235 Ma. Though *Silesaurus* is likely younger than this, the *Silesaurus* clade as a whole is much older (unpubl. data), and thus an age of 235 Ma (or slightly older, see below), represents an underestimate of the internode connecting the *Silesaurus* clade to Dinosauria. All taxa from the Hayden Quarry, *Plateosaurus*, *Efraasia*, *Liliensternus*, and *Zupaysaurus* were assigned an age of 215 Ma. Though the true ages of these taxa may not be contemporaneous, setting them equal for the purposes of this analysis prevents any particular mid-Norian continental fauna from contributing more, or less to nodal reconstructions in the temporally calibrated biogeographic analyses based solely on slight differences in branch lengths between it and the other mid-Norian faunas. *Eocursor* and *Coelophysis* were assigned an age of 204 Ma. We also applied a “soft constraint” of a minimum age of 220 Ma for the node Neotheropoda, based on the North American taxon *Camposaurus* from the *Placerias* Quarry (Nesbitt et al. 2007; age constraints from Irmis & Mundil 2008). Although there is significant uncertainty for all of the geologic ages of the taxa included in the analysis, our chosen point estimates are consistent with accepted relative ages of these taxa, and in most cases represent the mid-points of age uncertainty, thus representing relatively conservative absolute age estimates.

Temporal Calibration of Trees

Three different sets of branch lengths were chosen to temporally calibrate the trees for the DEC analyses. The first analysis (“No Temp”) set all branches equal to 1.0, and therefore remained agnostic regarding any temporal information from the phylogeny. This analysis is the most directly comparable to the DIVA analysis. The second analysis (“Strict Temp”) used point estimates of taxon ages and the phylogeny to temporally calibrate the tree, including only minimum length ghost lineages. Resulting zero length branches were arbitrarily set to 0.1, which is more than an order of magnitude smaller than the minimal possible difference between two taxa of different ages. The third analysis, (“Temp”) also used point estimates of taxon ages and the phylogeny to temporally calibrate the tree, but instead of including only minimal estimates of ghost

lineages, the internal calibration method of Brusatte et al. (2008) and Nesbitt (unpubl. dissertation) was used to spread the ages of zero-length lineage splitting events evenly between two internal calibration points (see also Ruta et al. 2006 for a discussion of this problem and similar methods). As this procedure cannot be applied to establish the age of the root of the tree, we arbitrarily set the age of the three branches leading from *Silesaurus* (the oldest taxon in the outgroup) to the root at 1.0 Ma each. Note that this is only slightly smaller (1.0 versus 1.33) for the lengths of the shortest branches in the tree inferred using the Brusatte et al. (2008) and Nesbitt (2009) method. This results in a root age for Dinosauriformes of 238 Ma. As noted above, we consider this an underestimate.

Areas

We chose to analyze biogeographic patterns at the level of continental faunas. Finer dissection of geographic areas would be possible, but would severely limit the statistical power of the analyses, and in general, avoiding over-division of areas in biogeographic areas is considered prudent (Ree & Smith 2008a). A prerequisite for biogeographic analysis is that designated areas maintain their identity through the time frame explored in the analysis, which can likely be assumed for continental-level areas in the Late Triassic, and is a further reason to avoid over-division of areas.

For both the DIVA and DEC analyses, we limited the size of inferred widespread ancestral ages to be no more than two areas. The tendency to infer widespread ranges at nodes deeper in the tree is a well-known bias in biogeographic methods derived from character optimization methods (Bremer 1992, 1995; Ronquist 1997, 2003; Ree et al., 2005; Ree & Smith 2008a; Clark et al. 2008). Given that: 1) none of our terminal taxa are present in more than a single range, 2) our area designation is geographically coarse (continent-level), and 3) plausible area connections have remained (relatively) constant through the time period in question (Late Triassic), we feel that restricting the reconstruction of widespread ranges to no more than two areas is a reasonable assumption. In both the DIVA and DEC analyses, allowing more than two-area widespread ranges typically only results in more uncertainty at deeper node reconstructions, and does not produce results that fundamentally conflict with those from the restricted analyses. Furthermore, for the DEC analyses, allowing widespread ranges that include more than two areas results in sub-optimal likelihood scores.

Analytic Biogeographic Methods

In recent years, biogeographic methods have been revolutionized by the co-opting of a diverse set of tools and methodology from ancestral character state reconstruction (Ronquist 1997; Nepokroeff et al. 2003; Ree et al. 2005; Olsson et al. 2006; McGuire et al. 2007; Pereira et al. 2007; Clark et al. 2008; Ree & Smith 2008). DIVA is a parsimony-based method for optimizing ancestral ranges on a phylogeny by minimizing the number of dispersal and local extinction events required to account for the observed ranges of terminal taxa (Ronquist 1997). However, vicariance maintains primacy in explaining disjunct distributions in DIVA, as it is assigned no cost relative to dispersal and local extinction, which are each assigned a cost that is specified a priori (Ronquist 1997; Ree et al. 2005). The DEC model is a likelihood method that specifies instantaneous rates of range transitions (dispersals and local extinctions) along phylogenetic branches and utilizes these to estimate the likelihoods of specific range inheritance scenarios at

cladogenetic events (Ree et al., 2005; Ree & Smith, 2008a). Given a temporally calibrated phylogeny with observed terminal taxon ranges, the DEC method integrates over all the possible range inheritance scenarios (see Ree et al., 2005: Fig.3) at internal nodes to estimate optimal rates of dispersal and local extinction, and optimal ancestral range reconstructions for individual nodes. These reconstructions and optimal dispersal and local extinction rates can then be treated as fixed, and the likelihood of the data for each range inheritance scenario can be iteratively recalculated at each node to produce a ranking of alternative scenarios at a single node, based on their relative contributions to the overall likelihood (Ree & Sanmartín 2009).

DIVA analyses were performed using DIVA 1.1a (Ronquist 1996), and DEC analyses were performed using Lagrange version 2 (Ree & Smith 2008b). Detailed descriptions of the two methods can be found in Ronquist (1997, 2002) for DIVA, and Ree et al. (2005) and Ree & Smith (2008a) for DEC.

South America/Europe Constraints

For each of the three temporally calibrated phylogenies specified above (“No Temp”, “Strict”, “Temp”), we performed additional DEC analyses with two specific constraints (labeled “No SE” below). In the DEC model, we explicitly disallowed the reconstruction of widespread ranges comprised of South America and Europe at internal nodes. The reasoning behind this constraint is that: 1) no widespread taxa are present in our terminal taxa, and 2) we consider it unlikely for a lineage to have established and then persisted in a widespread range formed of two geographically disjunct, continent-sized areas for millions of years. In addition, we also set dispersal rates between South America and Europe to zero for these constraint analyses. Given that the continental landmasses of South America and Europe were not in direct contact during the Late Triassic, this constraint essentially forces dispersals between the two areas to take place via North America or Africa.

Results and Key to the *Tawa* Biogeography Figures

Results of the DIVA and DEC analyses are provided in Figures S1-S6. The four continental areas represented are color-coded (red = South America; green = North America; yellow = Europe; blue = Africa). Below each node are the optimal ancestral area reconstructions. Only reconstructions within 2 log-likelihood units of the maximum for each node are shown; this is the conventional cutoff for assessing significance in likelihood differences (Edwards 1992). In cases where more than one area is reconstructed, areas are listed from top to bottom in the order of their contribution to the global likelihood for that node (i.e., areas at the top are more likely reconstructions than areas at the bottom, though not significantly so).

For the lineages leading to North American taxa, the scenario of range evolution that led to the presence of that taxon in North America is indicated to the right of the branch. Again, only scenarios falling within 2 log-likelihood units of the maximum are shown, and multiple scenarios are listed from top to bottom according to which are more likely. Single arrows indicate dispersal events to North America, and double arrows indicate either vicariant scenarios, or cases of allopatric speciation from an ancestrally widespread range that resulted in the lineage being present in North America (see also Ree et al. 2005: fig. 3). Single areas leading from a widespread area where one boxed

bears an “X” indicate scenarios where a widespread area was the range at the base of the lineage, and extinction in one area resulted in a North American range.

All analyses are consistent in rejecting scenarios of an endemic North American theropod radiation (see Main Text). The DIVA ancestral range reconstructions are nearly congruent with those of the DEC analysis imposing equal branch lengths (Fig. S1). In all cases where the DEC analysis only yields one statistically significant reconstruction, the DIVA analysis infers an identical reconstruction, with the exception of the node Neotheropoda, where DIVA yields two equally parsimonious reconstructions. In cases where more than one range reconstruction is considered plausible in the DEC analysis, DIVA also infers multiple equally parsimonious reconstructions, or a single parsimonious reconstruction that is identical to one of the DEC reconstructions. The various DEC analyses differ slightly in support for range reconstructions at individual nodes, but are consistent in providing high relative support for inferring South America as the ancestral range through much of the spine of the basal dinosaur tree. DEC analyses that do and do not incorporate temporal data allow us to assess the relative contributions of topology and time to this pattern, and reveal that it is both the phylogenetic relationships and the age of South American basal dinosaur taxa that supports these reconstructions. However, the effects of increased taxon sampling (notably within Sauropodomorpha) and uneven spatiotemporal sampling of the Late Triassic fossil record on the patterns recovered here have not been fully explored. A more detailed analysis and discussion of these results of the biogeographic analyses is in preparation.

Biogeographic Constraint Analyses

To assess the robustness of the biogeographic reconstructions inferred by the various DEC analyses, and to provide a more direct test of whether the HQ theropods form a portion of an endemic North American radiation (see main text), we designed several constraint analyses using the DEC model. For each of the 6 DEC datasets, we performed two constraint analyses. The first constraint analysis fixed North America as the ancestral range for the six nodes subtending the three HQ theropod lineages (“NA only” constraint in Table S1). The second constraint analysis (“NA included” constraint in Table S1) enforced that North America be included in the reconstructions for those six nodes (i.e., either as a North America only reconstruction, or as a widespread range that included North America). The first constraint is analogous to studies of character evolution that assess whether the presence of a particular character state in three disparate taxa is homologous. The second constraint is less strict, but addresses whether there is any continuity of the presence of North America in ancestral ranges subtending the three HQ theropods.

The results of these constraint analyses are given in Table S1. All constraint analyses resulted in significantly worse fits to the data, using the conventional cutoff value of two log-likelihood units (Edwards 1992). Only the “NA included” constraints for the two DEC datasets not incorporating temporal information yielded global likelihood scores that were close to the cutoff value (i.e. within 3 log-likelihood units). This suggests that the inclusion of temporal data into the DEC analyses has a further potential benefit of increasing the ability to statistically reject alternative biogeographic scenarios.

Table S1 also permits comparison of the global likelihood scores for the DEC models with and without the constraint disallowing South America/Europe widespread ranges and direct dispersal between South America and Europe. These dispersal/widespread range constrained analyses also result in significantly worse fit, though this tradeoff in fit must be balanced with our knowledge of the interconnections of geographical areas during the Late Triassic.

Table S1. Results of biogeographic constraint analyses.

DEC Dataset	Unconstrained -lnL	“NA only” Constrained – lnL	“NA included” Constrained – lnL
No Temp	35.21	47.73	38.02
No Temp(No SE)	41.32	50.55	43.54
Strict	29.49	63.82	41.39
Stict(No SE)	41.8	69.44	51.33
Temp	33.64	56.1	40.74
Temp(No SE)	42.11	59.4	48.11

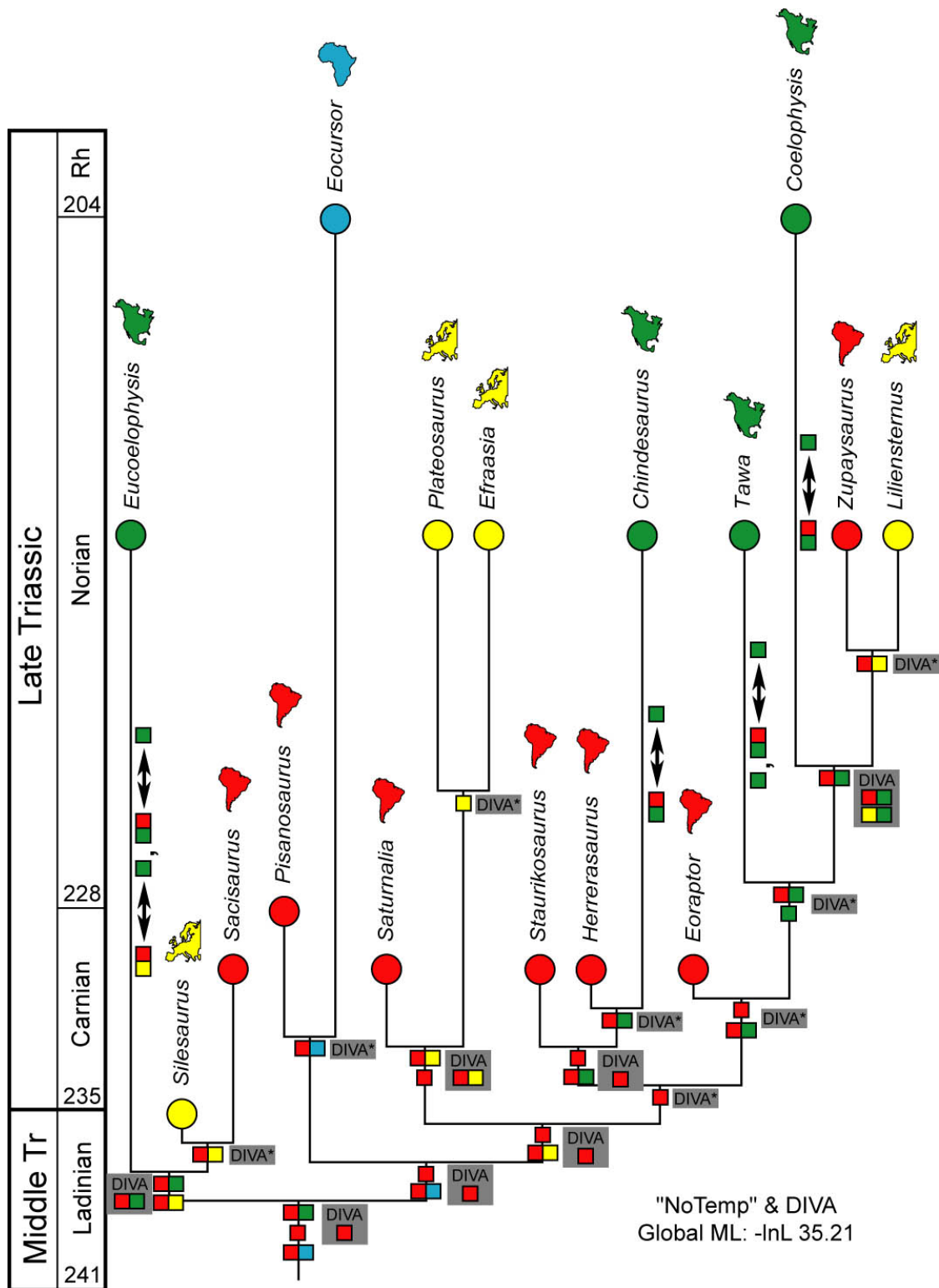


Figure S1. Ancestral range reconstructions for the DIVA and “NoTemp” DEC analyses. The phylogeny is temporally calibrated only for display purposes. All branch lengths were set equal in the biogeographic analyses. Asterisks next to the DIVA results indicate exact correspondence to the DEC results.

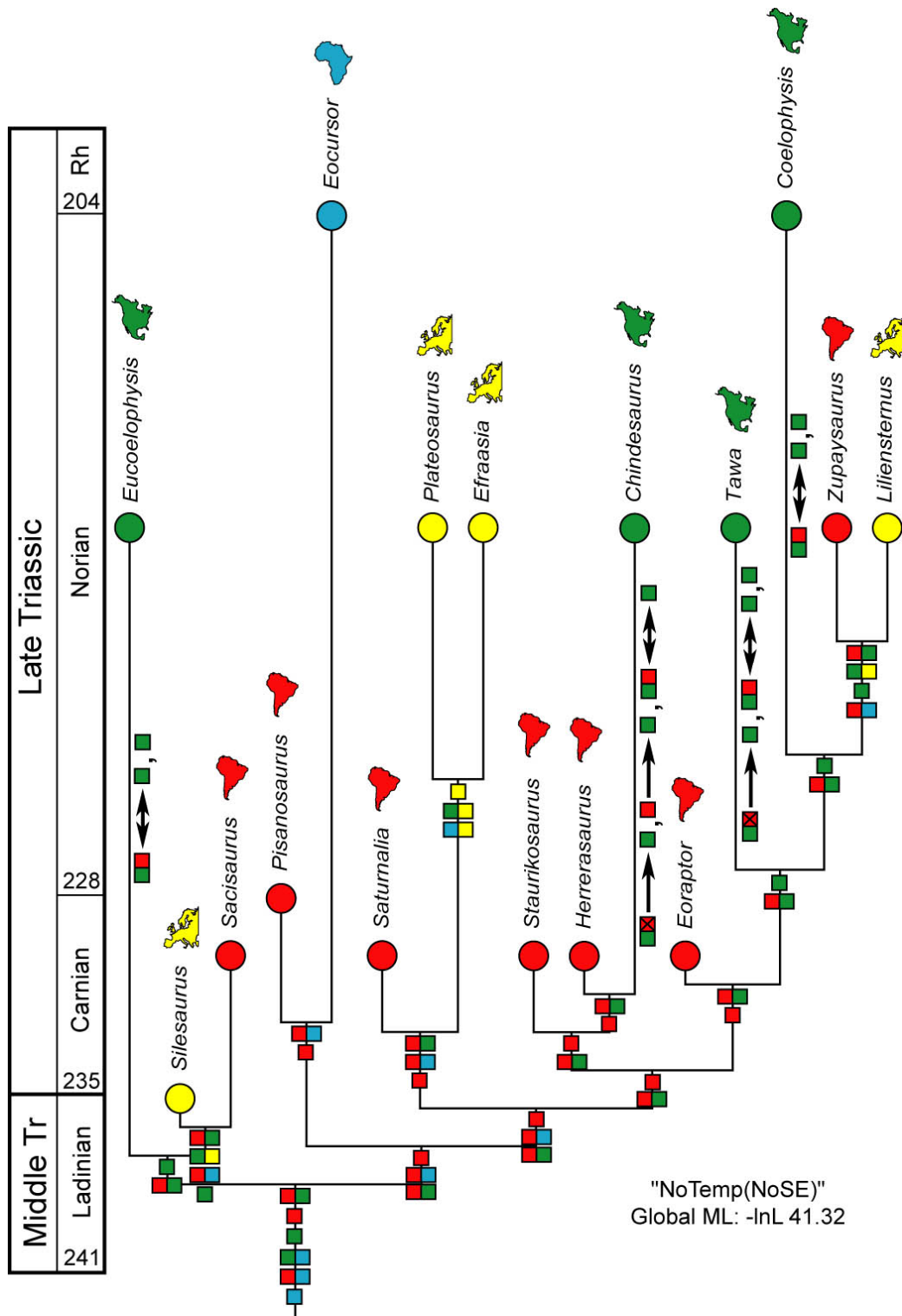


Figure S2. Ancestral range reconstructions for the “NoTemp (No SE)” DEC analysis. The phylogeny is temporally calibrated only for display purposes. All branch lengths were set equal in the biogeographic analyses.

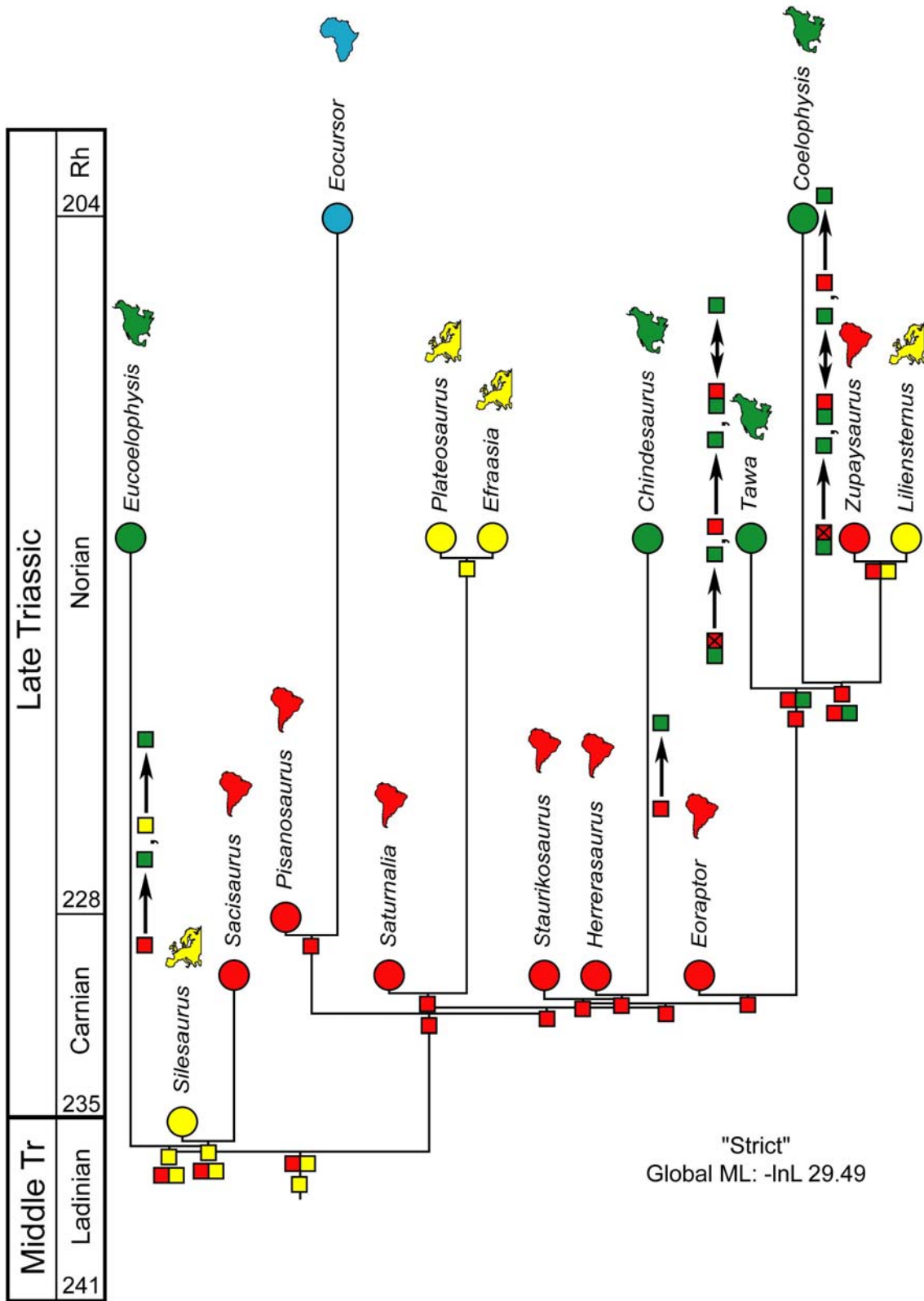


Figure S3. Ancestral range reconstructions for the “Strict” DEC analysis.

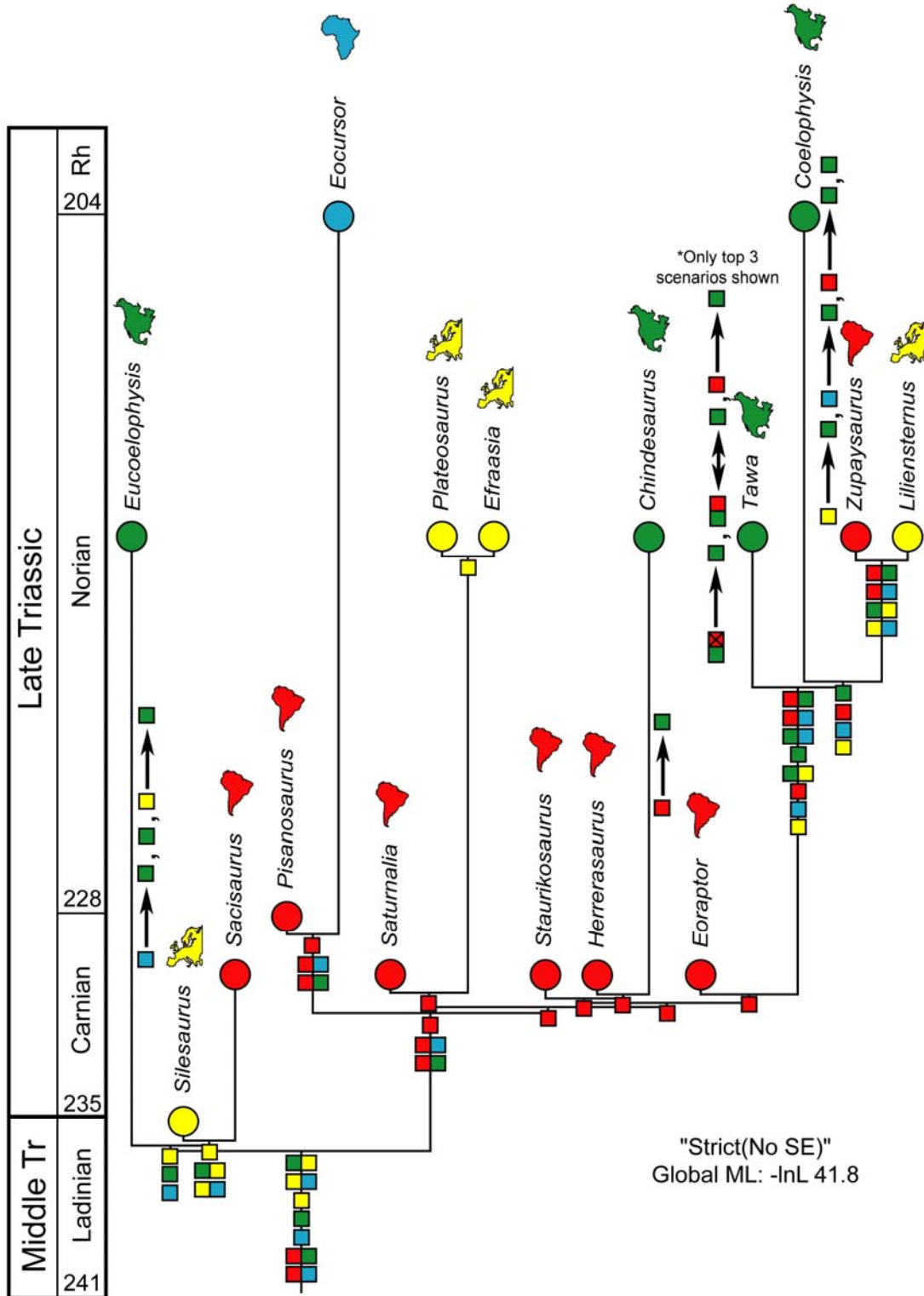


Figure S4. Ancestral range reconstructions for the "Strict (No SE)" DEC analysis. Note that many terminal range inheritance scenarios fell within the two log-likelihood unit cutoff of significance for the lineage leading to *Tawa*. Only the top three are shown here because of space constraints.

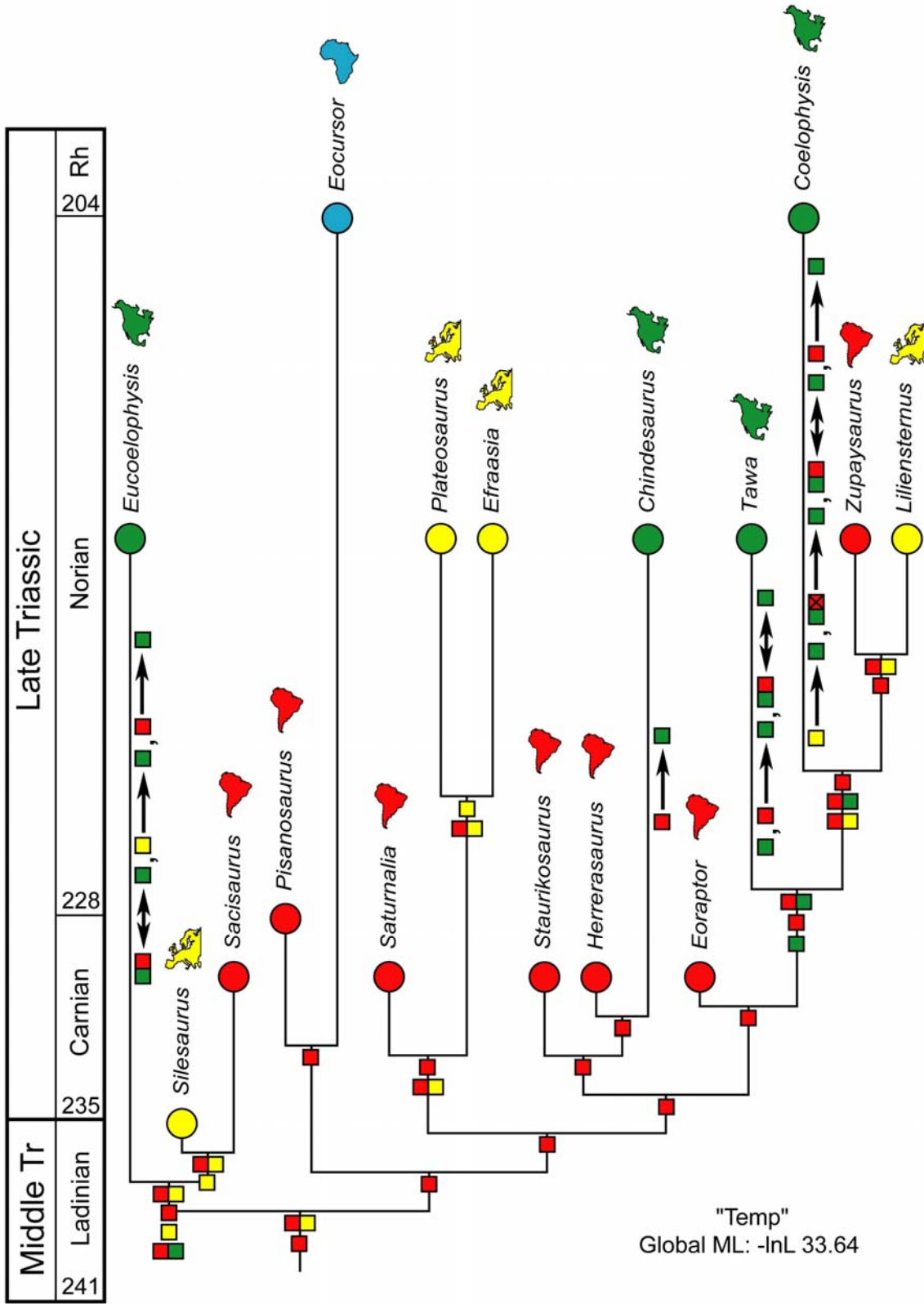


Figure S5. Ancestral range reconstructions for the "Temp" DEC analysis.

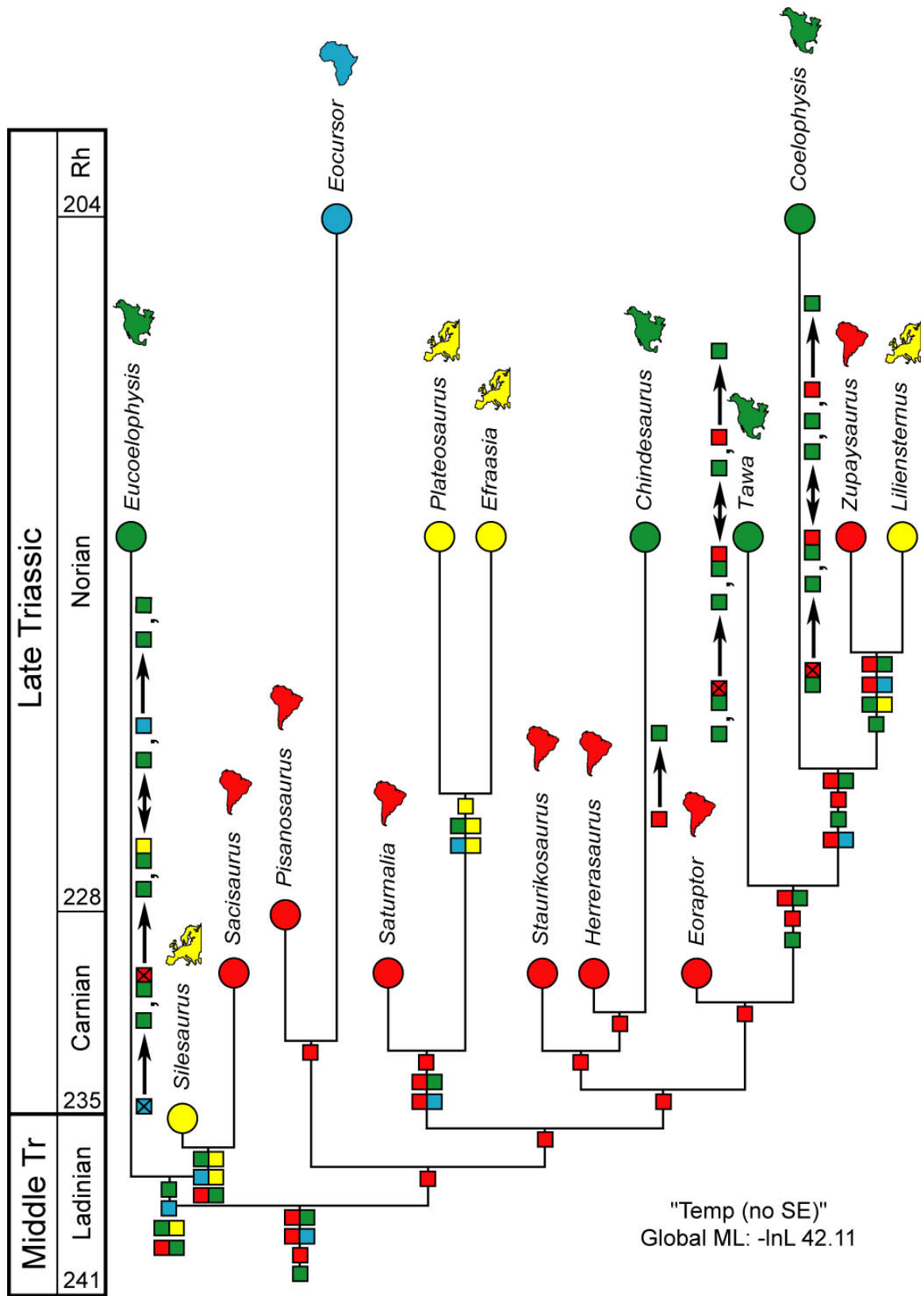


Figure S6. Ancestral range reconstructions for the “Temp (No SE)” DEC analysis.

4. Details of the phylogenetic analysis.

The phylogenetic analysis comprises 41 taxa and 315 characters. Nearly all taxa were observed firsthand by at least one of the authors. *Erythrosuchus* was constrained as the outgroup, and ingroup taxa included a variety of pseudosuchians, pterosaurs, basal dinosauromorphs, and dinosaurs. Specimen numbers or literature sources for each taxon are reported in Table S2. Characters are mainly derived from Gauthier (1986), Benton and Clark (1988), Sereno (1991), Sereno and Arcucci (1994), Novas (1996), Benton (1999), Rauhut (2003), Yates (2003), Butler (2005), Langer and Benton (2006), Smith et al. (2007), Irmis et al. (2007), Butler et al. (2008), and new and revised characters from Irmis (2008) and Nesbitt (2009).

The character-taxon matrix was assembled in Mesquite v.2.6 (Maddison and Maddison 2008) and is freely available on Morphobank (O’Leary and Kaufman 2007) as project 205. We analyzed our dataset using PAUP* 4.0b10 for Macintosh PPC (Swofford 2002). Trees were searched for using the parsimony criterion implemented under the heuristic search option using tree bisection and reconnection (TBR) with 10,000 random addition sequence replicates. Zero length branches were collapsed if they lack support under any of the most parsimonious reconstructions. All characters were equally weighted. Characters 17, 30, 67, 128, 174, 184, 213, 219, 231, 236, 248, 253, 254, and 273 represent nested sets of homologies and/or entail presence and absence information. These characters were set as additive (also marked as “ordered” in bold text following character description). Three most-parsimonious trees were found; we report the strict consensus of these trees here (Fig. S7). Relationships within Ornithischia and Tetanurae are unresolved. Tree statistics were calculated using TNT v. 1.0 (Goloboff et al., 2003; Goloboff et al. 2008). Bootstrap proportions were calculated using 10,000 bootstrap replicates with 10 random addition sequence replicates for each bootstrap replicate (Efron 1979, Felsenstein 1985). Bremer support decay indices were calculated in TNT.

Table S2. Specimens and literature sources for the scoring of taxa in the phylogenetic analysis. AMNH, American Museum of Natural History, New York; BNMH, The Natural History Museum, London; BP, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; CMNH, Cleveland Museum of Natural History, Cleveland, Ohio; FMNH, Field Museum of Natural History, Chicago, Illinois; GPIT, Institut und Museum für Geologie und Paläontologie, Tübingen, Germany; GR, Ghost Ranch Ruth Hall Museum of Paleontology, Ghost Ranch, New Mexico; IGM, Mongolian Institute of Geology, Ulaan Bataar, Mongolia; LACM, Los Angeles County Museum of Natural History, Los Angeles, California; MACN, Museo Argentinas Ciencias Naturales, Buenos Aires, Argentina; MB, Museum für Naturkunde der Humboldt Universität, Berlin, Germany; MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MCP, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNA, Museum of Northern Arizona, Flagstaff, Arizona; MSM, Arizona Museum of Natural History, Mesa, Arizona; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico; PEFO, Petrified Forest National Park, Arizona; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; PVL,

Instituto Miguel Lillo, Tucumán, Argentina; PVSJ, Museo de Ciencias Naturales, San Juan, Argentina; SAM, Iziko South African Museum, Capetown, South Africa; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TMM, Vertebrate Paleontology Laboratory, Texas Natural Science Center, Austin, Texas; TTUP, Texas Tech University, Lubbock, Texas; UCMP, University of California Museum of Paleontology, Berkeley, California; UMCZ, Museum of Zoology, Cambridge University, Cambridge, England; UMNH, Utah Museum of Natural History, Salt Lake City, Utah; UNC, Department of Geological Sciences, University of North Carolina at Chapel Hill, North Carolina; UNLR, Universidad Nacional de La Rioja, La Rioja, Argentina; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C.; YPM, Yale Peabody Museum, Yale University, New Haven, Connecticut; ZPAL, Instytut Paleobiologii PAN, Warsaw, Poland.

<u>Taxon</u>	<u>Source</u>
<i>Erythrosuchus africanus</i>	BMNH R3592, R8667; BP/1/ 5207
<i>Euparkeria capensis</i>	SAM 5867; SAM 6050; SAM 6047B; SAM 6049; SAM 6047A; UMCZ T692
<i>Reueltosaurus callenderi</i>	PEFO 33788, 34274, 34561, various other PEFO specimens
<i>Aetosaurus ferratus</i>	SMNS 5770 (block of at least 22 specimens), SMNS 5771, SMNS 18554
<i>Arizonasaurus babbitti</i>	MSM P4590, UCMP 36232
<i>Effigia okeeffeae</i>	AMNH FR 30587, AMNH FR 308588, AMNH FR 30859
<i>Batrachotomus kupferzellensis</i>	SMNS 52970, SMNS 80260-80339
<i>Postosuchus kirkpatricki</i>	TTUP 9000, TTUP 9002, UCMP various (from loc. A269)
<i>Dromicosuchus grillator</i>	UNC 15574
<i>Eudimorphodon</i> spp.	Wild 1978, Dalla Vecchia 2003, Wellnhofer 2003
<i>Dimorphodon macronyx</i>	BMNH R 1034, BMNH R 1035, BMNH 41212, YPM 350, YPM 9182
<i>Lagerpeton chanarensis</i>	UNLR 06, PVL 4619, PVL 4625
<i>Dromomeron gregorii</i>	TMM 31100-1306 (holotype), 31100-278, 31100-464, 31100-764, 31100-1234, 31100-1308, 31100-1314
<i>Dromomeron romeri</i>	GR 218-223, 234, 238-239
<i>Marasuchus lilloensis</i>	PVL 3870, PVL 3871
<i>Eucoelophysis baldwini</i>	NMNNH P-22298
<i>Sacisaurus agudoensis</i>	MCN PV10041 (holotype), PV10009-10011, PV10013-10016, PV10018-10020, PV10023-10025, PV10033, PV10042-10044, PV10061, PV10063, PV10075
<i>Silesaurus opelensis</i>	ZPAL Ab III 361, ZPAL Ab III 363, ZPAL Ab III 364, ZPAL various referred material from type locality
<i>Scutellosaurus lawleri</i>	MNA V175 (holotype), V1752; UCMP 130580; MCZ 8797
<i>Lesothosaurus diagnosticus</i>	BMNH RU B17, RU B23, R11956, R8501
<i>Eocursor parvus</i>	SAM PK-K8025
<i>Pisanosaurus mertii</i>	PVL 2577
<i>Heterodontosaurus tucki</i>	SAM PK-K337, PK-K1332
<i>Saturnalia tupiniquim</i>	MCP 3844-PV, MCP 3845-PV, MCP 3846-PV
<i>Efraasia minor</i>	SMNS 11838, SMNS 12354, SMNS 12667, SMNS 12668, SMNS 12684, SMNS 14881, SMNS 17928
<i>Plateosaurus engelhardti</i>	SMNS 13200, GPIT mounted skeletons
<i>Herrerasaurus ischigualastensis</i>	PVL 2566, PVSJ 373, PVSJ 407
<i>Chindesaurus bryansmalli</i>	PEFO 10395, GR 226
<i>Staurikosaurus pricei</i>	MCZ 1669
<i>Eoraptor lunensis</i>	PVSJ 512
<i>Tawa hallae</i>	see text
<i>Coelophysis bauri</i>	AMNH FR 7223, 7224, 7239, 7241, 7242; MNA V3315, MNA block; various LACM, CMNH, and CM specimens
" <i>Syntarsus</i> " <i>kayentakatae</i>	MNA V2623 (holotype); TMM 43588-1
<i>Liliensternus liliensterni</i>	MB.R.2175
<i>Zupaysaurus rougieri</i>	UNLR 076
<i>Cryolophosaurus ellioti</i>	FMNH PR1821
<i>Dilophosaurus wetherilli</i>	UCMP 37302 (holotype), 37303, 77270; Tykoski 2005
<i>Ceratosaurus nasicornis</i>	USNM 4735 (holotype); UMNH Cleveland-Lloyd material; Gilmore 1920; Madsen & Welles 2000
<i>Piatnitzkysaurus floresii</i>	PVL 4073 (holotype); MACN Pv CH895
<i>Allosaurus fragilis</i>	UCMP 147068 (cast of MOR 693); UMNH Cleveland- Lloyd material; Gilmore 1920;

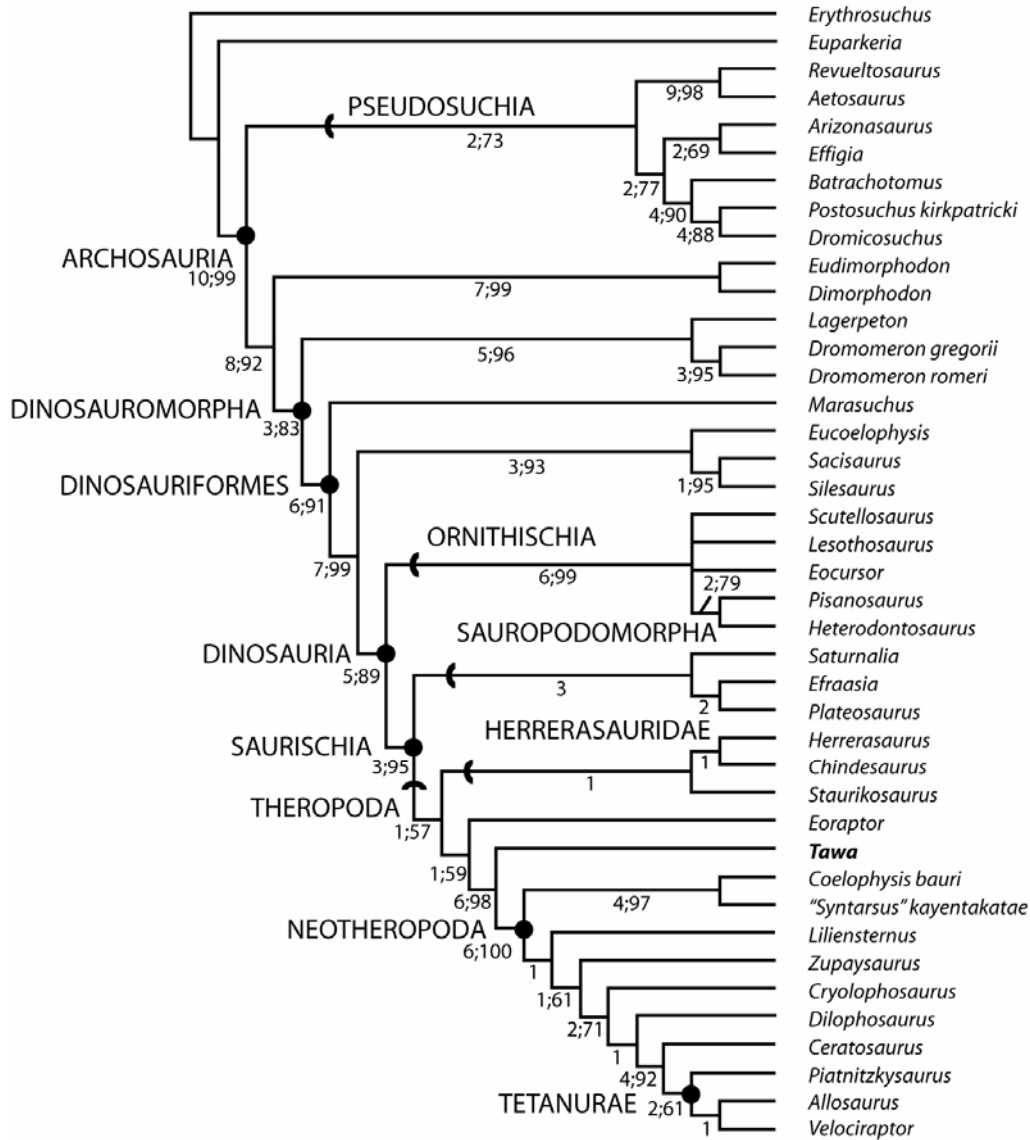


Figure S7. The relationships of *Tawa hallae*. Strict consensus of the three most parsimonious trees with a tree length of 872 steps. Bold numbers on the branches indicate Bremer support indices and percentages indicate bootstrap support when above 50%. Consistency Index (CI) = 0.427, Retention Index (RI) = 0.710.

Character List

- 1) Premaxilla, height: length ratio below external naris: .5-1.25 (0); <.5 (1); >1.25 (2).
Smith et al. 2007: 5; Irmis 2008: 9
- 2) Premaxilla, anterodorsal process (=nasal process), length: less than the anteroposterior length of the premaxilla (0); greater than the anteroposterior length of the premaxilla (1).
Nesbitt and Norell 2006; Nesbitt 2009: 1
- 3) Premaxilla, angle of the anterodorsal process (=nasal process) relative to the alveolar margin: more than 75 degrees (0); less than 70 degrees (1).
Smith et al. 2007: 6; Irmis 2008: 10
- 4) Premaxilla, posterodorsal process (=maxillary process, = subnarial process), length: less than or about the same as the anteroposterior length of the premaxilla (0); greater than the anteroposterior length of the premaxilla (1).
Nesbitt 2009: 2
- 5) Premaxilla, posterodorsal process (=maxillary process, = subnarial process): wide, plate-like (0); thin (1).
Parrish 1993; Clark et al. 2000; Olsen et al. 2000; Benton and Walker 2002; Sues et al. 2003; Clark et al. 2004; Nesbitt 2009: 3
- 6) Premaxilla, posterodorsal process (=maxillary process, = subnarial process): extends posteriorly to the external naris (0); restricted to the ventral border of the external naris (1).
Smith et al. 2007: 7; Irmis 2008: 13
- 7) Premaxilla, ventral process at the posterior end of the premaxillary body: absent (0); present (1).
Langer and Benton 2006; Nesbitt 2009: 5
- 8) Premaxilla-nasal suture, on the internarial bar: V-shaped (0); W-shaped (1).
Smith et al. 2007: 16; Irmis 2008: 17
- 9) Premaxillary teeth, number: 3(0); 4 (1); 5 (2); 6+ (3); 0 (4).
Nesbitt and Norell 2006; Nesbitt 2009: 6
- 10) Premaxillary teeth, serrations: present (0); absent (1).
Heckert et al. 1996; Parker 2007; Nesbitt 2009: 7
- 11) Premaxilla, teeth: present along entire length of the premaxilla (0); absent in the anterior portion of the premaxilla (1).

Smith et al. 2007: 17; Irmis 2008: 139

12) Premaxilla, narial fossa: absent or shallow (0); expanded in the anteroventral corner of the naris (1).

Sereno 1999; Langer and Benton 2006; Irmis et al. 2007; Nesbitt 2009: 9

13) Premaxilla-maxilla, subnarial gap between the elements: absent (0); present (1).

Gauthier 1986; Langer and Benton 2006; Nesbitt 2009: 11

14) Premaxilla-maxilla, subnarial foramen between the elements: absent (0); present and the border of the foramen is present on both the maxilla and the premaxilla (1); present and the border of the foramen is present on the maxilla but not on the premaxilla (2); present and the border of the foramen is present on the premaxilla but not on the maxilla (3).

Benton and Clark 1988; Parrish 1993; Juul 1994; Benton 1999; Nesbitt 2009: 12

15) Maxilla, facial portion anterior to anterior edge of antorbital fenestra: shorter than posterior portion (0); equal in length or longer than portion posterior to anterior edge of fenestra (1).

Clark et al. 2000; Olsen et al. 2000; Benton and Walker 2002; Clark et al. 2004; Sues et al. 2003; Clark et al. 2004; Nesbitt 2009: 14

16) Maxillary teeth, posterior edge of posterior maxillary teeth: concave or straight (0); convex (1).

Sues et al. 2003; Clark et al. 2004; Nesbitt 2009: 15

17) Maxillary tooth count: less than 12 (0); 12 - 18 (1); more than 18 (2). ORDERED
Smith et al. 2007: 3; Irmis 2008: 31

18) Maxilla, posterior extent of the maxillary tooth row: extends to approximately half of the anteroposterior length of the orbit (0); completely antorbital; tooth row ends anterior to the vertical strut of the lacrimal (1).

Smith et al. 2007: 35; Irmis 2008:147

19) Maxilla, posterior process: articulates ventral to the jugal (0); articulates into a slot on the lateral side of the jugal (1).

Nesbitt 2009: 16

20) Maxilla, dentition: present (0); absent (1).

Nesbitt and Norell 2006; Nesbitt 2009: 18

21) Maxilla, buccal emargination separated from the ventral margin of the antorbital fossa: absent (0); present (1).

Butler 2005, 2007; Irmis et al. 2006; Irmis et al., 2007; Nesbitt 2009: 23

22) Maxilla, anterodorsal margin: separated from the external naris by the premaxilla (0); borders the external naris (1).

Gauthier 1986; Langer and Benton 2006; Nesbitt 2009: 24

23) Maxilla, anterodorsal margin at the base of the dorsal process: convex or straight (0); concave (1).

Langer and Benton 2006; Nesbitt 2009: 25

24) Lateral surface of the maxilla: smooth (0); sharp longitudinal ridge present (1); bulbous longitudinal ridge present (2).

Gower 1999; Weinbaum and Hungerbühler 2007; Nesbitt 2009: 26

25) Maxilla, depth of the ventral portion of the antorbital fossa: less than or subequal to the depth of the maxilla below the ventral margin of the antorbital fossa (0); much greater than the depth of the maxilla below the ventral margin of the antorbital fossa (1).

Smith et al. 2007: 35; Irmis 2008: 27

26) Maxilla, posterior portion ventral to the antorbital fenestra: tapers posteriorly (0); has a similar dorsoventral depth as the anterior portion ventral to the antorbital fenestra (1); expands dorsoventrally at the posterior margin of the maxilla (2).

Nesbitt 2009: 27

27) Maxilla, promaxillary foramen: absent (0); present (1).

Rauhut 2003; Tykoski 2005; Smith et al. 2007: 32; Irmis 2008: 34; Nesbitt 2009: 28

28) Maxilla, dorsal (=ascending) process: tapers posterodorsally (0); remains the same width (1).

Nesbitt 2009: 29

29) Antorbital fenestra, anterior margin: gently rounded (0); nearly pointed (1).

Benton and Clark 1988; Benton and Walker 2002; Weinbaum and Hungerbühler 2007; Nesbitt 2009: 30

30) Maxilla, palatal processes: do not meet at the midline (0); meet at the midline (1); meet at the midline and expand anteriorly and posteriorly (2). ORDERED

Parrish 1993; Clark et al. 2000; Olsen et al. 2000; Benton and Walker 2002; Sues et al. 2003; Clark et al. 2004; Nesbitt 2009: 32

31) Nasals, posterior portion at the midline: convex or flat (0); concave (1).

Nesbitt 2009: 34

32) Nasal, dorsolateral margin of the anterior portion (just posterodorsal to the external naris): smoothly rounded (0); distinct anteroposteriorly ridge on the lateral edge (1).

Nesbitt 2009: 35

33) Nasal: does not possess a posterolateral process that envelops part of the anterior ramus of the lacrimal (0); possesses a posterolateral process that envelops part of the anterior ramus of the lacrimal (1).

Yates 2003; Langer and Benton 2006; Nesbitt 2009: 36

34) Nasal: does not form part of the dorsal border of the antorbital fossa (0); forms part of the dorsal border of the antorbital fossa (1).

Sereno et al. 1994; Langer and Benton 2006; Irmis et al. 2007; Nesbitt 2009: 37

35) Lacrimal: does not fold over the posterior/posterodorsal part of the antorbital fenestra (0); folds over the posterior/posterodorsal part of the antorbital fenestra (1).

Sereno 1999; Langer and Benton 2006; Nesbitt 2009: 38

36) Lacrimal, height: significantly less than the height of the orbit, and usually fails to reach the ventral margin of the orbit (0); as high as the orbit, and contacts the jugal at the level of the ventral margin of the orbit (1).

Rauhut 2003; Nesbitt 2009: 39

37) Lacrimal, orientation of long axis: sloping anterodorsally (0); erect or nearly vertical (1).

Smith et al. 2007:60; Irmis 2008: 47

38) Lacrimal 'horn': absent (0); present, forms dorsal crest above the orbit (1).

Smith et al. 2007: 52; Irmis 2008: 45

39) Lacrimal fenestra: absent (0); present (1).

Smith et al. 2007: 51; Irmis 2008: 44

40) Frontal, dorsal surface: flat (0); with longitudinal ridge along midline (1).

Wu and Chatterjee 1993; Clark et al. 2000; Olsen et al. 2000; Benton and Walker 2002; Sues et al. 2003; Clark et al. 2004; Nesbitt 2009: 42

41) Frontal, anterior portion: about as wide as the orbital margin or has a transversely aligned suture with the nasal (0); tapers anteriorly along the midline (1).

Nesbitt 2009: 43

42) Postfrontal: present (0); absent (1).

Gauthier 1986; Benton and Clark 1988; Juul 1994; Bennett 1996; Novas 1996; Benton 1999; Clark et al. 2000; Olsen et al. 2000; Benton and Walker 2002; Sues et al. 2003; Clark et al. 2004; Langer and Benton 2006; Nesbitt 2007; Irmis et al., 2007; Nesbitt 2009: 44

43) Quadratojugal: forms less than 80% of the posterior border of the lower temporal fenestra (0); more than 80% of the posterior border of the lower temporal fenestra (1).

Benton and Clark 1988; Parrish 1993; Nesbitt 2009: 45

44) Squamosal, posterior end: does not extend posterior to the head of the quadrate (0); extends posterior to the head of the quadrate (1).

Nesbitt 2009: 48

45) Squamosal: without distinct ridge on dorsal surface along edge of supratemporal fossa (0); with distinct ridge on dorsal surface along edge of supratemporal fossa (1).

Bonaparte 1982; Parrish 1993; Nesbitt 2009: 49

46) Squamosal, facet for the paroccipital process on the medial side of the posterior process: mediolaterally thin (0); rounded and thick (1).

Nesbitt 2009: 54

47) Squamosal, ventral process: wider than one quarter of its length (0); narrower than one quarter of its length (1).

Yates 2003; Langer and Benton 2006; Nesbitt 2009: 56

48) Parietals, upper temporal fenestrae separated by: broad, flat area (0); supratemporal fossa separated by a mediolaterally thin strip of flat bone (1); has supratemporal fossa separated by a "sagittal crest" (which may be divided by interparietal suture) (2).

Clark et al. 2000; Olsen et al. 2000; Benton and Walker 2002; Sues et al. 2003; Clark et al. 2004; Nesbitt 2009: 59

49) Postorbital, ventral termination of the ventral process: tapered (0); blunt (1).

Benton and Clark 1988; Juul 1994; Benton 1999; Alcober 2000; Benton and Walker 2002; Nesbitt 2009: 65

50) Postorbital-squamosal, contact: restricted to the dorsal margin of the elements (0); continues ventrally for much or most of the ventral length of the squamosal (1).

Nesbitt 2009: 66

51) Postorbital bar: composed both of the jugal and postorbital in nearly equal proportions (0); composed by mostly the postorbital (1).

Nesbitt 2009: 67

52) Jugal, anterior extent of the slot for the quadratojugal: well posterior of the posterior edge of the dorsal process of the jugal (0) at or anterior to the posterior edge of the dorsal process of the jugal (1).

Nesbitt 2009: 68

53) Jugal, anterior process: participates in posterior edge of antorbital fenestra (0); excluded from the antorbital fenestra by lacrimal or maxilla (1).

Clark et al. 2000; Olsen et al. 2000; Benton and Walker 2002; Sues et al. 2003; Clark et al. 2004; Rauhut 2003; Langer and Benton 2006; Nesbitt 2009: 69

54) Jugal, posterior process: lies dorsal to the anterior process of the quadratojugal (0); ventral to the anterior process of the quadratojugal (1); splits the anterior process of the quadratojugal (2); is split by the anterior process of the quadratojugal (3).

Nesbitt 2009: 71

55) Jugal, posterior termination: anterior to or at the posterior extent of the lower temporal fenestra (0); posterior to the lower temporal fenestra (1).

Nesbitt 2009: 72

56) Jugal, long axis of the body: nearly horizontal (0); anterodorsally inclined (1).

Heckert and Lucas 1999; Parker 2007; Nesbitt 2009: 74

57) Jugal, longitudinal ridge on the body: absent (0); present and sharp (1); rounded and broad (2); rounded and restricted to a bulbous ridge (3).

Nesbitt 2009: 75

58) Quadrate, head: partially exposed laterally (0); completely covered by the squamosal (1).

Sereno and Novas 1994; Juul 1994; Novas 1996; Benton 1999; Langer and Benton 2006; Nesbitt 2009: 78

59) Quadratojugal and quadrate, suture between the elements, foramen: present (0); absent (1).

Parrish 1991; Benton and Walker 2002; Nesbitt 2009: 79

60) Quadrate, angled: posteroventrally or vertical (0); anteroventrally (1).

Nesbitt 2007; Nesbitt 2009: 82

61) Pterygoid-ectopterygoid, articulation: ectopterygoid ventral to pterygoid (0); ectopterygoid dorsal to pterygoid (1).

Sereno and Novas 1994; Novas 1996; Benton 1999; Irmis et al. 2007; Nesbitt 2009: 84

62) Ectopterygoid, ventral recess: absent (0); present (1).

Gauthier 1986; Langer and Benton 2006; Nesbitt 2009: 86

63) Ectopterygoid, body: arcs anteriorly (0); arcs anterodorsally (1).

Nesbitt 2009: 87

64) Ectopterygoid: single-headed (0); double-headed (1).

Weinbaum and Hungerbühler 2007; Nesbitt 2009: 89

65) Basipterygoid, processes directed: anteriorly or ventrally at their distal tips (0); posteriorly at their distal tips (1).

Nesbitt 2009: 93

- 66) Parabasisphenoid, foramina for entrance of cerebral branches of internal carotid artery into the braincase positioned on the surface: ventral (0); lateral (1).
Parrish 1993; Gower and Sennikov 1996; Gower 2002; Nesbitt 2009: 95
- 67) Parabasisphenoid, plate: present and straight (0); present and arched anteriorly (1); absent (2). ORDERED
Gower and Sennikov 1996; Nesbitt 2009: 96
- 68) Parabasisphenoid, semilunar depression on the lateral surface of the basal tubera: present (0); absent (1).
Gower and Sennikov 1996; Nesbitt 2009: 98
- 69) Parabasisphenoid, recess (=median pharyngeal recess of some authors = hemispherical sulcus = hemispherical fontanelle): absent (0); present (1).
Nesbitt and Norell 2006; Nesbitt 2009: 100
- 70) Parabasisphenoid, anterior tympanic recess on the lateral side of the braincase: absent (0); present (1).
Makovicky and Sues 1998; Rauhut 2003; Nesbitt 2009: 101
- 71) Parabasisphenoid, between basal tubera and basipterygoid processes: approximately as wide as long or wider (0); significantly elongated at least 1.5 times longer than wide (1).
Rauhut 2003; Nesbitt 2007; Nesbitt 2009: 103
- 72) Basioccipital, portion of the basal tubera: rounded and anteroposteriorly elongated (0); blade-like and anteroposteriorly shortened (1).
Nesbitt 2009: 106
- 73) Opisthotic, paroccipital processes: no or slight dorsal and ventral expansion distally (0); markedly expanded dorsally at the distal ends (1).
Clark et al. 2000; Olsen et al. 2000; Benton and Walker 2002; Sues et al. 2003; Clark et al. 2004; Nesbitt 2009: 108
- 74) Opisthotic, paroccipital processes: directed laterally or dorsolaterally (0); directed ventrolaterally (1).
Rauhut 2003; Hwang et al. 2004; Smith et al. 2007: 90; Irmis 2008: 89; Nesbitt 2009: 110
- 75) Paroccipital processes, ventral rim of the bases: above or level with the dorsal border of the occipital condyle (0); situated at mid-height of occipital condyle or lower (1).
Smith et al. 2007: 91
- 76) Opisthotic, ventral ramus (= crista interfenestralis): extends further laterally or about the same as lateralmost edge of exoccipital in posterior view (0); covered by the lateralmost edge of exoccipital in posterior view (1).
Gower 2002; Nesbitt 2009: 111

77) Exoccipital, lateral surface: without subvertical crest (= metotic strut) (0); with clear crest (= metotic strut) lying anterior to both external foramina for hypoglossal nerve (XII)(1); with clear crest (= metotic strut) present anterior to the more posterior external foramina for hypoglossal nerve (XII) (2).

Gower 2002; Nesbitt 2009: 114

78) Exoccipitals: meet along the midline on the floor of the endocranial cavity (0); do not meet along the midline on the floor of the endocranial cavity (1).

Gower and Sennikov 1996; Gower 2002; Nesbitt 2009: 115

79) Vestibule, medial wall: incompletely ossified (0); almost completely ossified (1).

Gower 2002; Nesbitt 2009: 117

80) Lagenar/cochlea recess: absent or short and strongly tapered (0); present and elongated and tubular (1).

Gower 2002; Nesbitt 2009: 118

81) Supraoccipital: excluded from dorsal border of foramen magnum by mediodorsal midline contact between opposite exoccipitals (0); contributes to border of foramen magnum (1).

Gower 2002; Nesbitt 2009: 126

82) Foramen for trigeminal nerve and middle cerebral vein: combined and undivided (0); at least partially subdivided by prootic (1); fully divided (2).

Gower and Sennikov 1996; Gower 2002; Nesbitt 2009: 131

83) Foramen or groove passing above and into the dorsal end of the metotic foramen: absent (0); present (1).

Gower 2002; Nesbitt 2009: 132

84) Auricular recess: largely restricted to prootic (0); extends onto internal surface of epiotic/supraoccipital (1).

Gower 2002; Nesbitt 2009: 133

85) Skull length: less than 50% of length of the presacral vertebral column (0); more than 50% of length of the presacral vertebral column (1).

Sereno 1991; Benton 1999; Nesbitt 2009: 134

86) Skull length: longer than two-thirds of the femoral length (0); shorter than two-thirds of the femoral length (1).

Gauthier 1986; Langer and Benton 2006; Nesbitt 2009: 135

87) Antorbital fossa: restricted to the lacrimal and dorsal process of the maxilla (0); present on the lacrimal, dorsal process of the maxilla and the dorsolateral margin of the posterior process of the maxilla (the ventral border of the antorbital fenestra) (1).

Nesbitt 2009: 137

88) Post-temporal opening, size: equal or greater than half the diameter of the foramen magnum (0); less than half the diameter of the foramen magnum or absent (1).

Sereno and Novas 1994; Novas 1996; Benton 1999; Nesbitt 2009: 141

89) Orbit, shape: circular or elliptical (0); tall and narrow (the "keyhole-shaped orbit"; maximum width is less than half the maximum height)(1); with distinct ventral point surrounded by V-shaped dorsal processes of jugal (2).

Benton and Clark 1988; Parrish 1993; Gower 2000; Benton and Walker 2002; Nesbitt 2009: 142

90) Supratemporal fossa: absent anterior to the supratemporal fenestra (0); present anterior to the supratemporal fenestra (1).

Gauthier 1986; Novas 1996; Nesbitt 2009: 144

91) Postparietal(s): present (0); absent (1).

Juul 1994; Bennett 1996; Dilkes 1998; Nesbitt 2009: 146

92) Palpebral(s): absent (0); present (1).

Nesbitt 2009: 147

93) Predeantary: absent (0); present (1).

Sereno 1986; Butler et al. 2007, 2008; Irmis et al. 2007; Nesbitt 2009: 151

94) Anterior half of the dentary, position of the Meckelian groove: dorsoventral center of the dentary (0); restricted to the ventral border (1).

Nesbitt 2009: 152

95) Dentary, anterior extent of the Meckelian groove: ends well short of the dentary symphysis (0); present through the dentary symphysis (1).

Nesbitt 2009: 153

96) Dentary, dorsal margin of the anterior portion compared to the dorsal margin of the posterior portion of the dentary: horizontal (about in the same plane)(0); ventrally deflected (1); dorsally expanded (2).

Nesbitt 2009: 154

97) Dentary, anterior extremity: rounded (0); tapers to a sharp point (1).

Nesbitt 2009: 155

98) Articular: without dorsomedial projection posterior to the glenoid fossa (0); with dorsomedial projection separated from glenoid fossa by a clear concave surface (1); with dorsomedial projection continuous with the glenoid fossa (2).

Clark et al. 2000; Olsen et al. 2000; Benton and Walker 2002; Sues et al. 2003; Clark et al. 2004; Nesbitt 2009: 156

- 99) Articular, ventromedially directed process: absent (0); present (1).
Nesbitt 2009: 157
- 100) Articular, glenoid of the mandible located: level with dorsal margin of the dentary (0); well ventral of the dorsal margin of the dentary (1).
Gauthier 1986; Langer and Benton 2006; Nesbitt 2009: 158
- 101) Articular, foramen on the medial side: absent (0); present and medial to the glenoid (1).
Nesbitt 2009: 159
- 102) Surangular, ridge or process on lateral surface, anterior to jaw suture: absent (0); present, strong anteroposteriorly extended ridge (1).
Butler et al. 2008; Irmis 2008: 126
- 103) Coronoid process, dorsally expanded: absent (0); present (1).
Serenio 1986; Sereno 1999; Butler 2005; Butler et al. 2008; Irmis et al. 2007; Nesbitt 2009: 161
- 104) Mandibular fenestra: anteroposterior length more than maximum depth of dentary ramus but less than half the length of the mandible (0); greater than half the length of the mandible (1); reduced, anteroposterior length less than maximum depth of dentary ramus (2).
Butler 2005; Nesbitt and Norell 2006; Nesbitt 2009: 162
- 105) Splenial, foramen in the ventral part: absent (0); present (1).
Rauhut 2003; Langer and Benton 2006; Smith et al. 2007; Nesbitt 2009: 165
- 106) Dentary teeth: present along entire length of the dentary (0); absent in the anterior portion (1); completely absent (2).
Parrish 1994; Parker 2007; Nesbitt 2009: 166
- 107) Dentition: generally homodont (0); markedly heterodont (1).
Parrish 1993; Nesbitt 2009: 167
- 108) Tooth, serrations: present as small fine knife-like serrations (0); present and enlarged and coarser (lower density) = denticles (1).
Gauthier et al. 1988; Juul 1994; Dilkes 1998; Irmis et al. 2007; Nesbitt 2009: 168
- 109) Extensive planar wear facets across multiple maxillary/dentary teeth: absent (0); present (1).
Weishampel and Witmer 1990; Irmis et al 2007; Nesbitt 2009: 169
- 110) Medial or lateral overlap of adjacent crowns in maxillary and dentary teeth: absent (0); present (1).

Sereno 1986; Butler et al. 2008; Nesbitt 2009: 170

111) Tooth, crown: not mesiodistally expanded (0); mesiodistally expanded above root in cheek teeth (1).

Sereno 1986; Irmis et al 2007; Butler et al. 2008; Nesbitt 2009: 171

112) Moderately developed lingual expansion of crown (=cingulum) on maxillary/dentary teeth: absent (0); present (1).

Sereno 1986; Butler et al. 2008; Nesbitt 2009: 172

113) Maxillary and dentary crowns, shape: apicobasally tall and blade-like (0); apicobasally short and subtriangular (1).

Sereno 1986; Butler et al. 2008; Nesbitt 2009: 173

114) Tooth, implantation: teeth fused to the bone of attachment at the base (0); free at the base of the tooth (1).

Gauthier 1984; Benton and Clark 1988; Benton 1990; Bennett 1996; Nesbitt 2009: 174

115) Pterygoid, teeth, on palatal process of the pterygoid: present (0); absent (1).

Juul 1994; Gower and Sennikov 1997; Nesbitt 2009: 175

116) Postaxial intercentra: present (0); absent (1).

Gauthier 1984; Benton and Clark 1988; Sereno 1991a; Parrish 1993; Juul 1994; Bennett 1996; Nesbitt 2009: 177

117) Atlantal articulation facet in axial intercentrum, shape: saddle-shaped (0); concave with upturned lateral borders (1).

Gauthier 1986; Langer and Benton 2006; Nesbitt 2009: 178

118) Axis, dorsal margin of the neural spine: expanded posterodorsally (0); arcs dorsally, where the anterior portion height is equivalent to the posterior height (1).

Nesbitt 2009: 179

119) Axis, neural spine: sheet-like (0); anteroposteriorly reduced and rod-like (1).

Smith et al. 2007: 145; Irmis 2008: 157

120) Anterior cervical vertebrae, prezygapophyses: transverse distance between medial margins of prezygapophyses less than mediolateral width of the neural canal (0); medial margin of prezygapophyses situated lateral to the margins of the neural canal (1).

Smith et al. 2007: 156; Irmis 2008: 163

121) Cervical vertebrae, 3-5 centrum length: shorter or the same length as the mid-dorsal (0); longer than mid-dorsal (1).

Sereno 1991; Nesbitt 2009: 181

- 122) Cervical vertebrae, deep recesses on the anterior face of the neural arch, lateral to the neural canal (=prechonos of Welles 1984): absent (0); present (1).
Nesbitt 2009: 182
- 123) Third cervical vertebra, centrum length: subequal to the axis centrum (0); longer than the axis centrum (1).
Gauthier 1986; Langer and Benton 2006; Nesbitt 2009: 183
- 124) Anterior to middle cervical vertebrae, diapophysis and parapophysis: well separated (0); nearly touching (1).
Nesbitt 2009: 184
- 125) Anterior cervical vertebrae, neural arch, posterior portion ventral to the postzygapophysis: smooth posteriorly or has a shallow fossa (0); with a deep excavation with a thin bone lamina covering the anterior extent on the posterolateral surface (1).
Langer and Benton 2006; Nesbitt 2009: 185
- 126) Epipophyses: absent in post-axial anterior cervical vertebrae (0); present in post-axial anterior cervical vertebrae (1).
Gauthier 1986; Novas 1996; Langer and Benton 2006; Nesbitt 2009: 186
- 127) Epipophyses: absent in posterior cervical vertebrae (cervicals 6-9) (0); present in posterior cervical vertebrae (cervicals 6-9) (1).
Serenio et al. 1993; Langer and Benton 2006; Nesbitt 2009: 187
- 128) Cervical vertebrae, pneumatic features (=pleurocoels) in the anterior portion of the centrum: absent (0); present as deep fossae (1); present as foramina (2). ORDERED
Holtz 1994; Rauhut 2003; Smith et al. 2007: 149; Irmis 2008: 162; Nesbitt 2009: 188
- 129) Cervical vertebrae, rimmed depression on the posterior part of the centrum: absent (0); present (1).
Gauthier 1986; Rauhut 2003; Nesbitt 2009: 189
- 130) Cervical vertebrae, middle portion of the ventral keel: dorsal to the ventralmost extent of the centrum rim (0); ventral to the centrum rims (1).
Nesbitt 2009: 190
- 131) Cervical vertebrae, distal end of neural spines: expansion absent (0); present and laterally expanded in the middle of the anteroposterior length (1); present and expanded anteriorly so that the spine table is triangular or heart-shaped in dorsal view (2).
Gauthier 1984; Juul 1994; Nesbitt 2009: 191
- 132) Posterior cervical and/or dorsal vertebrae, hyosphene-hypantrum accessory intervertebral articulations: absent (0); present (1).
Gauthier 1986; Juul 1994; Benton 1999; Rauhut 2003; Langer and Benton 2006; Weinbaum and Hungerbühler 2007; Nesbitt 2009: 195

- 133) Cervical ribs: slender and elongated (0); short and stout (1).
Gauthier 1986; Benton and Clark 1988; Juul 1994; Benton 1999; Nesbitt 2009: 196
- 134) Cervical ribs, pneumatic excavations in head: absent (0); present (1).
Smith et al. 2007: 165; Irmis 2008: 170
- 135) Dorsal vertebrae, deep fossae and/or pneumatopores ("pleurocoels"): absent (0); present in anterior dorsals (1).
Smith et al. 2007: 170; Irmis 2008: 172
- 136) Anterior dorsal vertebrae, ventral keel: absent or very poorly developed (0); pronounced (1).
Smith et al. 2007: 170; Irmis 2008: 172
- 137) Dorsal vertebrae, neural spine distal expansion: absent (0); present with a flat dorsal margin (1); present with a rounded dorsal margin (2).
Nesbitt 2009: 197
- 138) Middle dorsal vertebrae, diapophyses and parapophyses: close to the midline (0); expand on stalks (1).
Nesbitt 2009: 199
- 139) Sacral centra: separate (0); co-ossified at the ventral edge (1).
Nesbitt 2009: 200
- 140) Sacral vertebrae, prezygapophyses and complimentary postzygapophyses: separate (0); co-ossified (1).
Nesbitt 2009: 201
- 141) Primordial sacral one, sacral rib: doesn't or weakly articulates with anteriorly directed process (=preacetabular process) of the ilium (0); articulates with the anteriorly directed process of the ilium (1).
Nesbitt 2005; 2007; Nesbitt 2009: 202
- 142) Sacral vertebrae, centra articular rims: present in sacrum (0); nearly obliterated (1).
Nesbitt 2007; Nesbitt 2009: 204
- 143) Trunk vertebrae: free from the sacrum (0); incorporated into the sacrum, with their ribs/transverse processes articulating with the pelvis (1).
Serenio et al. 1993; Langer and Benton 2006; Nesbitt 2009: 205
- 144) Caudal vertebrae: free from the sacrum (0); incorporated into the sacrum, with their ribs/transverse processes articulating with the pelvis (1).
Galton 1976; Langer and Benton 2006; Nesbitt 2009: 206

- 145) Insertion of a sacral vertebra between the first and second primordial sacral vertebrae: absent (0); present (1).
Nesbitt 2009: 207
- 146) Sacral ribs: almost entirely restricted to a single sacral vertebra (0); shared between two sacral vertebrae (1).
Nesbitt 2009: 208
- 147) First primordial sacral, articular surface of sacral rib: circular (0); C- shaped in lateral view (1).
Langer and Benton 2006; Nesbitt 2009: 209
- 148) Middle caudal vertebrae, accessory laminar process on anterior face of neural spine: absent (0); present (1).
Benton and Clark 1988; Juul 1994; Benton 1999; Benton and Walker 2002; Rauhut 2003; Irmis et al. 2007; Nesbitt 2009: 210
- 149) Distal caudal vertebrae, prezygapophyses: not elongated (0); elongated more than a quarter of the adjacent centrum (1).
Gauthier 1986; Rauhut 2003; Nesbitt 2007; Nesbitt 2009: 211
- 150) Forelimb-hindlimb length ratio: more than 0.55 (0); less than 0.55 (1).
Gauthier 1984; Sereno 1991; Juul 1994; Benton 1999; Nesbitt 2009: 212
- 151) Clavicles: present and unfused (0); fused into a furcula (1); clavicles absent (2).
Gauthier 1986; Sereno 1991; Benton 1999; Benton and Walker 2002; Nesbitt 2009: 213
- 152) Interclavicle: present (0); absent (1).
Gauthier 1986; Sereno 1991; Juul 1994; Benton 1999; Nesbitt 2009: 214
- 153) Scapula, entire anterior margin: straight/convex or partially concave (0); markedly concave (1).
Gower and Sennikov 1997; Nesbitt 2009: 217
- 154) Scapula, blade height versus distal width: less than 3 times distal width (0); more than 3 times distal width (1).
Sereno 1999; Nesbitt 2009: 218
- 155) Scapulocoracoid, anterior margin: distinct notch between the two elements (0); uninterrupted edge between the two elements (1).
Parrish 1993; Benton 1999; Nesbitt 2009: 221
- 156) Coracoid: subcircular in lateral view (0); with post-glenoid process (notch ventral to glenoid) (1).
Clark et al. 2004; Nesbitt 2009: 222

157) Coracoid, post-glenoid process: short (0); elongate and expanded posteriorly only (1).

Clark et al. 2004; Nesbitt 2009: 223

158) Coracoid, posteroventral portion: smooth (0); possesses a "swollen" tuber (=biceps tuber) (1).

Nesbitt 2009: 225

159) Glenoid, orientation: posterolaterally (0); directed posteroventrally (1).

Fraser et al. 2002; Nesbitt 2009: 227

160) Humerus, apex of deltopectoral crest situated at a point corresponding to: less than 30% down the length of the humerus (0); more than 30% down the length of the humerus (1).

Bakker and Galton 1974; Benton 1990; Juul 1994; Novas 1996; Benton 1999; Nesbitt 2009: 230

161) Humerus, length: longer than or subequal to 0.6 of the length of the femur (0); shorter than 0.6 of the length of the femur (1).

Novas 1993; Langer and Benton 2006; Nesbitt 2009: 231

162) Humerus, proximal head: confined to the proximal surface (0); posteriorly expanded and hooked (1).

Nesbitt 2009: 232

163) Humerus, proximal articular surface: continuous with the deltopectoral crest (0); separated by a gap from the deltopectoral crest (1).

Nesbitt, 2009: 233

164) Humerus, ectepicondylar flange: present (0); absent (1).

Nesbitt 2009: 234

165) Humerus, distal end width: narrower or equal to 30% of humerus length (0); greater than 30% of humerus length (1).

Langer and Benton 2006; Nesbitt 2009: 235

166) Ulna, lateral tuber (=radius tuber) on the proximal portion: absent (0); present (1).

Nesbitt 2009: 237

167) Ulna, distal end in posterolateral view: rounded and convex (0); squared off where the distal surface is nearly flat (1).

Nesbitt 2009: 238

168) Ulna, distal end: anteroposteriorly compressed or oval-shaped (0); with anterior expansion (1).

Nesbitt 2009: 239

169) Radius, distal end: convex (0); shallow longitudinal groove on the posterior side (1).
Nesbitt 2009: 240

170) Radius, length: longer than 80% of humerus length (0); shorter than 80% of humerus length (1).

Langer and Benton 2006; Nesbitt 2009: 241

171) Pteroid bone: absent (0); present (1).

Bennett 1996; Nesbitt 2009: 244

172) Longest metacarpal: longest metatarsal $>.5$ (0); $<.5$ (1).

Nesbitt 2009: 245

173) Metacarpals, proximal ends: overlap (0); abut one another without overlapping (1).

Clark et al. 2000; Olsen et al. 2000; Benton and Walker 2002; Sues et al. 2003; Clark et al. 2004; Nesbitt 2009: 246

174) Manual length (measured as the average length of digits I-III) accounts for: less than 0.3 of the total length of humerus plus radius (0); more than 0.3 but less than 0.4 of the total length of humerus plus radius (1); more than 0.4 of the total length of humerus plus radius (2). ORDERED

Gauthier 1986; Langer and Benton 2006; Nesbitt 2009: 247

175) Medialmost distal carpal: subequal other distal carpals (0); significantly larger than other distal carpals (1).

Gauthier 1986; Langer and Benton 2006; Nesbitt 2009: 248

176) Distal carpal V: present (0); absent (1).

Sereno 1999; Langer and Benton 2006; Nesbitt 2009: 249

177) Extensor pits on the proximodorsal portion of metacarpals I-III: absent or shallow and symmetrical (0); deep and asymmetrical (1).

Sereno et al. 1993; Langer and Benton 2006; Nesbitt 2009: 250

178) Metacarpal I, width at the middle of the shaft accounts for: less than 0.35 of the total length of the bone (0); more than 0.35 of the total length of the bone (1).

Bakker and Galton 1974; Langer and Benton 2006; Nesbitt 2009: 251

179) Digit I with metacarpal: longer than the ungual (0); subequal or shorter than the ungual (1).

Sereno 1999; Langer and Benton 2006; Nesbitt 2009: 252

180) Manual digit I, first phalanx: is not the longest non-ungual phalanx of the manus (0); is the longest non-ungual phalanx of the manus (1).

Gauthier 1986; Langer and Benton 2006; Nesbitt 2009: 253

181) Metacarpal I, distal condyles: approximately aligned or slightly offset (0); lateral condyle strongly distally expanded relative to medial condyle (1).

Bakker and Galton 1974, Langer and Benton 2006; Irmis et al., 2007; Nesbitt 2009: 254

182) Metacarpal II: shorter than metacarpal III (0); equal to or longer than metacarpal III (1).

Gauthier 1986; Langer and Benton 2006; Irmis et al. 2007; Nesbitt 2009: 256

183) Manual digits I-III: blunt unguals on at least digits II and III (0); trenchant unguals on digits I-III (1).

Gauthier 1986; Juul 1994; Benton 1999; Irmis et al. 2007; Nesbitt 2009: 257

184) Manual digit IV: five phalanges (0); four phalanges (1); three or two phalanges (2); one phalanx (3). ORDERED

Gauthier 1986; Benton and Clark 1988; Novas 1996; Benton 1999; Irmis et al. 2007; Nesbitt 2009: 258

185) Metacarpal IV: present (0); reduced to a nubbin or absent (1).

Gauthier 1986; Nesbitt 2009: 259

186) Metacarpal IV, shaft width: about the same width than that of metacarpals I-III (0); significantly narrower than that of metacarpals I-III (1).

Sereno et al. 1993; Langer and Benton 2006; Nesbitt 2009: 261

187) Manual digit IV length: less than or equal to 50% of total forelimb length (0); more than 50% of total forelimb length (1).

Bennett 1996; Irmis et al. 2007; Nesbitt 2009: 262

188) Manual digit V: possesses one or more phalanges (0); lacks phalanges (1); absent or reduced to a tiny nubbin (2).

Bakker and Galton 1974; Langer and Benton 2006; Irmis et al. 2007; Nesbitt 2009: 263

189) Ilium, supra-acetabular crest (=supra-acetabular rim): projects laterally or ventrolaterally (0); projects ventrally (1).

Gauthier 1986; Nesbitt 2009: 264

190) Ilium, distal extent of the supra-acetabular crest (=supra-acetabular rim): near or at the articular facet for the pubis (0); ends well proximal of the facet for the pubis (1).

NEW

191) Ilium, crest dorsal to the supra-acetabular crest: absent (0); present and divides the anterior (=preacetabular) process from the posterior (=postacetabular) process (1); confluent with anterior extent of the anterior (=preacetabular) process of the ilium (2).

Nesbitt 2009: 265

192) Ilium, anterior (=preacetabular, =cranial) process: short and does not extend anterior of the acetabulum (0); long and extends anterior of the acetabulum (1).

Nesbitt 2009: 269

193) Ilium, shape of the anterior (=preacetabular, =cranial) process: blunt and tapering dorsally (0); square-shaped (1).

Yates 2007: 247; Irmis 2008: 239

194) Ilium, posterior margin of the postacetabular process in lateral view: straight or convex (0); notched or indented (1).

Smith et al. 2007: 262; Irmis 2008: 255

195) Ilium, orientation: mainly vertically orientated (0-20°) (0); ventrolaterally deflected about 45°(1).

Benton and Clark 1988; Juul 1994; Benton and Walker 2002; Nesbitt 2009: 270

196) Ilium, distinct fossa present for the attachment of the m caudifemoralis brevis: absent (0); present as an embankment on the lateral side of the posterior portion of the ilium (1); present as a deep fossa on the ventral surface of postacetabular part of the ilium (2).

Gauthier and Padian 1985; Gauthier 1986; Juul 1994; Novas 1996; Benton 1999; Hutchinson 2001; Nesbitt 2009: 271

197) Ilium, ridge connecting the posterior portion of the supra-acetabular rim to the posterior portion of the ilium: absent (0); present (1).

Langer and Benton 2006; Nesbitt 2009: 272

198) Ilium, ventral margin of the acetabulum: convex (0); straight (1); concave (2).

Bakker and Galton 1974; Gauthier and Padian 1985; Gauthier 1986; Juul 1994; Novas 1996; Benton 1999; Benton et al. 2000; Fraser et al. 2002; Langer and Benton 2006; Nesbitt 2009: 273

199) Ilium, acetabular antitrochanter: absent (0); present (1).

Sereno and Arcucci 1994; Novas 1996; Benton 1999; Fraser et al. 2002; Irmis et al. 2007; Nesbitt 2009: 274

200) Ilium, dorsal margin dorsal to the supra-acetabular rim: rounded, or blade-like (0); flat (1).

Nesbitt 2009: 275

201) Ilium, dorsal portion: height about the same or shorter than the dorsal portion of the supra-acetabular rim to the pubis-ischium contact (0); expanded dorsally, height markedly taller than the dorsal portion of the supra-acetabular rim to the pubis-ischium contact (1).

Nesbitt 2009: 276

- 202) Ilium, ischiadic peduncle orientation: mainly vertical in lateral aspect (0); well expanded posteriorly to the anterior margin of the postacetabular embayment (1).
Langer and Benton, 2006; Nesbitt 2009: 277
- 203) Pubis, length: less than 70% of femoral length (0); more than 70% or more of femoral length (1).
Novas 1996; Nesbitt 2009: 278
- 204) Pubis, orientation: anteroventral (0); rotated posteroventrally to lie alongside the ischium (opisthopic) (1).
Serenio 1986; Butler et al. 2008b; Nesbitt 2009: 279
- 205) Pubis, prepubic process: absent, anterior margin unexpanded (0); present, anterior margin expanded into a process (1).
Serenio 1986; Butler et al. 2008b; Nesbitt 2009: 280
- 206) Pubis, length: shorter or subequal to the ischium (0); longer than ischium (1).
Benton and Clark 1988; Juul 1994; Novas 1996; Benton 1999; Benton and Walker 2002; Nesbitt 2009: 282
- 207) Pubis, distal end: unexpanded (0); expanded relative to the shaft (=pubis boot) (1).
Gauthier 1986; Serenio and Novas 1992; Juul 1994; Benton 1999; Rauhut 2003; Langer and Benton 2006; Nesbitt 2007; Nesbitt 2009: 283
- 208) Pubis, expanded distal margin: mediolaterally thick and rounded (0); mediolaterally thin (1).
Gauthier 1986; Juul 1994; Benton 1999; Nesbitt 2009: 284
- 209) Pubis, expanded distal margin: shorter than 33% of the length of the shaft of the pubis (0); greater than 33% of the length of the shaft of the pubis (1).
Nesbitt and Norell 2006; Nesbitt 2007; Nesbitt 2009: 285
- 210) Proximal portion of the pubis: articular surfaces with the ilium and the ischium continuous (0); articular surfaces with the ilium and the ischium separated by a groove or gap (1).
Nesbitt 2009: 286
- 211) Ischio-pubis contact: present and extended ventrally (0); present and reduced to a thin proximal contact (1); absent (2).
Benton and Clark 1988; Novas 1996; Nesbitt 2009: 287
- 212) Pubis, pubic apron, proximal portion: similar anteroposterior thickness as the rest of the pubic apron (0); thickened process (1).
Nesbitt 2005; 2007; Nesbitt 2009: 288

213) Pubis, mediolateral width of distal portion: nearly as broad as proximal width (0); significantly narrower than proximal width (1); mediolaterally compressed and not broader than anteroposteriorly deep (2). ORDERED

Galton 1976; Novas 1996; Sereno 1999; Langer and Benton 2006; Nesbitt 2009: 289

214) Ischium, medial contact with antimere: restricted to the medial edge (0); extensive contact but the dorsal margins are separated (1); extensive contact and the dorsal margins contact each other (2).

Nesbitt 2009: 291

215) Ischium, cross-section of the distal portion: thin, plate-like (0); rounded or elliptical (1); sub-triangular (2).

Sereno 1999; Langer and Benton 2006; Irmis et al. 2007; Nesbitt 2009: 293

216) Ischium, distal portion: unexpanded (0); expanded relative to the ischial shaft (=ischial boot) (1).

Smith and Galton 1990; Holtz 1994; Hutchinson 2001; Rauhut 2003; Langer and Benton 2006; Nesbitt 2009: 294

217) Ischium, obturator process: confluent with the pubic peduncle (0); offset from the pubic peduncle by a notch (1).

Gauthier 1986; Novas 1993; Rauhut 2003; Nesbitt 2009: 295

218) Ischium, ventral margin: continuous ventral margin (0); notch present (1).

Sereno et al. 1996; Rauhut 2003; Nesbitt 2009: 296

219) Ischium, proximal articular surfaces: articular surfaces with the ilium and the pubis continuous (0); articular surfaces with the ilium and the pubis continuous but separated by a fossa (1); articular surfaces with the ilium and the pubis separated by a large concave surface (2). ORDERED

Irmis et al. 2007; Nesbitt 2009: 297

220) Ischium, groove on the dorsolateral surface of the proximal part: absent (0); present (1).

Irmis et al 2007: 75; Irmis 2008: 275

221) Ischium length: about the same length or shorter than the dorsal margin of the iliac blade (minus the anterior process) (0); markedly longer than the dorsal margin of iliac blade (minus the anterior process) (1).

Juul 1994; Nesbitt 2009: 298

222) Tibia (or fibula)-femur length: femur longer or about the same length as the tibia/fibula (0); tibia longer (1).

Gauthier 1986; Sereno 1991a; Juul 1994; Benton 1999; Irmis et al. 2007; Nesbitt 2009: 299

223) Femur, proximal portion, anteromedial tuber: absent (0); small and rounded (1); offset medially (or posteriorly) relative to the posteromedial tuber (2); large and "hooked" posteriorly (3).

Gauthier 1986; Benton 1999; Clark et al. 2000; Olsen et al. 2000; Benton and Walker 2002; Sues et al. 2003; Clark et al. 2004; Nesbitt 2009: 300

224) Femur, proximal portion, posteromedial tuber: present and small (0); present and largest of the proximal tubera (1); absent (2).

Novas 1996; Nesbitt 2005; Irmis et al. 2007; Nesbitt 2009: 301

225) Femur, proximal portion, anterolateral tuber: present as an expansion (0); absent, the anterolateral face is flat (1).

Sereno and Arcucci 1994; Irmis et al. 2007; Nesbitt 2009: 302

226) Femur, medial articular surface of the head in dorsal view: rounded (0); flat/straight (1).

Nesbitt 2009: 303

227) Femur, ventral to the proximal head: smooth transition from the femoral shaft to the head (0); notch (1); concave emargination (2).

Sereno and Arcucci 1994; Novas 1996; Nesbitt 2009: 304

228) Femur, femoral head orientation (angle with respect to the transverse axis through the femoral condyles Parrish 1986): anterior ($60 - 90^\circ$) (0); anteromedial ($20 - 60^\circ$) (1); medial ($0 - 20^\circ$) (2).

Benton and Clark 1988; Hutchinson 2001a; Nesbitt 2009: 305

229) Femur, femoral head in medial and lateral views: rounded (0); hook-shaped (1).

Sereno and Arcucci 1994; Irmis et al. 2007; Nesbitt 2009: 306

230) Femur, dorsolateral margin of the proximal portion: smooth (0); sharp ridge (=dorsolateral trochanter of some) (1); rounded ridge (=dorsolateral trochanter of some) (2).

Nesbitt 2009: 307

231) Femur, anterior trochanter (=M. iliofemoralis cranialis insertion): absent (0); present and forms a steep margin with the shaft but is completely connected to the shaft (1); present and forms a steep margin with the shaft and separated from the shaft by a marked cleft (2). ORDERED

Bakker and Galton 1974; Gauthier 1986; Novas 1992; Juul 1994; Novas 1996; Benton 1999; Langer and Benton 2006; Nesbitt 2009: 308

232) Femur, medial articular facet of the proximal portion: rounded (0); straight (1).

Nesbitt 2009: 309

- 233) Femur, anterolateral side of the femoral head: smooth, featureless (0); ventral emargination present (1).
Serenio and Arcucci 1994; Irmis et al. 2007; Nesbitt 2009: 310
- 234) Femur, anterior trochanter shelf proximal to the fourth trochanter (insertion site for the *M. iliofemoralis externus*): absent (0); present (1).
Gauthier 1986; Rowe and Gauthier 1990; Novas 1992; 1996; Langer and Benton 2006; Nesbitt 2009: 311
- 235) Femur, posterolateral portion (= fossa trochanterica, = posterolateral depression, = facies antitrochanterica articularis) of the head: level with the greater trochanter (0); ventrally descended (1).
Novas 1996; Nesbitt 2009: 313
- 236) Femur, proximal surface: rounded and smooth (0); transverse groove that is straight (1); transverse groove that is curved (2). ORDERED
Ezcurra 2006; Nesbitt 2009: 314
- 237) Femur, fourth trochanter shape: mound-like and rounded (0); a sharp flange (1); absent, no distinct ridge for the attachment of the *M. caudifemoralis* (2).
Gauthier 1986; Benton and Clark 1988; Sereno 1991; Juul 1994; Bennett 1996; Benton 1999; Nesbitt 2009: 316
- 238) Femur, fourth trochanter: symmetrical, with distal and proximal margins forming similar low-angle slopes to the shaft (0); asymmetrical, with distal margin forming a steeper angle to the shaft (1).
Langer and Benton 2006; Nesbitt 2009: 317
- 239) Femur, angle between the lateral condyle and the crista tibiofibularis in distal view: obtuse (0); about a right angle (1).
Parker and Irmis 2005; Nesbitt 2009: 319
- 240) Femur, infrapopliteal ridge between medial femoral distal condyle and crista tibiofibularis: absent (0); present (1).
Smith et al. 2007: 304; Irmis 2008: 306
- 241) Femur, medial condyle of the distal portion: tapers to a point on the medial portion in distal view (0); smoothly rounded in distal view (1).
Nesbitt 2009: 320
- 242) Femur, surface between the lateral condyle and crista tibiofibularis on the distal surface: smooth (0); deep groove (1).
Nesbitt 2009: 322
- 243) Femur, bone wall thickness at or near mid-shaft: thickness/diameter >0.3 (0); thin; thickness/diameter <0.3, > 0.2 (1); very thin; thickness/diameter <0.2 (2).

Nesbitt 2009: 323

244) Femur, distal condyles of the femur divided posteriorly: less than 1/4 the length of the shaft (0); between 1/4 and 1/3 the length of the shaft (1).

Nesbitt 2009: 324

245) Femur, anterior surface of the distal portion: smooth (0); distinct scar orientated mediolaterally (1).

Nesbitt et al. 2009; Nesbitt 2009: 325

246) Femur, crista tibiofibularis (fibular condyle of Sereno & Arcucci 1994): smaller or equal in size to the medial condyle (0); larger than the medial condyle (1).

Nesbitt et al. 2009; Nesbitt 2009: 326

247) Femur, anteromedial corner of the distal end: rounded (0); squared off near 90° or acute >90° (1).

Nesbitt et al. 2009; Nesbitt 2009: 327

248) Tibia, proximal portion, cnemial crest: absent or just a slight bump (0); present and straight (1); present arcs anterolaterally (2). ORDERED

Benton and Clark 1988; Juul 1994; Novas 1996; Benton 1999; Irmis et al. 2007; Nesbitt 2009: 328

249) Tibia, proximal surface: flat or convex (0); concave, the posterior condyles of the tibia are separated from the cnemial crest by a concave surface (the cnemial process is proximally expanded) (1).

Nesbitt 2009: 329

250) Tibia, proximal surface of the lateral condyle: convex or flat (0); depressed (1).

Nesbitt 2009: 330

251) Tibia, lateral (fibular) condyle of the proximal portion: offset anteriorly from the medial condyle (0); level with the medial condyle at its posterior border (1).

Langer and Benton 2006; Irmis et al. 2007; Nesbitt 2009: 331

252) Tibia, lateral margin of the lateral condyle of the proximal portion: rounded (0); squared-off (1).

Nesbitt 2009: 332

253) Tibia, lateral side of the proximal portion: smooth (0); dorsoventrally oriented crest present (=fibular crest) and extends from the proximal articular surface (1);

dorsoventrally oriented crest present and clearly separated from the proximal articular surface (2). ORDERED

Gauthier 1986; Rauhut 2003; Nesbitt 2009: 333

254) Tibia, posterolateral flange of the distal portion: absent (0); present and nearly contacts or contacts fibula (1); present and extends well posterior to the fibula (2).

ORDERED

Novas 1992; Juul 1994; Benton 1999; Langer and Benton 2006; Irmis et al. 2007; Nesbitt 2009: 334

255) Tibia, posterolateral margin of the distal end: straight or convex (0); concave (1).
Irmis et al., 2007; Nesbitt 2009: 335

256) Tibia, posterior face of the distal end: rounded surface (0); distinct proximodistally oriented ridge present (1).

Nesbitt 2009: 336

257) Tibia, posterior side of the distal portion: smooth and featureless (0); dorsoventrally oriented groove or gap (1).

Nesbitt 2009: 337

258) Tibia, lateral side of the distal portion: smooth/rounded (0); proximodistally oriented groove (1).

Novas 1996; Nesbitt 2009: 338

259) Fibula, attachment site for the M. iliofibularis, location: near the proximal portion (0); near the mid point between the proximal and distal ends (1).

Sereno 1991; Nesbitt 2009: 340

260) Fibula, proximal end in proximal view: rounded or slightly elliptical (0); mediolaterally compressed (1).

Nesbitt 2009: 341

261) Fibula, anterior edge of the proximal portion: rounded (0); tapers to a point and arched anteromedially (1).

Nesbitt 2009: 342

262) Fibula, proximal portion in lateral view: symmetrical or nearly symmetrical (0); posterior part expanded posteriorly (1).

Nesbitt 2009: 343

263) Fibula, medial face of the distal portion: smooth (0); banked with an articular facet that articulates with the astragalus (1).

Nesbitt 2009: 344

264) Fibula, ridge on the medial side of the proximal end and oriented anterodistally: absent (0); present (1).

Smith et al. 2007: 315; Irmis 2008: 328

265) Fibula, deep groove on the medial side of the proximal portion: absent (0); present, medial side of fibula bears distinct deep fossa (1).

Smith et al. 2007: 314; Irmis 2008: 327

266) Fibula, distal end in lateral view: angled anterodorsally (asymmetrical) (0); rounded or flat (symmetrical) (1).

Nesbitt 2009: 345

267) Distal tarsal 4, transverse width: broader than distal tarsal 3 (0); subequal to distal tarsal 3 (1).

Sereno 1991; Juul 1994; Benton 1999; Nesbitt 2009: 347

268) Distal tarsal 4, size of articular facet for metatarsal V: more than half of lateral surface of distal tarsal 4 (0); less than half of lateral surface of distal tarsal 4 (1).

Sereno 1991; Novas 1996; Benton 1999; Nesbitt 2009: 348

269) Distal tarsal 4, posterior prong: blunt (0); pointed (1).

Langer and Benton 2006; Nesbitt 2009: 350

270) Distal tarsal 4, medial side: without a distinct medial process present in the anteroposterior middle of the element (0); with a distinct medial process present in the anteroposterior middle of the element (1).

Nesbitt 2009: 351

271) Distal tarsal 4, proximal surface: flat (0); distinct, proximally raised region on the posterior portion (=heel of Sereno and Arcucci 1994) (1).

Nesbitt 2009: 353

272) Astragalus, dorsally expanded process on the posterolateral portion of the tibial facet: absent or poorly expanded (0); expanded into a distinct, raised process (=posterior ascending process of Sereno and Arcucci 1994a) (1).

Sereno and Arcucci 1994; Nesbitt 2009: 355

273) Astragalus, anterior ascending flange (anterior process): absent (0); present and less than the height of the dorsoventral height of the posterior side of the astragalus (1); present and greater than the height of the dorsoventral height of the posterior side astragalus (2). ORDERED

Gauthier 1986; Novas 1992; 1996; Benton 1999; Rauhut 2003; Nesbitt 2009: 356

274) Astragalus, anteroposterior breadth of the astragalar ascending process: wedge-shaped/blocky (0); plate-like/laminar (1).

Smith et al. 2007: 323; Irmis 2008: 335

275) Astragalus, anterior hollow: shallow depression (0); reduced to a foramen or absent (1).

Nesbitt 2009: 357

- 276) Articular facet for the astragalus of the calcaneum lies: completely medial to the fibular facet (0); partially ventral to the fibular facet (1).
Parrish 1993; Nesbitt 2009: 358
- 277) Astragalus, proximal surface: lacks a marked rimmed and elliptical fossa posterior to the anterior ascending process (0); possesses a marked rimmed and elliptical fossa posterior to the anterior ascending process (1).
Langer and Benton 2006; Nesbitt 2009: 359
- 278) Astragalus, anteromedial corner shape: obtuse (0); acute (1).
Bonaparte 1976; Novas 1989; Sereno 1991; Juul 1994; Novas 1996; Benton 1999; Nesbitt 2009: 361
- 279) Astragalus, proximal articular facet for fibula occupies: more than 0.3 of the transverse width (0); less than 0.3 of the transverse width (1).
Langer and Benton 2006; Nesbitt 2009: 362
- 280) Astragalus, posterior groove: present (0); absent (1).
Sereno 1991; Nesbitt 2009: 363
- 281) Astragalus, tibial facet: concave or flat (0); divided into posteromedial and anterolateral basins (1).
Sereno 1991; Parrish 1993; Juul 1994; Benton 1999; Nesbitt 2009: 366
- 282) Astragalus-calcaneum, ventral articular surface: flat or slightly convex (0); concavoconvex with concavity on calcaneum (1); concavoconvex with concavity on astragalus (2).
Sereno 1991; Nesbitt 2009: 368
- 283) Astragalus-calcaneum, articulation: free (0); co-ossified (1).
Sereno and Arcucci 1994; Irmis et al. 2007; Nesbitt 2009: 370
- 284) Calcaneum, ventral articular surface for distal tarsal 4 and the distal end of the tuber: continuous (0); separated by a clear gap (1); separated by a gap with a ventral fossa (2).
Nesbitt 2009: 371
- 285) Calcaneum, articular facets for the fibula and astragalus: connected by a continuous surface (0); separated (1).
Nesbitt 2009: 372
- 286) Calcaneum, calcaneal tuber: present (0); absent (1).
Gauthier 1986; Sereno 1991; Juul 1994; Benton 1999; Nesbitt 2009: 373
- 287) Calcaneum, calcaneal tuber, distal end: rounded and unexpanded (0); flared, dorsally and ventrally (1).

Sereno 1991; Nesbitt 2009: 374

288) Calcaneum, calcaneal tuber, distal end: without dorsoventrally aligned median depression (0); with dorsoventrally aligned median depression (1).

Parrish 1993; Benton 1999; Nesbitt 2009: 375

289) Calcaneum, calcaneal tuber, shaft proportions at the mid-shaft of the tuber: taller than broad (0); about the same or broader than tall (1); just short of twice the mediolateral width of the fibular facet (2).

Sereno 1991; Parrish 1993; Juul 1994; Benton 1999; Nesbitt 2009: 376

290) Calcaneum, articular surface for the fibula: convex (0); convex and hemicylindrical shaped (1); concave (2).

Sereno 1991; Parrish 1993; Juul 1994; Novas 1996; Gower 1996; Benton 1999; Nesbitt 2009: 378

291) Calcaneum, shape: proximodistally compressed with a short posterior projection and medial process (0); transversely compressed, with the reduction of these projections (1).

Langer and Benton 2006; Nesbitt 2009: 379

292) Calcaneum, articular surfaces for fibula and distal tarsal IV: separated by a non-articular surface (0); continuous (1).

Sereno 1991; Juul 1994; Benton 1999; Nesbitt 2009: 380

293) Metatarsus, configuration: metatarsals diverging from ankle (0); compact metatarsus, with metatarsals II-IV tightly bunched (at least half of the length) (1).

Sereno 1991; Juul 1994; Benton 1999; Nesbitt 2009: 382

294) Longest metatarsal: shorter than 50% of tibial length (0); longer than 50% of tibial length (1).

Sereno 1991; Juul 1994; Benton 1999; Nesbitt 2009: 383

295) Metatarsals, midshaft diameters: I and V subequal or greater than II-IV (0); I and V less than II-IV (1).

Sereno 1991; Juul 1994; Novas 1996; Benton 1999; Nesbitt 2009: 384

296) Metatarsal I: reaches the proximal surface of metatarsal II (0); does not reach the proximal surface of metatarsal II and attaches onto the medial side of metatarsal II (1).

Gauthier 1986; Rauhut 2003; Nesbitt 2009: 385

297) Metatarsal I, length, relative to length of metatarsal III: 0-84% (0); 85% or more (1).

Sereno 1991; Benton 1999; Nesbitt 2009: 387

298) Metatarsal III, proximal end: does not back to the ventral side of metatarsals II and IV (0); backs metatarsals II and IV posteroventrally, resulting in a T-shaped proximal profile (1).

Carrano et al. 2002; Tykoski 2005; Nesbitt 2009: 389

299) Metatarsal III: longer than metatarsal II (0); subequal to metatarsal II (1).
Nesbitt 2009: 390

300) Metatarsal III, outline of the proximal articular surface: rectangular (0); hourglass-shaped (1).
Smith et al. 2007: 335; Irmis 2008: 369

301) Metatarsal IV, distal articulation surface: broader than deep to as broad as deep (0); deeper than broad (1).
Serenio 1999; Langer and Benton 2006; Nesbitt 2009: 391

302) Metatarsal IV, proximal portion, possesses an elongated lateral expansion that overlaps the anterior surface of metatarsal V: absent (0); present (1).
Serenio 1999; Langer and Benton 2006; Nesbitt 2009: 392

303) Metatarsal IV length: longer than metatarsal II (0); subequal or shorter than to metatarsal II (1).
Gauthier 1986; Nesbitt 2009: 395

304) Metatarsal V, dorsal prominence separated from the proximal surface by a concave gap: absent (0); present (1).
Nesbitt 2009: 397

305) Metatarsal V, 'hooked' proximal end: present (0); absent, and articular face for distal tarsal 4 subparallel to shaft axis (1).
Serenio 1991; Juul 1994; Benton 1999; Nesbitt 2009: 398

306) Metatarsal V, phalanges: present and has "fully" developed first phalanx (0); present and has a "poorly" developed first phalanx (1); without phalanges and tapers to a point (2).
Gauthier 1984; Parrish 1993; Nesbitt 2009: 399

307) Pedal unguals: weakly mediolaterally compressed, rounded or triangular in cross-section (0); dorsolaterally compressed (1); strongly mediolaterally compressed, with a sharp dorsal keel (2).
Serenio 1991; Nesbitt 2009: 400

308) Osteoderms, dorsal to the vertebral column: absent (0); present (1).
Gauthier 1984; Benton and Clark 1988; Serenio 1991; Juul 1994; Bennett 1996; Dilkes 1998; Benton 1999; Nesbitt 2009: 401

309) Osteoderms, presacral, dorsal, anterior edge: straight or rounded (0); with distinct anterior process (1).

Pisanosaurus mertii

????????????????1?1?01??0??
????????0?????????000001?01200?111111?1?????0?0??0000??00????????????????????
??0????????????????????2????????????
????????001??0000?0000010001011100?1?????01010?111??0?01???2111??0?01??????0
???????

Heterodontosaurus tucki

00010000001110110000100000000100000000011010002000003001000101?0121?11000011
1??0?001101111?0B000100120B111001111110000000100000?000211?0011100001?111
?0?111001101000101100010000112000?021000002100011110??01??100002011?0??????2
0?010110010?0000200001101??0110??111000?1?10?1?1?1?01?????11100?00101?1200
??????2

Lesothosaurus dianosticus

00010?0?30000011010010000000010000000001101000000000300001010100121010000??
1??10??00110111110000010112000101101111??000001000000??0001??0?111?0??1??11
0??1100?1000?01010??000?00??000000210?0102100011110??01??100002111100021012
0001011?0100000020000020101?111?00????001?100111??0?01???2111100000101???00
???????

Scutellosaurus lawleri

??0??0?????????10??01??000????????????????00??10??2????????00??????0??????0?????
1??????0?1?????110B0????1????01011011?10??00?00?0?000?00?00?0?0??00?00?11?
?0?000001101000??????0?????????????0?21000102?100111?????1?0?0?????1111000?1?12
000?0110010000002000002010?01?10001?????010100111?????01???21110?????0??????01
???000?

Saturnalia tupiniquim

?????????????????0????0?????????11?????????1?????????????????????1?????????0??
?????????1?????????0?????????001001001?1????0??0??100001??0000000000001001??10
00?111000111??010?????????????????0020000101100010011001100121002110100021021
00111110011?000020000111101011100111110010101111??0?01???2011110000011101?00
???????

Plateosaurus engelhardti

01001010200101010200001001000100111100000101001000000301000010100121010000001
101?20?0111?11001010001100010010110011111000010011000010010000000010010000110
00?1110011110001010101011111200000020000002100010011001100121002110100021021
0001111001100000200000111010111000111110010101111??0?01???2011010000011101100
???????

Efraasia minor

0?001?1010010101?20000?000000100??11000001?1001????00??1?000????0121010000001
1??1???011?01??000000?1?000?001001001?11??010?001100?01000000000000001001?110
?0?1110011110001010?01011?111?000?0020000002100010010??1100121002110100021021
000111100110000020000011101011100011111001010?111??0?01???2011010000011101100
??????1

Herrerasaurus ischigualastensis

20010?0010010100010000000000?0000100000?10100000000030010001?1?012111000000?
1??1????001101100??00000?100?000000001111000?01001100101??0020000000001011?11?
????1110110100000112011001101301010020000002100010011101101120002010101021021
00110110011?0000200100101010111001111110010101111??0?01???2011110000011101100
???????

Staurikosaurus pricei

??
?????????????????00000?00?00?000000001?1?????01?00?????000000000?00101?????
???002000000210001001110110111?00?011?00021011
0011111001??00002001001000101110001???
????????

Chindesaurus bryansmalli

??
??
??
??
0011011000?000020011010001?????????????????0101?1?1????????????????????????????????
????????

Eoraptor lunensis

00010?00100112000100000100000?0011111000?10100?0000013001000101?012?1?0?00???
?????????001?011000?00000?????000?00?0101?????001?0??0?0000200000?000?0?1?110
?0?11110110100010111??1001110??1010020000112?00110011??10011000??11??0??1?11
0?0??100??00020010?1000101?10??11111??10?0??1??0?0?????2?11110000?1?1?1?00
???????

Tawa hallae

1110000000111?0001000?0000000100??110000010100000001?30000?01?1001211?000000?
11?1001001?011000000000?00?000000001?111?011111111010100??000000?000?011?111
????11101101000001120010011012010101200001120001100?110?101?1??2??1200022011
0001210001110000200110100010111000111110010101111??0?01??211110000010101200
???????

Coelophysys bauri

1110111110111?0002000101100001?010111000010100100001130010?010100121111000011
1??00?0011011000?00000?100?0000000011111001111111110010000001000111010111111
?0?111101101000101121110011113010111211102121111100111011?11111021?1200021021
001121001111000021011111010111011111010010100111??1?01??2111110100101012?0
????0??

"Syntarsus" kayentakatae

1110111110111?000200010110000?00??1110?0010100100000130020?0??????0??000011
1??1??001101100?00??1001000000001?1?10011111111100?0?00??1??01111??11111
?10111101?01??0?01????1?????12010?1?2?1102121??1100111011?1?111?21?020002?021
0011210011110000210111111010110?111?101001010?111??1??1????111110?00101?????
???????

Liliensternus liliensterni

?????????????????000?000??1100?0?????????????????????0?????01?3?020??1110?????????????
????????????1?????000?0?????00100000000111??011??11010001??010?0?00??10??1??1?
?101111011010001011??1?1????????????1121110212001110011101101111??21?0200021012
00012100011?00002101111110101110001?????010100111??1??1??21111??000101?????
????????

Zupaysaurus rougieri

?????????????????0012000?0110100????11110100100?000000113010000????0?211?00000??
????????????11011?0??000?0?10??000?00?01?????0?????????????????????????????????
???
????????????????????????????????????11101?????0?1?????010100111??0??????2?????????????
????????

Dilophosaurus wetherelli

11101?11100?1?001100??00101001?0??11110??101000??00113000000????0121110001011
10??2??001111?00000001001?01000000001111000011111200010?0100000011101??1?111
?1011110010100010112??10011112010111211002121011100?110?1011111121?0200021?12
0001210001110?002101112110101110?1111010010100111??0?01???211111000010101200
??????1

Cryolophosaurus ellioti

??????????????01?00??1??0??0??1111101100??000000?3000?001?10?1?????00101?
??0??????1111?????010?10????0??0?01?1?????????12?001000100?????1??0??????
??????0??1????????????????????????????02?21?11??0????1??111??????2000210?2
00112100011?0?00?????1??0????????1?????01?10?1????1??1??211????????????????
??????1

Ceratosaurus nasicornis

20001011000100000100010000001001111110010100120000130000?01?100121110000011
11010??001111100??00000?10010000000011010010111111200010101011??01111?110?101
11011?????10??011??10??1?010?01211?0212??111000??110??111?21?0200021002
00010100111?00002100012110?01100100?????02110?111??1??????1110110100101?????
???????

Piatnitzkysaurus floresi

??????????????00?1000?00001001????????00????????????????????01211100?1111
1??2?1??1??1????????????????00000001?1?011?0111120001??11001?0011111??1??1?
?1011110010100?????????????????0?21100202111?00?1101??1111?121?0200022002
0001?100011?00002101112110100110101?10100?1????????????????2??1?????1???????
???????

Allosaurus fragilis

210010112001011011?000100210010111111100101000000001300000011100121110001111
1??02??001111100000001001001000000001111011101011120001011100000011111111101
0101111011010001011211101111?1??101211002021011100110111021111121?0200022002
0001010001110000210111211010111010111010021100111??0?01???2111011000110101200
??????1

Velociraptor mongoliensis

0100101110010010111000001010010011111100101001000000310000011100121?10011111
11?????001101100000000?100100000000111??11?????????10?01?01001111110?11101
?1111100110100000012111000111?1??10121100202101110111011?20010020102010220?2
00010100011100002101?12110?01?0010?11??02110?111??1?01????111011000010101200
??????1

Apomorphies

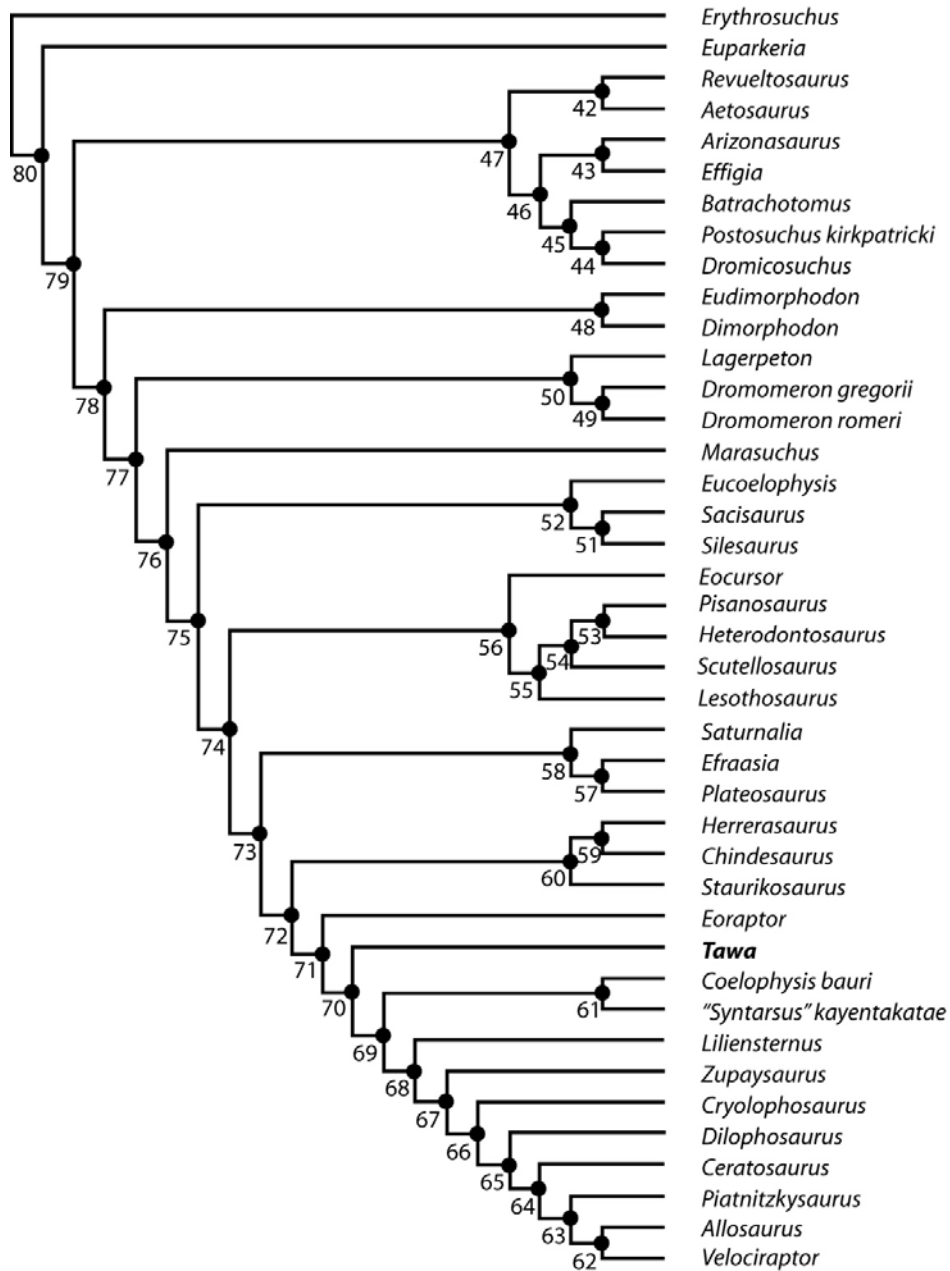


Figure S8. The relationships of *Tawa hallae*. Most parsimonious tree 2 (of 3) with a tree length of 872 steps (CI = .427; RI = .7100). Numbers refer to nodes in the apomorphy list.

Apomorphy List. Parentheses next to character number indicate whether the apomorphy in question has an unambiguous (U) optimization, or is optimized as an apomorphy under ACCTRAN (A), or DELTRAN (D), optimization.

Branch	Character	CI	Change
node_80 --> node_79	4 (A)	0.200	1 → 0
	9 (U)	0.308	0 → 1
	16 (A)	0.250	0 → 1
	22 (A)	0.167	0 → 1
	23 (A)	0.167	0 → 1
	30 (U)	0.500	0 → 1
	66 (U)	0.333	0 → 1
	67 (U)	0.500	1 → 2
	68 (U)	0.500	0 → 1
	77 (A)	0.667	0 → 1
	80 (U)	0.500	0 → 1
	87 (U)	1.000	0 → 1
	88 (A)	0.500	0 → 1
	91 (U)	1.000	0 → 1
	116 (U)	0.500	0 → 1
	156 (A)	0.250	0 → 1
	158 (U)	0.333	0 → 1
	166 (U)	0.333	0 → 1
	172 (U)	0.500	0 → 1
	178 (U)	0.333	1 → 0
	220 (A)	0.143	1 → 0
	223 (U)	1.000	0 → 1
	224 (A)	0.400	1 → 0
	241 (A)	0.250	0 → 1
	262 (U)	0.200	0 → 1
	271 (A)	0.333	0 → 1
	281 (U)	0.500	0 → 1
	282 (A)	1.000	0 → 1
	284 (U)	1.000	0 → 1
290 (A)	0.667	0 → 1	
292 (U)	1.000	0 → 1	
node_79 --> node_47	4 (D)	0.200	1 → 0
	17 (A)	0.143	0 → 1
	41 (A)	0.167	0 → 1
	57 (U)	0.273	0 → 2
	69 (U)	0.500	0 → 1
	77 (A)	0.667	1 → 2
	79 (A)	0.333	0 → 1
	92 (A)	0.333	0 → 1
	101 (U)	0.250	0 → 1

	156 (D)	0.250	0	→1
	167 (U)	0.500	0	→1
	169 (A)	0.500	0	→1
	250 (U)	1.000	0	→1
	257 (U)	1.000	0	→1
	271 (D)	0.333	0	→1
	282 (D)	1.000	0	→1
	285 (U)	1.000	0	→1
	287 (U)	1.000	0	→1
	290 (D)	0.667	0	→1
	299 (A)	0.500	0	→1
	307 (A)	0.500	0	→2
	308 (A)	0.250	0	→1
	312 (A)	1.000	0	→1
node_47 --> node_42	16 (D)	0.250	0	→1
	19 (U)	0.333	0	→1
	26 (U)	0.400	0	→2
	28 (U)	0.500	0	→1
	46 (U)	1.000	0	→1
	50 (U)	0.500	0	→1
	51 (U)	0.500	0	→1
	54 (U)	0.750	0	→2
	88 (A)	0.500	1	→0
	126 (A)	0.500	0	→1
	131 (A)	0.667	0	→2
	137 (A)	0.333	0	→1
	138 (A)	0.200	0	→1
	169 (D)	0.500	0	→1
	170 (U)	0.200	0	→1
	224 (A)	0.400	0	→1
	241 (A)	0.250	1	→0
	260 (A)	0.250	1	→0
	289 (U)	0.667	1	→2
	308 (D)	0.250	0	→1
	310 (U)	1.000	1	→0
	311 (U)	1.000	0	→1
	312 (U)	1.000	1	→2
	313 (U)	1.000	0	→1
	314 (U)	1.000	0	→1
	315 (U)	0.667	0	→2
node_47 --> node_46	14 (A)	0.375	0	→1
	16 (A)	0.250	1	→0
	79 (U)	0.333	0	→1
	83 (U)	1.000	0	→1
	98 (A)	0.667	0	→1
	99 (A)	0.200	0	→1

	132 (U)	0.333	0	→1
	141 (A)	0.500	0	→1
	145 (A)	0.200	0	→1
	155 (A)	0.500	0	→1
	168 (A)	1.000	0	→1
	191 (U)	1.000	0	→1
	195 (A)	0.333	0	→1
	203 (A)	0.500	0	→1
	206 (U)	0.333	0	→1
	207 (U)	0.333	0	→1
	211 (A)	0.667	0	→1
	214 (U)	0.400	0	→1
	215 (A)	0.333	0	→1
	216 (A)	0.250	0	→1
	220 (A)	0.143	0	→1
	221 (U)	0.500	0	→1
	224 (D)	0.400	1	→0
	236 (A)	0.222	0	→1
	239 (U)	1.000	0	→1
	276 (A)	1.000	0	→1
	299 (D)	0.500	0	→1
	301 (A)	0.250	0	→1
	303 (U)	0.250	0	→1
	309 (A)	1.000	0	→1
node_46 --> node_43	2 (A)	0.200	0	→1
	3 (A)	0.200	0	→1
	7 (U)	0.250	0	→1
	9 (A)	0.308	1	→4
	14 (A)	0.375	1	→2
	22 (D)	0.167	0	→1
	23 (D)	0.167	0	→1
	77 (A)	0.667	2	→0
	92 (A)	0.333	1	→0
	133 (A)	0.333	1	→0
	139 (A)	0.200	0	→1
	140 (U)	1.000	0	→1
	141 (D)	0.500	0	→1
	145 (D)	0.200	0	→1
	149 (A)	0.250	0	→1
	150 (A)	0.200	0	→1
	164 (A)	0.250	0	→1
	169 (A)	0.500	1	→0
	198 (U)	0.500	0	→2
	208 (U)	0.333	0	→1
	211 (U)	0.667	1	→2
	212 (U)	0.500	0	→1

	213 (U)	0.333	0	→1
	215 (D)	0.333	0	→1
	236 (D)	0.222	0	→1
	243 (U)	0.400	0	→1
	253 (A)	0.333	0	→1
	266 (A)	0.200	0	→1
	307 (A)	0.500	2	→1
	308 (A)	0.250	1	→0
node_46 --> node_45	1 (A)	0.222	0	→2
	14 (D)	0.375	0	→1
	29 (U)	1.000	0	→1
	31 (U)	1.000	0	→1
	32 (A)	0.333	0	→1
	34 (A)	0.167	0	→1
	37 (A)	0.200	0	→1
	40 (U)	1.000	0	→1
	41 (D)	0.167	0	→1
	45 (U)	1.000	0	→1
	48 (U)	0.500	0	→1
	49 (U)	1.000	0	→1
	64 (U)	1.000	0	→1
	72 (U)	1.000	0	→1
	73 (U)	0.500	0	→1
	82 (A)	0.500	0	→1
	84 (A)	0.500	0	→1
	88 (D)	0.500	0	→1
	89 (A)	0.333	0	→1
	98 (D)	0.667	0	→1
	99 (D)	0.200	0	→1
	148 (A)	0.333	0	→1
	168 (D)	1.000	0	→1
	195 (D)	0.333	0	→1
	211 (D)	0.667	0	→1
	216 (D)	0.250	0	→1
	241 (D)	0.250	0	→1
	259 (A)	0.500	0	→1
	276 (D)	1.000	0	→1
	284 (A)	1.000	1	→2
	304 (U)	0.500	0	→1
	308 (D)	0.250	0	→1
	309 (D)	1.000	0	→1
	312 (D)	1.000	0	→1
node_45 --> node_44	16 (U)	0.250	0	→1
	22 (A)	0.167	1	→0
	23 (A)	0.167	1	→0
	26 (U)	0.400	0	→1

	43 (U)	0.500	0	→1
	50 (U)	0.500	0	→1
	54 (U)	0.750	0	→1
	55 (U)	0.333	0	→1
	58 (U)	1.000	0	→1
	76 (A)	0.250	0	→1
	90 (U)	0.500	0	→1
	96 (A)	0.500	0	→2
	141 (A)	0.500	1	→0
	145 (A)	0.200	1	→0
	151 (A)	1.000	0	→2
	155 (D)	0.500	0	→1
	159 (U)	0.250	0	→1
	162 (U)	1.000	0	→1
	192 (A)	0.200	0	→1
	236 (A)	0.222	1	→0
	263 (U)	1.000	0	→1
	263 (D)	1.000	0	→1
	284 (D)	1.000	1	→2
	288 (U)	1.000	0	→1
	307 (A)	0.500	2	→0
node_79 --> node_78	42 (A)	0.333	0	→1
	53 (U)	0.333	1	→0
	61 (A)	1.000	0	→1
	63 (A)	1.000	0	→1
	65 (A)	0.500	1	→0
	76 (A)	0.250	0	→1
	94 (A)	0.333	0	→1
	108 (A)	0.250	0	→1
	113 (A)	0.500	0	→1
	118 (A)	0.250	0	→1
	154 (A)	0.333	0	→1
	163 (A)	0.167	0	→1
	164 (U)	0.250	0	→1
	183 (U)	0.500	0	→1
	199 (A)	0.143	0	→1
	220 (D)	0.143	1	→0
	222 (U)	0.167	0	→1
	241 (D)	0.250	0	→1
	243 (A)	0.400	0	→1
	266 (A)	0.200	0	→1
	267 (U)	1.000	0	→1
	268 (U)	1.000	0	→1
	275 (U)	1.000	0	→1
	278 (U)	1.000	0	→1
	280 (U)	0.500	0	→1

	283 (A)	0.143	0	→1
	286 (U)	0.500	0	→1
	290 (A)	0.667	1	→2
	293 (U)	0.500	0	→1
	315 (U)	0.667	0	→1
node_78 --> node_48	1 (A)	0.222	0	→1
	2 (U)	0.200	0	→1
	4 (D)	0.200	1	→0
	7 (A)	0.250	0	→1
	11 (U)	0.200	0	→1
	22 (D)	0.167	0	→1
	23 (D)	0.167	0	→1
	85 (U)	1.000	0	→1
	102 (U)	0.250	1	→0
	107 (U)	0.333	0	→1
	115 (A)	0.333	1	→0
	121 (U)	0.143	0	→1
	123 (A)	0.500	0	→1
	149 (U)	0.250	0	→1
	157 (U)	0.333	0	→1
	163 (D)	0.167	0	→1
	171 (U)	1.000	0	→1
	187 (U)	1.000	0	→1
	188 (A)	0.500	0	→1
	192 (U)	0.200	0	→1
	237 (A)	0.500	0	→2
	243 (A)	0.400	1	→2
	271 (A)	0.333	1	→0
	283 (D)	0.143	0	→1
	297 (U)	1.000	0	→1
	301 (A)	0.250	0	→1
	303 (A)	0.250	0	→1
	304 (U)	0.500	0	→1
node_78 --> node_77	4 (A)	0.200	0	→1
	22 (A)	0.167	1	→0
	23 (A)	0.167	1	→0
	54 (A)	0.750	0	→1
	100 (A)	0.250	0	→1
	111 (A)	0.250	0	→1
	133 (A)	0.333	1	→0
	152 (A)	1.000	0	→1
	159 (A)	0.250	0	→1
	182 (A)	0.250	0	→1
	184 (A)	0.667	1	→2
	235 (U)	0.333	0	→1
	248 (U)	1.000	0	→1

	294 (U)	0.250	0	→1
	305 (U)	1.000	0	→1
	306 (U)	0.667	0	→2
node_77 --> node_50	199 (A)	0.143	1	→0
	224 (A)	0.400	0	→1
	225 (U)	0.250	0	→1
	229 (U)	1.000	0	→1
	233 (U)	1.000	0	→1
	246 (U)	1.000	0	→1
	272 (U)	1.000	0	→1
	283 (D)	0.143	0	→1
	290 (D)	0.667	0	→2
node_50 --> node_49	242 (U)	0.250	0	→1
	243 (D)	0.400	0	→1
	245 (U)	1.000	0	→1
	247 (U)	1.000	0	→1
node_77 --> node_76	65 (D)	0.500	1	→0
	76 (D)	0.250	0	→1
	77 (D)	0.667	0	→1
	118 (D)	0.250	0	→1
	159 (D)	0.250	0	→1
	206 (U)	0.333	0	→1
	210 (U)	0.500	0	→1
	211 (U)	0.667	0	→1
	219 (U)	1.000	0	→1
	221 (U)	0.500	0	→1
	224 (D)	0.400	1	→0
	231 (U)	0.500	0	→1
	258 (U)	1.000	0	→1
	273 (U)	1.000	0	→1
	283 (A)	0.143	1	→0
node_76 --> node_75	16 (D)	0.250	0	→1
	61 (D)	1.000	0	→1
	70 (U)	1.000	0	→1
	84 (U)	0.500	0	→1
	100 (D)	0.250	0	→1
	111 (D)	0.250	0	→1
	117 (U)	0.500	0	→1
	132 (A)	0.333	0	→1
	133 (D)	0.333	1	→0
	145 (A)	0.200	0	→1
	191 (U)	1.000	0	→2
	196 (U)	0.400	0	→1
	198 (A)	0.500	0	→1
	203 (U)	0.500	0	→1
	213 (A)	0.333	0	→1

	214 (U)	0.400	0	→1
	220 (A)	0.143	0	→1
	227 (A)	1.000	0	→1
	230 (U)	0.400	0	→1
	236 (U)	0.222	0	→1
	254 (U)	0.500	0	→1
	261 (U)	1.000	0	→1
	266 (D)	0.200	0	→1
	271 (A)	0.333	1	→0
	281 (A)	0.500	1	→0
	290 (D)	0.667	0	→2
	295 (U)	1.000	0	→1
	301 (U)	0.250	0	→1
	303 (U)	0.250	0	→1
node_75 --> node_52	9 (A)	0.308	1	→2
	18 (A)	0.222	1	→0
	47 (A)	0.167	0	→1
	57 (A)	0.273	0	→2
	66 (A)	0.333	1	→0
	95 (A)	1.000	0	→1
	97 (A)	0.333	0	→1
	106 (A)	0.667	0	→1
	114 (A)	1.000	1	→0
	121 (A)	0.143	0	→1
	146 (A)	0.250	0	→1
	163 (A)	0.167	1	→0
	198 (D)	0.500	0	→1
	199 (A)	0.143	1	→0
	222 (A)	0.167	1	→0
	224 (A)	0.400	0	→2
	227 (D)	1.000	0	→1
	232 (U)	1.000	0	→1
	235 (U)	0.333	1	→0
	243 (D)	0.400	0	→1
	244 (U)	1.000	0	→1
	251 (U)	0.333	0	→1
	307 (A)	0.500	0	→1
node_52 --> node_51	18 (D)	0.222	1	→0
	95 (D)	1.000	0	→1
	97 (D)	0.333	0	→1
	106 (D)	0.667	0	→1
	113 (D)	0.500	0	→1
	114 (D)	1.000	1	→0
	226 (U)	1.000	0	→1
	253 (U)	0.333	0	→1
node_75 --> node_74	12 (A)	0.333	0	→1

	42 (D)	0.333	0	→1
	54 (U)	0.750	1	→3
	63 (D)	1.000	0	→1
	78 (U)	0.500	0	→1
	88 (D)	0.500	0	→1
	90 (U)	0.500	0	→1
	126 (U)	0.500	0	→1
	150 (U)	0.200	0	→1
	152 (D)	1.000	0	→1
	156 (A)	0.250	1	→0
	160 (U)	0.333	0	→1
	163 (D)	0.167	0	→1
	170 (U)	0.200	0	→1
	184 (D)	0.667	1	→2
	198 (U)	0.500	1	→2
	219 (U)	1.000	1	→2
	220 (D)	0.143	0	→1
	227 (U)	1.000	1	→2
	237 (U)	0.500	0	→1
	238 (U)	0.500	0	→1
	243 (A)	0.400	1	→0
	248 (U)	1.000	1	→2
	256 (A)	0.200	0	→1
	279 (U)	1.000	0	→1
node_74 --> node_56	9 (A)	0.308	1	→0
	15 (A)	0.333	0	→1
	21 (A)	0.500	0	→1
	41 (A)	0.167	0	→1
	92 (A)	0.333	0	→1
	93 (A)	1.000	0	→1
	94 (D)	0.333	0	→1
	103 (U)	1.000	0	→1
	108 (D)	0.250	0	→1
	110 (U)	0.333	0	→1
	113 (D)	0.500	0	→1
	118 (A)	0.250	1	→0
	132 (A)	0.333	1	→0
	138 (U)	0.200	0	→1
	143 (U)	0.333	0	→1
	144 (A)	0.333	0	→1
	145 (D)	0.200	0	→1
	154 (D)	0.333	0	→1
	176 (A)	0.500	1	→0
	192 (U)	0.200	0	→1
	204 (U)	0.500	0	→1
	205 (U)	0.500	0	→1

	210 (U)	0.500	1	→0
	231 (U)	0.500	1	→2
	254 (U)	0.500	1	→2
	256 (D)	0.200	0	→1
	291 (A)	0.500	0	→1
	315 (A)	0.667	1	→2
node_56 --> node_55	15 (D)	0.333	0	→1
	21 (D)	0.500	0	→1
	92 (D)	0.333	0	→1
	93 (D)	1.000	0	→1
	104 (U)	1.000	0	→2
	144 (D)	0.333	0	→1
	199 (D)	0.143	0	→1
	236 (U)	0.222	1	→0
	291 (D)	0.500	0	→1
node_55 --> node_54	11 (A)	0.200	0	→1
	13 (A)	0.250	0	→1
	48 (U)	0.500	0	→2
	71 (A)	0.333	0	→1
	137 (A)	0.333	0	→2
	173 (A)	0.500	0	→1
node_54 --> node_53	57 (A)	0.273	0	→1
	102 (U)	0.250	1	→0
	107 (A)	0.333	0	→1
	109 (U)	1.000	0	→1
	112 (U)	0.500	0	→1
	139 (A)	0.200	0	→1
	177 (A)	0.500	0	→1
	196 (A)	0.400	1	→0
	220 (A)	0.143	1	→0
	254 (U)	0.500	2	→1
node_74 --> node_73	12 (D)	0.333	0	→1
	14 (A)	0.375	0	→1
	33 (A)	0.500	0	→1
	34 (A)	0.167	0	→1
	35 (U)	1.000	0	→1
	36 (A)	0.333	0	→1
	76 (U)	0.250	1	→0
	94 (A)	0.333	1	→0
	105 (U)	1.000	0	→1
	113 (A)	0.500	1	→0
	123 (U)	0.500	0	→1
	127 (U)	0.500	0	→1
	132 (D)	0.333	0	→1
	145 (A)	0.200	1	→0
	147 (U)	1.000	0	→1

	154 (A)	0.333	1	→0
	174 (U)	0.667	0	→1
	180 (U)	0.500	0	→1
	181 (U)	1.000	0	→1
	199 (D)	0.143	0	→1
	207 (U)	0.333	0	→1
	215 (A)	0.333	0	→1
	242 (U)	0.250	0	→1
	269 (U)	0.500	0	→1
	270 (U)	1.000	0	→1
	277 (U)	0.500	0	→1
	302 (A)	0.500	0	→1
	306 (A)	0.667	2	→1
node_73 --> node_58	2 (A)	0.200	0	→1
	4 (A)	0.200	1	→0
	5 (A)	0.500	0	→1
	7 (A)	0.250	0	→1
	18 (A)	0.222	1	→2
	23 (A)	0.167	0	→1
	36 (D)	0.333	0	→1
	47 (U)	0.167	0	→1
	56 (A)	0.500	0	→1
	82 (A)	0.500	0	→2
	86 (U)	1.000	0	→1
	101 (A)	0.250	0	→1
	102 (A)	0.250	1	→0
	108 (D)	0.250	0	→1
	165 (U)	0.500	0	→1
	178 (A)	0.333	0	→1
	179 (A)	1.000	0	→1
	213 (A)	0.333	1	→0
	215 (U)	0.333	1	→2
	216 (U)	0.250	0	→1
	222 (U)	0.167	1	→0
	230 (U)	0.400	1	→2
	255 (U)	0.500	0	→1
	256 (D)	0.200	0	→1
	302 (D)	0.500	0	→1
node_58 --> node_57	4 (D)	0.200	1	→0
	5 (D)	0.500	0	→1
	7 (D)	0.250	0	→1
	14 (D)	0.375	0	→1
	18 (D)	0.222	1	→2
	56 (D)	0.500	0	→1
	102 (D)	0.250	1	→0
	178 (D)	0.333	0	→1

	179 (D)	1.000	0	→1
	182 (D)	0.250	0	→1
	196 (U)	0.400	1	→0
	294 (U)	0.250	1	→0
	306 (D)	0.667	2	→1
node_73 --> node_72	16 (U)	0.250	1	→0
	57 (A)	0.273	0	→1
	69 (U)	0.500	0	→1
	79 (A)	0.333	0	→1
	80 (A)	0.500	1	→0
	100 (U)	0.250	1	→0
	108 (A)	0.250	1	→0
	111 (U)	0.250	1	→0
	149 (U)	0.250	0	→1
	151 (A)	1.000	0	→1
	161 (U)	0.500	0	→1
	173 (U)	0.500	0	→1
	174 (A)	0.667	1	→2
	177 (U)	0.500	0	→1
	186 (U)	1.000	0	→1
	188 (U)	0.500	0	→1
	208 (U)	0.333	0	→1
	215 (D)	0.333	0	→1
	243 (A)	0.400	0	→1
	251 (U)	0.333	0	→1
	256 (A)	0.200	1	→0
node_72 --> node_60	1 (A)	0.222	0	→2
	33 (A)	0.500	1	→0
	34 (A)	0.167	1	→0
	36 (A)	0.333	1	→0
	118 (A)	0.250	1	→0
	170 (A)	0.200	1	→0
	182 (A)	0.250	1	→0
	184 (A)	0.667	2	→3
	196 (U)	0.400	1	→0
	213 (D)	0.333	0	→1
	220 (U)	0.143	1	→0
	234 (U)	0.167	0	→1
node_60 --> node_59	137 (A)	0.333	0	→2
	215 (A)	0.333	1	→2
	222 (A)	0.167	1	→0
	230 (U)	0.400	1	→2
	236 (U)	0.222	1	→0
	265 (A)	0.250	0	→1
node_72 --> node_71	13 (U)	0.250	0	→1
	14 (A)	0.375	1	→0

	24 (A)	0.333	0	→1
	33 (D)	0.500	0	→1
	36 (D)	0.333	0	→1
	37 (A)	0.200	0	→1
	53 (U)	0.333	0	→1
	122 (A)	0.500	0	→1
	143 (A)	0.333	0	→1
	197 (U)	0.500	0	→1
	202 (U)	1.000	0	→1
	223 (A)	1.000	1	→2
	236 (A)	0.222	1	→2
	291 (A)	0.500	0	→1
	302 (A)	0.500	1	→0
	306 (A)	0.667	1	→2
node_71 --> node_70	1 (U)	0.222	0	→1
	2 (U)	0.200	0	→1
	3 (U)	0.200	0	→1
	4 (U)	0.200	1	→0
	11 (A)	0.200	0	→1
	22 (A)	0.167	0	→1
	52 (U)	0.250	0	→1
	57 (A)	0.273	1	→0
	121 (U)	0.143	0	→1
	122 (D)	0.500	0	→1
	124 (U)	0.500	0	→1
	125 (U)	0.500	0	→1
	128 (U)	0.500	0	→1
	154 (U)	0.333	0	→1
	156 (A)	0.250	0	→1
	174 (D)	0.667	1	→2
	190 (U)	1.000	0	→1
	213 (D)	0.333	0	→1
	216 (A)	0.250	0	→1
	217 (A)	0.500	0	→1
	223 (D)	1.000	1	→2
	236 (D)	0.222	1	→2
	238 (U)	0.500	1	→0
	243 (D)	0.400	0	→1
	252 (U)	0.333	0	→1
	291 (D)	0.500	0	→1
node_70 --> node_69	5 (U)	0.500	0	→1
	7 (U)	0.250	0	→1
	8 (U)	0.500	0	→1
	18 (A)	0.222	1	→2
	24 (D)	0.333	0	→1
	25 (U)	0.333	0	→1

	37 (D)	0.200	0	→1
	57 (A)	0.273	0	→2
	76 (U)	0.250	0	→1
	143 (D)	0.333	0	→1
	144 (U)	0.333	0	→1
	145 (U)	0.200	0	→1
	151 (D)	1.000	0	→1
	175 (U)	1.000	0	→1
	182 (D)	0.250	0	→1
	189 (U)	0.333	0	→1
	192 (U)	0.200	0	→1
	193 (U)	1.000	0	→1
	194 (A)	0.500	0	→1
	196 (U)	0.400	1	→2
	201 (U)	0.500	0	→1
	216 (D)	0.250	0	→1
	217 (D)	0.500	0	→1
	222 (A)	0.167	1	→0
	249 (U)	1.000	0	→1
	253 (U)	0.333	0	→1
	255 (U)	0.500	0	→1
	256 (U)	0.200	0	→1
	264 (A)	0.500	0	→1
	269 (U)	0.500	1	→0
	277 (U)	0.500	1	→0
	283 (U)	0.143	0	→1
	296 (U)	1.000	0	→1
node_69 --> node_61	6 (U)	1.000	0	→1
	11 (D)	0.200	0	→1
	18 (D)	0.222	1	→2
	22 (D)	0.167	0	→1
	34 (A)	0.167	1	→0
	47 (U)	0.167	0	→1
	71 (A)	0.333	0	→1
	129 (U)	0.500	0	→1
	139 (U)	0.200	0	→1
	194 (D)	0.500	0	→1
	200 (A)	0.250	0	→1
	230 (U)	0.400	1	→2
	234 (U)	0.167	0	→1
	240 (U)	0.500	0	→1
	264 (D)	0.500	0	→1
	265 (U)	0.250	0	→1
	298 (A)	0.500	0	→1
node_69 --> node_68	11 (A)	0.200	1	→0
	39 (A)	0.500	0	→1

	44 (A)	0.250	1	→0
	62 (U)	1.000	0	→1
	81 (A)	0.333	1	→0
	82 (A)	0.500	0	→2
	99 (A)	0.200	0	→1
	118 (A)	0.250	1	→0
	136 (U)	1.000	0	→1
	156 (D)	0.250	0	→1
	218 (A)	0.500	0	→1
	222 (D)	0.167	1	→0
	231 (U)	0.500	1	→2
node_68 --> node_67	17 (U)	0.143	0	→1
	27 (U)	0.500	0	→1
	34 (D)	0.167	0	→1
	39 (D)	0.500	0	→1
	57 (A)	0.273	2	→0
	121 (U)	0.143	1	→0
	128 (A)	0.500	1	→2
	163 (A)	0.167	1	→0
	194 (A)	0.500	1	→0
node_67 --> node_66	18 (A)	0.222	2	→1
	38 (U)	1.000	0	→1
	52 (A)	0.250	1	→0
	74 (U)	0.500	0	→1
	89 (U)	0.333	0	→1
	128 (D)	0.500	1	→2
node_66 --> node_65	24 (U)	0.333	1	→0
	44 (A)	0.250	0	→1
	118 (D)	0.250	1	→0
	134 (A)	1.000	0	→1
	148 (A)	0.333	0	→1
	218 (D)	0.500	0	→1
	254 (U)	0.500	1	→2
node_65 --> node_64	1 (U)	0.222	1	→2
	3 (U)	0.200	1	→0
	13 (U)	0.250	1	→0
	25 (U)	0.333	1	→0
	47 (A)	0.167	0	→1
	52 (D)	0.250	1	→0
	79 (D)	0.333	0	→1
	99 (A)	0.200	1	→0
	120 (U)	1.000	0	→1
	134 (D)	1.000	0	→1
	139 (U)	0.200	0	→1
	146 (U)	0.250	0	→1
	153 (A)	0.333	1	→0

	189 (U)	0.333	1	→0
	230 (U)	0.400	1	→0
	236 (U)	0.222	2	→0
	264 (D)	0.500	0	→1
	273 (U)	1.000	1	→2
	274 (U)	1.000	0	→1
	294 (U)	0.250	1	→0
node_64 --> node_63	22 (A)	0.167	1	→0
	82 (D)	0.500	0	→2
	119 (U)	1.000	0	→1
	121 (A)	0.143	0	→1
	122 (U)	0.500	1	→0
	135 (A)	0.333	0	→1
	185 (A)	1.000	0	→1
	197 (U)	0.500	1	→0
	228 (U)	0.667	1	→2
	253 (U)	0.333	1	→2
	300 (A)	0.500	0	→1
node_63 --> node_62	15 (U)	0.333	0	→1
	19 (A)	0.333	0	→1
	75 (U)	1.000	0	→1
	124 (A)	0.500	1	→0
	153 (D)	0.333	1	→0
	163 (A)	0.167	0	→1
	185 (D)	1.000	0	→1
	213 (U)	0.333	1	→2

5. Further implications of *Tawa* for the relationships of theropods

To further explore the impact of *Tawa* on the reconstruction of basal saurhian relationships, we conducted a number of constraint analyses and taxon exclusion analyses with the phylogenetic dataset. Analyses were performed using PAUP* 4.0b10 for Macintosh PPC (Swofford 2002). Trees were searched for using the parsimony criterion implemented under the heuristic search option using tree bisection and reconnection (TBR) with 2,500 random addition sequence replicates. Zero length branches were collapsed if they lack support under any of the most parsimonious reconstructions. All characters were equally weighted.

The results of the taxon-exclusion analyses are given in Table S3. Removing *Tawa* from the dataset results in the recovery of trees that are topologically identical to the unconstrained MPTs. Excluding both *Tawa* and *Eoraptor* results in a monophyletic Coelophysoidea, with *Chindesaurus* as the sister-taxon to Neotheropoda, and *Herrerasaurus* and *Staurikosaurus* in a polytomy outside of this clade. Deleting *Tawa*, *Eoraptor*, and *Herrerasaurus*, or *Tawa*, *Eoraptor*, *Herrerasaurus*, *Staurikosaurus*, and *Chindesaurus* results in sets of MPTs that both affirm and reject coelophysoid monophyly *sensu lato* and ‘core’ coelophysoid monophyly (defined here as a clade of *Liliensternus*, *Coelophysis bauri*, and ‘*Syntarsus*’ *kayentakatae*). In general, it appears

that the combination of *Tawa* and *Eoraptor* and the transitional morphologies they possess are critical to rejecting coelophysoid monophyly for the phylogenetic dataset (Table S5).

Results of the constraint analyses are given in Table S4. Constraining *Chindesaurus*, *Tawa*, *C. bauri* and '*S.*'*kayentakatae* to be monophyletic represents the closest approximation for a test of the monophyly of the HQ theropods, and results in trees that are 24 steps longer than the unconstrained MPTs. Constraining a monophyletic clade of *Chindesaurus* and *Tawa* requires an additional 8 steps. Simply constraining *Chindesaurus*, *Tawa*, and Neotheropoda to be monophyletic only requires one additional step, and results in a topology of: (*Chindesaurus*, (*Tawa*, ((*C. bauri*, '*S.*'*kayentakatae*), Neotheropoda))), which brings up the possibility that the HQ theropods may form a paraphyletic grade near the base of Neotheropoda, though this would be contingent on a placement of the HQ coelophysoid as the sister-taxon to Neotheropoda in this topology, something we consider unlikely (unpubl. data). Constraining *Tawa*+Neotheropoda to be non-monophyletic produces trees that are 6 steps longer than the unconstrained MPTs, with *Chindesaurus* more closely related to Neotheropoda than to *Herrerasaurus* or *Eoraptor*.

Constraining *Herrerasaurus* and *Eoraptor* as basal saurischians (i.e., outside of Eusaurischia) results in a tree that is 7 steps longer, but *Tawa* is still recovered as a basal theropod. Constraining only *Herrerasaurus* as a basal saurischian produces trees 6 steps longer, with both *Herrerasaurus* and *Chindesaurus* outside of Eusaurischia, and *Staurikosaurus*, *Eoraptor*, and *Tawa* as basal theropods that are successively closer sister-taxa to Neotheropoda. Constraining *Tawa* to fall outside of Eusaurischia required an additional 15 steps, and resulted in a topology where *Tawa* is sister-taxon to Eusaurischia.

These results suggest that the recovery of *Chindesaurus* as a herrerasaurid and herrerasaurid monophyly are not strongly supported in this dataset. This can in part be attributed to the fairly incomplete nature of the *Chindesaurus* holotype, though some genuine character conflict is also present (e.g., the presence of cervical pleurocoels in *Chindesaurus*). However, the relationships of *Herrerasaurus*, *Eoraptor*, *Tawa* and Neotheropoda relative to each other appear to be well supported. Furthermore, the dataset strongly supports the non-monophyly of the Hayden Quarry theropods.

As noted above, one of the most significant results of our analysis was the failure to recover a monophyletic Coelophysoidea. Constraining a monophyletic Coelophysoidea *sensu lato* (i.e., coelophysids, *Liliensternus*, *Zupaysaurus*, and *Dilophosaurus*) resulted in trees 5 steps longer than our original analysis. Constraining a monophyletic core Coelophysoidea (coelophysids and *Liliensternus* only) required only one extra step. In both cases *Tawa* is still recovered as the sister-taxon to Neotheropoda. Although our phylogenetic dataset is not designed to provide a comprehensive test of coelophysoid monophyly, we find the results of the constraint and taxon-deletion analyses intriguing, and suggest that the mosaic of anatomical features present in *Tawa* (which possesses many 'classic' coelophysoid synapomorphies, as well as numerous neotheropod plesiomorphies) is primarily responsible for the recovery of a paraphyletic Coelophysoidea (Table S5; see also discussion in main text). Interestingly, four of the nine characters identified in Table S5 as putative coelophysoid synapomorphies are traits associated with the morphology of the premaxilla and anterior end of the snout. Previous

authors have suggested that, rather than representing a bauplan unique to a monophyletic clade, a ‘coelophysoid’ morphology may have been a plesiomorphic morphotype characterizing a paraphyletic grade of early theropods (Yates 2005; Smith et al. 2007b). Our results support this interpretation by confirming a broader distribution for ‘classic’ coelophysoid features in the basal theropods *Eoraptor* and *Tawa*. Accurately resolving basal theropod relationships, and also characterizing the distribution of potentially ecologically relevant traits (such as snout morphology) have critical implications for scenarios of turnover in theropod faunas at the Triassic-Jurassic (Olson et al. 2002) and Early-Mid Jurassic (Carrano and Sampson 2004) boundaries.

Table S3. Results of taxon-exclusion analyses.

Taxa Excluded	‘Core’ Coelophysoid Monophyly?	Coelophysoid Monophyly <i>sensu lato</i>
None	No	No
<i>Tawa</i>	No	No
<i>Eoraptor</i>	No	No
<i>Tawa, Chindesaurus</i>	No	No
<i>Tawa, Eoraptor</i>	Yes	Yes
<i>Tawa, Eoraptor, Herrerasaurus</i>	Equivocal	Equivocal
<i>Tawa, Eoraptor, Herrerasaurus, Staurikosaurus, Chindesaurus</i>	Equivocal	Equivocal
<i>Saturnalia, Tawa, Eoraptor, Herrerasaurus, Staurikosaurus, Chindesaurus</i>	Equivocal	Equivocal
<i>Tawa, Saturnalia</i>	No	No
<i>Eoraptor, Saturnalia</i>	No	No
<i>Tawa, Saturnalia, Eoraptor</i>	Yes	Yes
<i>Zupaysaurus, Cryolophosaurus</i>	Equivocal	No
<i>Tawa, Zupaysaurus, Cryolophosaurus</i>	Equivocal	Equivocal
<i>Eoraptor, Zupaysaurus, Cryolophosaurus</i>	Equivocal	No

Table S4. Results of constraint analyses.

Constraint	Number of Trees	Tree Length
None	3	872
<i>Chindesaurus, Tawa, C. bauri, ‘S.’kayentakatae</i> monophyly	6	+4
<i>Chindesaurus, Tawa, Neotheropoda</i> monophyly	3	+1
<i>Chindesaurus, Tawa</i> monophyly	3	+6
<i>C. bauri, ‘S.’kayentakatae, Liliiensternus, Zupaysaurus, Cryolophosaurus, Dilophosaurus</i> monophyly	6	+5
<i>C. bauri, ‘S.’kayentakatae, Liliiensternus</i> monophyly	9	+1
<i>Tawa, Neotheropoda</i> non-monophyly	3	+6

<i>Herrerasaurus, Chindesaurus</i> non-monophyly	10	+1
Herrerasauridae non-monophyly	10	+1
<i>Herrerasaurus, Eoraptor</i> outside of Eusaurischia	1	+7
<i>Herrerasaurus</i> outside of Eusaurischia	3	+6
<i>Tawa</i> outside of Eusaurischia	1	+15
<i>Tawa</i> outside of <i>Herrerasaurus, Eoraptor</i> , Neotheropoda	3	+14
<i>Tawa</i> outside of <i>Eoraptor</i> , Neotheropoda	9	+8

Table S5. Characters optimized as synapomorphies of more inclusive theropod clades in the MPTs that are optimized as synapomorphies of Coelophysoidea when *Eoraptor* and *Tawa* are excluded from the dataset. The letter “U”, “A”, or “D” after the character indicates whether it represents an unambiguous synapomorphy, or a synapomorphy under ACCTRAN or DELTRAN optimization, respectively. Synapomorphies are described in the format: “Character number: plesiomorphic state → derived state”.

Coelophysoid Synapomorphies with <i>Eoraptor, Tawa</i> Excluded	<i>Eoraptor, Tawa, Neotheropoda</i> Synapomorphies in MPTs	<i>Tawa, Neotheropoda</i> Synapomorphies in MPTs
1. 2→1 (U)		1. 0→1 (U)
2. 0→1 (D)		2. 0→1 (U)
3. 0→1 (U)		3. 0→1 (U)
13. 0→1 (U)	13. 0→1 (U)	
24. 0→1 (U)	24. 0→1 (A)	
52. 0→1 (U)		52. 0→1 (U)
122. 0→1 (D)		122. 0→1 (D)
197. 0→1 (D)	197. 0→1 (U)	
236. 0→2 (U)	236. 1→2 (A)	236. 0→2 (D)

6. Supporting online material references.

- Bakker, R. T., and P. M. Galton. 1974. Dinosaur monophyly and a new class of vertebrates. *Nature* **248**:168-172.
- Bennett, S. C. 1996. The phylogenetic position of the Pterosauria within Archosauromorpha. *Zoological Journal of the Linnean Society* **118**:261-308
- Benton, M. J. 1990. Origin and interrelationships of dinosaurs; pp. 11-30 in D. B. Weishampel, P. Dobson, and H. Osmolska (eds.), *The Dinosauria*. University of California Press, Berkeley.
- Benton, M. J. 1999. *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. *Philosophical Transactions of the Royal Society of London, Series B* **354**:1423-1446.

- Benton, M. J., and J. M. Clark. 1988. Archosaur phylogeny and the relationships of the Crocodylia. Pages 295-338 in *The Phylogeny and Classification of Tetrapods. Volume 1: Amphibians, Reptiles, Birds*. Clarendon Press, Oxford.
- Benton, M. J., and A. D. Walker. 2002. *Erpetosuchus*, a crocodile-like basal archosaur from the Late Triassic of Elgin, Scotland. *Biological Journal of the Linnean Society* **136**:25-47.
- Bonaparte, J. F. 1976. *Pisanosaurus mertii* Casimiquela and the origin of the Ornithischia. *Journal of Paleontology* **50**:808-820.
- Bremer, K. 1992. Ancestral areas: A cladistic reinterpretation of the center of origin concept. *Systematic Biology* **41**:436-445.
- Bremer, K. 1995. Ancestral areas: Optimization and probability. *Systematic Biology* **44**:255-259.
- Butler, R. J. 2005. The 'fabrosaurid' ornithischian dinosaurs of the upper Elliot Formation (Lower Jurassic) of South Africa and Lesotho. *Zoological Journal of the Linnean Society* **145**:175-218.
- Butler, R. J., P. Upchurch, and D. B. Norman. 2008. The phylogeny of the ornithischian dinosaurs. *Journal of Systematic Palaeontology* **6**:1-40.
- Carrano, M. T., and S. D. Sampson. 2004. A review of coelophysoids (Dinosauria: Theropoda) from the Early Jurassic of Europe, with comments on the late history of the Coelophysoidea. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 2004:537-558.
- Carrano, M. T., S. D. Sampson, and C. A. Forster. 2002. The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* **22**:510-534.
- Clark, J. M., and H.-D. Sues. 2002. Two new basal crocodylomorph archosaurs from the Lower Jurassic and the monophyly of the Sphenosuchia. *Zoological Journal of the Linnean Society* **136**:77-95.
- Clark, J. M., X. Xing, C. A. Forster, and Y. Wang. 2004. A Middle Jurassic 'sphenosuchian' from China and the origin of the crocodylian skull. *Nature* **430**:1021-1024.
- Clark, J. M., H.D. Sues, and D.S. Berman. 2000. A new specimen of *Hesperosuchus agilis* from the Upper Triassic of New Mexico and the interrelationships of basal crocodylomorph archosaurs. *Journal of Vertebrate Paleontology* **20**:683-704.

- Clark, J. R., R. H. Ree, M. E. Alfaro, M. G. King, W. L. Wagner, and E. H. Roalson. 2008. A comparative study in ancestral range reconstruction methods: retracing the uncertain histories of insular lineages. *Systematic Biology* **57**:693-707.
- Dilkes, D. W. 1998. The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. *Philosophical Transactions of the Royal Society of London Series B* **353**:501-541.
- Donoghue, M. J., and B. R. Moore. 2003. Toward an integrative historical biogeography. *Integrative and Comparative Biology* **43**:261-270.
- Edwards, A. W. F. 1992. Likelihood. Johns Hopkins University Press, Baltimore.
- Efron, B. 1979. Bootstrap methods: another look at the jackknife. *The Annals of Statistics* **7**:1-26.
- Ezcurra, M. D. 2006. A review of the systematic position of the dinosauriform archosaur *Eucoelophysis baldwini* Sullivan and Lucas, 1999 from the Upper Triassic of New Mexico, USA. *Geodiversitas* **28**:649-684.
- Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**:783-791.
- Galton, P. M. 1976. Prosauropod dinosaurs (Reptilia: Saurischia) of North America. *Postilla* **169**:1-98.
- Gauthier, J. A. 1984. A cladistic analysis of the higher systematic categories of Diapsida University of California Berkeley, Berkeley, 564 pp.
- Gauthier, J. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences* **8**:1-55.
- Gauthier, J., and K. Padian. 1985. Phylogenetic, functional, and aerodynamic analyses of the origin of birds and their flight; pp. 185–197 in J. H. O. M.K. Hecht, G. Viohl and P. Wellnhofer (ed.), *The Beginning of Birds*. Freunde des Jura Museums, Eichstatt.
- Gauthier, J. A., A. G. Kluge, and T. Rowe. 1988. Amniote phylogeny and the importance of fossils. *Cladistics* **4**:105-209.
- Goloboff, P.A., J.S. Farris, and K. Nixon. 2003. TNT: Tree analysis using new technologies. Program and documentation available from the authors and at <http://www.zmuc.dk/public/phylogeny>.
- Goloboff, P., J. Farris, and K. Nixon. 2008. TNT: a free program for phylogenetic analysis. *Cladistics* **24**:774-786.

- Gower, D. J. 2002. Braincase evolution in suchian archosaurs (Reptilia: Diapsida): Evidence from the rauisuchian *Batrachotomus kupferzellensis*. *Zoological Journal of the Linnean Society* **136**:49-76.
- Gower, D. J., and A. G. Sennikov. 1997. *Sarmatosuchus* and the early history of the Archosauria. *Journal of Vertebrate Paleontology* **17**:60-73.
- Grande, L. 1985. The use of paleontology in systematics and biogeography, and a time control refinement for historical biogeography. *Paleobiology* **11**: 234-243.
- Heckert, A. B., and S. G. Lucas. 1999. A new aetosaur (Reptilia: Archosauria) from the upper Triassic of Texas and the phylogeny of aetosaurs. *Journal of Vertebrate Paleontology* **19**:50-68.
- Holtz, T. R. J. 1994. The phylogenetic position of the Tyrannosauridae: implications for theropod systematics. *Journal of Paleontology* **68**:1100-1117.
- Humphries, C. J. and M. C. Ebach. 2004. Biogeography on a dynamic earth. Pages 67-86 in *Frontiers of Biogeography New Directions in the Geography of Nature* (M. V. Lomolino and L. R. Heaney, eds). Sinauer Associates, Massachusetts.
- Hutchinson, J. R. 2001a. The evolution of pelvic osteology and soft tissues on the line to extant birds. *Zoological Journal of the Linnean Society* **131**:123-168.
- Hutchinson, J. R. 2001b. The evolution of femoral osteology and soft tissue on the line to extant birds (Neornithes). *Zoological Journal of the Linnean Society* **131**:169-197.
- Hwang SH, Norell, M.A., Quiang, J., and Keqin, G. 2004. A large compsognathid from the Early Cretaceous Yixian Formation of China. *Journal of Systematic Paleontology* **2**:13-30.
- Irmis, R. B. 2008. Perspectives on the origin and early diversification of dinosaurs. Unpublished PhD Dissertation. Integrative Biology, University of California Berkeley, 434 pp.
- Irmis, R. B., S. J. Nesbitt, K. Padian, N. D. Smith, A. H. Turner, D. Woody, and A. Downs. 2007. A Late Triassic dinosauriform assemblage from New Mexico and the rise of dinosaurs. *Science* **317**: 358-361.
- Irmis, R. B., and R. Mundil. 2008. New age constraints from the Chinle Formation revise global comparisons of Late Triassic vertebrate assemblages. *Journal of Vertebrate Paleontology* **28** (supplement to 3):95A.
- Juul, L. 1994. The phylogeny of basal archosaurs. *Paleontologia Africana* **31**:1-38.

- Langer, M. C., and M. J. Benton. 2006. Early dinosaurs: A phylogenetic study. *Journal of Systematic Palaeontology* **4**:309-358.
- Long, R. A., and P. A. Murry. 1995. Late Triassic (Carnian and Norian) tetrapods from the southwestern United States New Mexico Museum of Natural History and Science Bulletin **4**:1-254.
- Maddison, W. P. and D. R. Maddison. 2008. Mesquite: a modular system for evolutionary analysis. V2.5. <http://mesquiteproject.org>.
- Martinez, R. N., and O. A. Alcobar. 2009. A basal sauropodomorph (Dinosauria: Saurischia) from the Ischigualasto Formation (Triassic, Carnian) and the early evolution of Sauropodomorpha. *PLoS ONE* **4(2)**: 1-12.
- McGuire, J. A., C. C. Witt, D. L. Altshuler, and J. V. Remsen. 2007. Phylogenetic systematics and biogeography of hummingbirds: Bayesian and maximum likelihood analyses of partitioned data and selection of an appropriate partitioning strategy. *Systematic Biology* **56**:837–856.
- Mundil, R. 2007. Critical view of the calibration of the Triassic time scale. *New Mexico Museum of Natural History and Science Bulletin* **41**: 314-315.
- Neopokroeff, M., K. J. Sytsma, W. L. Wagner, and E. A. Zimmer. 2003. Reconstructing ancestral patterns of colonization and dispersal in the Hawaiian understory tree genus *Psychotria* (Rubiaceae): A comparison of parsimony and likelihood approaches. *Systematic Biology* **52**:820–838.
- Nesbitt, S. J. 2005. The osteology of the Middle Triassic pseudosuchian archosaur *Arizonasaurus babbitti*. *Historical Biology* **17**:19-47.
- Nesbitt, S. J. 2007. The anatomy of *Effigia okeeffeae* (Archosauria, Suchia), theropod convergence, and the distribution of related taxa. *Bulletin of the American Museum of Natural History* **302**:1-84.
- Nesbitt, S. J. 2009. The early evolution of archosaurs: Relationships and the origin of major clades. Unpublished PhD Dissertation. Earth and Environmental Sciences, Columbia University, New York, 675 pp.
- Nesbitt, S. J., and M. A. Norell. 2006. Extreme convergence in the body plans of an early suchian (Archosauria) and ornithomimid dinosaurs (Theropoda). *Proceedings of the Royal Society of London B* **273**:1045-1048.
- Nesbitt, S. J., R. B. Irmis, and W. G. Parker. 2007. A critical re-evaluation of the Late Triassic dinosaur taxa of North America. *Journal of Systematic Palaeontology* **5**:209-243.

- Nesbitt, S. J., R. B. Irmis, W. G. Parker, N. D. Smith, A. H. Turner, and T. Rowe. 2009. Hindlimb osteology and distribution of basal dinosauromorphs from the Late Triassic of North America. *Journal of Vertebrate Paleontology* **29**:498-516.
- Norell, M. A. 1992. Taxic origin and temporal diversity: the effect of phylogeny. Pages 89-119 in *Extinction and Phylogeny* (M. J. Novacek and Q. Wheeler, eds). Columbia University Press, New York.
- Novas, F. E. 1989. The tibia and tarsus in Herrerasauridae (Dinosauria, incertae sedis) and the origin and evolution of the dinosaurian tarsus. *Journal of Paleontology* **63**:677-690.
- Novas, F. E. 1992. Phylogenetic relationships of basal dinosaurs, the Herrerasauridae. *Palaeontology* **63**:51-62.
- Novas, F. E. 1996. Dinosaur monophyly. *Journal of Vertebrate Paleontology* **16**:723-741.
- O'Leary, M. A., and S. G. Kuaufman. MorphoBank 2.5: Web application for morphological phylogenetics and taxonomy. <http://www.morphobank.org>.
- Olsen, P. E., H.-D. Sues, and M. A. Norell. 2000. First record of *Erpetosuchus* (Reptilia: Archosauria) from the Late Triassic of North America. *Journal of Vertebrate Paleontology* **20**:633-636.
- Olsson, U., P. Alström, M. Gelang, P. G. Ericsson, and P. Sundberg. 2006. Phylogeography of Indonesian and Sino-Himalayan bush warblers (*Cettia*, Aves). *Molecular Phylogenetics and Evolution* **41**:556-561.
- Parker, W. G. 2007. Reassessment of the Aetosaur '*Desmotosuchus*' *chamaensis* with a reanalysis of the phylogeny of the Aetosauria (Archosauria: Pseudosuchia). *Journal of Systematic Palaeontology* **5**:41-68.
- Parker, W. G., and R. B. Irmis. 2005. Advances in Late Triassic vertebrate paleontology based on new material from Petrified Forest National Park, Arizona; pp. 45-58 in A. B. Heckert and S. G. Lucas (eds.), *Vertebrate Paleontology in Arizona*. New Mexico Museum of Natural History and Science, Albuquerque.
- Parrish, J. M. 1993. Phylogeny of the Crocodylotarsi, with reference to archosaurian and crurotarsan monophyly. *Journal of Vertebrate Paleontology* **13**:287-308.
- Parrish, J. M. 1994. Cranial osteology of *Longosuchus meadei* and the phylogeny and distribution of the Aetosauria. *Journal of Vertebrate Paleontology* **14**:196-209.
- Pereira, S.L., K. P. Johnson, D. H. Clayton, and A. J. Baker. 2007. Mitochondrial and nuclear DNA sequences support a Cretaceous origin of Columbiformes and a

- dispersal-driven radiation in the Paleogene. *Systematic Biology* **56**:656–672.
- Rauhut, O. W. M. 2003. The interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Palaeontology* **69**:1-214.
- Ree, R. H., and I. Sanmartín. 2009. Prospects and challenges for parametric models in historical biogeographical inference. *Journal of Biogeography*. In Press.
- Ree, R. H., and S. A. Smith. 2008a. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology* **57**:4-14.
- Ree, R. H., B. R. Moore, C. O. Webb, and M. J. Donoghue. 2005. A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution* **59**:2299-2311.
- Ronquist, F. 1997. Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology* **46**:195-203.
- Ronquist, F. 2003. Parsimony analysis of coevolving species associations. Pages 22-64 in *Tangled trees: phylogeny, cospeciation, and coevolution* (R. D. M. Page, ed). University of Chicago Press, Chicago.
- Rowe, T., and J. Gauthier. 1990. Ceratosauria; pp. 151-168 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*. University of California Press, Berkeley.
- Sereno, P. C. 1986. Phylogeny of the bird-hipped dinosaurs (Order Ornithischia). *National Geographic Society Research* **2**:234-256.
- Sereno, P. C. 1991. Basal archosaurs: phylogenetic relationships and functional implications. *Society of Vertebrate Paleontology Memoir* **2**:53 pp.
- Sereno, P. C. 1999. The evolution of dinosaurs. *Science* **284**:2137-2147.
- Sereno, P. C., and A. B. Arcucci. 1994. Dinosaur precursors from the Middle Triassic of Argentina: *Lagerpeton chanarensis*. *Journal of Vertebrate Paleontology* **13**:385-399.
- Sereno, P. C., and F. E. Novas. 1994. The skull and neck of the basal theropod *Herrerasaurus ischigualastensis*. *Journal of Vertebrate Paleontology* **13**:451-476.
- Sereno, P. C., C. A. Forster, R. R. Rogers, and A. M. Monetta. 1993. Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria. *Nature* **361**:64-66.

- Smith, D. K., and P. M. Galton. 1990. Osteology of *Archaeornithomimus asiaticus* (Upper Cretaceous, Iren Dabasu Formation, People's Republic of China. *Journal of Vertebrate Paleontology* **10**:255-265.
- Smith, N. D., P. J. Makovicky, W. R. Hammer, and P. J. Currie. 2007. Osteology of *Cryolophosaurus ellioti* (Dinosauria: Theropoda) from the Early Jurassic of Antarctica and implications for early theropod evolution. *Zoological Journal of the Linnean Society* **151**:377-421.
- Sues, H.-D., P. E. Olsen, J. G. Carter, and D. M. Scott. 2003. A new crocodylomorph archosaur from the Upper Triassic of North Carolina. *Journal of Vertebrate Paleontology* **23**:329-343.
- Swofford, D.L. 2002. PAUP*: Phylogenetic Analysis Using Parsimony. V4.0b10. Sinauer Associate, Inc., Sunderland, Massachusetts.
- Turner, A. H. 2004. Crocodyliform biogeography during the Cretaceous: evidence of Gondwana vicariance from biogeographical analysis. *Proceedings of the Royal Society of London, Biological Sciences* **343**:2003-2009.
- Tykoski, R. S. 2005. Anatomy, ontogeny, and phylogeny of coelophysoid theropods. PhD thesis/dissertation, Jackson School of Geosciences, University of Texas, Austin, 553 pp.
- Upchurch, P., C. A. Hunn, and D. B. Norman. 2002. An analysis of dinosaurian biogeography: evidence for the existence of vicariance and dispersal patterns caused by geological events. *Proceeding of the Royal Society of London, Biology* **269**:613-621.
- Upchurch, P., P. M. Barrett, and P. M. Galton. 2007. A phylogenetic analysis of basal sauropodomorph relationships: implications for the origin of sauropod dinosaurs. *Special Papers in Palaeontology* **77**:57-90.
- Weinbaum, J. C., and A. Hungerbühler. 2007. A revision of *Poposaurus gracilis* (Archosauria: Suchia) based on two new specimens from the Late Triassic of the southwestern U.S.A. *Paläontologische Zeitschrift* **81/2**:131-145.
- Weishampel, D. B., and L. M. Witmer. 1990. Heterodontosauridae.; pp. 486-497 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*. University of California Press, Berkeley.
- Yates, A. M. 2003. A new species of the primitive dinosaur *Thecodontosaurus* (Saurischia: Sauropodomorpha) and its implications for the systematics of early dinosaurs. *Journal of Systematic Palaeontology* **1**:1-42.

Yates, A. M. 2005. A new theropod dinosaur from the Early Jurassic of South Africa and its implications for the early evolution of theropods. *Palaeontologia Africana* 41:105-122.

Yates, A. M. 2007. The first complete skull of the Triassic dinosaur *Melanorosaurus* Haughton (Sauropodomorpha: Anchisauria). *Special Papers in Palaeontology* 77:9-55.