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Chapter 7: A New Coelurosaurian Theropod from the La Buitrera Fossil Locality of Río Negro, Argentina

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Abstract

A new coelurosaurian theropod, *Alnashetri cerropoliciensis*, is reported here based on articulated hind limbs of a single individual discovered at the locality of La Buitrera (Candeleros Formation, Cenomanian–Turonian), Río Negro Province, Argentina. The new taxon differs from other coelurosaurs in the possession of a low ridge that separates the rostral tibial surface from the outer face of the lateral malleolus, and which extends proximally beyond the tip of the ascending process of the astragalus, and in the possession of ventral notches on the hemicondyles of the distal articulations on pedal phalanges III-1 and III-2. *Alnashetri* is easily distinguished from the dromaeosaurid *Buitreraptor*, the only other known small theropod from La Buitrera. Phylogenetic analysis supports alvarezsaurid affinities. The evidence supporting this relationship comes from the detailed anatomy of the ankle, however, and this concentration of character support within a single anatomical region may bias our results. If our proposed phylogenetic placement is accurate, *Alnashetri* antedates all other Argentinian alvarezsaurids and indicates that alvarezsaurids were present in the Neuquén Basin throughout the entire Late Cretaceous.

Introduction

Non-avian coelurosaurian theropods were largely unknown and considered to be absent from the Mesozoic record of South America until the 1990s. The recognition of both alvarezsaurid and paravian theropods from Late Cretaceous strata of Argentina in the mid-1990s (Novas, 1996, 1997; Novas & Puerta, 1997) challenged the paradigm that Laurasian and Gondwanan dinosaur faunas of the Cretaceous were comprised of distinct and vicariously distributed lineages (Bonaparte, 1986). Since the initial discoveries of *Alvarezsaurus* (Bonaparte, 1991) and *Unenlagia* (Novas & Puerta, 1997), several more alvarezsaurid (Novas, 1997; Salgado et al., 2009; Agnolin et al., 2012) and dromaeosaurid (Makovicky et al., 2005; Novas & Pol, 2005; Novas et al., 2009) taxa and specimens have been discovered principally from the Late Cretaceous Neuquén Group of northern Patagonia.

The oldest unit within the Neuquén Group is the Cenomanian–Turonian Candeleros Formation, which has produced a rich fauna of both large and small dinosaurs and other vertebrates (Leanza et al., 2004). The bulk of the known small- to medium-sized vertebrates derive from a large tract of exposures of the upper Candeleros Formation on the Río Negro shore of the Ezequiel Ramos Mexía reservoir known as La Buitrera (Fig. 1), which were discovered by the second author in 1999.

In 2005, the senior author discovered a partial skeleton of a very small theropod dinosaur at La Buitrera, comprising parts of both hind limbs, but with the left more complete than the right. Preparation of the specimen has revealed that it can be distinguished from other Cretaceous theropods of South

America and elsewhere. In this paper we describe and name this new taxon.

Institutional Abbreviations

FMNH, Field Museum of Natural History, Chicago; IGM, Institute of Geology, Mongolia, Ulaanbataar (currently held at American Museum of Natural History, New York); MPCA, Museo Provincial Carlos Ameghino, Cipoletti; MUCPV, Museo de Ciencias Naturales, Universidad del Comahue, Neuquén (currently repositated at Centro Paleontológico los Barreales); MCF-PVPH, Museo Carmen Funes, Plaza Huincul; UA, Université de Antananarivo, Antananarivo.

Systematic Paleontology

Theropoda Marsh, 1891
Coelurosauria Von Huene, 1926
Maniraptora Gauthier, 1986
Alvarezsauridae Bonaparte, 1991
Alnashetri cerropoliciensis gen. et sp. nov.

Holotype

MPCA-477—Partial left femur, distal portions of left and right tibiae, right fibula, proximal tarsals of both ankles, a nearly complete right metatarsus, proximal and distal parts of the left metapodials, left pedal digit III.

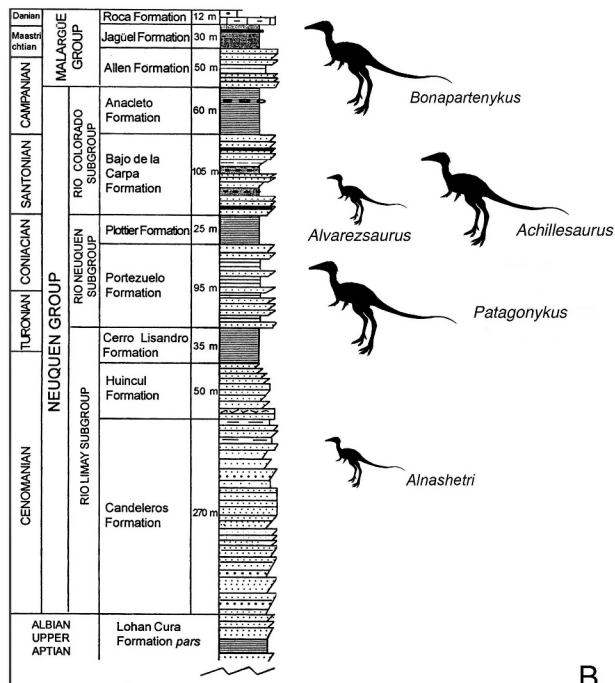
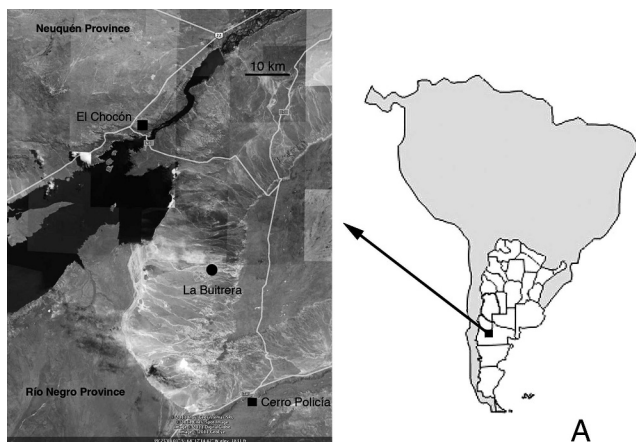


FIG. 1. (A) Satellite map of the La Buitrera locality, with inset providing geographic context within South America. (B) Stratigraphy of the Upper Cretaceous Neuquén Group calibrated against the geologic timescale, and showing which formations yield alvarezsaurid remains. The silhouettes approximate relative size of taxa. Specific specimen and coordinate data for La Buitrera specimens are on file with the second author. Map sourced from Google Earth.

Etymology

Alnashetri, meaning “slender thighs” in the Günün-a-kunna dialect of the Tehuelchan language, in reference to long and slender hind limbs of the holotype. The specific name is coined in honor of the nearby hamlet of Cerro Policia, whose residents have generously assisted fieldwork efforts at La Buitrera since the locality was discovered by the second author in 1999.

Diagnosis

A small non-avian coelurosaur exhibiting the following two autapomorphies: presence of a low ridge on the distal end of the tibia, which separates the rostral surface for articulation with the astragalus from the outer face of the lateral malleolus,

and which extends up the shaft of the tibia dorsal to the tip of the ascending process of the astragalus. Small notches extending ventrally from the collateral ligament pits at the base of the distal articular hemicondyles on phalanges III-2 and III-3 appear to be unique to *Alnashetri* among described non-avian theropods.

Locality and Horizon

The specimen was found at the “Hoyada de los esfenodontes” sublocality, part of the main fossiliferous locality of La Buitrera, about 30 km south of the village of El Chocón (Fig. 1). It was recovered from massive red sandstones that form the upper part of the Candeleros Formation, close to the contact with the Huincul Formation. However, the specimen comes from the lower levels of the outcrops in this region, where the lowermost section of the Candeleros Formation is not exposed. This unit produces a rich fauna of small vertebrates, including dozens of specimens of the large eilenodontine rhynchocephalian *Prionsphenodon avelasi* (Apesteguía & Novas, 2003), the basal snake *Najash rionegrina* (Apesteguía & Zaher, 2006), the notosuchian crocodile *Araripesuchus buitreaensis* (Pol & Apesteguía, 2005), several specimens of the unenlagiine dromaeosaurid *Buitreraptor gonzalezorum* (Makovicky et al., 2005), and also mammals (Rougier et al., 2011) and pterosaurs. Many of the small vertebrate fossils recovered from this unit are articulated, suggesting that they were entombed by rapid overbank flooding events (Apesteguía, 2008). The Candeleros Formation is regarded as Cenomanian–Turonian in age (Leanza et al., 2004).

Description

The proximal half of the left femur is preserved (Fig. 2). An isolated fragment of bone has a shape suggestive of being the femoral head. It is roughly conical in form and has a broken triangular base, with the most prominent point likely representing the ventral edge of the femoral neck. If this inference is correct, the neck of the femur would have been relatively short and thick. Its surface is generally rounded, except for a flat zone surrounding the break, and the entire fragment ends in a rounded but eroded apex. The femur is missing the proximal part of both the anterior and greater trochanters. There is no evidence of a groove separating the anterior and greater trochanters, and it is likely that the trochanters were separated by only a small notch as in the alvarezsauroid *Patagonykus* (Novas, 1997), or not at all. Only the base of the anterior trochanter is preserved. It arises just below the level of the neck for the femoral head. The preserved section of the anterior trochanter is straight (Fig. 2A), but protrudes only very slightly beyond the femoral shaft, and there is no evidence of an accessory trochanter as observed in several coelurosaurian lineages including ornithomimosaurs (Makovicky et al., 2010), tyrannosauroids (FMNH PR 2081), and *Microvenator* (Makovicky & Sues, 1998). A small neurovascular foramen occupies the medial face of the shaft slightly anterior and distal to the anterior trochanter (Fig. 2A). A fourth trochanter is absent (Fig. 2A) as in many Maniraptora, including Paraves and parvicursorine alvarezsaurids. The trochanteric shelf (Hutchinson, 2001) is also

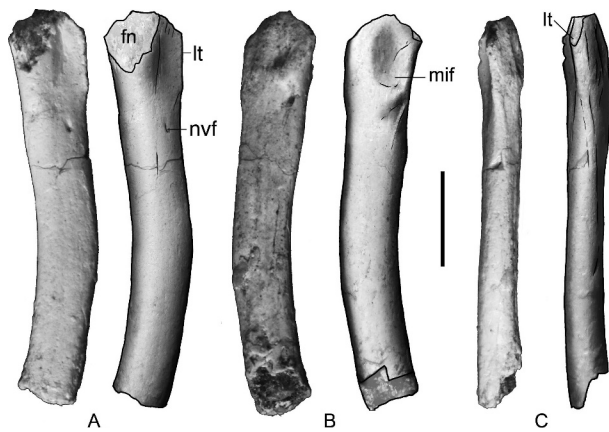


FIG. 2. Partial left femur of the holotype specimen (MPCA 477) of *Alnashetri cerropoliciensis* in (A) medial, (B) lateral, and (C) rostral views. Abbreviations: fn, femoral neck; lt, lesser trochanter; mif, insertion for m. iliofemoralis; nvf, neurovascular foramen. Scale bar = 1 cm.

reduced and represented by a low mound on the lateral face of the femur (Fig. 2C) located just below the level of the neck for the femoral head. Similar development of the trochanteric shelf is observed in a number of basal tetanurans, but not in paravian taxa, which bear a prominent and dorsally directed tubercle. The preserved section of the femoral shaft is mediolaterally compressed and much wider in lateral view than in rostral view (Fig. 2). The lateral and posterior surfaces of the shaft are nearly continuous, only separated by a rounded posterolateral edge, unlike most alvarezsaurids, in which the caudal face of the shaft is flat between the posterolateral ridge and the fourth trochanter (MUCPV 53; Novas, 1997). The medial surface is largely flat, and separated from the anterior and posterior sides by more conspicuous and marked edges. Consequently, the transverse section of the shaft is elliptical in cross section immediately below the anterior trochanter and more elliptical to D-shaped at the level of the midshaft. The shaft is strongly bowed distally as is typical of Maniraptora.

The right tibia (Fig. 3) is more complete than the left, though both are missing the proximal end including the cnemial and fibular crests. The shaft is cylindrical and slightly bowed medially. The distal end bears a shallow groove for articulation with the astragalus, and is only slightly expanded across the malleoli. The triangular depression for articulation with the ascending process of the astragalus is offset laterally with its apex toward the lateral border of the tibia (Fig. 4B). In contrast, most coelurosaurs lack a well-defined medial ridge on the tibia that buttresses the astragalus ascending process, and the rostral aspect of the distal tibia is flat. However, the tibia of *Mononykus* (IGM 7/106) exhibits a well-defined groove for reception of the ascending process of the astragalus.

A low ridge extends along the shaft of the tibia toward the distal end and defines the border between the lateral and rostral faces of the distal tibia (Fig. 4B). It is about twice as long as the ascending process of the astragalus, which it braces distally. To the best of our knowledge, all other coelurosaurs lack an extended ridge that reaches above the ascending process of the astragalus along this part of the tibial shaft, although the fibula may obscure such a ridge in articulated specimens. We interpret the extent of this ridge to be an autapomorphy of *Alnashetri*. The distal end of the tibia is only

slightly wider than the tibial shaft and does not flare broadly as in, e.g., ornithomimosaur, oviraptorosaurs, and tyrannosauroids. The tibia is trapezoidal and block-like in distal view, as in some enantiornithine birds and the parvicursorine taxa *Shuvuuia* and *Mononykus*, but unlike the more rostrocaudally flattened distal tibiae of most other maniraptorans (e.g., Norell & Makovicky, 1999, figure 11). The caudal surface of the distal end is marked by low medial and lateral ridges extending towards the malleoli and defining a shallow sulcus between them. The outer malleolus of the tibia is broad and about as wide as the maximum width of the calcaneum. In this regard, *Alnashetri* resembles the condition observed in parvicursorine taxa such as *Mononykus*, whereas most other non-avian coelurosaurs have an outer malleolus that is narrower than the calcaneum (Novas, 1997).

A short distal section bordering the right ankle is the only part of the fibula preserved with MPCA 477 (Fig. 3). The fibula clearly reached the ankle as in most non-avian theropods, but unlike parvicursorine taxa. The articulation between the distal fibula and the proximal tarsals is not preserved in MPCA 477.

The astragalus is restricted to the extensor face of the tibia in distal view unlike the majority of coelurosaurs (Fig. 4E), in which the astragalus wraps over much of the distal end of the tibia. The astragalus is also largely restricted to the rostral face of the tibia in *Achillesaurus* (Martinelli & Vera, 2007), *Shuvuuia* (Suzuki et al., 2002), and the Tugrikin Shireh alvarezsaurid (IGM 100/1305) though it wraps further onto the distal surface of the tibia in *Mononykus* (IGM 107/6) and *Patagonykus* (MCF-PVPH 53). The astragalus articular surface is smaller than the exposed end of the tibia in distal view, an unusual proportion among theropods, although this is in part due to poor preservation and possible breakage of the bottom of the astragalus. The ascending process is more complete on the left ankle, and is tall and triangular as in other coelurosaurs. Its lateral edge is relatively straight for most of its length and parallels the lateral edge of the tibia (Fig. 4B). The medial edge is inclined dorsolaterally as revealed by the underlying groove on the rostral face of the tibia. The astragalus of *Alnashetri* lacks the robust buttress for articulation with the distal fibula observed in *Patagonykus* (Novas, 1997) and *Achillesaurus* (Martinelli & Vera, 2007), nor is there evidence for a cup-like depression on the calcaneum for reception of the end of the fibula as seen in ornithomimosaur, *Patagonykus*, and tyrannosauroids.

The calcaneum is fused to the astragalus in *Alnashetri* (Figs. 3, 4) and the lateral face of the calcaneum on the better preserved left ankle appears to be flat and smooth. The lateral condyle of the astragalocalcaneum is distinctly taller than the medial one, a condition also observed in the basal alvarezsaurids *Patagonykus* and *Alvarezsaurus* (Martinelli & Vera, 2007, figure 9). By contrast, the proximal tarsal condyles are generally subequal in height in most coelurosaurian theropods, including dromaeosaurids (IGM 100/985), oviraptorosaurs (IGM 100/3003), tyrannosauroids (FMNH PR 2081), and parvicursorine alvarezsaurids (IGM 106/7), with the notable exception of a juvenile troodontid (Currie & Peng, 1993). The medial condyle of the astragalocalcaneum of *Alnashetri* is narrow and terminates in a sharp arc as in the parvicursorines *Albinykus* (Nesbitt et al., 2011) and *Mononykus* (Perle et al., 1994), and it projects farther anteriorly than the broader lateral condyle. The condyles are separated rostrally by a wide and deep sulcus forming a deep saddle in end view (Fig. 4E) as in the alvarezsaurids *Shuvuuia* and *Mononykus*, but in contrast

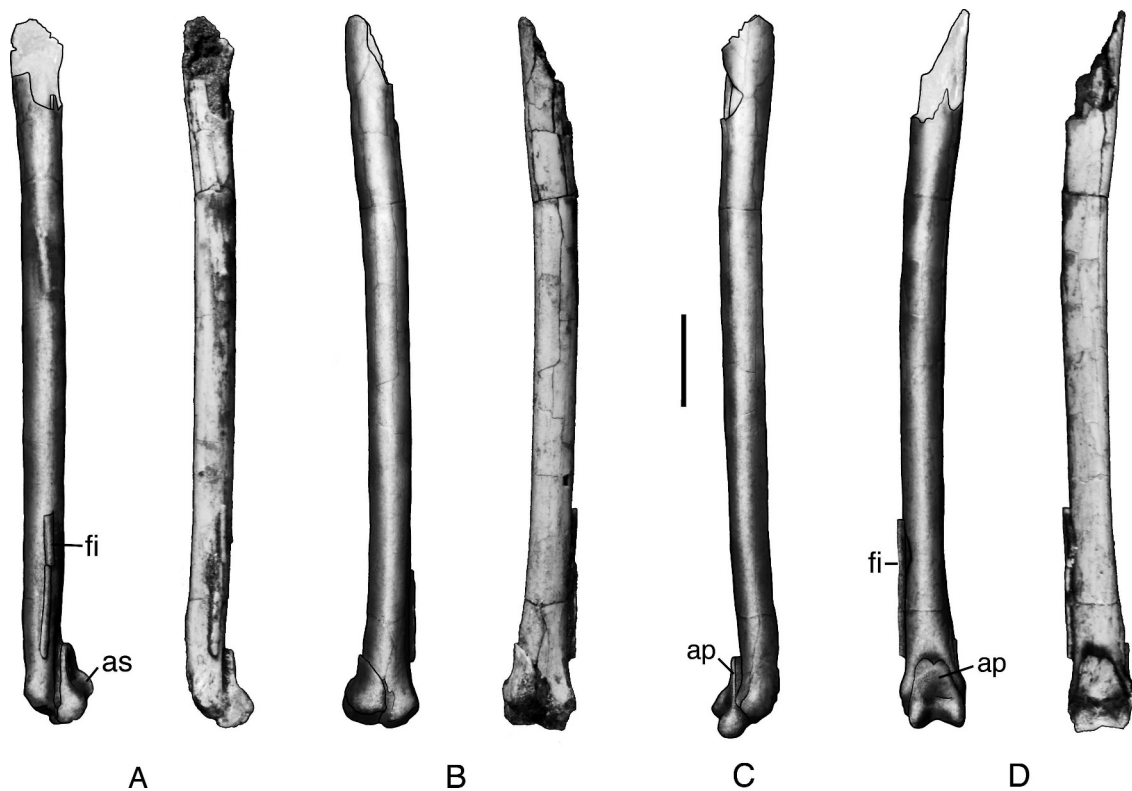


FIG. 3. Right tibia, fibula, and proximal tarsals of the holotype specimen (MPCA 477) of *Almashetri cerropoliciensis* in (A) lateral, (B) caudal, (C) medial, and (D) rostral views. Note that medial view is represented by drawing only, whereas all other views are represented by drawing and photograph. Abbreviations: as, astragalus; ap, ascending process of the astragalus; fi, fibula. Scale bar = 1 cm.

to the majority of other non-avian coelurosaurs. However, unlike these parvicursorine taxa, there is no tendinal fossa on the extensor surface of the sulcus that separates the condyles in *Almashetri* (Figs. 4B, 5B). The supracondylar fossa is very

broad and deep laterally and is truncated laterally by the tall lateral condyle, which it excavates medially. Naish and Dyke (2004) noted that a large, elliptical, and laterally situated supracondylar fossa is a synapomorphy of alvarezsaurids. A

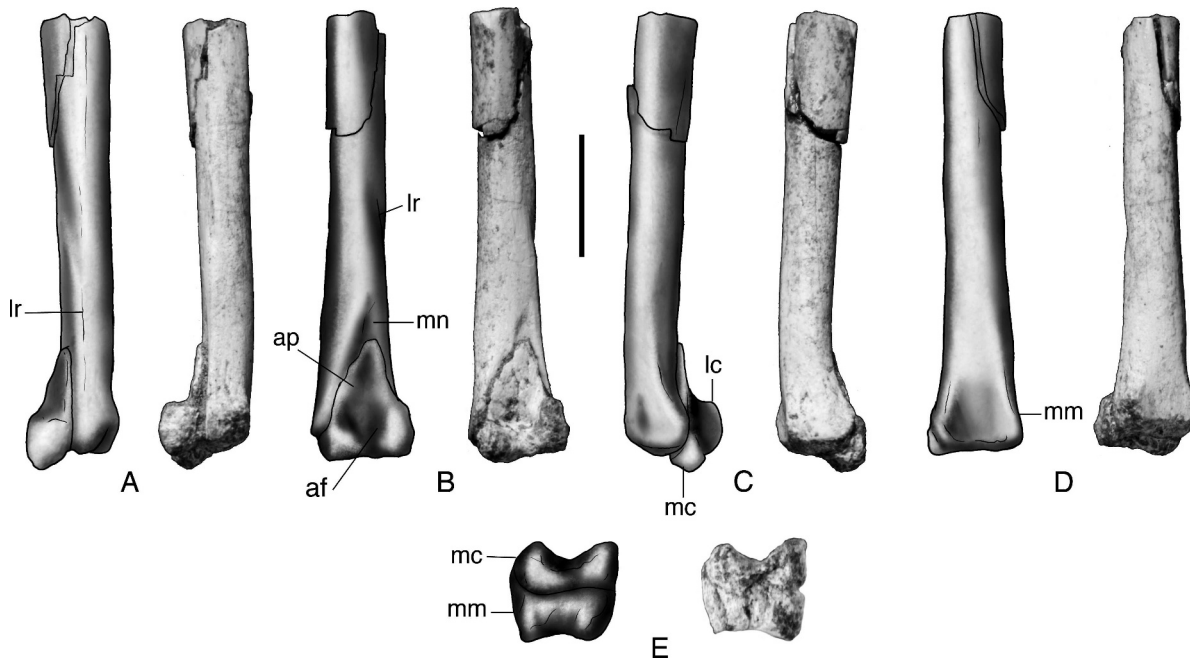


FIG. 4. Left tibia and astragalocalcaneum of the holotype specimen (MPCA 477) of *Almashetri cerropoliciensis* in (A) lateral, (B) rostral, (C) medial, (D) caudal, and (E) distal views. Abbreviations: af, fossa at base of ascending process; ap, ascending process of astragalus; lc, lateral condyle; lr, lateral ridge; mc, medial condyle; mm, medial malleolus; mn, medial notch on tibia for reception of ascending process of astragalus. Scale bar = 1 cm.

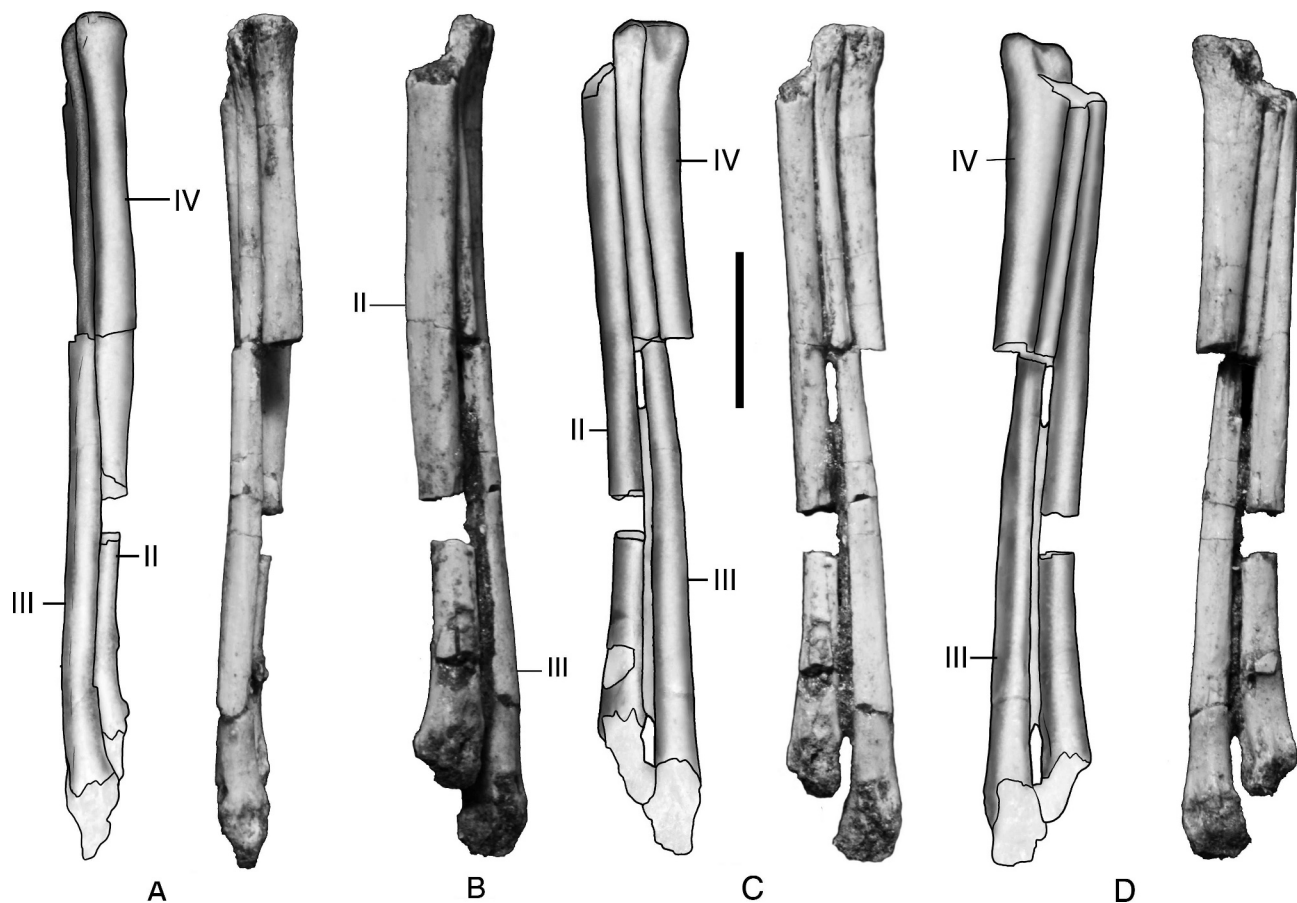


FIG. 5. Right metatarsus of the holotype specimen (MPCA 477) of *Alnashetri cerropolicencis* in (A) lateral, (B) medial, (C) rostral, and (D) caudal views. Note that medial view is represented by photograph only, whereas all other views are accompanied by half-tone drawings. Abbreviations: II–IV, metatarsals II–IV. Scale bar = 1 cm.

similar deep excavation of the medial face of the lateral condyle is observed in the alvarezsaurids *Achillesaurus* (Martinielli & Vera, 2007), *Patagonykus* (Novas, 1997; MCF-PVPH 47), and to a lesser extent in *Alvarezsaurus* (MUCPV 54). The fossa bears a small pit at its deepest point in *Alnashetri*. Several accessory fossae are observed on the better-preserved left ankle of *Patagonykus* (Novas, 1997), and the depression is also marked by pitting in the parvicursorine *Mononykus* (IGM 106/7). Such pits are not limited to alvarezsaurid taxa, however, and pits are also observed within a fossa at the base of the ascending process of the astragalus in *Tyrannosaurus rex* (FMNH PR 2081), and a single pit can be observed within the supracondylar groove of the unenlagiine *Rahonavis* (UA 8656). No distal tarsals are preserved with the holotype specimen of *Alnashetri*.

The right metatarsus (Fig. 5) is fairly complete, whereas only fragments of the left one were recovered. Metatarsal (MT) II is incomplete proximally on the right foot, but the proximal end is preserved on the left side. The proximal articulation is slightly expanded relative to the shaft and is roughly square in end view. The shaft is mediolaterally compressed and deeper in the extensor–plantar plane. The lateral and medial surfaces of the shaft converge posteriorly to form a low plantar crest. This crest reaches its maximum depth along the middle of the shaft, and is posteriorly convex in lateral view. Below the midshaft, the crest attenuates and is replaced by a rounded border. The shaft is slightly curved and laterally concave.

Alnashetri does not possess an arctometatarsalian foot, and MT III is exposed along the full length of the foot. Metatarsal III has a proximal articulation that is deeper than wide in end view, with straight medial and lateral edges (Fig. 5). The shaft is slender and is constricted at midlength, but still fully exposed in both plantar and extensor views as in *Alvarezsaurus*. The shaft is slightly medially curved in extensor view. The distal half of the shaft bears narrow facets on its medial and lateral faces for articulation with the shafts of MT II and MT IV, respectively (Fig. 6A). The facet for MT II extends farther distally than that for MT IV, suggesting that the shaft of MT IV diverges laterally from the axis of the metatarsus distally as is observed in *Alvarezsaurus* (MUCPV 54). This condition differs from parvicursorines as well as from outgroups, in which the flattened zone of contact for MT IV reaches roughly the same level as that for MT II. The shaft adjacent to the distal articulation exhibits a gentle anteriorly convex curvature (Fig. 6A, C), which serves to bring the distal articulation into the same plane as the articulation of MT II and MT IV in distal view. A similar curvature of the distal part of MT III is observed in *Albertonykus* (Longrich & Currie, 2009) and *Xixianykus* (Xu et al., 2010). The distal articulation is preserved on the left element, and is narrow in extensor view (Fig. 6C). A break extends obliquely through the articulation, rendering it uncertain as to whether it is ginglymoid or not. A shallow, but conspicuous extensor fossa lies proximal to the intercondylar groove.

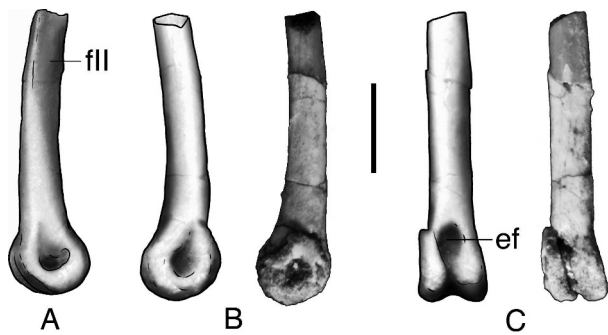


FIG. 6. Distal end of right metatarsal III of the holotype specimen (MPCA 477) of *Alnashetri cerropoliciensis* in (A) medial, (B) lateral, and (C) rostral views. Note that medial view is represented by half-tone drawing only, whereas the other views are represented by photographs accompanied by half-tones. Abbreviations: ef, extensor fossa; fII, facet for metatarsal II. Scale bar = 5 mm.

Only the proximal half of the left MT IV is preserved. Both its proximal articulation and shaft are more robust than the corresponding parts of the other two major metatarsals. The proximal part of the shaft is mediolaterally expanded in plantar view. In end view, the proximal articular surface is slightly triangular and mainly expanded mediolaterally.

Three articulated phalanges from the left foot (Fig. 7) likely represent the end of digit III, given their slender proportions and the symmetrical appearance of their shafts and articular surfaces. Phalanx III-2 is elongate with a shaft that is slightly constricted at midlength. The distal collateral ligament fossae are relatively large. A conspicuous extensor pit is observed on the dorsal surface just proximal to the condyles. Small notches are present immediately proximal to the distal articulation on the medioventral and lateroventral borders of the shaft (Fig. 7), and represent a unique trait of *Alnashetri*. Phalanx III-3 is almost as long as III-2 (Fig. 8). As in phalanx III-2, notches are observed proximoventral to the collateral ligament fossae. The ungual is incomplete, but is clearly the shortest element in the toe. The flexor tubercle is deep and positioned close to the proximal articulation (Fig. 7). The dorsal edge of the ungual is relatively straight in lateral view, whereas the lower edge is deeply concave. In ventral view, the lower face of the ungual is formed as a low ridge adjacent to the tubercle, but becomes more rounded distally.

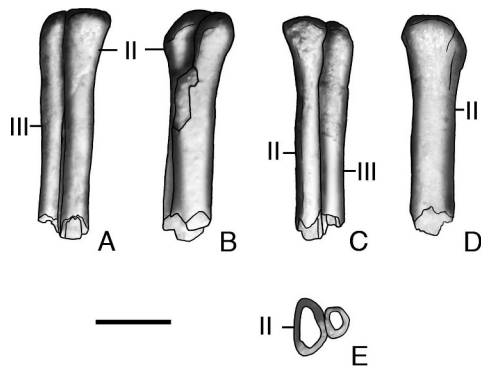


FIG. 7. Proximal ends of left metatarsals II and III of the holotype specimen (MPCA 477) of *Alnashetri cerropoliciensis* in (A) caudal, (B) lateral, (C) rostral, and (D) medial views. (E) Distal cross sections of the preserved sections. Abbreviations: II–III, metatarsals II–III. Scale bar = 5 mm.

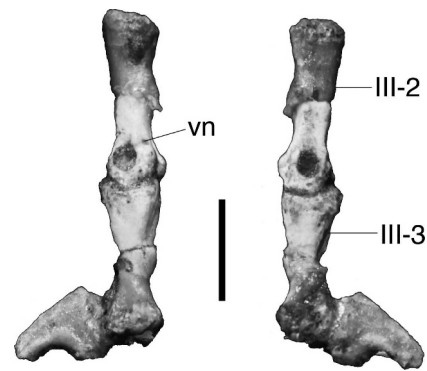


FIG. 8. Right pedal digit III of the holotype specimen (MPCA 477) of *Alnashetri cerropoliciensis*: Left, medial view; Right, lateral view. Abbreviations: III-2, phalanx III-2; III-3, phalanx III-3; vn, ventral notch on distal articulation below ligament pit. Scale bar = 5 mm.

Phylogenetic Methods and Results

Due to its fragmentary nature, the holotype skeleton of *Alnashetri* lacks clear-cut synapomorphies that would allow unambiguous referral to a particular coelurosaurian clade, necessitating a more comprehensive analysis to determine its affinities. As a first pass, we added *Alnashetri* to a recent and relatively comprehensive cladistic matrix used to explore coelurosaurian interrelationships (Zanno & Makovicky, 2011). This preliminary analysis found *Alnashetri* to nest within Alvarezsauroidea. To further explore this potential relationship, we added four recently described alvarezsaurid taxa (*Linhenykus* Xu et al., 2011; *Xixianykyus* Xu et al., 2010; *Albinykus* Nesbitt et al., 2011; and *Bonapartenykus* Agnolin et al., 2012) and eight characters with relevance for *Alnashetri* or for alvarezsaurid relationships to the matrix. Several other alvarezsaurid taxa were omitted either due to their highly incomplete preservation, including *Albertonykus* (Longrich & Currie, 2009), *Ceratonykus* (Alifanov & Barsbold, 2009), and *Kol* (Turner et al., 2009), or because of a lack of sufficiently detailed description (*Haplocheirus*). The first category of omissions is less likely to have an impact on the position of *Alnashetri* as these taxa all exhibit an arctometatarsal pes and are therefore more derived alvarezsaurids than is *Alnashetri*. The omission of *Haplocheirus* is of greater concern as it is considered the basalmost alvarezsaurid (Choiniere et al., 2010) and is therefore critical for understanding trait distributions at the base of the clade. The basal Argentinean taxon *Achillesaurus* (Martinelli & Vera, 2007) was not included as a separate terminal taxon, as it may be a junior synonym of *Alvarezsaurus*, which is known from the same formation and from which it differs trivially. Because we could not code the majority of traits for *Haplocheirus* from the brief preliminary description (Choiniere et al., 2010), and because information on *Alnashetri* is restricted to the hind limb, the results of our present analysis should be viewed as provisional. The character list and data matrix (in Nexus or TNT formats) are available upon request from the senior author, or online at <http://fieldmuseum.org/users/peter-makovicky>.

The data matrix was analyzed with parsimony using TNT (Goloboff et al., 2008), with all characters treated as unordered. Analysis was performed using the following parameters: searches employing the Tree Bisection and Reconnection algorithm were run on 200 randomly generated

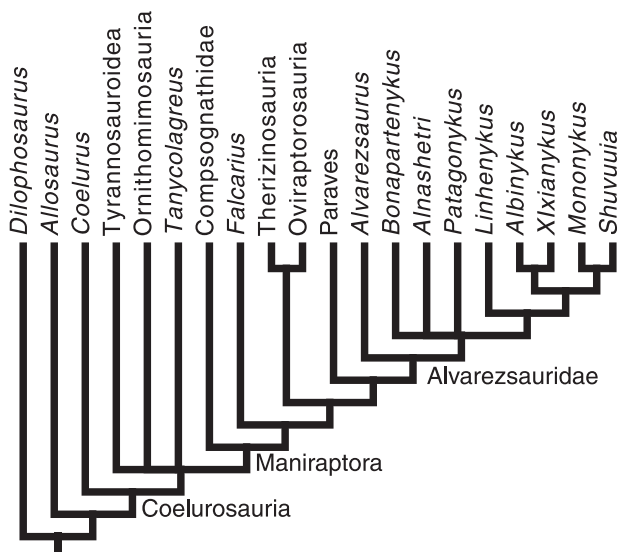


FIG. 9. Strict consensus of 28,980 most-parsimonious trees derived from the phylogenetic analysis of 304 characters in 80 coelurosaurian and outgroup taxa. Clades outside of Alvarezsauridae have been collapsed to suprageneric lineages for simplicity. Clade names follow usage and definitions by Sereno et al. (2005) and Choiniere et al. (2010). All shown relationships have a Bremer support of 1, although some nodes within collapsed clades enjoy higher support.

Wagner trees, with 10 trees for held at each iteration. The analysis produced 390 most-parsimonious trees (MPTs) with a length of 1052 steps, the consensus of which is shown in Figure 9. Further branch swapping using the Subtree Pruning and Regrafting strategy was performed on the recovered 390 MPTs, resulting in a total population of 28,980 MPTs, but the additional resolutions caused no changes to consensus topology, indicating that all MPTs derive from a single tree island. *Alnashetri* is recovered as a basal alvarezsaurid, falling within a basal polytomy of other Argentinean taxa from the Neuquén Basin. The character support for this placement, and a qualitative evaluation of it, will be presented in the Discussion.

Discussion

Alnashetri represents only the second coelurosaurian taxon known from the rich La Buitrera fauna. This locality has produced a remarkable diversity of small vertebrates (e.g., Apesteguía & Novas, 2003; Apesteguía & Zaher, 2006; Rougier et al., 2011), but Coelurosauria was only known from several specimens of the unenlagiine dromaeosaurid *Buitreraptor* (Makovicky et al., 2005; Gianechini & Apesteguía, 2011) prior to the preparation of *Alnashetri*. *Alnashetri* can clearly be distinguished from *Buitreraptor* in its lack of a pronounced lateral ridge or tuber (= posterior trochanter of Gauthier [1986]) on the proximal femur. With few exceptions such as *Vorona*, almost all paravian taxa exhibit a prominent lateral tuber regardless of size or developmental stage. A large lateral tuber is observed in specimens of *Buitreraptor* with femoral lengths ranging from approximately 80 mm to approximately 150 mm, and can thus be confidently interpreted as ontogenetically invariant. Currie and Peng (1993) also noted the presence of a large lateral tuber on the hind limb of a

juvenile troodontid, and all specimens of *Archeopteryx* exhibit a prominent tuber regardless of size (Wellnhofer, 1974; Mayr et al., 2007).

Alnashetri also differs from *Buitreraptor* in traits of the tibia, proximal tarsals, and metatarsus. The lateral malleolus of the tibia is relatively broad and flat with little or no lateral projection in *Alnashetri*, whereas it is narrow and projects as a pointed process beyond the fibula and lateral margin of the astragalocalcaneum in *Buitreraptor* (MPCA 238). The astragalocalcaneum of *Alnashetri* differs significantly from that of *Buitreraptor* in having asymmetrical condyles with the lateral one taller than the medial one, and in the possession of an expanded fossa at the base of the ascending process, bearing a small pit presumably for insertion of tendons of the foot extensor musculature (Nesbitt et al., 2011). The third metatarsal of *Alnashetri* is more uniformly exposed in caudal view than in *Buitreraptor*, where the diaphysis of MT III is pinched distally between MT II and MT IV. The diaphysis of MT III has a gently rounded rostral face rather than flat to concave rostral shaft surface as observed in the unenlagiines *Buitreraptor* (MPCA 238) and *Rahonavis* (UA 8656), and the proximal half of the shaft of the third metatarsal is not rostroplantarly compressed as in *Buitreraptor* (MPCA 238).

Although the preserved parts of the anatomy are limited, the holotype of *Alnashetri* does exhibit two autapomorphies. The first of these is an expanded longitudinal ridge that separates the rostral and lateral faces of the distal tibial shaft and extends well above the top of the ascending process of the astragalus. Many other coelurosaurians such as ornithomimosaurids (*Beishanlong*, Makovicky et al., 2010), dromaeosaurids (*Velociraptor* IGM 100/985; *Rahonavis* UA 8656), alvarezsaurids (*Achillesaurus*, Martinelli & Vera, 2007; *Shuvuua*, IGM 100/1305), and oviraptorosaurs (*Conchoraptor* IGM 100/3003) have a sharp edge separating the rostral and lateral faces of the lateral malleolus of the tibia, but the ridge is restricted to the articular surface for the astragalocalcaneum and does not extend above the proximal tarsals. *Alnashetri* also appears to be unique in having small notches or indentations on the edges of the lateral and medial hemicondyles of the distal articulations on phalanges III-2 and III-3, proximoventral to the collateral ligament pits. Such notches have not been reported in other coelurosaurian taxa to our knowledge, although detailed information on phalangeal anatomy is admittedly scant for many taxa.

Besides unenlagiine dromaeosaurids, other coelurosaurian clades known from South America include avialans, alvarezsaurids, and compsognathids. Although *Alnashetri* resembles Cretaceous stem avialans in lacking a fourth trochanter and in having a block-like distal ankle with rostrally projected astragalocalcaneal condyles, it differs in having a fibula that reaches the ankle and in having narrower astragal condyles separated by a wide sulcus. Furthermore, unlike South American enantiornithines (Chiappe & Walker, 2002) and many other stem birds such as *Patagopteryx* (Chiappe, 2002), it lacks a lateral tubercle on the proximal ends of the femur. Although the Malagasy stem avialan *Vorona* also lacks a lateral tubercle, its fibula does not reach the ankle and it has a fully fused tarsometatarsus with a proximolateral foramen between MT III and MT IV (Forster et al., 2002) unlike *Alnashetri*. *Alnashetri* differs from compsognathids and several other non-paravian coelurosaurian lineages such as tyrannosauroids, ornithomimosaurids, and therizinosaurids in the absence of a fourth trochanter, and the probable partial or

complete development of a trochanteric crest. It furthermore is distinguishable from these clades in the more block-like outline of the ankle in distal view, with rostrally projected astragalar condyles separated by a deep saddle-like sulcus.

Our phylogenetic analysis posits *Alnashetri* as a basal alvarezsaurid in a polytomy with two other Argentinean basal alvarezsaurids, *Bonapartenykus* and *Patagonykus*. Eleven unambiguous synapomorphies (characters [chars.] 112, 114, 117, 157, 164, 181, 265, 297, 298, 299, 301; see character list) unite alvarezsaurid taxa in our phylogenetic result, but only three of these (chars. 297, 298, 299) can be scored in *Alnashetri*. These three synapomorphies include: asymmetrical astragalocalcaneal articulation with a taller lateral condyle (char. 297, shared with *Alvarezsaurus*, *Patagonykus*, and *Albinykus*, reversed in *Mononykus* and *Shuvuuiia*); presence of a laterally displaced expanded fossa at the base of the ascending process of the astragalus (char. 298, shared with *Patagonykus*, *Alvarezsaurus*, and *Mononykus*, absent in *Shuvuuiia* and *Albinykus*, not observable in other taxa due to preservation); and presence of small pits, presumably for tendinal insertion, within the supracondylar groove or fossa (char. 299, shared with *Mononykus*, *Patagonykus*, and probably *Alvarezsaurus*, although preservation is poor in the latter, absent in *Shuvuuiia*, unknown in other alvarezsaurids).

Although we find unambiguous character support for placing *Alnashetri* within the Alvarezsauridae, all of these traits derive from the ankle and may therefore be functionally interrelated and therefore not fully independent of each other. Nevertheless, *Alnashetri* does exhibit other traits, such as reduction or absence of a fourth trochanter, only a small cleft between anterior (lesser) and greater trochanters or no separation at all, and absence of a lateral ridge and posterior trochanter that are all compatible with alvarezsaurid anatomy, though these characters also enjoy a wider distribution among coelurosaurian theropods. We also note that there are a few other anatomical traits in *Alnashetri* that are only known in some alvarezsaurid taxa among maniraptorans. For example, the rostral face of the distal tibia bears a clearly delimited depression for reception of the astragalar ascending process in the holotype of *Mononykus*, as in *Alnashetri*, and Agnolin et al. (2012) noted that the distal tibia of *Bonapartenykus* bears an oblique ridge for reception of the medial edge of the ascending process. Such structures cannot be evaluated in *Patagonykus*, *Albinykus*, *Linhenykus*, and *Xixianykus* and *Alvarezsaurus* due to fusion or articulation between the tibia and proximal tarsals, or due to preservation, and they are absent *Shuvuuiia* and virtually all maniraptoran outgroups.

Alnashetri predates all other South American alvarezsaurids by 5 to 10 million years. All other described alvarezsaurids from Argentina derive from younger strata within the Neuquén Group of Neuquén and Río Negro provinces. Should future discoveries confirm our preliminary phylogenetic findings, the discovery of *Alnashetri* within the lowest unit of the Neuquén Group provides evidence that this clade was present in the Neuquén Basin throughout the entire span of the Late Cretaceous (Salgado et al., 2009; Agnolin et al., 2012) and that alvarezsaurids were a stable, if rare, component of South American Late Cretaceous faunas.

The holotype skeleton of *Alnashetri* is remarkably small and comparable to *Shuvuuiia* in size. Besides *Ligabueino*, it is the smallest non-avian theropod yet collected from Argentina, although it is impossible to determine if the holotype represents a juvenile individual or not without histological sampling of

the long bones. By contrast, *Achillesaurus*, *Patagonykus*, and *Bonapartenykus* represent relatively large taxa, whereas the holotype of *Alvarezsaurus* derives from a young juvenile (and is possibly a senior synonym of *Achillesaurus*). Continued fieldwork and future discoveries hopefully will provide more information on the anatomy of *Alnashetri* and allow a more definitive evaluation of its affinities and its significance for understanding biogeography and evolutionary trends such as body size evolution within alvarezsaurids.

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