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Editors' choice

The early fossil record of dinosaurs in North America: A new neotheropod from the base of the Upper Triassic Dockum Group of Texas

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The dinosaur record from the stratigraphically-lowest portions of Upper Triassic deposits of western North America is poor and only consists of a handful of fragmentary hind limb elements. Here we present an articulated segment of the ankle region of a dinosaur that consists of the distal ends of the tibia and fibula and a complete astragalocalcaneum. Additionally, we suggest that an isolated femur and maxilla from the same locality may belong to the same taxon. Using the most comprehensive analysis of early theropod relationships currently available, we determined that the new specimen pertains to a coelophysoid neotheropod (i.e., more closely related to *Coelophysis bauri* than to *Allosaurus fragilis*). The stratigraphic position of the locality where the new specimen was discovered is equivalent to the famous Otis Chalk localities and this set of localities likely predates the rest of the Dockum Group and possibly the entirety of the fossiliferous portion of the Chinle Formation on the Colorado Plateau. Therefore, the new specimen represents one of the oldest neotheropods. Accordingly, neotheropods were present at or just after the onset of both the Chinle Formation and Dockum Group deposits.

Key words: Dinosauria, Archosauria, Neotheropoda, phylogeny, Norian, Otis Chalk, North America.

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Introduction

The early dinosaur record from the Upper Triassic has greatly improved over the last twenty five years (Brusatte et al. 2010; Langer et al. 2010; Irmis 2011; Benton et al. 2014; Langer 2014). Specifically, the well preserved and nearly complete remains of early saurischian dinosaurs from the Ischigualasto Formation in Argentina (Casamiquela 1967; Sereno and Novas 1992; Sereno et al. 1993; Martínez and Alcober 2009; Ezcurra 2010a; Martinez et al. 2011) and Santa Maria sequence in southern Brazil (Colbert 1970; Bonaparte 1999; Langer et al. 1999; Leal et al. 2004; Cabreira et al. 2011) have greatly improved our understanding of the detailed anatomy, phylogenetic relationships, and character transformations among the earliest members of Dinosauria. The wealth of information derived from the most complete early dinosaurs from these deposits now allows more fragmentary records of dinosaurs from other portions of Pangea to be incorporated into larger studies of early dinosaur macroevolutionary patterns (e.g., Brusatte et al. 2008).

The record of early dinosaurs from the Upper Triassic of the western portion of North America is relatively poor compared to the South American record, and only two species-level taxa (*Coelophysis bauri*, Colbert 1989 and *Tawa hallae*, Nesbitt et al. 2009b) are known from both substantial cranial and postcranial material. Nearly the entire record of the early dinosaurs from North America consists of fragmentary or isolated limb bones (e.g., Hunt et al. 1998; Nesbitt et al. 2007; Nesbitt and Chatterjee 2008) or partial skeletons consisting of mainly hindlimb material (Padian 1986). Although the record is fragmentary, a number of substantial revisions of previous identifications (e.g., Ezcurra 2006; Nesbitt and Chatterjee 2008) of a higher diversity of early dinosaurs (Hunt et al. 1998) determined that the Upper Triassic dinosaur record of North America consists solely of what are currently considered theropod dinosaurs (Nesbitt et al. 2007; 2009b; Irmis et al. 2007a; Ezcurra and Brusatte 2011). Of the

published records, most occur in the upper half of the Chinle Formation and Dockum Group, and comparatively very few specimens have been identified from the lower portion of these Upper Triassic units. *Camposaurus arizonensis* (Hunt et al. 1998; Ezcurra and Brusatte 2011), a specimen from the *Placerias* Quarry in eastern Arizona, is the only named dinosaur from lower part of the Chinle Formation, dated to ~220 Ma (Ramezani et al. 2014), and thus far, no theropod has been reported from the equivalent or possibly older deposits of the Dockum Group.

Here we describe an articulated tibia, fibula and astragalocalcaneum of a dinosaur attributed to a new taxon of neotheropod dinosaur from near the famous Otis Chalk localities in the Dockum Group in western Texas, USA (Fig. 1). An isolated partial maxilla and isolated partial femur collected at the same locality may either belong to the same individual or species-level taxon. Within the Dockum Group, the stratigraphic position of this locality is hotly debated, but appears to be one of the lowest vertebrate producing localities in the Dockum Group and, in turn, the specimen may be one of the oldest neotheropod records to date.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; CM, Carnegie Museum of Natural History, Pittsburg, USA; GR, Ghost Ranch Ruth May Museum of Paleontology, Ghost Ranch, USA; MB, Museum für Naturkunde der Humboldt Universität, Berlin, Germany; MCP, Museu de Ciências e Tecnologia, Porto Alegre, Brazil; NMT, National Museum of Tanzania, Dar es Salaam, Tanzania; PEFO, Petrified Forest National Park, Petrified Forest, USA; PULR, Paleontología, Universidad Nacional de La Rioja, Argentina; PVSJ, División de Paleontología de Vertebrados del Museo de Ciencias Naturales y Universidad Nacional de San Juan, Argentina; QG, Zimbabwe Natural History Museum, Bulawayo, Zimbabwe; SAM, Iziko South African Museum, Cape Town, South Africa; TMM, Vertebrate Paleontology Laboratory, University of Texas at Austin, USA; UCMP, University of California Museum of Paleontology, Berkeley, USA; ZPAL, Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland.

Other abbreviations.—CI, consistency index; LAG, line of arrested growth; MPT, most parsimonius tree; RI, retention index.

Geological and geographical setting

The exact geographic coordinates of the locality (Dockum Site 7 General = HO-7-1-41; locality TMM 41936) of the new dinosaur specimen is unknown, but was reported to occur about eight miles southeast of Big Spring, Howard County, Texas (TMM archives). The locality was discovered and collected by the Works Progress Administration paleontology team tasked to collect vertebrate fossils in Texas from

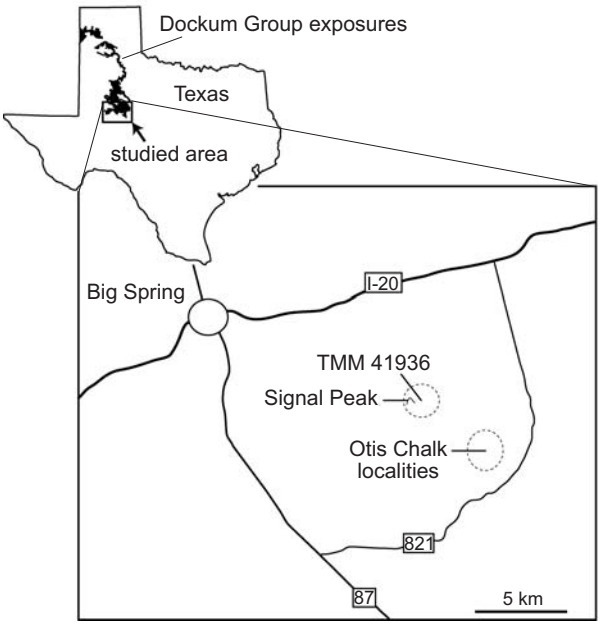


Fig. 1. Map of the type locality of *Lepidus praecisio* gen. et sp. nov. near Signal Peak, southeast of Big Spring, Texas. The dotted circle is the approximate area that holotype came from and its relationship to the famous Otis Chalk localities.

1939−1941. According to the field logs of the 1941 work in Howard County, Texas, Dockum Site 7 General (locality TMM 41936), its fossils were collected during the middle of February of 1941 (TMM unpublished field report).

Using Google Earth (accessed on 30 April 2014) and 7.5 minute topographical maps (provided by the U.S. Geological Survey), we were able to deduce that the specimens were mostly likely found in the vicinity of Signal Peak (Moss Creek Lake Quadrangle, Texas-Howard Co., 7.5 minute series). Here, the Triassic exposures occur on the edges of the eponymous topographic feature and in small outcrops in the immediate area. The Triassic beds in this area are mapped as the same unit as those in the classic Otis Chalk localities (Lehman and Chatterjee 2005), a set of highly fossiliferous localities that have produced tens of species-level taxa (Gregory 1945; Elder 1978; Stocker 2013a) and the assemblage form the basis for the Otischalkian land-vertebrate faunachron (Hunt and Lucas 1991; Lucas 1998). Higher stratigraphic units or vertebrate fossils indicating a younger age (e.g., the phytosaur *Machaeroprosopus pristinus*) have not been reported from the area.

The correlation of exposures of Upper Triassic strata in the area of Otis Chalk, Howard County (~15 miles east southeast of Big Spring; Fig. 1), to the rest of the Dockum Formation remains unresolved because of the lack of outcrop linking the Otis Chalk area to other sections of the Dockum Group. For example, Lehman (1994) correlated the exposures of Triassic rocks in the Otis Chalk area with the Cooper Canyon Member found around Post, Texas (Garza County) in the middle part of the Dockum Group, based on lithostratigraphy, whereas Lucas and Anderson (1993a, b) correlated

the exposures of Triassic rocks in the Otis Chalk area to the base of the Dockum Formation (= "pre-Tecovas horizon") based on biostratigraphy. Recent interest in correlating the Otis Chalk fossil beds with the rest of the Dockum Formation has resulted in somewhat of a compromise between the two entrenched hypotheses. Martz (2008), followed by Stocker (2013a), hypothesized that the Cooper Canyon Member encompasses nearly all of the Upper Triassic strata in Garza County to Howard County, Texas, and that the Otis Chalk localities, and surrounding area, should be correlated to near the base of the Cooper Canyon Member. Therefore, based on current knowledge of correlations of Dockum Group strata, the Otis Chalk localities are located low in the Dockum Group.

As with the stratigraphic level of the Otis Chalk localities, the age is also difficult to narrow down because there are no radioisotopic dates available for the Dockum Group. Currently, the age of the Otis Chalk localities is only calculated based on biostratigraphy of vertebrates (Hunt and Lucas 1991; Stocker 2013a, b). The presence of *Paleorhinus* (sensu Stocker 2013a, b; Butler et al. 2014) at the Otis Chalk localities with the absence of *Leptosuchus* (sensu Stocker 2010) suggest an age older than that recovered from the leptosuchomorph-bearing strata of the Blue Mesa Member of the Chinle Formation (Parker and Martz 2011). Given that the base of the Blue Mesa Member has been radiometrically dated to ~223 Ma (Irmis et al. 2011; Ramezani et al. 2011, 2014), the Otis Chalk localities are probably at least older than 223 Ma, or at the youngest, lower Norian. Additionally, palynomorphs have not been reported from the Otis Chalk area, thus hampering independent means of correlation. The age of the Otis Chalk localities could be older, but at this time it is not clear without any means of temporal evaluation from biostratigraphically-independent data (Stocker 2013a).

Material

All of the specimens from TMM 41936 were found on the surface and none of the bones were collected in situ. The red mudstone matrix covering each specimen, the quality of bone preservation, and the white to yellow general color of each specimen indicates that all of the specimens originated from the same locality and general horizon, as described in the field reports of Grayson Meade (TMM unpublished field report). Dozens of fragments were collected, including limb bone fragments, unidentified fragments, the theropod material described here, and dozens of small archosauromorph vertebrae. Few of the elements are identifiable beyond Archosauromorpha. Nonetheless, we have positively identified from this assemblage the theropod described here, a pseudosuchian tibia that shares synapomorphies with shuvosaurids (TMM unnumbered; Nesbitt 2007), a partial phytosaur premaxilla (TMM unnumbered), and the distal end of a drepanosaurid femur (TMM unnumbered).

Systematic paleontology

Archosauria Cope, 1869 sensu Gauthier and Padian 1985

Theropoda Marsh, 1881 sensu Gauthier 1986

Neotheropoda Bakker, 1986 sensu Sereno 1998

Coelophysoidea Nopsca, 1928 sensu Sereno et al. 2005

Genus *Lepidus* nov.

Type species: *Lepidus praecisio* gen. et sp. nov.; monotypic, see below.

Etymology: From Latin *lepidus*, fascinating, gender masculine.

Diagnosis.—As for the type species.

Lepidus praecisio sp. nov.

Fig. 2.

Etymology: From Latin *praecisio*, fragment or scrap; in reference to the common preservation of early dinosaurs from North America as bony fragments.

Holotype: TMM 41936-1.3, articulated distal ends of the left tibia and fibula and a left astragalocalcaneum (Fig. 2).

Type locality: Dockum Site 7 General (TMM locality 41936), just northeast of the classic Otis Chalk localities, Howard County, Texas (see above) (Fig. 1).

Type horizon: Otis Chalk area, Dockum Group, Upper Triassic

Referred material.—TMM 41936-1, fragment of left femoral shaft (Fig. 3), TMM 41936-1.1, partial left maxilla (Fig. 4).

Diagnosis.—*Lepidus praecisio* gen. et sp. nov. possesses an autapomorphically well-developed posterior pyramidal process on the astragalus that delimits the posterolateral margin of the tibial facet and the posteromedial portion of the facet of the fibula, and is separated from the proximal surface of the calcaneum by a shallow notch that opens dorsolaterally. Additionally, *Le. praecisio* shares the following combination of plesiomorphic and synapomorphic character states with Neotheropoda (character enumeration follows that of Nesbitt et al. 2009b and Ezcurra and Brusatte 2011): fused astragalus and calcaneum (283-1); low anterior ascending process of the astragalus (273-1); calcaneum mediolaterally compressed (291-1); proximodistally extended ridge on the posteromedial surface of the tibia (256-1); distinct scar on the anterior surface of the distal end of the tibia (333-1).

Furthermore, *Le. praecisio* can be differentiated from other Upper Triassic North American theropods by other features beyond the autapomorphies listed above. *Lepidus praecisio* is differentiated from *Camposaurus arizonensis* by the lack of an oval depression (= medial fossa of Ezcurra and Brusatte 2011) on the medial surface of the astragalus. *Lepidus praecisio* is differentiated from *Coelophysis bauri*, the "Padian *Coelophysis*" (UCMP 129618), and *Chindesaurus bryansmalli* by the less laterally expanded posterolateral process (= lateral malleolus) of the distal end of the tibia. *Lepidus praecisio* is differentiated from *Tawa hallae* by the

presence of a proximodistally oriented ridge on the posteromedial surface of the tibia.

Description.—TMM 41936-1.3: The articulated tibia, fibula and astragalocalcaneum of *Le. praecisio* are well preserved with fine details of muscle scars and articulation surfaces (Fig. 2). The astragalus and the calcaneum are clearly fused together with no sign of any sutural surface or cleft. The fibula is in articulation with the astragalocalcaneum whereas the tibia is in near articulation with the astragalocalcaneum but slightly displaced laterally by about 0.5 millimeters.

Tibia: In overall morphology, the tibia resembles that of neotheropods. The anterior surface of the bone has a very well developed tuberosity just proximomedially to the anterior ascending process of the astragalocalcaneum (= anterior diagonal tuberosity of Ezcurra and Brusatte 2011) (Fig. 2). The tuberosity is well pronounced from the anterior surface of the tibia and the external surface consists of striated bone fibers oriented proximolaterally. A similar tuberosity, but comparatively less-developed, is present in the same position in *Camposaurus arizonensis* (Ezcurra and Brusatte 2011), the Hayden Quarry coelophysoid (GR 227), *Coelophysis bauri* (AMNH FR 30614, 30615) and *Coelophysis rhodesiensis* (cast of QG 1) but absent in *Tawa hallae* (Nesbitt et al. 2009), *Eodromaeus murphi* (Martinez et al. 2011), and *Herrerasaurus ischigualastensis* (PVSJ 373). The facet for reception of the ascending process of the astragalus of TMM 41936-1.3 is straight and slanted proximomedially at an angle about 15° to the mediolateral horizontal plane in anterior view. The medial surface of the tibia lacks the diagonal, anteriorly bowed tuberosity present in *Ca. arizonensis* (Ezcurra and Brusatte 2011), the Hayden Quarry coelophysoid (GR 227), and more weakly developed in *Co. rhodesiensis* (cast of QG 1). The distal end of the tibia possesses a distinct proximodistally oriented ridge on the posteromedial surface (Fig. 2), as occurs in neotheropods (Langer and Benton 2006) and *Eodromaeus murphi* (PVSJ 562), but absent in *T. hallae* (Nesbitt et al. 2009), *Chindesaurus bryansmalli* (PEFO 33982), and *H. ischigualastensis* (PVSJ 373). The lateral malleolous of TMM 41936-1.3 is weakly developed beyond the shaft of the tibia and is lobe-shaped in posterior view, contrasting with the more expanded and tabular-shaped process of *Zupaysaurus rougieri* (Ezcurra and Novas 2007), *Liliensternus liliensterni* (MB R2175), and *Co. bauri* (Colbert 1989: AMNH uncatalogued). The posteromedial corner of the distal end has a distinct notch for reception of a posteromedial process on the astragalus, as occurs in several neotheropods (e.g., *Co. bauri*, AMNH FR 7239) but not in *T. hallae* (Nesbitt et al. 2009b) and *H. ischigualastensis* (PVSJ 373). The notch in *Le. praecisio* is considerably deeper in *Li. liliensterni* (MB R2175) and *Zupaysaurus rougieri* (Ezcurra and Novas 2007). Furthermore, the presence of the notch creates a sigmoidal articulation (ventrally concave on the anterior half and convex posteriorly) surface with the astragalocalcaneum when viewed in medial view (Fig. 2). The lateral surface of the distal end of tibia lacks the longitudinal sharp ridge present in *Ca. arizonensis* (Ezcurra and Brusatte 2011). The lateral malleolous appears to contact the fibula in posterior view, but this condition seems to be an artefact as a result of the lateral displacement of the tibia (see above). Therefore, the condition of TMM 41936-1.3 seems to differ from that of *Coelophysis rhodesiensis* (cast of QG 1) and *Co. bauri* (CM 11894) in which the fibula and the tibia contact each other proximal to the articulation with the astragalocalcaneum.

Fibula: The distal end of fibula is expanded anteroposteriorly in lateral view (Fig. 2). The distal end of the bone is asymmetric in lateral view, where the anterior portion is more distally expanded than the posterior portion. This is in contrast to the continuously convex and near symmetrical distal end of the fibulae present in *Ca. arizonensis* (UCMP 34498), *Li. liliensterni* (MB R2175), *Co. bauri* (AMNH FR 30614 *Co. rhodesiensis* (cast of QG 1), *Zupaysaurus rougieri* (PULR 076), *T. hallae* (Nesbitt et al. 2009), and *Dilophosaurus wetherilli* (UCMP 37302). The lateral surface of the fibula is smooth and lacks the distinct scar present in *T. hallae* (Nesbitt et al. 2009b). In lateral view, the distal end of the fibula is slightly larger than that of its facet with the astragalocalcaneum. In anterior view, the distal end of fibula expands slightly medially and, as a result, likely slightly overlapped the anterior surface of the ascending process of the astragalus. The shaft of the fibula is mediolaterally- and to a lesser degree, anteroposteriorly compressed relative to the shaft of the tibia.

Astragalocalcaneum: The astragalus and calcaneum of *Le. praecisio* are fused into an astragalocalcaneum (Fig. 2), as also occurs in hypothesized mature individuals of early neotheropod dinosaurs (e.g., *Ca. arizonensis*, UCMP 34498; *Co. bauri*, AMNH FR 30614, 30615; *Co. rhodesiensis*, cast of QG 1; *Zupaysaurus rougieri*, PULR 076). The ascending process is dorsoventrally short, about one-third the height of the astragalar body (Fig. 2). The anterior surface of the ascending process of the astragalus lacks the large fossa present in most basal neotheropods (e.g., *Co. bauri*, AMNH FR 30576; *Z. rougieri*, PULR 076; *D. wetherilli*, UCMP 37302). However, there is a subcircular blind pit between the base of the ascending process and the astragalar body that is likely homologous to the larger fossa commonly present in early neotheropods. The anterior surface of the astragalar body possesses a very faint swelling of the horizontal tuberosity present in *Ca. arizonensis* (Ezcurra and Brusatte 2011), the Hayden Quarry coelophysoid (GR 227) and *Co. rhodesiensis* (QR 1) (= horizontal large tuberosity of Ezcurra and Brusatte 2011). The anteromedial corner of the astragalar body is acutely angled like all dinosauromorphs (Langer and Benton 2006), but has an angle closer to 90° than the more pointed anteromedial corner present in *Ca. arizonensis* (Ezcurra and Brusatte 2011). The medial surface of the astragalar body is nearly flat with long, paralleled bone fibers decorating the surface. In contrast, in *Ca. arizonensis*, the Hayden Quarry coelophysoid, *Co. rhodesiensis* and *D. wetherilli* the medial surface of the astragalus possesses an oval fossa (Ezcurra and Brusatte 2011). The astragalus of TMM 41936-1.3 is nearly

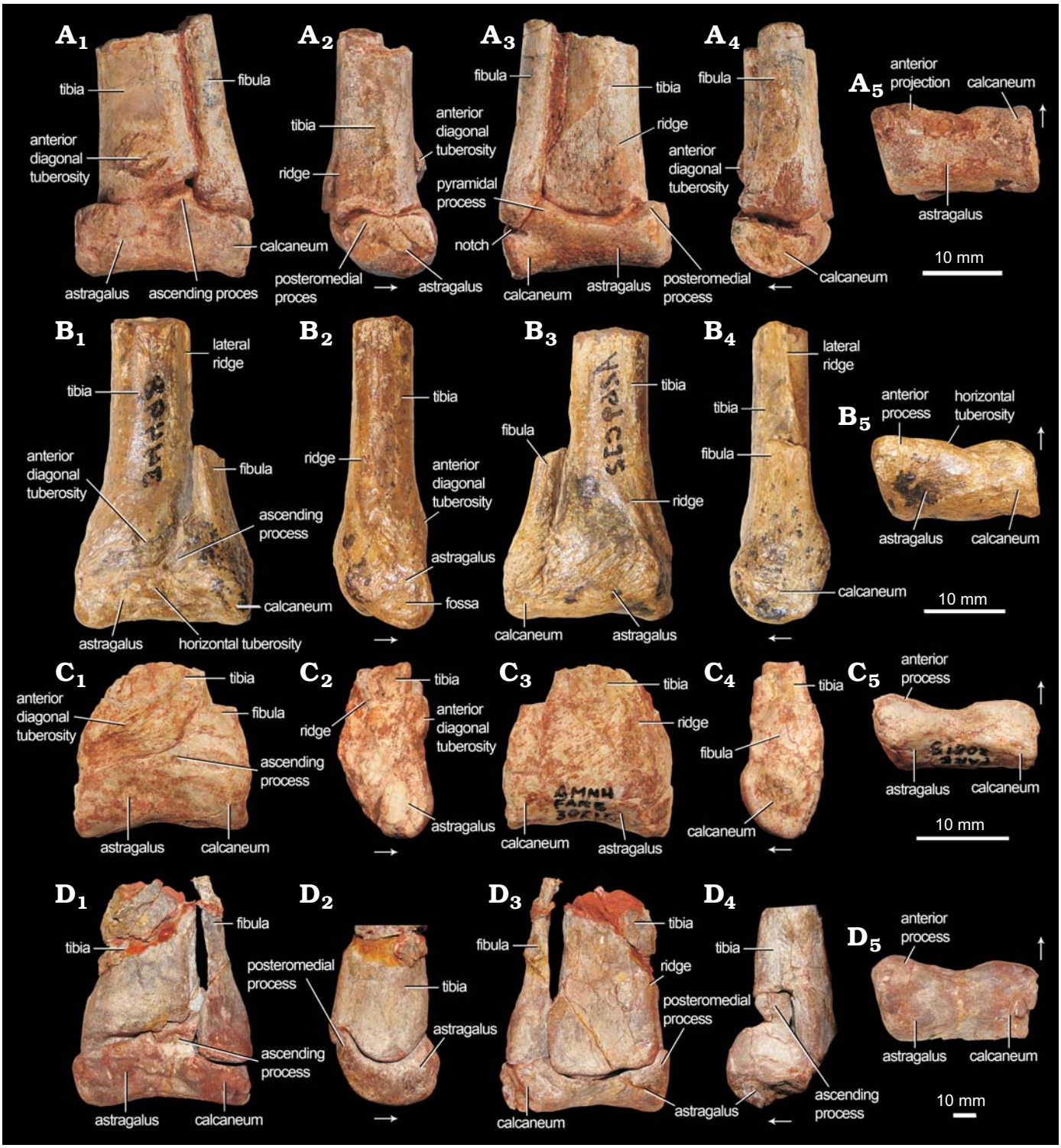


Fig. 2. Comparisons of almost naturally articulated ankle complexes of neotheropods. **A**. *Lepidus praecisio* gen. et sp. nov., Otis Chalk area, Dockum Group, Late Triassic (TMM 41936-1.3). **B**. *Camposaurus arizonensis* Hunt, Lucas, Heckert, Sullivan, and Lockley, 1998, *Placerias* Quarry, Chinle Formation, Late Triassic UCMP 34498), reversed. **C**. *Coelophysis bauri* Cope, 1887, *Coelophysis* Quarry, Chinle Formation, Late Triassic (AMNH FARB 30615). **D**. *Zupaysaurus rougieri* Arcucci and Coria, 2003, Colorados Formation, Late Triassic (PULR 076), reversed. Left (A, C) and right (B, D) tibia, fibula, and astragalocalcaneum in anterior (A_1–D_1), medial (A_2–D_2), posterior (A_3–D_3), lateral (A_4–D_4), and ventral (A_5–D_5) views, arrows indicate anterior direction.

symmetric in medial view, with similarly distally developed anterior and posterior sides, resembling the condition present in most basal neotheropods (e.g., *Co. bauri*, AMNH FR 30576, 30614; *Co. rhodesiensis*, cast of QG 1; *Li. lilienster-ni*, MB R2175; *Z. rougieri*, PULR 076; *D. wetherilli*, UCMP 37302). In contrast, in *Ca. arizonensis* the anterior edge of the astragalus is much more distally expanded than the posterior side in medial view (UCMP 34498). The posteromedial

corner of the astragalus of *Le. praecisio* possesses a low and blunt dorsally directed process (= posteromedial process of Ezcurra and Nova 2007) (Fig. 2), which contrasts with the more dorsally projected and pyramidal posteromedial process present in *Z. rougieri* (Ezcurra and Novas 2007) and *Li. liliensterni* (MB R2175). In posterior view, the pyramidal structure that delimits the posterolateral margin of the tibial facet and the posteromedial portion of the facet of the fibula is very well developed (Fig. 2), contrasting with the condition present in other early neotheropods (e.g., *Coelophysis bauri*, AMNH FR 30576; *Co. rhodesiensis*, Raath 1977: pl. 26d; *Li. liliensterni*, MB R2175; *Z. rougieri*, PULR 076; *D. wetherilli*, UCMP 37302), and is an autapomorphy of *Le. praecisio*. The posterior pyramidal process is of similar height to the anterior ascending process. The posterior pyramidal process may connect to the anterior ascending process, but this cannot be determined given that the tibia and fibula were preserved in tight articulation with the astragalocalcaneum. This posterior pyramidal process is separated from the proximal surface of the calcaneum by a shallow notch that opens dorsolaterally into a posterior sulcus (Fig. 2), which is also not present in any other dinosaur observed by us.

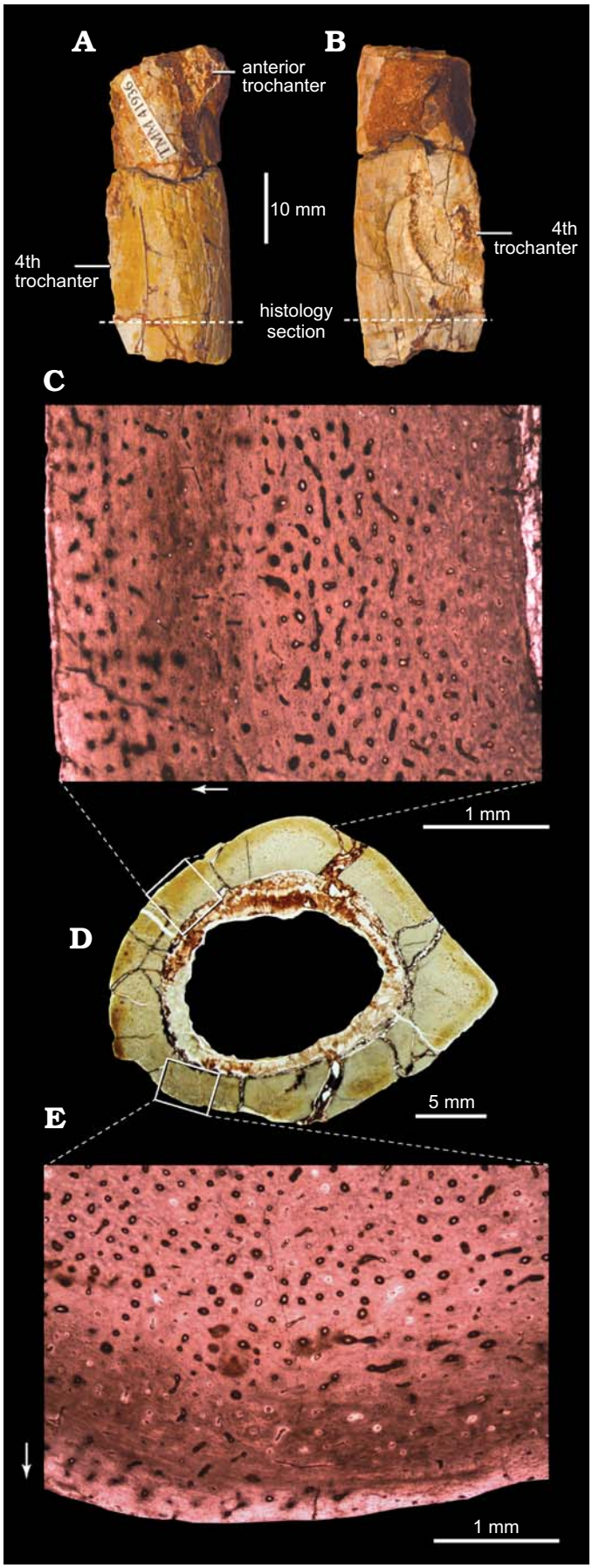
Based on the position of the posterior pyramidal process, the calcaneal portion of the astragalocalcaneum should be strongly transversely compressed as in neotheropods and unlike the condition present in *Herrerasaurus ischigualastensis* (PVSJ 373). The lateral margin of the proximal articular surface of the calcaneum is concavo-convex from anterior to posterior. The latter is a result of the asymmetric distal end of fibula, a condition that differs from that observed in most early neotheropods (see above). The lateral surface of the calcaneum portion of the astragalocalcaneum is mostly covered by a shallow concavity, which is subdivided by a low, anteriorly curved ridge as in a theropod specimen (UCMP 152645) from the Upper Triassic Canjilon Quarry (Nesbitt and Stocker 2008). The ventral surface of the astragalocalcaneum is strongly anteroposteriorly convex. The ventral margin of the astragalocalcaneum is only weakly transversely concave in anterior or posterior views.

Femur: The proximal half of the femoral shaft possibly referable to *Le. praecisio* is preserved in two pieces (Fig. 3). The base of the anterior trochanter is similar to that of ornithosuchids (Bonaparte 1971), early dinosauromorphs (Nesbitt et al. 2009a), silesaurids (ZPAL Ab III/361/23; Dzik 2003), and other early dinosaurs (Novas 1996). The base of the anterior trochanter is highly rugose and proportionally mediolaterally wider than in other dinosauromorphs (Fig. 3A, B). The specimen lacks a trochanteric shelf. The medially extending fourth trochanter is symmetrical in anterior view, where the proximal and distal portions have similar angles relative to the shaft, as in *Tawa hallae* and neotheropods (Langer and Benton 2006; Nesbitt et al. 2009b). The well separated fourth trochanter from the shaft differs from that of the low, mound-like structure in some silesaurids (*Silesaurus opolensis*; Dzik 2003). The fourth trochanter begins immediately distal the level of the base of the anterior trochanter. The trochanter is blade-like, being strongly transversely compressed, contrasting with the proportionally thicker and distally expanded fourth trochanters of ornithischians (e.g., *Heterodontosaurus tucki*, SAM-PK-K1332) and early saurischians (e.g., *Saturnalia tupiniquim*, MCP 3844-PV, Langer 2003; *Herrerasaurus ischigualastensis*, PVSJ 373, Novas 1994). The fourth trochanter originates close to the medial margin of the shaft and trends diagonally towards the lateral margin of the shaft. The most distal tip of the fourth trochanter is not preserved, but it seems that it does not reach the lateral margin of the shaft. Immediately medially to the base of the fourth trochanter there is a very well developed muscle scar, which is delimited by a semilunate shelf, resembling the condition present in other saurischians (e.g., *S. tupiniquim*, MCP 3844-PV; *Li. liliensterni*, MB R2175). The shaft has a convex, slightly developed anteromedial edge, but it clearly contrasts with the sharp keel present in *H. ischigualastensis* (PVSJ 373).

The histological section of the referred femur was taken at the base of the fourth trochanter, and the entire cross-section of the femur was recorded in two histological sections (Fig. 3A, B). The shaft has a quite thin cortex in cross-section; with a cortex (anterior and posterior parts of shaft = 1.75 mm) to diameter (~10.75 mm) ratio ~0.167.

Overall, the structure of the original bony tissues is well preserved and little, if any, recrystallization is present (Fig. 3C–E). The medullary cavity is free of trabeculae. The cortex is like that of early theropods (Padian et al. 2001; Ricqlès et al. 2003) and most Triassic dinosauromorphs (Werning et al. 2011) in terms of overall composition of boney tissues, vascularization, and cortex thickness. The cortex is composed entirely of woven-fibered primary bone tissue without any evidence of remodeling. The majority of vascular canals are longitudinal primary osteons with at least one, but no more than two, lamellae. Rarely, the longitudinal primary canals possess circumferential anastomoses that connect either one or two canals.

The bone is well vascularized and is comparable to the long bones of *Co. bauri* (AMNH FR unnumbered) and the "Padian *Coelophysis*" (UCMP 129618) but does show variation in vascularization densities across the cortex. Vascularization densities decrease in the outer cortex compared to the inner cortex. In comparison with the "Padian *Coelophysis*" (UCMP 129618), the femoral tissues of *Le. praecisio* clearly have less of a plexiform configuration in the inner cortex, but the overall bone tissue orientations are similar. The osteocyte lacunae surround the longitudinal primary canals but do not appear to be arranged circumferentially around the canals. The woven-fibered boney tissue is similar throughout most of the cortex without any interruptions (i.e., lines of arrested growth), indicating that the specimen was not a mature individual at the time of its death. Furthermore, the lack of lines of arrested growth (LAGs) does not allow an age to be estimated. The absence of LAGs indicates that the individual was in its first year of life when it died or grew throughout its life without laying down any LAGs. The absence of LAGs



in femora about the size of that of *Le. praecisio* appears to be rather common among early dinosauriforms (e.g., *Coelophysis bauri* and *Asilisaurus kongwe*; Christopher Griffin and SJN unpublished data). The outermost cortex (i.e., the outer 10% of the radius of the cortex) has a slight transition to more parallel-fibered bone but no external fundamental system is present. No secondary osteons are present in the cortex as in the dinosauriform *A. kongwe* and the neotheropods *Co. bauri* (AMNH FR unnumbered) and the "Padian *Coelophysis*" (UCMP 129618).

TMM 41936-1.1: The left partial maxilla (Fig. 4) consists of the main body of the bone missing the distal tip of the anterior process, posterior half of the posterior (= horizontal) process, and the distal end of the dorsal (= ascending) process. In lateral view, the anterior portion of the maxilla is triangular with a low, sloping anterodorsal straight margin, a straight and horizontal ventral margin, and a posteriorly tapering anterior portion of the posterior process. The lateral surface of the maxilla bears a distinct antorbital fossa (Fig. 4) separated from the dorsal process by a thin ridge that curls posteriorly, creating a slight pocket. The extent of the lateral exposure of the antorbital fossa in TMM 41936-1.1 differs from the minute lateral exposure of the antorbital fossae of *Tawa hallae* (GR 241), *Herrerasaurus ischigualastensis* (PVSJ 407), and *Daemonosaurus chauliodus* (CM 76821). This ridge continues ventrally, becomes less pronounced and turns posteriorly about half the dorsoventral distance from the ventral edge. More posteriorly, the antorbital fossa is only separated from the rest of the body of the maxilla by a low ridge, thus lacking the alveolar ridge present in several early saurischians (e.g., *Eoraptor lunensis*, PVSJ 512; *Zupaysaurus rougieri*, PULR 076; *Li. liliensterni*, MB R2175; *Co. bauri*, AMNH FR 7224; *Co. rhodesiensis*, QG1; *Eodromaeus murphi*, PVSJ 561). Overall, the shape of the ridge demarcating the antorbital fossa is "squared-off" as in the putative sauropodomorph *Eoraptor lunensis* (Sereno et al. 2013), and some basal neotheropods (e.g., *Z. rougieri*, Ezcurra 2007; "*Syntarsus*" *kayentakatae*, MNA V2623; *Co. rhodesiensis*, cast of QG1; Rauhut 2003). The promaxillary foramen observed in some neotheropods (Rauhut 2003) and small fossae within the antorbital fossa are clearly absent in TMM 41936-1.1. The straight dorsal margin of the posterior process of the maxilla forms the ventral margin of the antorbital fenestra. Although incomplete because of the loss of part of the dorsal process of the maxilla, the preserved anterior extent of the antorbital fenestra suggests that the angle of the anterior portion of the antorbital fenestra was acute unlike the condition in *T. hallae* (GR 241), *Eodromaeus murphi* (PVSJ 560), *Eoraptor lunensis* (Sereno et al. 2013), *Co. bauri* (CM 31374),

Fig. 3. The referred left femur of neotheropod *Lepidus praecisio* gen. et sp. nov., Otis Chalk area, Dockum Group, Late Triassic (TMM 41936-1.3) in anterior (**A**) and posterior (**B**) views and the bone tissues of the femur (**D**) through the entire cortex on the anterolateral side (**C**) and the middle and outer cortex on the posterolateral side (**D**). Arrows indicate the direction of the external surface of the femur.

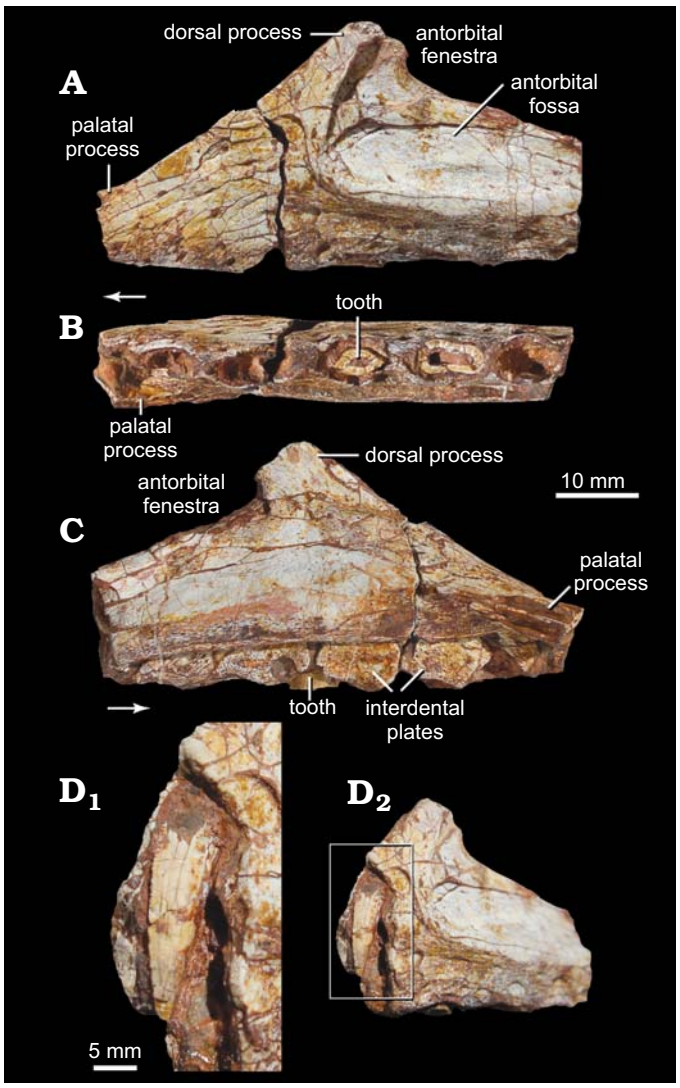


Fig. 4. Partial left maxilla of an archosaur (TMM 41936-1.1), Otis Chalk area, Dockum Group, Late Triassic, found with and possibly referable to neotheropod *Lepidus praecisio* gen. et sp. nov., in lateral (**A**), ventral (**B**), and medial (**C**) views, arrows indicate anterior direction. **D**. A replacement tooth in labial view within the fourth alveolus in anterolateral view (D_2), close up (D_1).

and *H. ischigualastensis* (PVSJ 407). The anterior portion of the maxilla tapers anteroventrally, but the shape of its anteriormost portion is not known because it is slightly broken. The preserved portion of the anterior process is nearly flat laterally as in *Co. bauri* (CM 31374), but with no indication that there was any ventral (as in *Dilophosaurus wetherilli*; Welles 1984) or lateral (as in *Protosuchus richardsoni*; Colbert and Mook 1951) notch. Anteriorly, the angle between the ventral margin and the anterodorsal margin of the anterior process is about 35° relative to the ventral margin. This angle is comparable to that of *Co. bauri* (CM 31374) and *Co. rhodesiensis* (cast of QG1), and contrasts with the lower angle present in "*S.*" *kayentakatae* (ca. 20°; MNA V2623) and the higher one present in *Z. rougieri* (ca. 45°; PULR 076). The thin anterodorsal margin is nearly straight and it is not clear if the maxilla participated in the external naris as in most early neotheropods (Tykoski and Rowe 2004), but there is no facet for reception of the posterior (= maxillary) process of the premaxilla so it is conceivable that the maxilla (TMM 41936-1.1) could have participated in the external naris. The straight anterodorsal border of the dorsal process resembles that of *Co. bauri* (CM 31374). Two rows of nutrient foramina are present near the ventral edge of the maxilla, one row 1–2 millimeters above the ventral margin, and another paralleling and just ventral to the low ridge separating the antorbital fossa from the rest of the posterior process of the maxilla.

The medial surface of the maxilla is well preserved. The main body of the medial surface is smooth with few distinguishing features, without an antrum anterior to the anterior margin of the antorbital fenestra. A distinct step paralleling the ventral margin of the bone separates the medially inflated main body from the interdental plates and tooth-bearing margin. Each interdental plate is polygonal with a ventrally directed vertex, bears some small irregular striations, is dorsoventrally low, and there is no evidence of fusion across each plate (Fig. 4). The distinct palatal process of the maxilla is located at the anterior margin of the medial side and the lateral edge of the process is clearly separated from the medial side of the anteriormost portion of the maxilla (a bit of matrix was left in this area to stabilize the anteriormost portion of the maxilla) (Fig. 4). Medially, the articulation surface of the palatal process has two deep longitudinal grooves separated from each other by a very thin ridge. The entire long axis of the palatal process projects anteroventrally with an angle of 10° relative to the horizontal ventral margin of the maxilla as in *T. hallae* (GR 241); most other early dinosaur maxillae are either broken in this area or the area is covered by other cranial elements (e.g., *Co. bauri*). This anteroventral deflection of the process suggests that the premaxilla may have been downturned, resembling the condition present in coelophysids (Colbert 1989), *Z. rougieri* (Ezcurra 2007), and *D. wetherilli* (UCMP 37303).

The preserved portion of the maxilla contains seven alveoli, where the anteriormost alveolus is only partially preserved (Fig. 4B). The alveoli are oval with the long axis oriented anteroposteriorly. The size of the alveoli increase through the first four positions and then each alveolus posterior to the third position remain similar in size. Alveoli five and six preserve the root in situ, but the crowns are completely missing (Fig. 4). An unerupted tooth crown is preserved within the fourth alveolus (Fig. 4D), and the tip of a replacement tooth is visible between interdental plates medial to the broken tooth in the sixth alveolus. The mesial edge of the crown of the unerupted tooth is convex whereas the distal edge is concave, resulting in a recurved crown. It is also labiolingually compressed. Fine serrations extend along both mesial and distal carina, and there are four serrations per millimeter in the visible portions of the crown, matching serration densities documented in *Lophostropheus airelensis* (Ezcurra and Cuny 2007) and *D. wetherilli* (Welles 1984), but much coarser than those of *Co. bauri* (Colbert 1989) or *T. hallae* (Nesbitt et al. 2009).

The formal attribution of this maxilla to *Le. praecisio* (TMM 41936-1.3) is nearly impossible given that the maxilla does not preserve any unambiguous synapomorphies or unique character combinations with neotheropods or even with dinosauromorphs. Nevertheless, the morphology of TMM 41936-1.1 is not present in any known Otis Chalk taxa that preserve skulls, or those taxa otherwise found in the Dockum Group or Chinle Formation. The presence of an antorbital fenestra and fossa on the posterior portion of the maxilla clearly places the specimen within Archosauria (Nesbitt 2011). Furthermore, the character states described above are consistent with, but not exclusive to, neotheropods. Thus, our very tentative referral of the maxilla (TMM 41936-1.1) to the same taxon as TMM 41936-1.3 can only be tested with the discovery of new material from the older Upper Triassic deposits of the Otis Chalk area or strata of a similar age.

Geographic and stratigraphic range.—Type locality and horizon only.

Phylogenetic relationships

To test the phylogenetic relationships of *Lepidus praecisio*, we utilized the original dataset of Nesbitt et al. (2009b) as modified by Ezcurra and Brusatte (2011). We further modified the version presented in Ezcurra and Brusatte (2011) by updating scorings of taxa based on discovered coding errors, new interpretations following extensive descriptions (e.g., *Eoraptor lunensis*; Sereno et al. 2013), and further personal observations (see SOM 1 in Supplementary Online Material available at http://app.pan.pl/SOM/app60-Nesbitt_Ezcurra_SOM.pdf). In addition, we added four characters and the recently published early theropod taxon *Eodromaeus murphi* (Martinez et al. 2011). The resulting matrix consists of 343 characters and 45 total taxa (SOM 2). We scored *Le. praecisio* as two different terminals, one including only the holotypic specimen TMM 41936-1.3 (ankle complex) and another terminal including the holotype and tentatively referred specimens (femur and maxilla). We were able to score 26 out of 343 characters for the holotype and 47 characters for the combined terminal.

The outgroup choice follows Nesbitt et al. (2009b) and the following multistate characters were ordered: 17, 30, 67, 128, 174, 184, 213, 219, 231, 236, 248, 253, 254, 273, 329, and 343. The data matrix was analyzed under equally weighted parsimony using TNT 1.1 (Goloboff et al. 2008). A heuristic search of 1,000 replications of Wagner trees (with random addition sequence) followed by TBR (tree bisection and reconnection) branch swapping (holding 10 trees per replicate) was performed. Zero length branches among all of the recovered MPTs (most parsimonious trees) were collapsed (i.e., rule 1 of Coddington and Scharff 1994). Two alternative analyses were conducted, one including only the holotype of *Le. praecisio* and a second including its holotype and tentatively referred specimens.

Our analysis of the data matrix that includes the holotype of *Le. praecisio* resulted in 6 MPT of 1058 steps, with a CI (consistency index) 0.5311 and a RI (retention index) 0.8250 (Fig. 5). The best score was hit 773 times out of the 1000 replications. We find *Le. praecisio* as a coelophysid neotheropod more closely related to *Co. bauri* than to "*Syntarsus*" *kayentakatae*. More specifically, *Le. praecisio* falls into a polytomy with *Co. bauri* and *Co. rhodesiensis* + *Ca. arizonensis*. *Lepidus praecisio* is supported as a member of the clade of *Eodromaeus murphi* + Neotheropoda because the posterolateral margin of the distal end of the tibia is concave (character 255-1) and the posterior face of the distal end of the tibia has a distinct proximodistally oriented ridge (character 256-1). The position of *Le. praecisio* within Coelophysidae is supported by the presence of a diagonal tuberosity on the anterior surface of the distal end of tibia (character 333-1).

The comparable scores of *Le. praecisio* and *Co. bauri* are nearly identical and in fact, they only differ in one scoring difference: *Co. bauri* is scored as having a deeply concave ventral margin of the astragalus (state 0) whereas *Le. praecisio* is scored as having a only slightly concave or straight ventral margin of the astragalus (state 1) in character 336. Indeed, one of the most parsimonious trees finds TMM 41936-1.3 as the sister-taxon of *Co. bauri*. However, both taxa differ in several characters described above, including the autapomorphic characters described in the diagnosis.

The phylogenetic position of *Le. praecisio* as a saurischian more closely related to *Coelophysis* than *Eodromaeus murphi*, *Tawa hallae*, *Chindesaurus bryansmalli*, and herrerasaurids is rather well supported (Table 1). The Bremer

Table 1. Bremer index and bootstrap frequency supports for Saurischia and its less inclusive nodes of the strict consensus of the recovered MPTs for the phylogenetic analysis with only the holotype of *Lepidus praecisio* scored. The phylogenetic position of *L. praecisio* as a saurischian more closely related to *Coelophysis* than *Eudromaeus murphi*, *Tawa hallae*, *Chindesaurus bryansmalli*, and herrerasaurids is rather well supported. GC, group present/contradicted.

Node	Bremer index	Absolute bootstrap frequency	GC bootstrap frequency
Saurischia	2	69%	63%
Sauropodomorpha	1	41%	19%
Saturnalia+*Plateosaurus*	5	94%	93%
Efraasia+*Plateosaurus*	2	81%	80%
Theropoda	2	41%	32%
Herrerasauridae	1	29%	7%
Chindesaurus+Neotheropoda	1	13%	12%
Tawa+Neotheropoda	1	35%	25%
Eodromaeus+Neotheropoda	1	29%	8%
Neotheropoda	2	69%	63%
Coelophysoidea	1	35%	28%
Lepidus praecisio +*Coelophysis*	1	49%	42%
Camposaurus+*C. rhodesiensis*	1	47%	34%
Dilophosaurus+Averostra	2	48%	41%
Averostra	3	75%	68%
Tetanurae	2	69%	60%

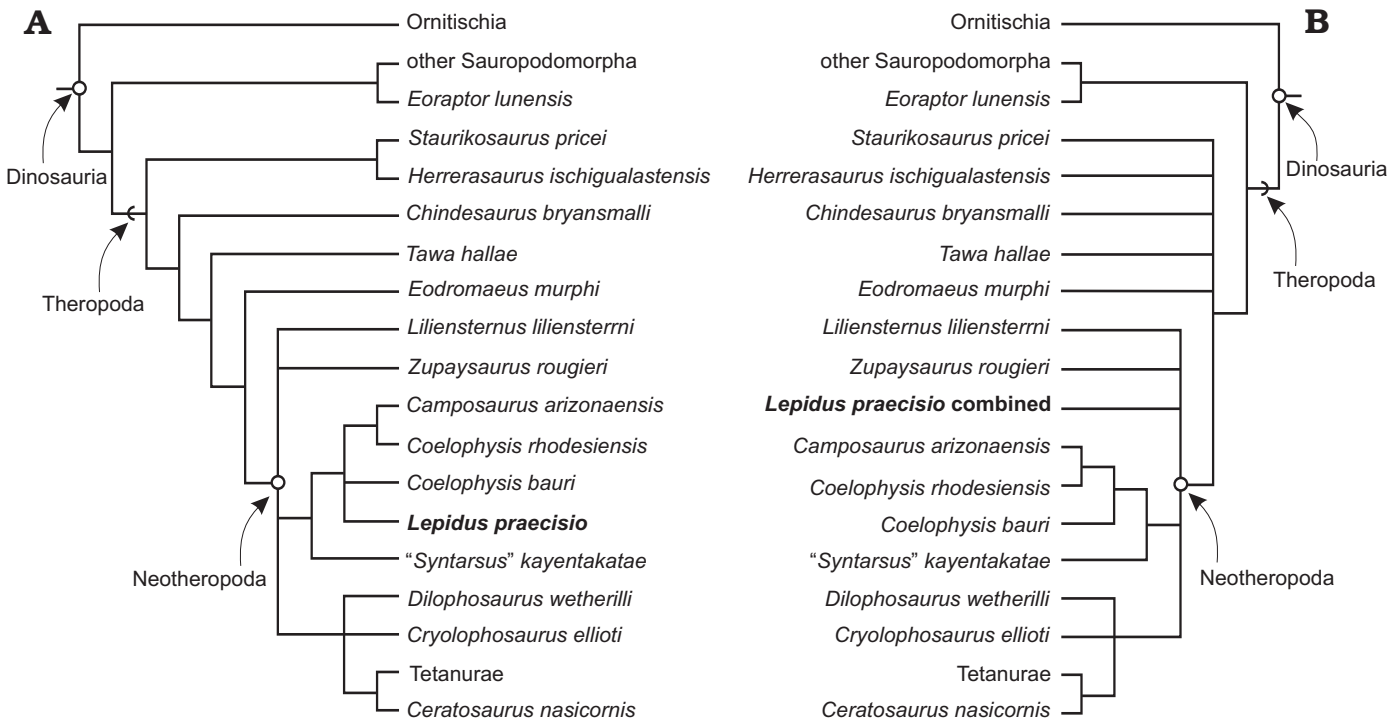


Fig. 5. Phylogenetic relationships of early theropod dinosaurs recovered here highlighting the phylogenetic position of *Lepidus praecisio* gen. et sp. nov. with the holotype only (**A**), simplified strict consensus of six MPTs, TL = 1058, CI = 0.5311, RI = 0.8250) or with all of the hypothesized material (**B**), simplified strict consensus of 18 MPTs, TL = 1061, CI = 0.5383, RI = 0.8303). The original taxon list and relationships outside of Dinosauria and within Ornithischia are exactly the same as that of Nesbitt et al. (2009b).

support of Neotheropoda is 2 and the absolute and GC (group present/contradicted) bootstrap frequencies provide moderate support at 69% and 63%, respectively. Indeed, under suboptimal constrained topologies, three additional steps are necessary to break the monophyly of *Le. praecisio* and other neotheropods. *Lepidus praecisio* is supported as a member of Neotheropoda by the following synapomorphies (character enumeration follows that of Nesbitt et al. 2009b and Ezcurra and Brusatte 2011): fused astragalus and calcaneum (283-1); low anterior ascending process of the astragalus (273-1); calcaneum mediolaterally compressed (291-1); proximodistally extended ridge on the posteromedial surface of the tibia (256-1); and distinct scar on the anterior surface of the distal end of the tibia (333-1). In addition, six additional steps are necessary to find *Le. praecisio* as a herrerasaurid or sister-taxon of *Ch. bryansmalli*, and five extra steps to place it as the sister-taxon of *T. hallae*. However, the support for the recovered phylogenetic relationships of *Le. praecisio* as a neotheropod is particularly weak. Only one additional step is necessary to recover *Le. praecisio* as the sister-taxon of *Ca. arizonensis*, of "*Syntarsus*" *kayentakatae*, as the most basal coelophysoid or even as the sister-taxon of Neotheropoda. This result is not unexpected given that *Le. praecisio* was only scored from an ankle complex. Future discoveries may shed light on the phylogenetic position of this taxon, but currently available data strongly support its position as a neotheropod or its sister taxon.

The structure of our strict consensus differs from both the results of Nesbitt et al. (2009b) and Ezcurra and Brusatte (2011). The modification of scores of *Eoraptor lunensis* based on the comprehensive description of Sereno et al. (2013) resulted in the removal of the taxon as a close relative of *Tawa hallae* + Neotheropoda and placed it as the earliest diverging member of Sauropodomorpha. The herrerasaurids *Herrerasaurus ischigualastensis* and *Staurikosaurus pricei* were found in a clade as the sister taxon to other Theropoda, but the controversial *Chindesaurus bryansmalli* is now more closely related to neotheropods. Furthermore, *Liliensternus liliensterni* and *Zupaysaurus rougieri* are still found in a polytomy with the clade containing coelophysids as in Ezcurra and Brusatte (2011), whereas they were found closer to *Allosaurus fragilis* in Nesbitt et al. (2009b). Here, we find *Eodromaeus murphi* as the sister taxon of neotheropods instead of *T. hallae*, contrasting with the analysis of Martinez et al. (2011). The differences in the relationships of early theropods here, in Ezcurra and Brusatte (2011), and in Nesbitt et al. (2009b), demonstrate that much work remains to elucidate the phylogenetic relationships of the earliest theropods.

The second phylogenetic analysis that included the holotype and tentatively referred specimens of *Le. praecisio* as a single terminal (= *L. praecisio* combined) resulted in 18 MPT of 1061 steps, with a CI 0.5383 and a RI 0.8303 (Fig. 5). The best score was hit 686 times out of the 1000 replications. The topology of the strict consensus tree is very similar to that of the original analysis but with two differences. First, a polytomy was found at the base of Theropoda, composed of *E. murphi*, *T. hallae*, *Ch. bryansmalli*, and herrerasaurids. Second, *Le. praecisio* was recovered in an unresolved position

at the base of Neotheropoda, together with *Z. rougieri*, *Li. liliensterni*, Coelophysoidea, and other neotheropods closer to averostrans. However, in all of 18 MPTs *Le. praecisio* was found within Coelophysoidea and in some of these trees as the sister-taxon of *Li. liliensterni* at the base of the group. Indeed, the strict reduced consensus tree generated after the a posteriori pruning of *Z. rougieri* shows *Le. praecisio* as a basal member of Coelophysoidea. The polytomy at the base of Neotheropoda is a result of the alternative positions of *Z. rougieri* and *Li. liliensterni* inside or outside Coelophysoidea and the sister-taxon relationship recovered between *Le. praecisio* and *Li. liliensterni* in one of the MPTs. Accordingly, the addition of the tentatively referred specimens of *Le. praecisio* to the data matrix still supports the position of the new species as a neotheropod and a coelophysoid, but in a more basal position among coelophysoids than suggested by the holotype alone.

Discussion and conclusions

Dinosaur remains from Upper Triassic rocks of North America are rare compared to the abundance of the remains of other contemporary archosaurs (Nesbitt et al. 2007; Irmis et al. 2011). However, the Triassic dinosaur fossil record is improving especially because of reanalysis of previously discovered specimens either as already published or previously unreported remains (Hunt et al. 1998; Ezcurra 2006; Parker et al. 2006; Nesbitt et al. 2007; Irmis et al. 2007b). Furthermore, renewed field collections in dinosaur rich areas in the western United States has produced a wealth of new data (Heckert et al. 2003; Irmis et al. 2007a; Nesbitt et al. 2009b). This trend is likely driven by recent advances in recognizing the differences between dinosaurs and convergent pseudosuchians (e.g., *Effigia okeeffeae*; Nesbitt and Norell 2006; Nesbitt 2007) and other distantly related taxa (*Azendohsaurus*; Flynn et al. 2010), and piecing out plesiomorphic character states from synapomorphies that distinguishes dinosaurs from their closest relatives, non-dinosaurian dinosauromorphs (e.g., *Eucoelophysis baldwini*; Ezcurra 2006; Nesbitt et al. 2007).

Although the overall record of dinosaur evolution in North America is improving, the dinosaur sample becomes increasingly desolate deeper in the Late Triassic, particularly in the Dockum Group. Dinosaur remains from the same or similar stratigraphic position as the Otis Chalk locality in lowermost levels of the Dockum Group have been reported before (Elder 1978; Long and Murry 1995), but only recently has their assignment been confirmed by a synapomorphic approach (Stocker 2013a). Here, *Lepidus praecisio* represents the first confirmed member of Neotheropoda from the base of the Dockum Group. Furthermore, *Le. praecisio* does not appear to be present among the dinosaurian sampling from the nearby Otis Chalk quarries. The one of the two possible theropods known from Otis Chalk Quarry 3 are represented by an isolated femoral head (TMM 31100-523; Long and Murry 1995; Hunt et al. 1998; Nesbitt et al. 2007; Stocker 2013a) similar to that of the holotype of the much younger *Chindesaurus bryansmalli* (Long and Murry 1995). However, the assignment of TMM 31100-523 to *Ch. bryansmalli* is not well supported given only a few observable character states, and the character states that are present in TMM 31100-523 do not differentiate this specimen from *H. ischigualastensis* and *Ch. bryansmalli*. Our phylogenetic analysis predicts that the femur of *Le. praecisio* would be more like that of *Co. bauri* from that of *H. ischigualastensis*. Using this reasoning, we conclude that *Le. praecisio* is different from the dinosaurian taxon represented by TMM 31100-523.

The second dinosaurian taxon from Otis Chalk Quarry 3 comprises an associated femur (TMM 31100-545), tibia (TMM 31100-1324), and other isolated limb bones (Stocker 2013a). The femur and tibia are similar in morphology to those of theropods outside of Neotheropoda (e.g., *Tawa hallae*; Nesbitt et al. 2009b), but appear to be more closely related to neotheropods than herrerasaurids (Stocker 2013a). The tibia of TMM 31100-1324 is the only element that can be compared directly to *Le. praecisio* and it is clear that TMM 31100-1324 lacks a proximodistally-oriented ridge on the posteromedial side. Thus, these dinosaurian remains (TMM 31100-545 and TMM 31100-1324) do not represent the same taxon as *Le. praecisio.*

The identification of *Le. praecisio* as a neotheropod dinosaur indicates that the clade was present near the onset of deposition of the Dockum Group (or at least the lowest fossiliferous localities). The uncertainty of the age of the bottom of the Dockum Group hampers the comparison of the timing of the earliest dinosaurs in North America. Yet, the presence of a neotheropod in the lower Dockum Group is in agreement with the neotheropod assignment of *Camposaurus arizonensis* from the lower levels of the Chinle Formation (Hunt et al. 1998; Nesbitt et al. 2007; Ezcurra and Brusatte 2011). Therefore, neotheropod dinosaurs were also part of the tetrapod assemblages during the onset of deposition of the Chinle Formation.

Lepidus praecisio also helps fill a gap in global Triassic theropod record. The important theropod records from the fossil rich Ischigualasto Formation in Argentina only documents non-neotheropod theropods (e.g., *Eodromaeus murphi* and *H. ischigualastensis*; but see Langer and Benton 2006 for a different interpretation of the systematic position of *H. ischigualastensis* as non-theropod saurischian) whereas the conformably younger lying Los Colorados Formation only records a single member of Neotheropoda (*Zupaysaurus rougieri*) and an indeterminate theropod (Bonaparte 1971). In contrast, *Le. praecisio* demonstrates that the early dinosaur assemblages of North America comprised a mixture of neotheropods (e.g., *Camposaurus arizonensis*, *Coelophysis*) and their proximate outgroups (i.e., herrerasaurids and *Tawa hallae*) for the duration of the Norian stage (Nesbitt and Chatterjee 2008). This faunal composition resembles that present in coeval beds of Europe (Niedźwiedzki et al. 2014), but clearly contrasts with most European assemblages in the

absence of sauropodomorphs. On the other hand, herrerasaurids seem to have disappeared regionally in the middle-late Norian of South America (e.g., Los Colorados, Caturrita, and lower Elliot formations; Langer et al. 2010). Accordingly, the herrerasaurid-neotheropod assemblages of Europe and North America suggest stronger paleobiogeographic affinities between these areas than with those of Gondwana (pending future discoveries because of the biases of the fossil record), as was suggested by previous quantitative biogeographic analyses (Ezcurra 2010b).

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