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ARTICLE

TAXONOMIC REVISON OF THE BASAL NEORNITHISCHIAN TAXA *THESCELOSAURUS* AND *BUGENASAURA*

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ABSTRACT—Considerable controversy surrounds the taxonomy and phylogenetic relationships of Maastrichtian basal neornithischian taxa from North America. Discovery of previously unrecognized cranial material from the paratype specimen of *Thescelosaurus neglectus* (USNM 7758), along with the examination of two new specimens that preserve nearly complete skulls and mandibles, allows for reevaluation of specimens previously referred to *Thescelosaurus* that preserve cranial material, including the holotypes of *Bugenasaura infernalis* (SDSM 7210) and *Parksosaurus warreni* (ROM 804). A phylogenetic analysis was conducted that included as terminals the holotypes of *B. infernalis* and *P. warreni*, the type series of *T. neglectus,* and six specimens previously referred to *Thescelosaurus*. This analysis is the first to recover a clade containing all basal neornithischian taxa from the Cretaceous of North America, within which *P. warreni* is recovered as the sister taxon to a *Thescelosaurus* clade whose monophyly is supported by five cranial autapomorphies. The results of this analysis support: (1) the synonymization of *Bugenasaura* with *Thescelosaurus*; (2) the removal of ROM 804 from *Thescelosaurus*; and (3) the validity of *Thescelosaurus garbanii* and its referral to *Thescelosaurus* despite its fragmentary nature. Currently, *Parksosaurus* and *Thescelosaurus* are the only basal neornithischian taxa definitively known from Maastrichtian age sediments of North America, while other basal neornithischian taxa proposed to demonstrate fossorial behavior (i.e., *Orodromeus*, *Oryctodromeus*, and *Zephyrosaurus*) are known from Campanian and older sediments. This temporal segregation may support previous hypotheses of an environmental or ecological shift during the latest Cretaceous in North America.

INTRODUCTION

The taxonomic diversity of basal neornithischians (stem based definition of Sereno, 1998) in North America during the Maastrichtian (70.6 to 65.5 Ma; Weishampel et al., 2004; Gradstein et al., 2004) remains controversial despite recent attempts to provide clarity to this issue (Galton, 1995, 1997, 1999). An array of species have been named and repeatedly revised as parts of three taxa (*Bugenasaura*, *Parksosaurus*, and *Thescelosaurus*), and the referral of individual specimens to these species remains fluid (Gilmore, 1913; Parks, 1926; Sternberg, 1937, 1940; Morris, 1976; Galton, 1995). Currently, no consensus exists on the systematic positions of these taxa. For instance, *Thescelosaurus* has been placed within a monophyletic Hypsilophodontidae (sensu Sereno, 1998; Figs. 1A, B, F) or basal to Iguanodontia (sensu Sereno, 2005; Figs. 1C, D, E). New information from previously unreported cranial material from the paratype specimen of *Thescelosaurus neglectus* (USNM 7758), the name bearing species of the taxon *Thescelosaurus*, and two new specimens allow identification of previously unrecognized cranial characters that facilitate a taxonomic revision of previously described *Bugenasaura*, *Parksosaurus*, and *Thescelosaurus* species.

The type series of *Thescelosaurus neglectus* (Gilmore, 1913) consists of a nearly-complete postcranial skeleton named as the holotype (USNM 7757) and a second, fragmentary postcranial skeleton (USNM 7758) assigned as the paratype. Both specimens were collected from the Lance Formation of Wyoming (Maastrichtian; 70.6 to 65.5 Ma; Weishampel et al., 2004; Gradstein et al., 2004) and between these two specimens all postcranial elements are represented with the exception of the anterior cervical vertebrae and coracoids. However, no cranial material was identified from either specimen (Gilmore, 1913; Gilmore, 1915). An array of additional specimens have since been referred to this species from the Lance (Gilmore, 1915), Hell Creek (Gilmore, 1915; Morris, 1976; Galton, 1997; Fisher et al., 2000), Scollard (Sternberg, 1940; Galton, 1974b), and Frenchman (Galton, 1974b, 1989) formations of North America.

Three additional species of *Thescelosaurus* have been described: *Thescelosaurus warreni*, Parks, 1926, *Thescelosaurus edmontonensis*, Sternberg, 1940, and *?Thescelosaurus garbanii*, Morris, 1976. Sternberg (1937) designated the holotype of *Thescelosaurus warreni*, ROM 804, the type of a new taxon, *Parksosaurus*, because he considered the differences present between it and *T. neglectus* greater than those he identified between *T. edmontonensis* and *T. neglectus*. Galton (1974a, 1995) argued that the differences noted by Sternberg (1940) between *T. edmontonensis* and *T. neglectus* fell within the range of individual variation exhibited by other closely related taxa (e.g., *Dryosaurus altus*, *D. lettowvorbecki*, and *Hypsilophodon foxii*; Galton, 1974a, 1981); therefore, he considered *T. edmontonensis* to be a subjective junior synonym of *T. neglectus*.

Morris (1976) described a partial left hind limb and associated cervical and dorsal vertebrae (LACM 33542) from the Hell

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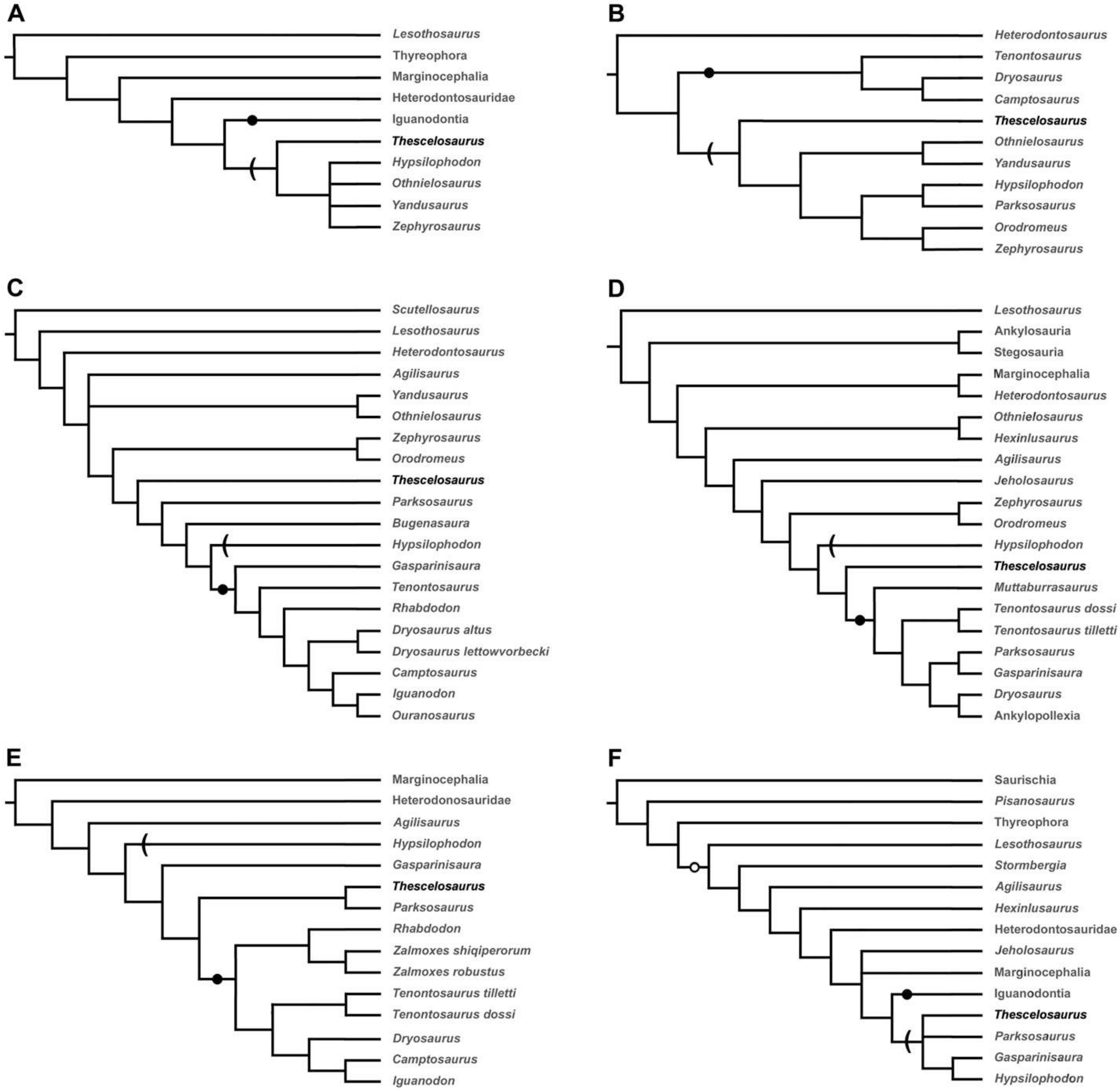
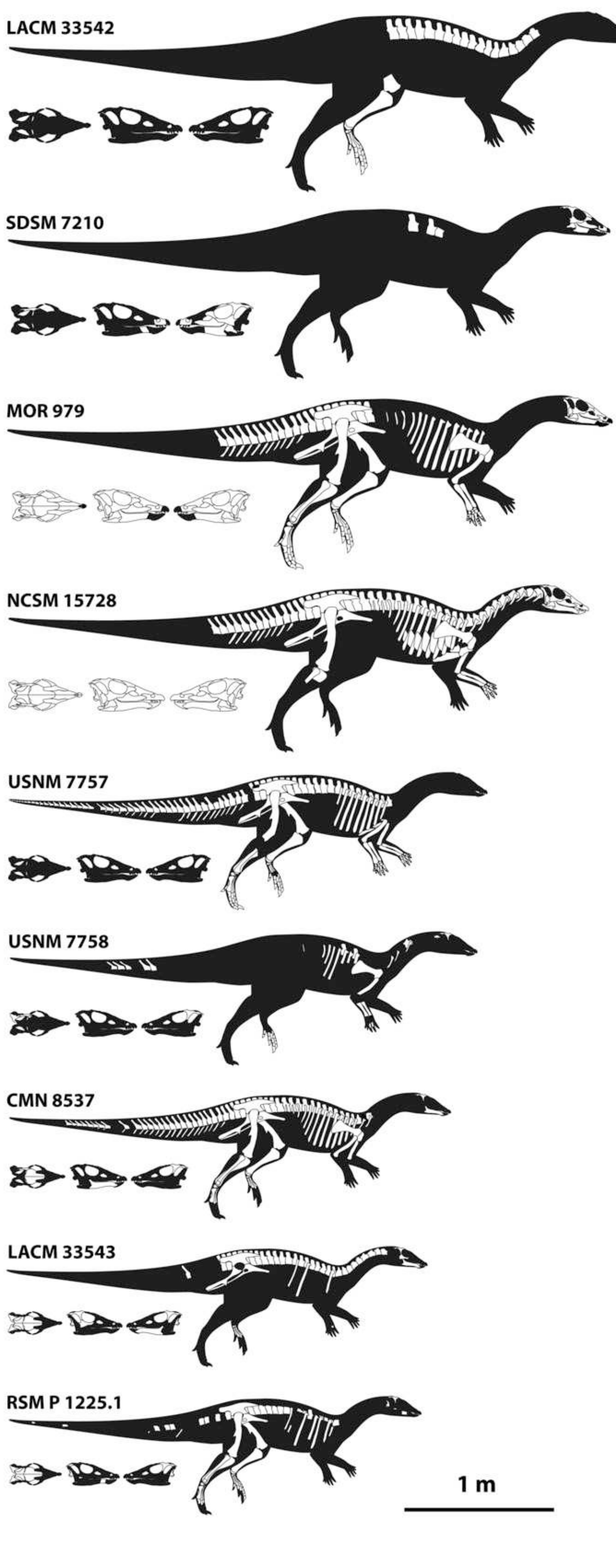


FIGURE 1. Overview of the position of *Thescelosaurus* in previously published phylogenetic analyses. **A**, phylogeny from Sereno (1986) modified to focus on the position of 'hypsilophodontid' taxa; **B**, single most parsimonious tree (MPT) from Weishampel and Heinrich (1992); **C**, majority rule consensus tree of three MPTs from Scheetz (1999); **D**, majority rule consensus tree of ten MPTs from Buchholz (2002); **E**, strict consensus of two MPTs from Weishampel et al. (2003); **F**, majority rule consensus of twenty–three MPTs from Butler (2005). The empty circle indicates the position of the stem-based clade Neornithischia (sensu Sereno, 1998) in Butler (2005). Black circles indicate the position of the stem–based clade Iguanodontia (sensu Sereno, 2005) and the curved lines denote the position of the stem–based clade Hypsilophodontidae (sensu Sereno, 1998).

Creek Formation as a new species, *?Thescelosaurus garbanii*, which was tentatively referred to *Thescelosaurus* based on general similarity with the hind limb. Morris (1976) also described a partial skull with fragmentary mandibles and associated postcrania (SDSM 7210) from the Hell Creek Formation, which he proposed may represent a previously undescribed species. This specimen lacks material that can be directly compared to the type series of *T. neglectus* and the holotype of *T. garbanii* and the only cranial material known from *Thescelosaurus* at that time was the fragmentary material preserved with the holotype of *T. edmontonensis* (CMN 8537). For these reasons he referred SDSM 7210 to *Thescelosaurus* sp. rather than erect a new species. Sues (1980) concurred and stated that this specimen should remain unnamed until new material was discovered that facilitated its comparison with the type series of *T. neglectus*. Galton (1995) made SDSM 7210 the holotype of *Bugenasaura infernalis* and tentatively referred the holotype of ?*Thescelosaurus garbanii* (LACM 33542) to this new species, despite the lack of comparable material between these specimens.



The taxonomy of *Bugenasaura*, *Parksosaurus,* and *Thescelosaurus* has not been revised since Galton (1995). Since then, two important specimens have been discovered that preserve nearly complete skulls and mandibles (NCSM 15728 referred to *T. neglectus* and MOR 979 referred to *B. infernalis*; Fisher et al., 2000; Horner, 2001), enhancing our knowledge of the anatomy of these taxa. These new specimens, combined with data obtained from the newly recognized skull material from USNM 7758, allow for a new phylogenetic analysis and taxonomic revision of eight specimens previously referred to these taxa (Fig. 2) that preserve material from the skull and/or tarsus (Parks, 1926; Sternberg, 1940; Galton, 1974b, 1989, 1997, 1999; Morris, 1976; Fisher et al., 2000; Horner, 2001). Two partial dentaries (AMNH 5020 and CMN 9534) that were referred to *T. neglectus* by Galton (1974b, 1997) will not be considered because no dentary characters were found to be diagnostic of a *Thescelosaurus* clade in this analysis. The postcranial anatomy of these taxa will only be briefly discussed as reexamination of the postcrania of these and other referred specimens is ongoing.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; **CMN**, Canadian Museum of Nature, Ontario; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; **LACM**, Los Angeles County Museum, California; **MOR**, Museum of the Rockies, Montana; **NCSM**, North Carolina Museum of Natural Sciences, North Carolina; **SDSM**, South Dakota School of Mines and Technology, South Dakota; **RSM**, Royal Saskatchewan Museum, Saskatchewan; **USNM**, United States National Museum, Washington, D.C.

Anatomical Abbreviations—aes, origin of m. adductor externus superficialis; **ar**, anterior ramus of postorbital; **f**, frontal; **fl**, flange; **ib**, irregular bosses; **jr**, jugal ramus of postorbital; **pfs**, postorbital-frontal suture; **pp**, postorbital projection into orbit; **pr**, posterior ramus of postorbital; **pss**, postorbital-squamosal suture; **qp**, quadratic process; **sh**, socket for head of quadrate; **stf**, supratemporal fenestra.

CLADISTIC METHODOLOGY

A new phylogenetic analysis was conducted that evaluated: (1) character support for a monophyletic *Thescelosaurus* clade; (2) removal of ROM 804 from *Thescelosaurus*; and (3) the relationships of LACM 33542, the holotype of *Thescelosaurus garbanii* (Appendices 1, 2; Fig. 3; Table). This analysis used the Varricchio et al. (2007) dataset, which is based on that of Scheetz (1999). The following modifications were made to this dataset: included six characters originally proposed by Galton (1997, 1999) to diagnose *Thescelosaurus*, added two new characters, and incorporated character scorings based on personal observations (see Appendix 1). The terminal taxa "*Bugenasaura"* and *"Thescelosaurus"* (Fig. 3A) from Scheetz (1999) were removed from this analysis because they were scored from both the type series and referred specimens and the current analysis aims to reassess these referrals. The chimeric terminal taxon *Yandusaurus* (largely scored from material now referred to *Hexinlusaurus*) was replaced with the terminal taxon *Hexinlusaurus*, which was scored only from the holotype material. *Parksosaurus* was also completely rescored from ROM 804. The holotype material of *Bugenasaura infernalis* and *Parksosaurus warreni*, the

← FIGURE 2. Diagram illustrating the relative size and completeness of all specimens referred to *Thescelosaurus* by this study. Bones present in each specimen are colored white. Skeletons are scaled isometrically based on femur and tibia length when available. Skeletons lacking both tibiae and femora were scaled using the following elements: anteroposterior width of orbit for SDSM 7210; length of the dentary for LACM 33543; and length of the humerus for USNM 7758. Proportions for each specimen represent those of USNM 7757 and do not illustrate proportion changes that would be effected due to allometric scaling.

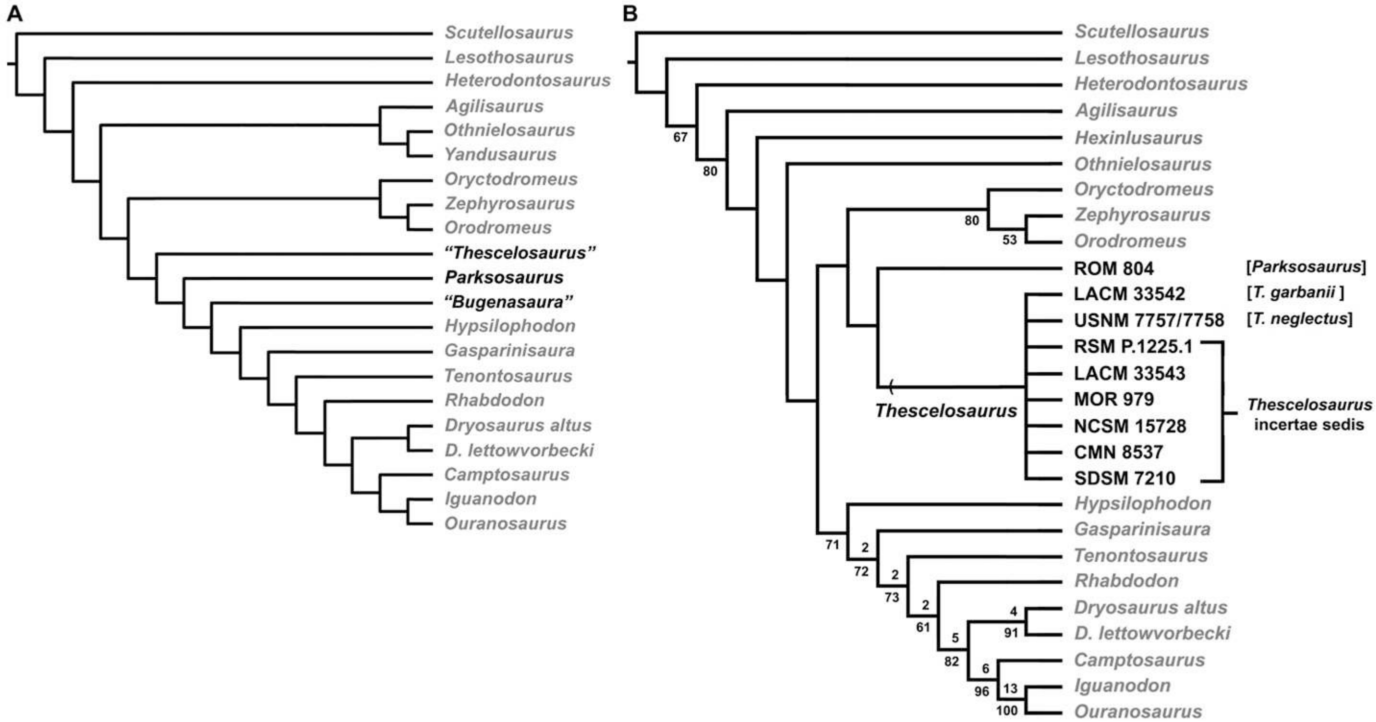


FIGURE 3. Phylogenetic analysis supporting the monophyly of a *Thescelosaurus* clade, synonymization of *Bugenasaura* with *Thescelosaurus*, and the placement of *Thescelosaurus garbanii* within a *Thescelosaurus* clade. **A**, single MPT from Varricchio et al. (2007); **B**, strict consensus of 748 MPTs with a length of 366, retention index (RI) of 0.67, and a consistency index (CI) of 0.50 resulting from analysis of the new dataset constructed for this investigation. On the second tree, Bremer support values are positioned above the nodes and bootstrap values are below the nodes. Quotations were added to *Thescelosaurus* and *Bugenasaura* in the Varricchio et al. (2007) tree to indicate that those terminal taxa were scored from both the type series and referred material. The taxonomic referrals of the nine terminals under investigation are listed to the right of their respective specimen numbers.

type series of *Thescelosaurus neglectus*, and six specimens previously referred to these taxa were included as terminals in this analysis (see the Table and Appendix 2 for the list of specimens and their respective scorings and Figure 2 for material preserved in each specimen). All characters were run unordered, but additional analysis demonstrated that alternative ordering of characters did not affect the placement of the nine terminals under investigation here (unpub. data). *Scutellosaurus* was selected as the outgroup taxon for this analysis because it has been consistently placed outside the Neornithischia by prior analyses (e.g., Sereno, 1986, Butler, 2005). The analysis was run in the program TNT (Goloboff et al., 2008) using the implicit enumeration search option that recovers all most parsimonious trees (MPTs). Seven hundred forty-eight MPTs (tree length = 366) were recovered and the resulting strict consensus tree is presented in Figure 3B. A bootstrap analysis (1000 replicates) was run and Bremer support values were calculated using PAUP*v.4.0b10 (Swofford, 2002). The results of this analysis are used to support the taxonomic referrals given in the Systematic Paleontology section below.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
ORNITHISCHIA Seeley, 1887
NEORNITHISCHIA Cooper, 1985 (sensu Sereno, 1998)
THESCELOSAURUS Gilmore, 1913

Bugenasaura Galton, 1995:308.

TABLE. Review of character data supporting synonymization of *Bugenasaura* with *Thescelosaurus* and for removing ROM 804, the holotype of *Parksosaurus warreni*, from *Thescelosaurus*.

Specimen	Original Taxonomic Assignment	Current Taxonomic Assignments	125	126	127	128	129	130	131	132	133
USNM 7757	*Thescelosaurus neglectus*	*Thescelosaurus neglectus*	—	—	—	—	—	1	—	—	—
USNM 7758	*Thescelosaurus neglectus*	*Thescelosaurus neglectus*	—	1	—	—	—	—	—	—	—
NCSM 15728	*Thescelosaurus neglectus*	*Thescelosaurus* sp.	1	1	1	1	1	—	1	1	1
MOR 979	*Bugenasaura infernalis*	*Thescelosaurus* sp.	1	—	—	—	1	1	1	1	1
SDSM 7210	*Bugenasaura infernalis*	*Thescelosaurus* sp.	1	—	—	—	—	—	1	1	—
CMN 8537	*Thescelosaurus edmontonensis*	*Thescelosaurus* sp.	1	1	1	—	1	1	—	—	—
LACM 33543	*Thescelosaurus neglectus*	*Thescelosaurus* sp.	—	—	1	1	1	—	—	1	—
RSM P.1225.1	*Thescelosaurus neglectus*	*Thescelosaurus* sp.	1	1	1	1	—	1	—	1	—
LACM 33542	*?Thescelosaurus garbanii*	*Thescelosaurus garbanii*	—	—	—	—	—	—	—	—	—
ROM 804	*Thescelosaurus warreni*	*Parksosaurus warreni*	—	0	—	—	0	0	0	0	0

The presence or absence of nine characters was traced: Seven proposed by Galton (1997, 1999; characters 125-131) and two new characters (132-133) identified in this analysis. Each character is described in Appendix 1 and listed by its respective number in the dataset. **Abbreviations**: **0**, character state zero is present (see Appendix 1); **1**, character state one is present (see Appendix 1); **-**, character state not preserved or unable to be scored.

Type Species—*Thescelosaurus neglectus* Gilmore, 1913.

Distribution—Frenchman Formation, Saskatchewan; Hell Creek Formation, Montana and South Dakota; Lance Formation, Wyoming; Scollard Formation, Alberta (all Maastrichtian age [70.6–65.5 Ma]; Weishampel et al., 2004; Gradstein et al., 2004).

Emended Diagnosis—Each of the characters proposed below is followed by (character number:state present) from Appendix 1 and illustrated in Figure 4. The following proposed autapomorphies comprise characters optimized as unique to a *Thescelosaurus* clade relative to all other analyzed taxa: frontals wider at midorbital level than across posterior margin (126:1); dorsolaterally directed process on surangular (129:1); prominent, horizontal ridge on maxilla with at least the posterior portion covered by a series of coarse, rounded, obliquely inclined ridges (131:1); depressed posterior half of ventral edge of jugal covered laterally with obliquely inclined ridges (132:1); foramen in dorsal surface of prefrontal dorsomedial to articulation surface for palpebral that opens into the orbit (133:1). Two additional characters are currently uniquely known for parts of the *Thescelosaurus* clade, but are unable to be evaluated for its sister taxon *Parksosaurus*: dorsal edge of opisthotic indented by deep, 'Y-shaped' excavation in dorsal view (127:1); palpebral dorsoventrally flattened and rugose along the medial and distal edges (125:1). The latter character is also present in an otherwise distinct basal neornithischian specimen from China housed at IVPP (CAB pers. obs.) whose relationships have not yet been evaluated. Only NCSM 15728 displays all proposed autapomorphies for *Thescelosaurus* (see Fig. 4 and Table), but subsets are preserved in all other referred specimens.

Two additional characters are optimized as local apomorphies of the *Thescelosaurus* clade, but occur convergently within major neornithischian subclades: angle between ventral margin of braincase (occipital condyle, basal tubera, and basipterygoid processes) and a line drawn through center of the trigeminal foramen and posterodorsal hypoglossal foramen less than fifteen degrees (128:1); and femur longer than tibia (130:1). The former is found in Iguanodontia and the latter occurs in both Iguanodontia and Marginocephalia.

Comments—As shown in the Table, the proposed diagnostic sets of characters identified by previous authors (Galton, 1997, 1999) from the type series of *Thescelosaurus neglectus* (USNM 7757, 7758) and the holotype of *Bugenasaura infernalis* (SDSM 7210) represent morphologies observed on distinct, non-comparable cranial elements preserved in these specimens. None of these previously proposed characters can be assessed in both the type series of *Thescelosaurus neglectus* and the holotype of *Bugenasaura infernalis*. No character conflict exists between these specimens or among any of the seven referred specimens examined here aside from ROM 804, which is placed outside of a *Thescelosaurus* clade (Fig. 3B). Thus, *Bugenasaura* is proposed to be a subjective junior synonym of *Thescelosaurus*, a conclusion that is also supported by

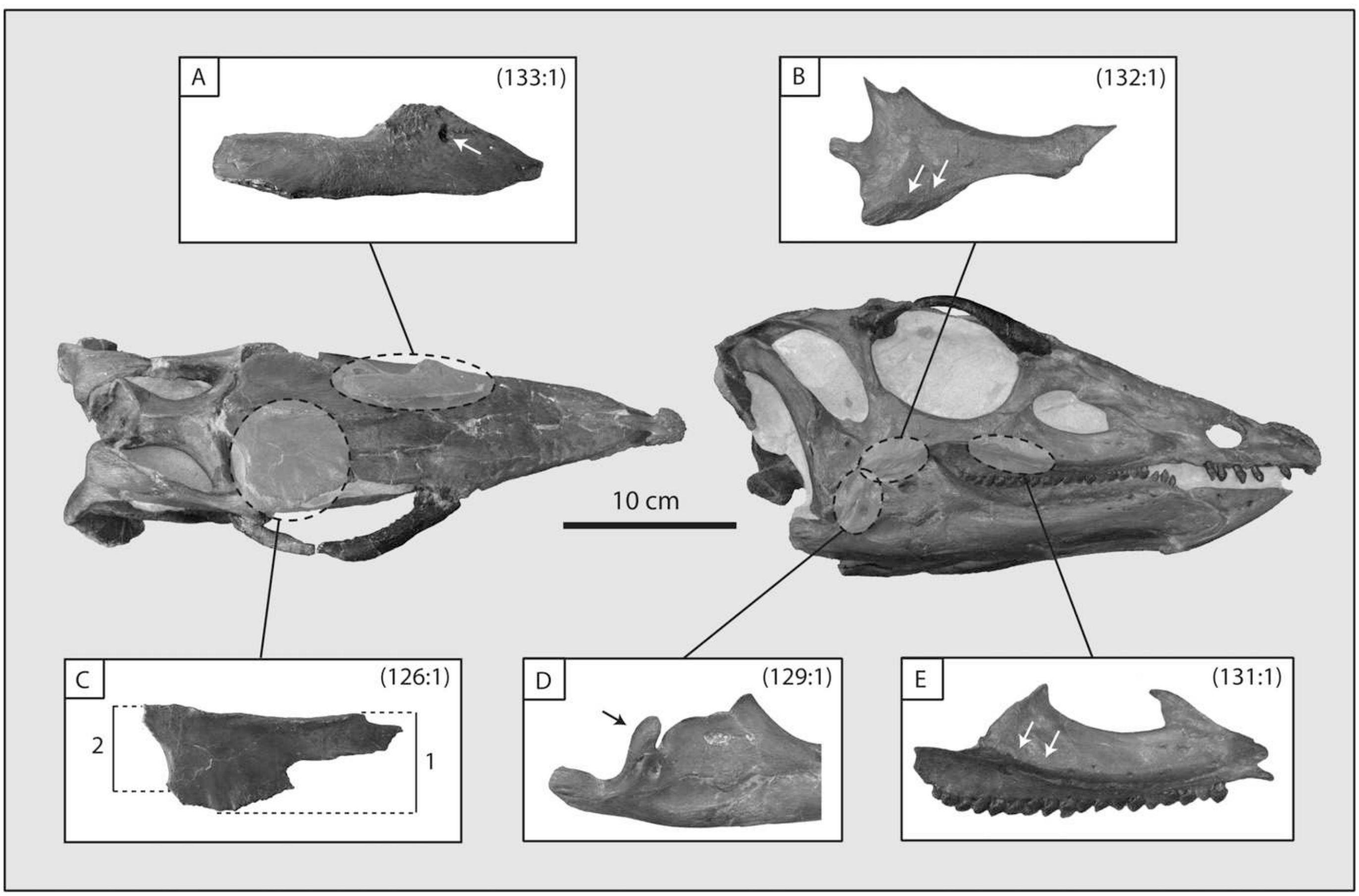


FIGURE 4. The five autapomorphies of *Thescelosaurus* as seen on the skull of NCSM 15728 in dorsal (left) and lateral (right) views. **A**, foramen in dorsal surface of prefrontal dorsomedial to articulation surface for palpebral that opens into the orbit (133:1); **B**, depressed posterior half of ventral edge of jugal covered laterally with obliquely inclined ridges (132:1); **C**, frontals wider at midorbital level (1) than across posterior end (2) (126:1); **D**, dorsolaterally directed process on surangular (129:1); **E**, prominent, horizontal ridge on maxilla with at least the posterior portion covered by a series of coarse, rounded, obliquely inclined ridges (131:1).

the placement of the holotype of *Bugenasaura infernalis* in a *Thescelosaurus* clade (Fig. 3B).

Three characters proposed by Galton (1997, 1999) to diagnose either *Thescelosaurus neglectus* or *Bugenasaura infernalis* were not found to diagnose a *Thescelosaurus* clade nor presently support species differentiation within that clade. These characters were not included in the analysis for the reasons described below. The presence of "numerous secondary ridges that form two converging crescentic patterns" on the maxillary and dentary teeth (buccal and lingual surfaces, respectively) was proposed by Galton (1997:253) to diagnose *T. neglectus*. This character was excluded because this morphology was found to vary across the maxillary and dentary dentition of individual specimens of *Thescelosaurus* (e.g., NCSM 15728). The degree of development of a prominent ridge on the dentary (proposed to diagnose *B. infernalis*; Galton, 1999) varies continuously between evaluated specimens. This variation, without discernibly distinct cutoffs, may be due to ontogenetic differences, but this hypothesis remains to be tested (see Discussion).

The degree of participation of the supraoccipital in the dorsal margin of the foramen magnum (proposed to diagnose *T. neglectus*; Galton, 1997) may be a useful character for analyzing the relationships of basal neornithischians and deserves further investigation. However, its distribution is complex and it does not appear to diagnose a *Thescelosaurus* clade or *T. neglectus*. For example, in RSM P.1225.1, the supraoccipital barely participates in the dorsal margin of the foramen magnum, but in LACM 33543 there is a notch in the dorsal border of the foramen magnum and the supraoccipital just touches the dorsal-most extent of this notch. The presence of this notch, along with other differences in the braincase of these specimens not discussed here, may later prove to be of diagnostic value at the species level within *Thescelosaurus*, but at this time sufficient data regarding the morphology of this region is not available from most specimens due to preservational issues and incomplete preparation.

THESCELOSAURUS NEGLECTUS Gilmore, 1913:1.

Holotype—USNM 7757: nearly complete postcranial skeleton.

Paratype—USNM 7758: fragmentary skeleton including parts of skull (Figs. 4, 5).

Locality—USNM 7757: Collected by J. B. Hatcher and W. H. Utterback in 1891 from Doegie Creek, Niobrara County, Wyoming. USNM 7758: Collected by O. A. Peterson in 1889 from Lance Creek, Niobrara County, Wyoming.

Distribution—Lance Formation of Wyoming (Maastrichtian age [70.6–65.5 Ma]; Weishampel et al., 2004; Gradstein et al., 2004).

Referred Specimens—None.

Emended Differential Diagnosis—This species differs from *Thescelosaurus garbanii* in: retention of calcaneum participation in midtarsal joint.

Emended Description of Type Series—Three previously unrecognized cranial bones were identified in material from paratype specimen USNM 7758. These consist of a partial left squamosal, partial left postorbital, and a fragmentary piece of frontal (Figs. 5, 6). Although all three of these bones are incomplete, sufficient morphological detail is preserved to provide important insights into the cranial anatomy of *Thescelosaurus neglectus*.

The dorsal surface of the squamosal is slightly inclined medially. The facet for the posterior ramus of the postorbital is dorsally directed (Fig. 5B) and the midpoint of the posterior edge of this facet is raised into a narrow flange that would have overlapped the midsection of the articulated postorbital (Fig. 5A, B). The postorbital would have been visible medial and lateral to this flange in dorsal view. In dorsal view, the posterior edge of

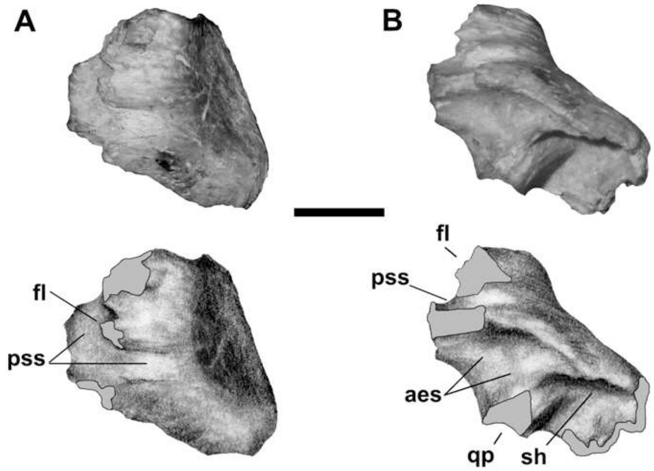


FIGURE 5. Squamosal from USNM 7758. **A**, photograph (top) and illustration (bottom) in dorsal view; **B**, photograph (top) and illustration (bottom) in lateral view. Areas shaded in grey indicate damaged regions of the bone. Scale bar equals 1 cm.

the squamosal is deeply concave (Fig. 5A). The lateral half of the postorbital-squamosal facet extends to the edge of this concavity as a broad, shallow groove. Ventral to this concavity the articulation surface for the paroccipital process (opisthotic) faces posterolaterally and consists of a raised, rugose surface. The quadrate facet is a deep socket dorsolaterally enclosed by a small wall of bone that would have covered the tip of the quadrate head in lateral view. The origin of the m. adductor externus superficialis (sensu Galton, 1974a) is developed as a conspicuous facet dorsal to the remains of the quadratic process and the edge of the lateral temporal fenestra (Fig. 5B). The ventrally directed quadratic process is not preserved, and the medial portion of the squamosal is also missing.

The postorbital is triradiate, but only the anterior ramus is completely preserved (Fig. 6A). The posterodorsal margin of the orbit is arcuate and marked with numerous small bosses that extend into the orbit (Fig. 6B). Near the base of the anterior ramus the edge of the orbital margin bears an anteroventrally

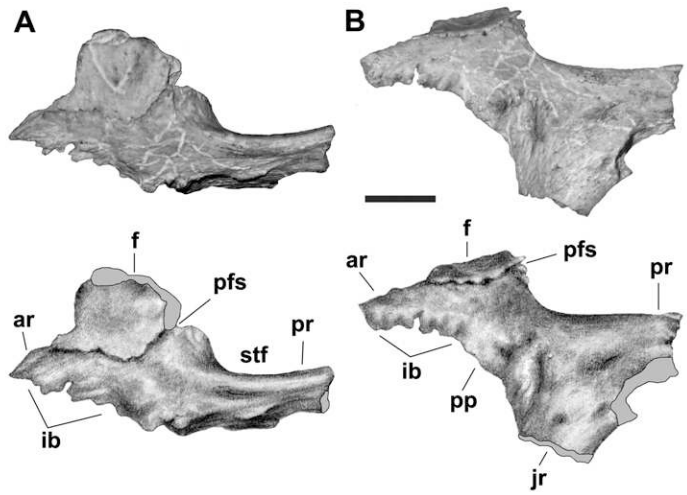


FIGURE 6. Postorbital and frontal from USNM 7758. **A**, photograph (top) and illustration (bottom) in dorsal view; **B**, photograph (top) and illustration (bottom) in lateral view. Areas shaded in grey indicate damaged regions of the bone. Scale bar equals 1 cm.

directed projection (Fig. 6B). An irregular, rugose, 'C-shaped' ridge of bone extends onto the lateral surface of this projection, possibly indicating a point of attachment for the palpebral or a secondary palpebral (if present). The ventrolateral surface of the postorbital is covered with a series of small ridges that vary in orientation and extend dorsally to a short horizontal ridge (Fig. 6B). The postorbital excludes the frontal from the anterolateral corner of the supratemporal fenestra (Fig. 6A). The articular surface for the frontal is complex, marked with a set of interlocking anteroposteriorly oriented ridges and grooves.

A small piece of the frontal is preserved that articulates with the preserved section of the postorbital. As noted, the surfaces of the postorbitofrontal contact bear interlocking anteroposteriorly-oriented ridges and grooves. The shape of the postorbitofrontal suture, specifically the lateral flaring of the anterior tip of the postorbital, indicates that the frontals would have been transversely wider at midorbit level than across their posterior end (Fig. 6A).

Comments—All characters previously proposed to differentiate the species *T. neglectus* by Galton (1997) are here found either to be synapomorphies of a clade *Thescelosaurus* (see above) or are broadly distributed within neornithischian taxa. Due to the fragmentary nature of the holotype of *T. garbanii*, the only other species of *Thescelosaurus* found to be valid by this analysis (see below), the anatomy of the hind limb and anterior vertebral column alone can be used to differentiate these two species. While *T. neglectus* is currently based on a differential diagnosis including a single character, further examination of the postcranial anatomy of this species and future referral of more complete specimens to *T. garbanii* may illuminate additional traits that will further differentiate these two species, or, ideally, diagnose *T. neglectus*.

THESCELOSAURUS GARBANII Morris, 1976

?Thescelosaurus garbanii Morris, 1976:100, figs. 3a–c, 5d–f.

Holotype—LACM 33542: Five posterior cervical and eleven anterior dorsal vertebrae, left pes, tarsus, tibia, fibula, and distal end of femur (Morris, 1976:figs. 3a–c, 5d–f; Galton, 1995:figs. 2e–f).

Locality—Discovered by Harli Garbani from LACM Locality v3152; T. 21N, R.42E, NE/2, NW/4, Sec. 22, Garfield County, Montana.

Distribution—Hell Creek Formation of Montana (Maastrichtian [70.6–65.5 Ma]; Weishampel et al., 2004; Gradstein et al., 2004).

Diagnosis—Autapomorphy of species: calcaneum excluded from midtarsal joint by laterally expanded astragalus.

Comments—Morris (1976) designated LACM 33542 the holotype of *?Thescelosaurus garbanii* based upon its general similarity to the hind limb of *T. neglectus*, but noted that the fragmentary nature of this specimen prevents the recognition of autapomorphies of any known basal neornithischian taxon. It was later tentatively referred to *Bugenasaura infernalis* by Galton (1995, 1999); however, LACM 33542 contains no elements directly comparable to the holotype of *B. infernalis*. The synonymization of *Bugenasaura* with *Thescelosaurus* places this species back within the latter taxon.

The exclusion of the calcaneum from the surface of the midtarsal joint is unique to LACM 33542, as indicated by comparisons to the structure of the tarsal region in CMN 8537, MOR 979, RSM P.1225.1, and USNM 7757. The analysis shown in Figure 3B places this specimen within a *Thescelosaurus* clade, supporting the prior tentative referral of this species to this taxon (Morris, 1976). These results support the recognition of *T. garbanii* as a valid species, though much of its anatomy remains poorly understood.

THESCELOSAURUS incertae sedis

Referred Specimens—CMN 8537, LACM 33543, MOR 979, NCSM 15728, SDSM 7210, RSM P.1225.1

Comments—The six referred specimens listed above each preserve multiple autapomorphies of *Thescelosaurus* (see Emended Diagnosis of *Thescelosaurus* and Table), but cannot be referred with certainty to one of the two species described above for reasons given below.

The holotype of *B. infernalis,* SDSM 7210, consists of an incomplete skull including premaxillae, maxillae, palpebral, prefrontal, lacrimal, jugal, quadratojugal, postorbital, ectopterygoid, pterygoid, dentary, surangular, coronoid, splenial, and prearticular as well as four dorsal vertebrae and two manual phalanges (see Fig. 2) collected from the Hell Creek Formation of South Dakota (Morris, 1976:figs. 5a–c; Galton, 1999:figs. 1–2, pl. 1). SDSM 7210 preserves neither the squamosal nor the tarsal region (Fig. 2), preventing direct comparison to the type series of *T. neglectus* and the holotype of *T. garbanii*. However, the discovery of specimens MOR 979 and NCSM 15728, which are indistinguishable from SDSM 7210, allow the morphology of SDSM 7210 to be indirectly compared to the holotype of *T. garbanii* and the type series of *T. neglectus*. The analysis in Figure 3B places this specimen within a monophyletic *Thescelosaurus* clade, supporting the synonymization of *Bugenasaura* with *Thescelosaurus*.

The synonymization of *Bugenasaura* with *Thescelosaurus* results in a new taxonomic combination: *Thescelosaurus infernalis*. This raises the question of whether the holotype (SDSM 7210) is sufficiently diagnostic or if this species should be considered a nomen dubium. Galton (1999) described two features of the premaxillae of SDSM 7210, which are damaged anteriorly, dorsally, posteriorly, and along much of the oral margin, that may distinguish this species from *T. neglectus*. Five alveoli are preserved on each side and extend to the anterior-most tip of the preserved portion of the premaxilla. Galton (1999) suggested that the close spacing of the anterior-most left and right alveoli ($\sim$ 5 mm) and their anterolateral orientation indicate this specimen only had five premaxillary teeth and may have lacked an anterior edentulous region. The only other specimen referred to *Thescelosaurus* that preserves a significant portion of the premaxillae is NCSM 15728. This specimen possesses elongate premaxillae that contain six alveoli and an anterior edentulous region that is approximately three tooth positions long. Computed Tomography (CT) scans of NCSM 15728 (CAB unpubl. data) show that the three anterior-most alveoli on each side arise within one millimeter of the premaxillary suture and extend anterolaterally from the midline. Therefore, the close spacing and orientation of the anterior-most alveoli in SDSM 7210 does not necessitate the presence of only five premaxillary teeth or the lack of an anterior edentulous region in this specimen; instead, it may indicate a significant loss of bone from the lateral and anterior portions of this element due to postmortem damage. No other unique features are recognized in this specimen. As a result, *T. infernalis* is considered a nomen dubium.

RSM P.1225.1 consists of a partial skull including a palpebral, frontals, parietal, a complete left squamosal (Fig. 7), a partial right squamosal, postorbital, pterygoid, dentary, and partial braincase as well as portions of the postcranial skeleton (Fig 2) collected from the Frenchman Formation of Saskatchewan (Galton, 1989:figs. 3g–l, 4k, pl. 4 [figs. 1–8]; Galton, 1997:figs. 3a–e, 4, pl. 1–2). The majority of the anterior ramus of the postorbital is not preserved, but enough of the orbital margin is present to determine a lack of irregular bosses seen in *T. neglectus*. The postorbital-squamosal suture on the squamosal is more anteriorly positioned than in *T. neglectus* (Fig. 7A). On the floor of this suture several anterioposteriorly-oriented ridges and grooves are present (Fig. 7A), unlike in *T. neglectus* where the

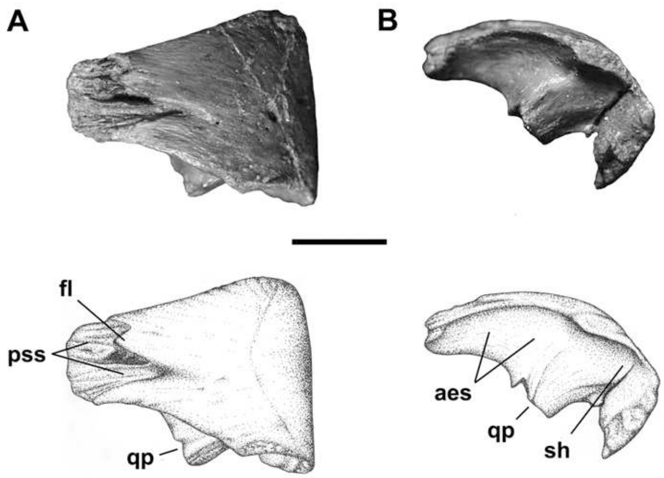


FIGURE 7. Squamosal from RSM P.1225.1. **A**, photograph (top) and illustration (bottom) in dorsal view; **B**, photograph (top) and illustration (bottom) in lateral view. Scale bar equals 1 cm.

floor of this facet is smooth. A portion of the posterior edge of this suture is raised into a narrow flange that would have slightly overlapped the midsection of the articulated postorbital (Fig. 7A). In dorsal view (Fig. 7A), the posterior edge of the squamosal is transversely wide and broadly convex, as opposed to the deep, dorsomedially directed concavity present in *T. neglectus*. In lateral view (Fig. 7B), the posterodorsal corner of the squamosal is broadly rounded as opposed to the angular condition observed in *T. neglectus* (Fig. 5B). This specimen differs from *Thescelosaurus garbanii* in that the calcaneum participates in the midtarsal joint.

Specimen RSM P.1225.1 appears to be distinctly different from *T. neglectus* (based on the squamosal and postorbital) and *T. garbanii* (based on the midtarsal joint). Despite these differences, we feel that erecting a new species for receipt of this specimen would be premature until the postcranial anatomy of this specimen is compared in more detail to *T. neglectus* and other specimens here referred to *Thescelosaurus*, in order to determine if additional differences exist. Also, this specimen displays some similarities to CMN 8537 (e.g., shape of the frontal), the holotype of *Thescelosaurus edmontonensis* (currently referred to *Thescelosaurus* incertae sedis), that may unite these two specimens as a single species. If this is the case, then *T. edmontonensis* would have taxonomic priority over a newer species based on RSM P.1225.1. Thus, until the anatomy of this specimen is examined in more detail and its relationship to CMN 8537 is clarified, this specimen should remain unnamed.

LACM 33543 consists of a partial skull including frontals, parietal, squamosal, partial braincase, ectopterygoids, jugals, and incomplete mandibles as well as a partial postcranial skeleton (see Fig. 2) collected from the Hell Creek Formation of Montana (Morris, 1976:figs. 1–2, 4; Galton, 1989:fig. 4k; Galton, 1997:figs. 3f, 5–7). The presence of two right jugals indicates that this specimen comprises material from two differently sized individuals (Morris, 1976). The squamosal was not described by Morris (1976) and only figured in lateral view by Galton (1997). The tarsal region is lacking and the squamosal has not been examined by the authors, preventing comparison to the holotype material of *T. garbanii* and *T. neglectus* as well as RSM P.1225.1.

CMN 8537, the holotype of *Thescelosaurus edmontonensis*, consists of a partial skull including frontals, parietal, postorbital, partial braincase, a mandible containing only replacement teeth, and associated premaxillary, maxillary, and dentary teeth along with a relatively complete postcranial skeleton (see Fig. 2) collected from the Scollard Formation of Alberta, Canada (Sternberg, 1940:figs. 1–18; Galton, 1974b:figs. 1a–i, pl. 1 [figs. 3–6, 9–12]; Morris, 1976: fig. 3e; Galton, 1995:figs. 1b–c,2b–d, 3; Galton, 1997:figs. 1–2). The calcaneum of CMN 8537 participates in the midtarsal joint, contrasting with the structure of the holotype of *T. garbanii*. The squamosals are not preserved and the postorbital is fragmentary, preventing detailed comparison to *T. neglectus*.

MOR 979 consists of a nearly complete skull, mandibles, and postcranial skeleton (see Fig. 2) collected from the Hell Creek Formation of Montana (Horner, 2001:unnumbered figure on p. 129). The postorbital differs from *T. neglectus* in lacking the irregular bosses extending into the orbit and from both *T. neglectus* and RSM P.1225.1 in lacking the anterior inflation into the orbit (Fig. 3B). The squamosals are damaged and incompletely prepared, preventing comparison to *T. neglectus* and RSM P.1225.1. The tarsal region of MOR 979 is intact and visible in lateral view on the right hind limb. The calcaneum is not excluded from the midtarsal joint, contrasting with the autapomorphic condition seen in *T. garbanii*. This specimen facilitated the indirect comparison of SDSM 7210 to the type series of *T. neglectus* and the holotype of *T. garbanii* as its cranial morphology is indistinguishable from that of SDSM 7210.

NCSM 15728, which preserves a complete skull, mandibles, and partial postcranial skeleton (see Fig. 2), was collected from the Hell Creek Formation of South Dakota (Fisher et al., 2000: figs. 1–2). This is the only specimen that preserves all five autapomorphies proposed here to diagnose a *Thescelosaurus* clade (Table). The postorbital differs from *T. neglectus* in lacking the irregular bosses along the orbital margin and the anteriolaterally directed bend at the tip of the anterior ramus of the postorbital. The general structure of the postorbital-squamosal suture more closely resembles that of *T. neglectus* than RSM P.1225.1. A prominent lateral expansion on the posterior edge of the squamosal is present, but this area is damaged in both *T. neglectus* and RSM P.1225.1. A large, anteriorly projecting sheet of bone on the squamosal arises from the posterior edge of the postorbital-squamosal facet and overlaps the medial two-thirds of the postorbital-squamosal suture, obscuring much of the medial and dorsal surfaces of the posterior ramus of the postorbital. This contrasts with the small, centrally placed flange of bone seen in *T. neglectus*. The structure of the squamosal distinguishes NCSM 15728 from both *T. neglectus* and RSM P.1225.1, but it lacks the necessary material to compare to *T. garbanii*. This specimen facilitated the indirect comparison of SDSM 7210 to the type series of *T. neglectus* as its cranial morphology is indistinguishable from that of SDSM 7210.

PARKSOSAURUS Sternberg, 1937

Type Species—*Thescelosaurus warreni* Parks, 1926.
Distribution—Horseshoe Canyon Formation, Alberta (Maastrichtian [70.6–65.5 Ma]; Weishampel et al., 2004; Gradstein et al., 2004).
Diagnosis—As for type and only known species.

PARKSOSAURUS WARRENI (Parks, 1926)

Thescelosaurus warreni Parks, 1926:figs. 1–18, pl. 1–2.
Parksosaurus warreni (Parks, 1926): Sternberg, 1937.

Holotype—ROM 804: partial skull and partial postcranial skeleton.
Locality—One half mile from the Red Deer River, on the east side, immediately south of the road to Rumsey ferry, 100 feet above the level of the water (Parks, 1926).
Distribution—Horseshoe Canyon Formation, Alberta (Maastrichtian [70.6–65.5 Ma]; Weishampel et al., 2004; Gradstein et al., 2004).
Referred Specimens—None.

Diagnosis—This species was diagnosed by Galton (1995) as follows: deep posterior process of premaxilla; extensive sutural contact between maxilla and nasal; small, oval antorbital fenestra; squamosal transversely wide; well-enamelled surface of cheek teeth has numerous low, rounded ridges. Further preparation and study of ROM 804 is currently underway by other authors (D. Evans pers. comm.) that will provide more information about the anatomy of this species.

Comments—*Parksosaurus warreni* was originally described by Parks (1926) as *Thescelosaurus warreni*, but was removed from *Thescelosaurus* by Sternberg (1937). One prior analysis (Fig. 1E) and the analysis presented in Figure 3B place *Parksosaurus* and *Thescelosaurus* as sister taxa, but this conflicts with the placement of these taxa in three other analyses (Figs. 1B–D). The holotype and only known specimen of *P. warreni*, ROM 804, lacks all of the proposed autapomorphies of *Thescelosaurus* described above (Table; characters 126, 129, 131, 132, and 133) and the presence or absence of two other characters (Table; characters 125 and 127) cannot be determined due to the preservation of this specimen. Based upon this evidence and the placement of ROM 804 outside of a *Thescelosaurus* clade (Fig. 3B), the removal of this species from *Thescelosaurus* is supported.

DISCUSSION

Newly recognized material from the paratype specimen of *Thescelosaurus neglectus* (USNM 7758) facilitated a taxonomic revision of all specimens that preserve cranial material previously referred to *Thescelosaurus*. For the first time six specimens (not including the type series of *T. neglectus* and the hypodigm of *T. garbanii*) are confidently referred to this taxon based upon the presence of shared apomorphies. These results shape future directions for the evaluation of basal neornithischian taxa and provide insight into the diversity of latest Cretaceous dinosaurian ecosystems in North America. They also raise questions about ontogenetic issues effecting further taxonomic revision of these and other basal neornithischian species.

This phylogenetic analysis is the first to recover a clade containing all known Cretaceous basal neornithischian taxa from North America, exclusive of all other taxa (Fig. 3B). The basalmost divergence within this clade is between two morphologically distinct subclades, one comprised of taxa proposed to be adapted to a fossorial mode of life (Varricchio et al., 2007) and the other that includes the relatively large-bodied *Thescelosaurus* clade. These two subclades are both morphologically and temporally distinct. The proposed fossorial *Orodromeus*, *Oryctodromeus*, and *Zephyrosaurus* have been recovered exclusively from sediments of Campanian age or older (70.6 Ma and older; Norman et al., 2004; Weishampel et al., 2004; Gradstein, 2004), while definitive fossil material referred to *Parksosaurus* and *Thescelosaurus* based on shared apomorphies is currently known only from the Maastrichtian (65.5-70.6 Ma; Weishampel et al., 2004; Gradstein, 2004), a fact that has been largely overlooked in the published literature. This temporal segregation may signify an important environmental change during the latest Cretaceous, as proposed by Lehman (2001 and references therein), that favored the larger-bodied forms such as *Parksosaurus* and *Thescelosaurus* over potentially fossorial taxa. Alternatively, this apparent temporal disparity may simply be a byproduct of the incompleteness of the fossil record. While this issue deserves detailed consideration by future investigations, the answer is beyond the scope of this discussion.

The specimens here evaluated and found to be part of a *Thescelosaurus* clade represent a marked range in size (approximately 2.5 to 4 meters; Fig. 2). Given this size range, the possibility that these individuals represent different ontogenetic stages of development must be taken into consideration in any taxonomic evaluation of these specimens. Differences noted between the type series of *T. neglectus* and RSM P.1225.1, which may represent a new species of *Thescelosaurus*, are considered potentially taxonomically informative because the similar size of these two specimens reduces the probability that they represent two distinct ontogenetic stages of the same species. By contrast, differences noted between the specimens here referred to *Thescelosaurus* incertae sedis must be examined with caution, as these specimens exhibit a much more disparate variation in size. Until either the ontogenetic stage of each of these specimens is determined or osteological changes that correlate with ontogenetic stage of development are identified, morphological differences noted between these specimens (e.g., shape of posterior margin of the frontals) should only be considered of diagnostic value when observed in specimens of similar size.

This investigation is a crucial step in a thorough reevaluation of the anatomy, ontogeny, and systematic position of the taxon *Thescelosaurus*. These results emphasize: (1) the need to base specimen referrals on shared apomorphies; (2) that erecting species based on specimens that lack material directly comparable to the hypodigm or type series material of known species should be avoided; and (3) that caution must be exercised when comparing specimens of differing size due to the possible effects of ontogeny. The next step in this process will be the thorough anatomical description of RSM P.1225.1 and NCSM 15728 that will seek to: (1) clarify the taxonomic relationships of these specimens; and (2) identify postcranial autapomorphies of the taxon *Thescelosaurus* to supplement the cranial characters identified above.

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APPENDIX 1. Description of characters used for the phylogenetic analysis of basal neornithischian relationships. See Scheetz (1999) for a detailed discussion of the distribution of character states for characters 1 through 123.

1. Length of jugal wing on quadrate greater than 20% quadrate length (0), less than 20% (1).
2. Quadrate notch absent (0), present (1).
3. Length of the articulation between the quadrate and quadratojugal greater than or equal to 50% length of quadrate (0), between 50% and 25% (1), contact 25% or less (2).
4. Dorsal head of the quadrate recurved posteriorly (0), straight (1).
5. Pterygoid wing on quadrate greater than 25% length of quadrate (0), less than 25% (1).
6. Jugal or quadratojugal meets the quadrate near the distal end (0), above distal end (1), well above distal end (2).
7. Ventral condyles of quadrate dorsomedially sloped or horizontal (0), dorsolaterally sloped (1).
8. Pterygoid wing emerges at the dorsal head of the quadrate (0), below the dorsal head of the quadrate (1).
9. The ventral extent of the jugal wing ends at or near distal condyles of quadrate (0), above distal condyles (1), well above the distal condyles (2).
10. Groove on the base of the posterior side of the pterygoid wing of the quadrate absent (0), groove or fossa present (1).
11. Lateral pit in mid-quadrate shaft present (0), absent (1).
12. Ventral process on squamosal less than 30% length of the quadrate (0), greater than 30% (1).
13. Quadrate leans posteriorly (0), oriented vertically (1).
14. Jugal fails to articulate with quadrate (0), jugal articulates with quadrate (1).
15. Quadratojugal height normal to short (0), tall and narrow (1).
16. Quadratojugal foramen absent (0), present (1).
17. Exoccipital contributes to part of occipital condyle (0), occipital condyle entirely composed of basioccipital (1).
18. Orbital edge of postorbital smooth (0), striated and rugose orbital edge (1).
19. Postorbital non-robust (0), robust postorbital (1).
20. Orbital margin of the postorbital arcuate (0), anteriorly directed inflation along upper half of the orbital margin of the postorbital (1).
21. Socket for the head of the laterosphenoid occurs along frontal-postorbital suture (0), only in postorbital (1), socket absent (2).
22. Combined width of frontals less than 150% frontal length (0), greater than 150%.
23. Frontals arched over the orbits (0), dorsally flattened frontals (1).
24. Frontal contacts orbit along more than 25% of total frontal length (0), less than 25% (1).
25. Ratio of frontal length to nasal length greater than 120% (0), between 120% and 60% (1), less than 60% (2).
26. Frontals positioned over all of orbit (0), frontals only over the posterior half of orbit (1).

27. Six premaxillary teeth (0), five premaxillary teeth (1), no premaxillary teeth (2).
28. Oral margin of the premaxila non-flared (0), slightly flared oral margin of the premaxilla (1), everted oral margin of the premaxilla (2).
29. Posterolateral recess in the posterior end of the premaxilla for receipt of the anterolateral boss of the maxilla absent (0), present (1).
30. Premaxilla does not contact lacrimal (0), premaxilla contacts lacrimal (1).
31. Non-packed maxillary teeth (0), lack of space between adjacent maxillary teeth up through the occlusional margin (1).
32. Maxillary and dentary teeth not inset (0), maxillary and dentary teeth at least modestly inset (1).
33. Maxillary tooth roots straight (0), curved (1).
34. Cingulum present on maxillary tooth crowns (0), no cingulum on maxillary teeth (1).
35. Distinct neck present below maxillary crown (0), crown tapers to root (1).
36. Maxillary teeth independently occlude (0), maxillary teeth form a continuous occlusal surface (1).
37. Maxillary teeth lingually concave (0), lingually convex (1).
38. Maxillary teeth with centrally placed apical ridge (0), posteriorly-set apical ridge (1).
39. Maxillary teeth equally enameled on both sides (0), enamel restricted to one side (1).
40. Anterior end of the maxilla exhibits a spike-like process that inserts into the posterior end of the premaxilla (0), anterior end of maxilla bears an anterodorsal sulcus to receive the posterior portion of the premaxilla (1).
41. Maxillary crowns relatively low spade-like, rectangular, or triangular (0), high diamond-shaped maxillary tooth crowns (1).
42. Jugal contacts antorbital fenestra (0), jugal excluded from bordering antorbital fenestra (1).
43. Greatest posterior expanse of the jugal greater than ¼ skull height (0), less than ¼ skull height (1).
44. Jugal horn or boss absent (0), present (1).
45. Anterior process of jugal straight (0), dorsally curved (1).
46. Maxillary process on the medial side of jugal medially projected and modestly arched (0), presence of a straight groove for insertion of the posterior flange of the jugal (1), anteromedially projected and arched (2).
47. Ectopterygoid articular facet on medial jugal consists of a deep groove (0), rounded scar (1).
48. In lateral view anterior end of jugal ends above maxilla (0), inserts within maxilla (1).
49. Jugal forms an oblique to right angle bordering the anteroventral corner of the infratemporal fenestra (0), acute angle (1).
50. Jugal barely touches lacrimal (0), jugal meets lacrimal with more contact (1), lacrimal-jugal butt joint (2).
51. Position of the anterior tip of dentary positioned high (0), mid height (1), near lower margin of dentary (2), below lower margin (3), well below lower margin (4).
52. Apical ridge on dentary teeth anteriorly or centrally positioned (0), posteriorly positioned (1).
53. Dentary tooth crowns possess primary and some secondary ridges (0), dentary crown possess primary, secondary, and tertiary ridges (1).
54. Dentary teeth possess ridges on both sides of crown (0), ridges on only one side (1).
55. Dentary teeth with enamel on both sides (0), enamel primarily on one side (1).
56. Dentary crowns possess denticles supported by ridges (0), not all denticles supported by ridges (1).
57. Dentary teeth possess a modest cingulum (0), no cingulum on dentary teeth (1).
58. Dentary tooth roots round in cross-section (0), oval (1), squared (2), squared and grooved (3).
59. Dentary tooth roots straight (0), curved (1).
60. Dentary crowns rectangular, triangular, or leaf-shaped (0), crowns lozenge-shaped (1).
61. Dentaries straight in dorsal view (0), dentaries arched medially (1).
62. Post-coronoid elements make up 35-40% of the total length of the lower jaw (0), 25-35% (1), less than 25% (2).
63. Ratio of dentary height (just anterior to the rising coronoid process) divided by length of dentary between 15-20% (0), 20-35% (1).
64. Predentary possesses a single posteroventral process (0), posteroventral process paired or bifurcate (1).
65. External mandibular fenestra present (0), absent (1).
66. Surangular foramen absent (0), present (1).
67. Dorsal margin of the surangular convex or diagonal (0), concave in lateral view (1).
68. Nuchal crest on supraoccipital present (0), absent (1).
69. Supraoccipital forms greater than 5% of the margin of the foramen magnum (0), less than 5% (1), does not contribute to dorsal margin (2).
70. Basioccipital ventral keel absent (0), present (1).
71. Foramen magnum occupies over 30% of the width of occipital condyle (0), 20-30% (1), less than 20% of occipital condyle (2).
72. Floor of braincase on basioccipital flat (0), arched (1).
73. Median ridge on floor of braincase on the basioccipital absent (0), present (1).
74. Basioccipital tubera extend further ventrally than the basisphenoid (0), level (1).
75. Basisphenoid shorter than basioccipital (0), equal in size (1), longer than basioccipital (2).
76. Foramen for cranial nerve V notches the anteroventral edge of the prootic (0), foramen nearly, or completely, enclosed in prootic (1).
77. Cervical vertebrae plateocoelous to amphicoelous (0), opisthocoelous (1).
78. Neural spine anteriorly positioned or centered over the dorsal centrum (0), posteriorly positioned (1).
79. Transition in dorsal ribs between a near vertical orientation of the tuberculum and capitulum to a horizontal orientation occurs within ribs 2-4 (0), 5-6 (1), 6-8 (2).
80. Twelve dorsal vertebrae (0), 15 dorsal vertebrae (1), 16 dorsal vertebrae (2), 17 dorsal vertebrae (3).
81. Four sacral vertebrae (0), five sacral vertebrae (1), six sacral vertebrae (2), seven sacral vertebrae (3).
82. Sacral neural spines less than twice the height of the centrum (0), neural spines between two and two and a half times the height of the centrum (1), greater than two and a half times (2).
83. Sacral spines lean posteriorly (0), slightly anteriorly (1).
84. Pubis does not articulate with the sacrum (0), pubis supported by sacral rib (1), pubis supported by sacral centrum (2).
85. Caudal ribs borne on centrum (0), on neurocentral suture (1), on neural arch (2).
86. Ossified hypaxial tendons on the tail absent (0), present (1).
87. First caudal vertebrae bears longest rib (0), longest rib posterior to the first (1).
88. Caudal neural spines positioned over centrum (0), neural spines extend beyond own centrum (1).
89. Scapular spine low or broad (0), sharp and pronounced (1).
90. Coracoid width divided by length less than 60% (0), between 70 and 100% (1), greater than 100% (2).
91. Coracoid foramen enclosed within coracoid (0), open along coracoid-scapula suture (1).
92. Sternals cresent-shaped (0), hatchet-shaped (1).
93. Olecranon process on ulna low (0), moderately developed (1), relatively high (2).
94. Shaft of ulna triangular or oval in cross section (0), cylindrical (1).
95. Shaft of ulna straight (0), bowed (1).
96. Manual phalangeal formula 2-3-4-3-0 (0), 2-3-4-2[3]-1 (1), 2-3-4-3-2 (2), 2-3-4-2-2 (3), 2-3-4-2-1 (4), 2-3-3-2-1 (5), 2-3-3-2-4 (6).
97. Unfused carpus (0), fused carpus (1).
98. Acetabulum high to normal (0), vertically short and long (1).
99. Ischiac peduncle of ilium not supported by sacral rib (0), ischiac peduncle articulates with sacral rib (1).
100. Shaft on ischium flat and blade-like (0), bar-like (1).
101. Distal end of ischium lacks an expanded foot (0), distal foot present (1).
102. Ischium lacks an obturator process (0), obturator process present and placed 60% down the shaft of ischium (1), placed 50% down the shaft (2), placed 40% down the shaft (3), placed with the proximal 30% of the ischial shaft (4).
103. Pubic peduncle of ischium larger than iliac peduncle (0), iliac peduncle of ischium as large or larger than pubic peduncle (1).
104. Anterior process of pubis absent (0), present and rod-like or sword like (1), dorsoventrally expanded prepubis (2).
105. Anterior process of pubis straight when present (0), upturned anterior process (1).
106. Femur lacks a neck-like constriction below the femoral head (0), constriction present (1).
107. Lesser trochanter of femur lower or equal to greater trochanter (0), higher than greater trochanter(1).
108. Lesser trochanter of femur anterior and medial of greater trochanter (0), anterior and somewhat lateral to lesser trochanter (1).

109. Greater trochanter of femur laterally convex (0), laterally flattened (1).
110. Anterior intercondylar groove on the distal femur absent (0), modest intercondylar groove present (1), well-developed intercondylar groove (2).
111. Lateral distal condyle width divided by medial distal condyle width on femur approximately 100% (0), 80-60% (1), 59-50% (2), 49-40% (3), 39-30% (4), 29-20% (5).
112. Both proximal lateral condyles on the tibia equal in size (0), fibular condyle smaller (1), only one lateral condyle present (2).
113. Cnemial crest of tibia rounded (0), sharply defined (1).
114. Midshaft of tibia triangular in cross-section (0), round in cross-section (1).
115. Fibula shaft elliptical or round in cross-section (0), D-shaped in cross-section (1).
116. Astragalus bears a short ascending process (0), triangular and tooth-like (1), spike-like (2), relatively large (3).
117. Posterior side of astragalus low (0), high (1).
118. Anterior side of astragalus high (0), moderate (1), low (2).
119. Angle between the tibial and fibular articular facets on the calcaneum greater then 120 degrees (0), less than 120 degrees (1).
120. Medial distal tarsal blocky in dorsal view (0), thin and rectangular (1), round (2).
121. Medial distal tarsal does not articulate over the proximal end of metatarsal II (0), medial distal tarsal articulates over a least a portion of the proximal end of metatarsal II (1).
122. Lateral distal tarsal square in dorsal view (0), kidney-shaped (1).
123. Four functional (i.e., bear phalanges) digits in the pes (0), three functional digits in the pes (1).
124. Premaxillae unfused (0), fused (1).
125. Palpebral dorsoventrally flattened and rugose along the medial and distal edges: absent (0), present (1).
126. Frontals wider across posterior end than at midorbit level (0), wider at midorbital level (1).
127. Presence of a 'Y-shaped' indentation on the dorsal edge of opisthotics: absent (0), present (1).
128. Angle formed by a line drawn along the ventral edge of the braincase (occipital condyle, basal tubera, and basipterygoid processes) and a line drawn through center of the trigeminal foramen and posterodorsal hypoglossal foramen: greater than fifteen degrees (0), less than fifteen degrees (1).
129. Dorsolaterally directed process on the lateral surface of the surangular: absent (0), present (1).
130. Ratio of femur length to tibia length: less than one (0), greater than one (1).
131. Presence and structure of a horizontal ridge on the maxilla: absent or smooth when present (0), present with at least the posterior portion covered by a series of obliquely inclined ridges (1).
132. Posterior half of ventral edge of jugal offset ventrally and covered laterally with obliquely inclined ridges: absent (0), present (1).
133. Foramen in the prefrontal positioned dorsomedial to the articulation surface for the palpebral that opens into the orbit: absent (0), present (1).

APPENDIX 2. Character codings for the 27 terminal taxa used in the analysis shown in Figure 3B. Modified from Scheetz (1999) and Varricchio et al. (2007). Question marks indicate lack of information for that taxon.

	1 0	2 0	3 0	4 0	5 0	6 0	7 0
Scutellosaurus	??????????	??????0000	??????00??	00?000000?	0?????????	0000000000	0?000?????
Heterodontosaurus	?00000??0?	000000?0?0	?0001000?1	11??11?00?	00010??001	0001101100	001000000?
Lesothosaurus	000000000?	0000000000	0000000000	0000000100	00000??001	0000000000	0000000000
Agilisaurus	?001??????	???000????	?0001011??	01?000?10?	01?01??110	??????????	????10????
Hexinlusaurus	0000??????	??10000001	?00010???0	?1?000?10?	01100??11	1?0??????0	1?0???00?
Othnielosaurus	??????????	??????0000	?00??0????	010000010?	0???0???1?	1000000000	1?001????0
Zephyrosaurus	0010001001	01?0??0101	0010?0101?	1100001?00	0?1110000?	?000000000	1?1????001
Orodromeus	0010001101	0100000101	1000?0111?	0100000000	0111000002	2000000000	1010110101
Parksosaurus	001?01?010	1000000000	?01010???0	011000110?	01000??11	?000000000	011011??0?
Hypsilophodon	000002002?	?000010?0	0000101000	1100111110	01000??111	2011110010	111011?001
Tenontosaurus	0000100?00	0011010??0	10101022?0	1111111110	01000??111	2001111211	001111?121
Dryosaurus altus	0120020100	?011000??0	1000102200	1111111111	1000010001	2111111111	1011101001
Dryosaurus lettowvorbecki	1120020121	1011000???	?000102201	??????????	???0010101	2111111111	1011111001
Rhabdodon	?010?10000	1?????????	??????200?	11?1?11100	0?????????	1001101210	1?11111??1
Iguanodon	1101120120	1010101?10	2111212201	1111111111	1100021112	4111111311	1201111020
Ouranosaurus	110112002?	?010101010	1111212201	11?????1?1	?010021112	3111???11	1100111120
Camptosaurus	01?0120120	1111?00010	1011102201	1111111111	1100001111	3111111311	1111111000
Gasparinisaura	1000?2??2?	?00011?000	??00??????	11?111?1??	11?00??1?1	3?????????	?01?110000
Oryctodromeus	001???1000	??????????	??????111?	010000???0	0??001??1?	200???0?00	1?0????001
USNM 7757/7758	??????????	???????101	??????????	??????????	??????????	??????????	??????????
RSM P.1225.1	??????????	??????0?0?	??1??0????	??????????	??????????	??????????	???????101
LACM 33542	??????????	??????????	??????????	??????????	??????????	??????????	??????????
SDSM 7210	??????????	????????0?	???????2??	11?000??0?	01?00?00?2	?0?0000?10	?????10???
NCSM 15728	1?1001??1?	0000010101	?010100210	110?00?1?0	01100?0012	20?00001?0	0111110111
MOR 979	??11?00???	?01000?000	?000?0???0	11??00??0?	01100???02	2???00???0	0????00?1?
CMN 8537	??????????	???????001	?00???????	????0??10?	0?????????	20?000???0	0?1?110?1?
LACM 33543	??????????	??????0???	??0???????	??????????	?1?00?????	2?????????	0?????0111

(*continued*)

APPENDIX 2. (*Continued*).

	80	90	100	110	120	130	133
Scutellosaurus	??????????	1????0??01	0?0??00??0	0?1??00001	0????0????	??00?????0	???
Heterodontosaurus	???0?0??00	0???0000?1	??200200?0	100000?100	0?0??????0	0000000000	000
Lesothosaurus	00??10????	2????0?0?1	0?00010000	0000000000	00???3?001	0?000000?0	000
Agilisaurus	?????????1	1???10??0?	0??????110	03?110010?	?????0????	0?0000??00	000
Hexinlusaurus	0?????00?1	1???1??1?1	0?000?0??0	0301000100	??0?01???1	1?0?00???0	000
Othnielosaurus	101???00?1	100010?101	000?0?0010	0301010100	1?00?21011	1100?????0	???
Zephyrosaurus	110120000?	???210?111	0?00???1?0	????10111	1?00100201	10010000?0	000
Orodromeus	1101110001	2002100111	00110?0110	0201010110	1000120001	100000??00	000
Parksosaurus	01???0?0?2	2???12010?	00??????10	0111110110	??0??0?0?1	??0??0??00	000
Hypsilophodon	01?010?001	2001121101	1010130010	0101010100	2100010011	1100000000	000
Tenontosaurus	20?0001112	1100110101	0000150110	1312110102	3201000211	1000000001	000
Dryosaurus altus	2000011111	2100200100	10100?1111	1402111102	3100?31011	1110000000	000
Dryosaurus lettowvorbecki	21002111?1	2?01201100	10101????1	1402111102	3????31?1?	0?10000000	000
Rhabdodon	?000??01??	210210?100	0?101??111	101??10102	2200?012?2	0110??????	???
Iguanodon	2000201123	2201101102	112?061111	1412110102	5211001202	01100001?1	???
Ouranosaurus	00002?1123	22??0??102	11210?1110	1412100102	4211001212	??10000001	000
Camptosaurus	2011000102	22101?1101	1010121111	1412110102	?20100120?	0?10000101	000
Gasparinisaura	2?????????	1001110101	0???0??110	?311011110	1201000212	11100???00	00?
Oryctodromeus	110??11121	30022?1111	0?100??11?	???1010110	?100100???	???1??0??0	?0?
USNM 7757/7758	???????0?2	1?00?1?1??	??00?20010	0?11110111	??00??0???	1?0??1???1	???
RSM P.1225.1	0??1?0?0??	?????1?1??	???????01?	???1110111	??00??0???	??0?1111?1	?1?
LACM 33542	??????????	??????????	??????????	?????????1	??000000?1	1?0???????	???
SDSM 7210	??????????	??????????	??????????	??????????	??????????	???01?????	11?
NCSM 15728	0??1?110??	3000?11100	0000??0010	0301110111	2?????????	???11111?	111
MOR 979	??????????	??0??11?00	0?00??00?0	0??1?101??	??000000?1	??0?1???11	111
CMN 8537	?????????2	2?0??11100	0??????010	0??111011?	??0????0??	????111?11	???
LACM 33543	0??????1??	??????????	???????010	030?1?????	??????????	??????111?	?1?