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ARTICLE

A NEW SPECIMEN OF *VELOCISAURUS UNICUS* (THEROPODA, ABELISAUROIDEA) FROM THE PASO CÓRDOBA LOCALITY (SANTONIAN), RÍO NEGRO, ARGENTINA

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ABSTRACT—Abelisauroids are the most abundant theropods in the Cretaceous beds of Patagonia. They are traditionally subdivided into large-sized Abelisauridae and smaller Noasauridae. Here, we describe a new specimen of the small enigmatic abelisauroid *Velocisaurus unicus* Bonaparte, 1991, which was previously known from a single incomplete specimen from Neuquén City, Neuquén Province, Patagonia. The new material comes from the Santonian Bajo de la Carpa Formation (Late Cretaceous) at the Paso Córdova locality, Río Negro Province. It comprises an almost complete left hind limb and offers novel information about the anatomy of this poorly known abelisauroid. The new material shows that *Velocisaurus* is remarkable in having a very short, stout, and anteriorly bowed femur, which has a notably subtriangular cross-section at its proximal end. The tibia is long and slender, and the anterior surface of the distal end is anteroposteriorly flat and transversely expanded, with an enlarged surface for the ascending process of the astragalus. The pes has a stout third metatarsal, rod-like metatarsals II and IV, and highly modified phalanges of digit IV. The unique combination of characters of *Velocisaurus* indicates that this taxon belongs to a still poorly understood radiation of gracile-limbed abelisauroids. The inclusion of *Velocisaurus* in a comprehensive phylogenetic analysis recovers a monophyletic Noasauridae, but with only very weak support. Detailed analysis of features supporting the inclusion of *Velocisaurus* within Noasauridae is discussed, and their implications for abelisauroid phylogeny are revisited.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

Abelisauroids represent a major radiation of carnivorous dinosaurs that were highly diverse during the Cretaceous on Gondwanan land masses (Bonaparte, 1991a, 1996; Carrano and Sampson, 2008; Novas, 2009; Novas et al., 2013). Although complete or nearly complete skeletons of several members of this clade are known, the taxonomic relationships of basal abelisauroids remain largely unresolved (Rauhut, 2003; Wilson et al., 2003; Carrano and Sampson, 2008; Canale et al., 2009; Novas et al., 2004, 2013; Novas, 2009; Pol and Rauhut, 2012). Noasauridae is a poorly known clade of abelisauroids originally erected by Bonaparte and Powell (1980) to include the single genus and species *Noasaurus leali*, from the Maastrichtian (Late Cretaceous) of Salta Province, Argentina. Later, Bonaparte (1996) tentatively included the small-sized *Ligabueino andesi* from Neocomian beds of Patagonia within noasaurids. More recently, Sampson et al. (2001) described nearly complete and abundant individuals of the noasaurid *Masiakasaurus knopfleri*, from the Late Cretaceous of Madagascar (Carrano et al., 2002, 2011). Several analyses included fragmentary and poorly known specimens coming from diverse Cretaceous beds mainly from Gondwanan landmasses, as well as some potential records in Europe within Noasauridae (Sampson et al., 1998, 2001; Coria and Salgado, 2000; Wilson et al., 2003; Carrano et al., 2011; Novas et al., 2004; Agnolin and Martinelli, 2007; Carrano and Sampson, 2008; Canale et al., 2009; Pol and Rauhut, 2012; Tortosa et al., 2013). The monophyly of Noasauridae has been criticized by some authors (e.g., Novas, 2009; Novas et al., 2013) who suggest that this clade may include a paraphyletic or polyphyletic assemblage of small-sized, unrelated basal abelisauroids.

Velocisaurus unicus is among the most poorly known forms assigned to Noasauridae. This taxon was described by Bonaparte (1991b) on the basis of a nearly complete hind limb from the Late Cretaceous (Santonian) of Neuquén City, at Neuquén Province, Patagonia, Argentina. In his original description, Bonaparte (1991b) recognized the unique morphology of this tiny dinosaur and assigned it with reservations to the clade Ceratosauria, at the same time erecting the new family Velocisauridae. Bonaparte (1991b) considered *Velocisaurus* to be an extremely cursorial theropod based on the morphology of the metatarsals and the flat pedal claws. More recently, Rauhut (2003) considered *Velocisaurus* to be an abelisauroid and he indicated that it was of interest as one of the few small theropods known from the Cretaceous of Gondwana. Later, *Velocisaurus* was proposed to be closely related to Noasauridae (Agnolin et al., 2003, 2004; Carrano and Sampson, 2008; Agnolín and Chiarelli, 2010; Carrano et al., 2011). Furthermore, Carrano and Sampson (2008) suggested that, due to the incomplete nature and absence of clear autapomorphies, *Velocisaurus unicus* may be regarded as an indeterminate noasaurid. However, based on its locality and age,

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these authors considered *V. unicus* tentatively as a valid taxon. It is worth mentioning that none of the previous authors made a detailed consideration of its phylogenetic relationships.

The aim of the present contribution is to describe a new specimen of *Velocisaurus unicus*. The new individual consists of an incomplete hind limb that sheds light on the morphology of this theropod and allows interpretation of some features that were previously unknown or misinterpreted due to the poor preservation of the holotype and, up to this point, only available specimen. In addition, *Velocisaurus* is included for the first time in a comprehensive data matrix of abelisauroid theropods, and its implications for abelisauroid phylogeny are discussed.

MATERIALS AND METHODS

With the aim to elucidate the phylogenetic affinities of *Velocisaurus unicus*, we coded this taxon into a comprehensive abelisauroid data matrix (Pol and Rauhut, 2012). The discovery of the new specimen, together with the reevaluation of the holotype, allowed reevaluation of several character states from the data matrix of Pol and Rauhut (2012) regarding *Velocisaurus* (Appendix 1; Supplementary Data). The following characters were changed from the Pol and Rauhut (2012) scorings as follows: (192) Size of iliofibularis tubercle on fibula: moderate (0), large (1) (changed from '?' to '1'); (194) morphology of astragalar ascending process: blocky (0), laminar (1) (changed from '?' to '1'); (196) horizontal groove across the anterior face of the astragalar condyles: absent or weak (0), pronounced (1) (changed from '1' to '?'); (199) height of ascending process of the astragalus relative to depth of astragalar body: less or equal (0), greater (1) (changed from '?' to '1'); (203) morphology of lateral and medial grooves on pedal unguals: single (0), double (1) (changed from '?' to '1'); and (205) ventral surface of pedal unguals with a well-developed flexor tubercle, and usually flat (0), or without flexor tubercle and with a ventral depression in its proximal end (1) (changed from '?' to '1').

The phylogenetic analysis was performed using TNT 1.1 (Goloboff et al., 2008). All characters were equally weighted and treated as unordered. Heuristic searches were performed after 1000 replicates of Wagner trees using random addition sequence followed by tree bisection and reconnection (TBR) branch swapping, holding 100 trees per replicate. Furthermore, we performed an additional round of TBR branch swapping that resulted in the same number of trees and tree indexes. We follow Pol and Rauhut (2012) in excluding *Genusaurus* and *Kryptops* from the analysis because of their fragmentary nature.

Institutional Abbreviations—**MPCN**, Museo Patagónico de Ciencias Naturales, General Roca, Río Negro, Argentina; **MUCPv**, Museo de la Universidad Nacional del Comahue, Neuquén, Neuquén, Argentina.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1888
THEROPODA Marsh, 1881
CERATOSAURIA Marsh, 1884
ABELISAUROIDEA Bonaparte, 1991a
VELOCISAURUS UNICUS Bonaparte, 1991a

Holotype—MUCPv-41, a nearly complete right hind limb, including tibia, astragalus, metatarsals II, III, and IV, and most pedal phalanges (Bonaparte, 1991b).

Referred Specimen—MPCN-PV-370, incomplete left hind limb, including femur, tibia, metatarsals II, III, and IV, several pedal non-ungual phalanges, and digit IV pedal claw.

Locality and Horizon—The new specimen reported here comes from beds of the Late Cretaceous Bajo de la Carpa Formation, Río Colorado Subgroup, Neuquén Group (Santonian; Bonaparte, 1991b; Garrido, 2012). The fossiliferous locality that yielded the referred specimen is Paso Córdova, at Río Negro Province, Patagonia, Argentina (Fig. 1).

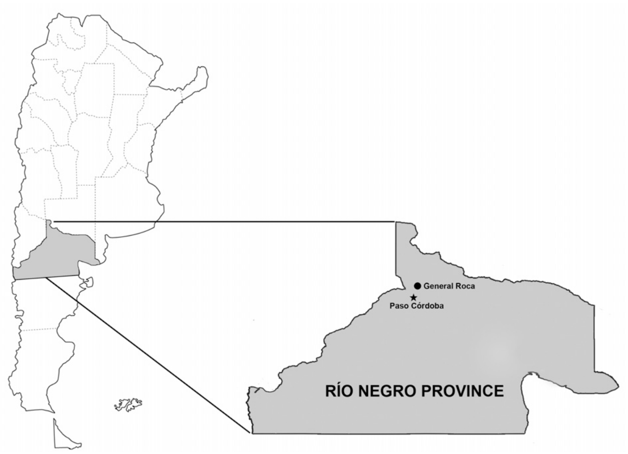


FIGURE 1. Map of Río Negro Province showing the Paso Córdoba locality where MPCN-PV-370 was found.

Emended Diagnosis—Small-sized theropod (Table 1) dinosaur diagnosable by the following combination of characters (autapomorphies marked by an asterisk, *): femur with proximal end showing a strongly subtriangular cross-section with lateral and medial surfaces converging anteriorly and resulting in a thick dorsoventral crest*; tibia coelurosaur-like, long and slender, with its distal end anteriorly flat, bearing a large surface to accommodate a tall and wide ascending process of the astragalus; metatarsals II and IV with rod-like shafts, differing from the laminar outer metatarsals present in other small abelisauroids*; and pedal phalanx IV-1 anteroposteriorly short, dorsoventraly tall, transversely compressed on its dorsal half, and medially curved*.

Features of the tibia, metatarsals, and pedal phalanges are shared between the holotype and the newly referred specimen, indicating that both specimens represent the same taxon. The morphology of the femur is unknown in the holotype specimen (Fig. 2).

DESCRIPTION

Femur

The femur (Fig. 3) is abraded at its proximal and distal ends. It is a robust element with very pronounced muscle scars. The shaft is straight in anterior view and anteriorly bowed in lateral view. Proximally, the shaft is notably subtriangular in cross-section; the medial and lateral surfaces of the bone are anteriorly convergent and form a very thick longitudinal crest along the proximal third of the bone shaft. In posterior view, the medial and lateral margins of the shaft are represented by prominent ridges that extend to the distal end of the bone. The shaft becomes subrectangular in cross-section near the distal end of the bone.

The femoral head is poorly preserved, but the preserved portion suggests that it was oriented about 45° anteromedially with respect to the shaft of the bone, as occurs in non-tetanuran theropods (Rauhut, 2003).

Although it is incompletely preserved, the greater trochanter was confluent with the femoral head. Only the base of the lesser trochanter is preserved. It is anteriorly positioned and separated from the greater trochanter by a deep and wide cleft. The preserved portion of the trochanter is strongly rugose, as in *Majungasaurus* (Carrano, 2007). A large nutrient foramen is present distal to the lesser trochanter. Also distal to the lesser trochanter, and posterolaterally

TABLE 1. Measurements (in mm) of preserved elements of MPCN-PV-370.

Element	Total length	Proximal width	Distal width	Anteroposterior width at mid-length	Transverse width of shaft at mid-length	Proximal dorsoventral height	Dorsoventral height at mid-shaft	Distal dorsoventral height
Femur	112.11	18.80	16.48	—	—	—	—	—
Tibia	142.65	13.66	19.96	—	—	—	—	—
MT-III	85.70	7.42	10.36	—	—	—	—	—
MT-II	—	5.79	—	1.86	2.68	—	—	—
MT-IV	—	—	—	4.38	3.93	—	—	—
Ph II-1	21.01	6.47	5.33	—	—	8.14	4.85	4.25
Ph III-1	16.80	7.84	6.60	—	—	6.07	3.94	3.97
Ph IV-1	12.41	4.39	5.40	3.25	4.39	—	4.27	4.09
Ph IV-2	12.04	5.10	—	—	—	6.10	3.89	—
Ph IV-5	11.23	3.54	—	—	—	5.49	—	—

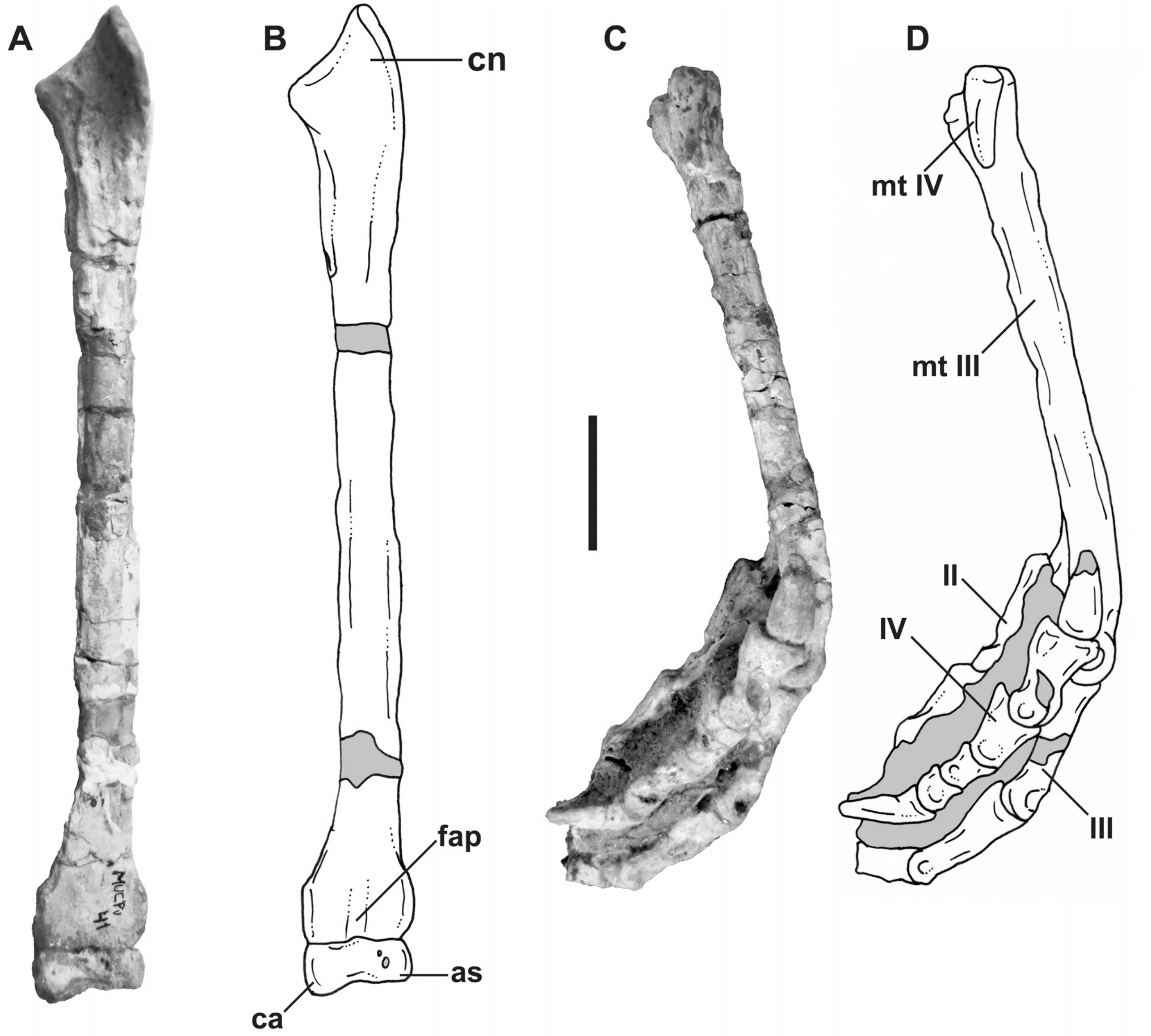
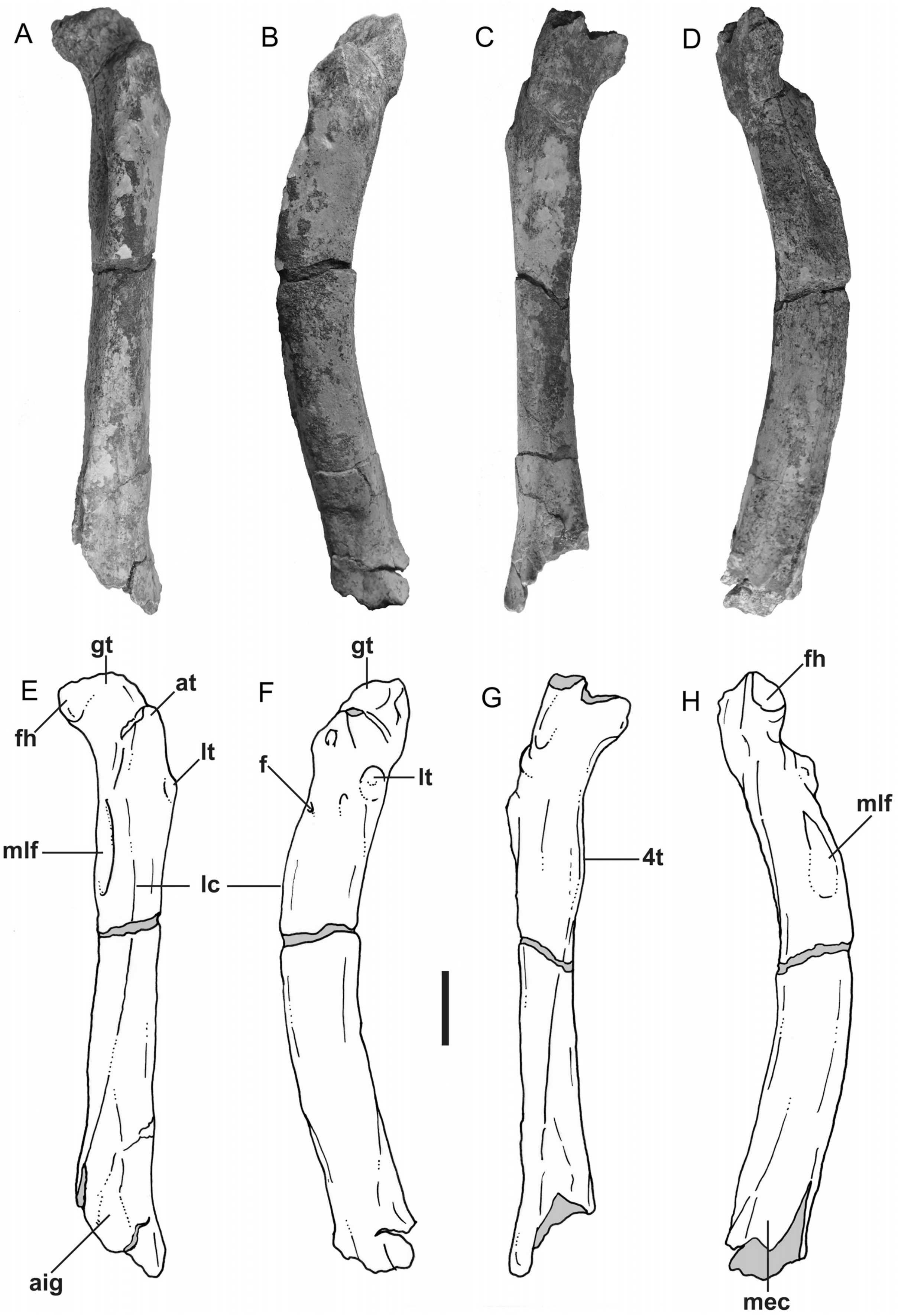


FIGURE 2. Holotype of *Velocisaurus unicus* (MUCPv-41). **A**, right tibia in anterior view; **B**, line drawing of right tibia in anterior view; **C**, right foot in lateral view; **D**, line drawing of the right foot in lateral view. Gray indicates matrix. **Abbreviations**: **as**, astragalus; **ca**, calcaneum; **cn**, cnemial crest; **fap**, facet for the ascending process of the astragalus; **mt III**, metatarsal III; **mt IV**, metatarsal IV; **II–IV**, digits II through IV. Scale bar equals 2 cm.


A
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positioned, a small rugose tubercle represents the accessory trochanter, possibly related to the insertion of the M. iliofemoralis externus (Hutchinson, 2001). This tubercle is not connected with the lesser trochanter, so a continuous trochanteric shelf is absent as in other abelisauroids (Carrano, 2007).

A small but distinct fourth trochanter is present. It forms a strong longitudinal ridge that extends posteromedially along the shaft. It shows some well-developed rugosities on its medial surface, possibly related to the insertion of the M. caudofemoralis brevis (Hutchinson, 2001).

Medial to the fourth trochanter, a large, deep, and well-defined fossa is present that probably served as the attachment site of the M. caudofemoralis longus (Carrano et al., 2002). A similar fossa is also present in *Masiakasaurus* and *Ligabueino* (Bonaparte 1996; Carrano et al., 2002). This fossa is anteriorly bounded by the thick longitudinal crest that constitutes the anterior surface of the femoral shaft.

The anterior intercondylar groove is well developed and extends for almost half of the femur length. Although most of the distal end is broken off, a small shallow groove on the laterodistal end of the bone represents the fibular condylar groove.

The mediodistal crest is represented by a small portion of its proximal tip, which suggests that it was strongly dorsoventrally extended as in other ceratosaurs (Carrano and Sampson, 2008). This crest is posteriorly delimited by a shallow and wide groove.

Tibia

The proximal and distal ends of the tibia are badly damaged. The tibia (Fig. 4) is a long and straight element, gently bowed laterally and posteriorly. The shaft is anteroposteriorly compressed and subelliptical in cross-section at its midpoint. The anterior surface of the shaft is remarkably flat, more so than in *Masiakasaurus*, which is a condition also found in coelurosaurs (Novas et al., 2013).

Proximally, only the base of the fibular condyle is preserved, whereas the medial condyle is completely missing. Distal to the lateral condyle, on the posterior face of the shaft, a deep and small depression that likely represents a nutritive foramen is present. The cnemial crest is represented only by its base, which indicates that the crest was rather robust and well developed. It rises from the medial side of the shaft and is anteriorly oriented. Mediodistal to the base of the cnemial crest, there is a short and thin ridge that probably served for the insertion of M. flexor tibialis internus (Carrano and Hutchinson, 2002). The lateral fossa is shallow and transversely wide, delimited medially by the base of the cnemial crest and laterally by the fibular crest.

The fibular crest is well developed and located at the same level as the base of the cnemial crest. It is connected to the proximal end of the bone by a smooth ridge, as typically occurs in non-tetanuran theropods (Rauhut, 2003). Distal to the fibular crest, a well-developed fibular articular surface is present. This longitudinal surface is rugose, well defined, and anteroposteriorly wide. There is a poorly defined gap separating the fibular crest from the fibular facet, whereas in *Masiakasaurus* this gap is more extensive (Carrano et al., 2002).

Medial to the proximal end of the fibular facet, a faint groove extends proximodistally along the shaft, a condition shared with the holotype specimen. It shows well-defined margins, and its proximal half is located near the lateral margin of the shaft and is slightly medially oriented. This groove might represent the intermuscular line described for *Masiakasaurus* and *Tyrannosaurus*, which delimits the anterior origin of the M. tibialis (Carrano and Hutchinson, 2002; Carrano et al., 2002).

The surface for articulation with the ascending process of the astragalus is flat and lacks a proximal transverse step, as also observed in the holotype specimen (Bonaparte, 1991b). Although the ascending process of the astragalus is not preserved in any of the *Velocisaurus* specimens, the astragalar facet on the anterior surface of the distal tibia suggest that it was probably scale-like, tall, transversely wide, and anteroposteriorly compressed, as previously suggested by Bonaparte (1991b) for the holotype specimen. The distal end of the tibia shows a faint dorsoventral median ridge, as occurs in other abelisauroids (Novas, 2009). Only the bases of the distal malleoli are preserved. In distal view, the tibia is subtriangular in contour, transversely wide, and strongly anteroposteriorly compressed.

Fibula

The fibula (Fig. 5) is only represented by a damaged portion of the proximal end. As in abelisauroids, an expanded iliofibularis tubercle is present (Rauhut, 2003). Distal to this tubercle the fibular shaft becomes abruptly narrow towards its distal end, a condition similar to that in coelurosaurs (Novas et al., 2013).

Metatarsals

The metatarsals (Fig. 6) are poorly preserved: Metatarsal III lacks its proximal end and its distal end is incomplete, and metatarsals II and IV lack their proximal halves and show badly damaged distal ends. Metatarsals I and V are not preserved. Metatarsal III is very large and is the stoutest element of the pes, as in the type specimen. Its proximal half is very robust and shows a slight anterior expansion. This dorsoventrally exposed metatarsal III indicates an antarctometatarsalian pes, as typically occurs in noasaurids (Carrano and Sampson, 2008). On the proximal third of the bone, the posterior surface of the shaft is transversely wider than the anterior surface. The posterior surface becomes narrower towards its distal end, giving room to the articulation for the distal end of metatarsals II and IV. Due to the posterior narrowing of metatarsal III, its medial and lateral surfaces are obliquely oriented and converge slightly posteriorly, a feature also present in the holotype. The distal articular surface of metatarsal III is very poorly preserved, but it appears to be dorsoventrally low, as occurs in other abelisauroids (de Valais et al., 2003).

Although they are poorly preserved, it can be said that metatarsals II and IV are greatly reduced in thickness, a trait that was noticed by Bonaparte (1991b) in the original description of *Velocisaurus*. The shafts are rod-like, differing from the laminar outer metatarsals present in other small abelisauroids such as *Masiakasaurus* and *Noasaurus* (Bonaparte and Powell, 1980; Sampson et al., 2001). The shaft of metatarsal II is thinner than that of metatarsal IV, as occurs in the holotype specimen (Bonaparte, 1991b). The distal end of metatarsal II appears to be transversely wider and more robust than that of metatarsal IV. Although it is very poorly preserved, the distal end of metatarsal IV was probably reduced and appears to lack a distal ginglymous, a condition also observed in the holotype specimen (Bonaparte, 1991b). The posterior surfaces of metatarsals II, III, and IV are nearly straight, which indicates that the entire posterior surface of the metapodium was probably flat along its length.

← FIGURE 3. Left femur of *Velocisaurus unicus* (MPCN-PV-370) in anterior (**A**), lateral (**B**), posterior (**C**), and medial (**D**) views. Line drawings of MPCN-PV-370 in anterior (**E**), lateral (**F**), posterior (**G**), and medial (**H**) views. Gray indicates matrix. **Abbreviations**: **aig**, anterior intercondylar groove; **at**, accessory trochanter; **f**, foramen; **fh**, femoral head; **gt**, greater trochanter; **lc**, longitudinal crest; **lt**, lesser trochanter; **mec**, medial epicondylar groove; **mlf**; median large fossa; **4t**, fourth trochanter. Scale bar equals 2 cm.

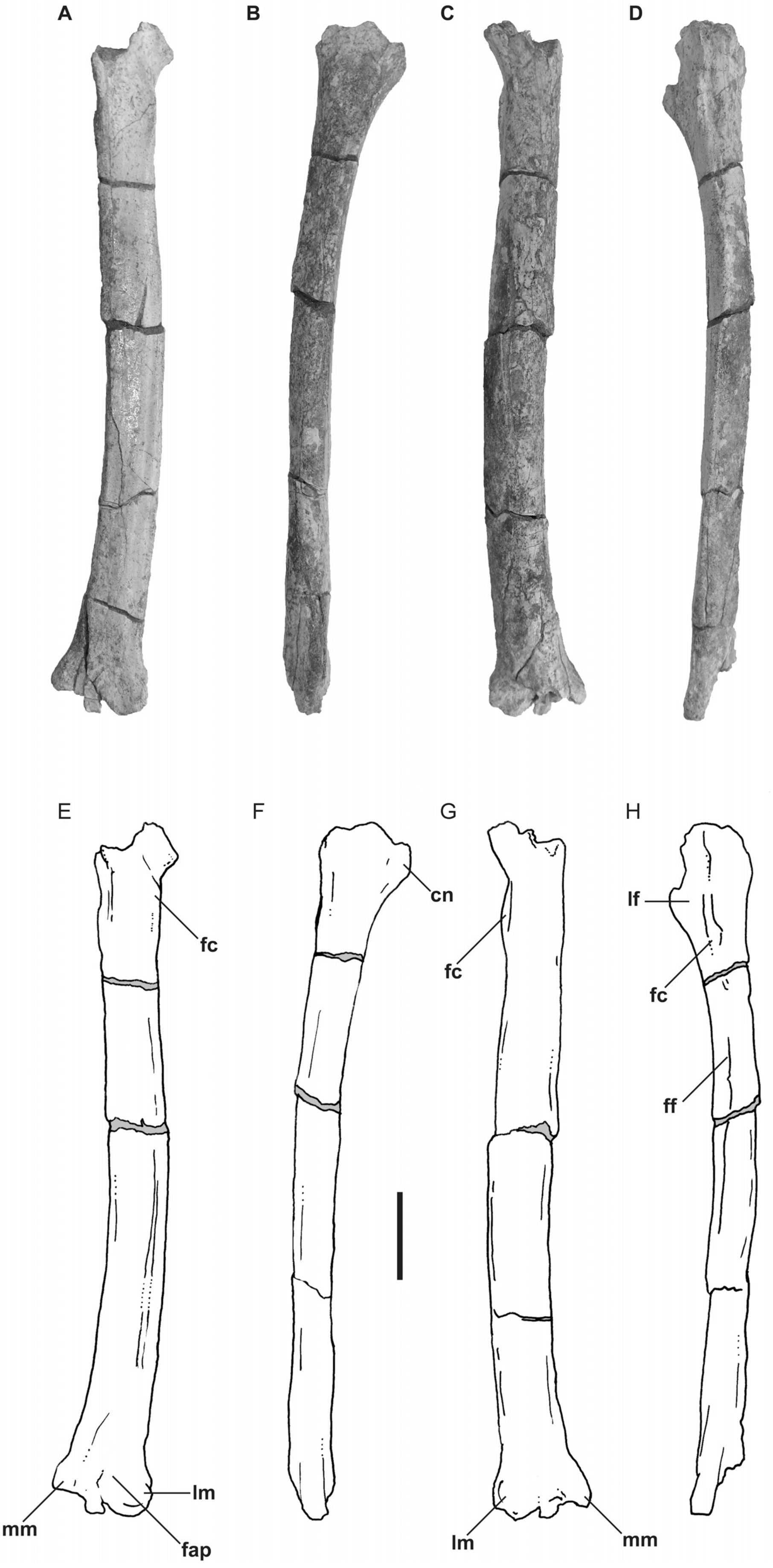

FIGURE 4. Left tibia of *Velocisaurus unicus* (MPCN-PV-370) in anterior (**A**), medial (**B**), posterior (**C**), and lateral (**D**) views. Line drawings of MPCN-PV-370 in anterior (**E**), medial (**F**), posterior (**G**), and lateral (**H**) views. Gray indicates matrix. **Abbreviations**: **cn**, cnemial crest; **fap**, facet for ascending process of the astragalus; **fc**, fibular crest; **ff**, fibular facet; **lf**, lateral fossa; **lm**, lateral malleolus; **mm**, medial malleolus. Scale bar equals 2 cm.

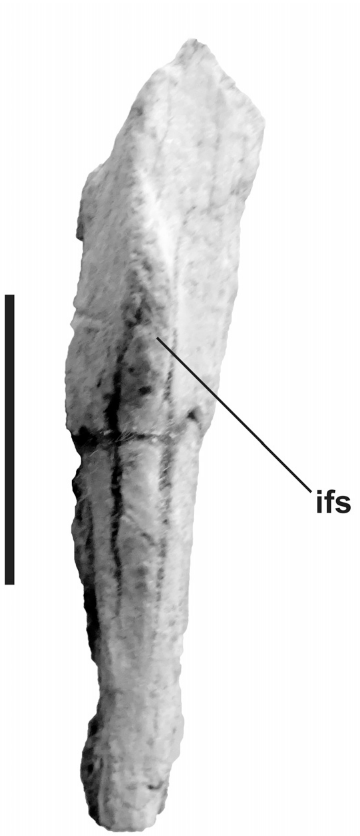

FIGURE 5. Left fibula of *Velocisaurus unicus* (MPCN-PV-370) in anterior view. **Abbreviation: ifs**, scar for M. iliofibularis. Scale bar equals 1 cm.

Phalanges

Several pedal phalanges have been preserved. Phalanx II-1 (Fig. 7) is the longest of the available elements. It is long and slender and, on its dorsal surface, bears a well-developed hyperextensor pit for the insertion of M. extensor digitorum (sensu Carrano and Hutchinson, 2002). It is slightly asymmetrical and shows a dorsoventrally deep proximal end as in the type specimen. The contact with metatarsal II is represented by a single shallow concavity lacking a proximal dorsoventral keel. Proximally, in plantar view, two longitudinal subparallel ridges are present. The medial one is somewhat larger and more distally extended than the lateral one, forming a short proximal process as in *Majungasaurus* (Carrano, 2007). The distal ginglymous is well defined, and the ligamental pits are well developed, the lateral one being deeper than the medial one.

Phalanx III-1 (Fig. 8) is shorter and stouter than phalanx II-1; this phalanx is slightly shorter than the equivalent element in the holotype specimen; the hyperextensor pits are large, deep, and subtriangular in contour. The ligamental pits are subequal in size and morphology. The dorsal surface of the phalanx is nearly straight in lateral view. The proximal articular surface lacks a dorsoventral keel.

Digit IV phalanges are the shortest of the pes. All phalanges have a dorsoventrally high shaft with a concave medial surface. Phalanx IV-1 (Fig. 9) is short and medially tilted in its distal end. The shaft has a very slender dorsal surface that is transversely narrower than the ventral surface. The phalanx has a well-developed ventral process on its proximomedial corner. This process exhibits an excavation on its medial surface. The proximal articular surface for contact with mt IV is slightly subtriangular in contour, with an oblique main axis that is ventromedially to laterodorsally oriented. The proximal articular surface is represented by a very deep concavity, a peculiar condition unmatched in other theropods. The hyperextensor pit is well developed, deep, and anteroposteriorly long. The distal ginglymous shows the medial arc much more developed than the lateral one. The medial ligament pit is much deeper than the lateral one. This strong asymmetry and medial tilting of the phalanx appear to be features unique to *Velocisaurus*, as they are observed in both the holotype and the referred specimen. The distal ginglymous is very deep and well defined and shows a connection between the extensor pit and the median groove of the distal articular trochlea.

Phalanx IV-2 is subequal in length with phalanx IV-1. The proximal articular surface shows two concavities for articulation with phalanx IV-1, and a median keel is present. The distal articular surface is missing.

The ungual of digit IV (Fig. 10) is similar to that of previously known abelisauroids (Novas and Bandyopadhyay, 2001). The ungual is slightly ventrally curved. The proximal articular facet is composed of two very shallow concavities separated by a low and poorly developed dorsoventral keel. The dorsal tubercle is well developed and finger-like. There is no ventral flexor tubercle; instead, a ventral fossa is present on the plantar surface of the ungual. Typical 'Y'-shaped vascular grooves are present on the lateral and medial sides of the ungual.

DISCUSSION

The Taxonomic Validity of *Velocisaurus unicus*

Bonaparte (1991b, 1996) described *Velocisaurus unicus* and included it in its own family: Velocisauridae. He assigned this genus with reservations to Ceratosauria on the basis of a robust metatarsal III. He also suggested that *Velocisaurus* was a strongly cursorial form and had non-predatory habits and consequently may be distinguished from Noasauridae by lacking raptorial pedal claws. At that time the available unguals of *Noasaurus* were erroneously interpreted as belonging to the pes (Agnolin and Chiarelli, 2010). However, Carrano and Sampson (2008) considered that *Velocisaurus* has no clear autapomorphies and concluded that it was probably a valid taxon based only on its geological and geographical provenance. In contrast to this proposal, the specimen here described allows us to recognize several autapomorphic features (below, in bold) for *Velocisaurus* that are unknown in other abelisauroids.

Femur with proximal end showing a strong subtriangular cross-section with lateral and medial bone surfaces converging strongly anteriorly, resulting in a proximodistally extended and thick crest—As occurs in other theropods, most abelisauroids (e.g., *Carnotaurus, Xenotarsosaurus*; Bonaparte et al., 1990; Martínez et al., 1986) have an ovoid cross-section of the femoral shaft. In *Masiakasaurus*, the proximal half of the shaft is subtriangular in contour, with the apex pointing anteriorly (Carrano et al., 2002). Evans et al. (2014) described an isolated femur from the Kem Kem beds of Morocco (Cenomanian) that they refer to Noasauridae. This femur shares with *Masiakasaurus* and *Velocisaurus* a subtriangular proximal shaft section. *Velocisaurus* is very similar to *Masiakasaurus* and the Moroccan specimen in this respect. However, in *Velocisaurus*, the anterior apex of the shaft forms a very thick and proximodistally extended crest unknown in other theropods, including the aforementioned taxa.

Tibia, long and slender, with its distal end anteriorly flat and bearing a large surface to accommodate a scale-like ascending process of the astragalus—Abelisauroids (e.g., *Indosuchus, Majungasaurus*) show a proportionally robust tibia with stout shaft and broad proximal and distal ends (Novas et al., 2004). In some abelisauroids (e.g., *Pycnonemosaurus, Indosuchus, Majungasaurus*), and also probably *Masiakasaurus* (Carrano et al.,

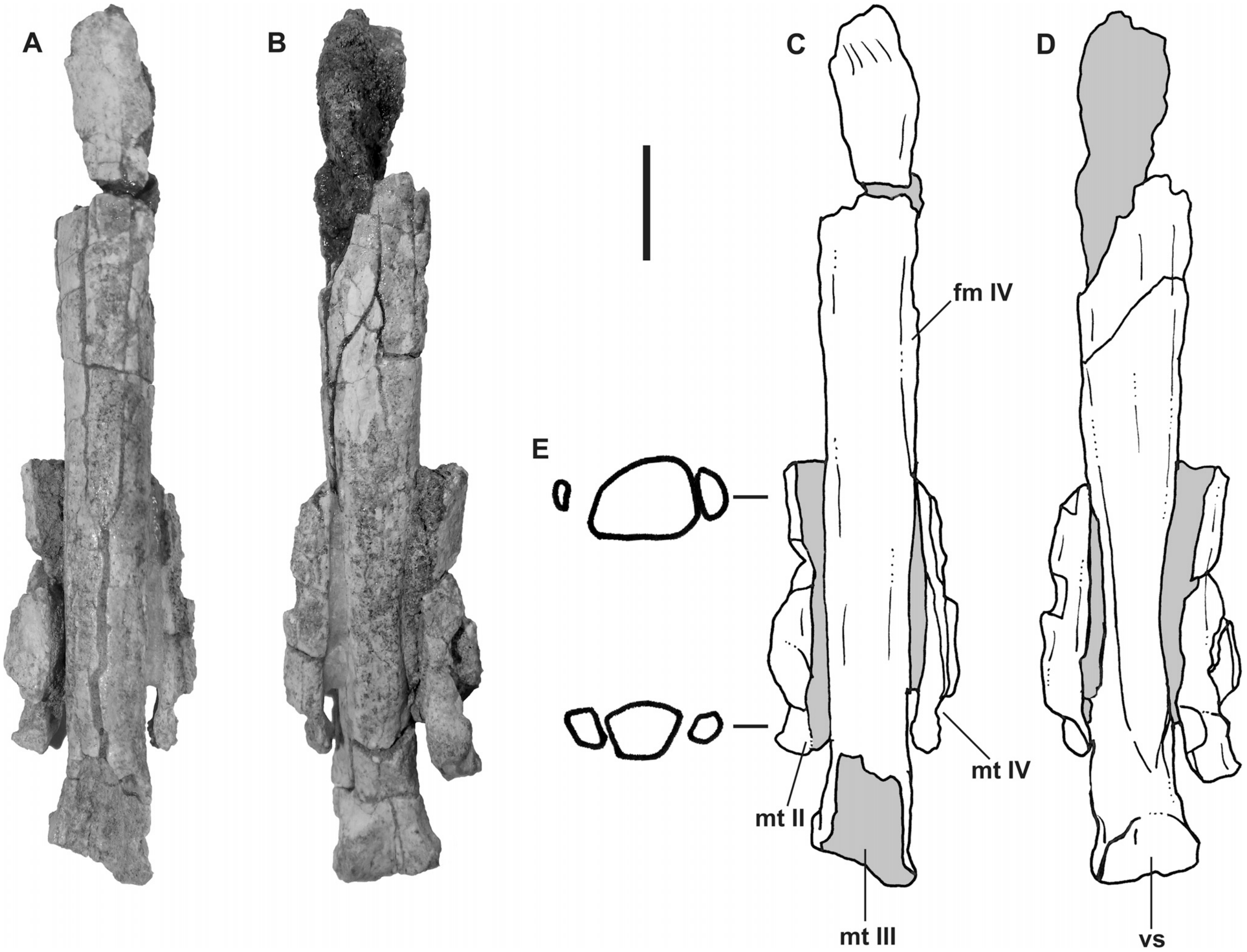

FIGURE 6. Left metatarsus of *Velocisaurus unicus* (MPCN-PV-370) in anterior (**A**) and posterior (**B**) views. Line drawings of MPCN-PV-370 in anterior (**C**) and posterior (**D**) views. Metatarsal shafts cross-sectional (**E**) view at two levels. Gray indicates matrix. **Abbreviations**: **fm IV**, facet for mt IV; **vs**, ventral sulcus. Scale bar equals 1 cm.

2002), there exists an oblique ridge for the articulation of the ascending process of the astragalus, a plesiomorphic feature shared with basal tetanurans (Ezcurra et al., 2010). In other abelisauroids (e.g., *Aucasaurus*) and *Velocisaurus*, the ascending process of the astragalus was probably transversely broad, occupying most of the distal surface of the shaft, a condition paralleled in coelurosaurian theropods (Ezcurra et al., 2010). However, in *Skorpiovenator* and *Aucasaurus*, the ascending process is subrectangular in contour (Canale et al., 2009; Ezcurra et al., 2010). In the case of *Velocisaurus*, the ascending process of the astragalus has not been preserved in any available specimen. However, the anterior surface of the distal end of the tibia is notably flat and shows a very tall subtriangular facet for the ascending process of the astragalus, a condition unmatched by remaining named abelisauroids. This fact was noted by Bonaparte (1991b) who reconstructed a very large and subtriangular ascending process. Along the same line of thought, Carrano et al. (2011) mentioned that the holotype specimen of *Velocisaurus* likely had a laminar ascending process, as evidenced from the broken base on the astragalar body and a flat contact area on the anterior surface of the distal tibia. This morphology is not found in any known abelisauroid and is strongly reminiscent of that of derived coelurosaurs such as deinonychosaurs and ornithomimids (Rauhut, 2003), as well as the basal tetanuran *Chuangdongocoelurus* (He, 1984).

In this regard, isolated tibiae coming from the Upper Jurassic of Africa referred by Rauhut (2005) to Abelisauroidea are very gracile and similar to *Velocisaurus* in gross morphology. These bones may indicate the presence of taxa related to *Velocisaurus* at that locality.

Very thin and rod-like metatarsals II and IV—*Velocisaurus* differs from other abelisauroids in the unique combination of characters present in the metatarsus. Bonaparte (1991b) included the unique proportions of the metatarsals in the diagnosis of *Velocisaurus*, in which metatarsal III was more than three times the width of metatarsals II and IV, which are transversely reduced. Bonaparte (1991b) indicated that this peculiar configuration of the metatarsus was probably related to extreme cursorial capabilities, similar to that of extant Rheidae. This condition was also considered diagnostic for *Velocisaurus* by Rauhut (2003) and Novas (2009); on the other hand, Carrano and Sampson (2008) proposed that this morphology was widespread among noasaurids. In this regard, *Elaphrosaurus, Masiakasaurus*, and *Noasaurus* show a transversely compressed and laminar proximal half of metatarsal II (Carrano et al., 2002). However, in *Velocisaurus*, the shaft of metatarsal II is rod-like and suboval

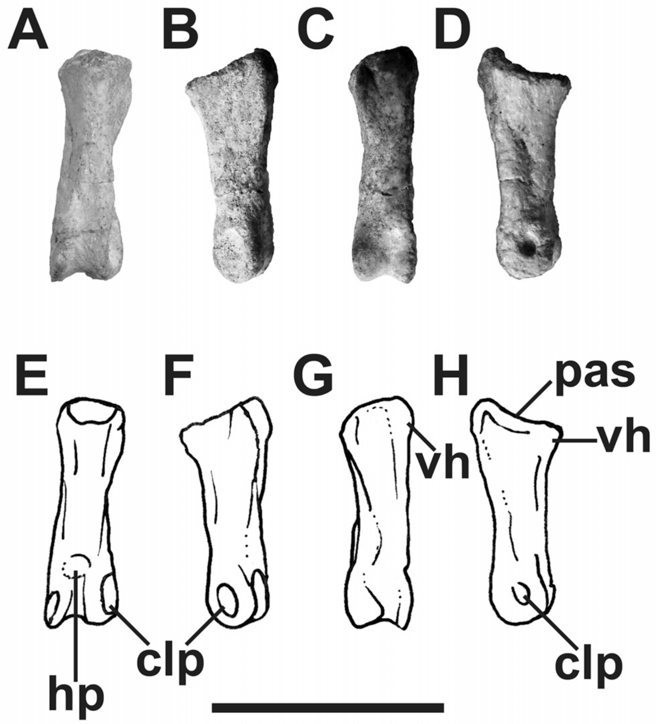

FIGURE 7. Left pedal phalanx II-1 of *Velocisaurus unicus* (MPCN-PV-370) in dorsal (**A**), lateral (**B**), ventral (**C**), and medial (**D**) views. Line drawings of MPCN-PV-370 in dorsal (**E**), lateral (**F**), ventral (**G**), and medial (**H**) views. **Abbreviations**: **clp**, collateral ligament pit; **das**, distal articular surface; **hp**, hyperextensor pit; **pas**, proximal articular surface; **vh**, ventral heel. Scale bar equals 1 cm.

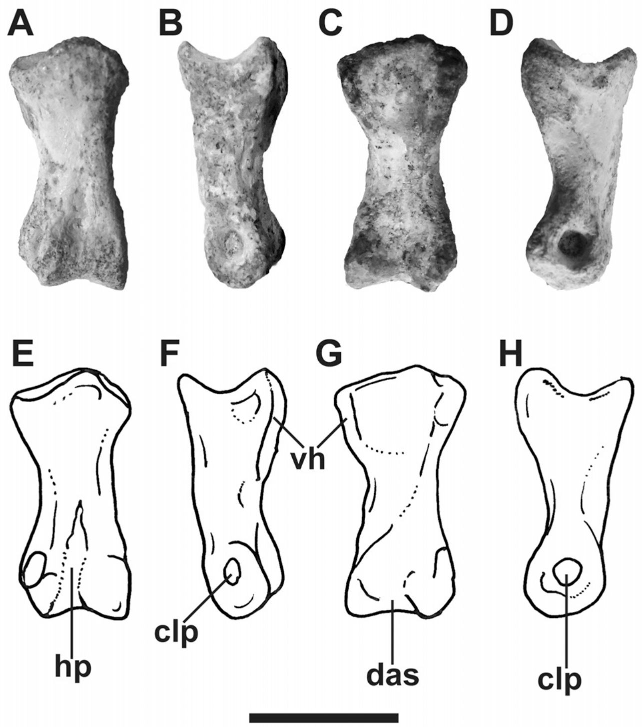

FIGURE 8. Left pedal phalanx III-1 of *Velocisaurus unicus* (MPCN-PV-370) in dorsal (**A**), lateral (**B**), ventral (**C**), and medial (**D**) views. Line drawings of MPCN-PV-370 in dorsal (**E**), lateral (**F**), ventral (**G**), and medial (**H**) views. **Abbreviations**: **clp**, collateral ligament pit; **das**, distal articular surface; **hp**, hyperextensor pit; **vh**, ventral heel. Scale bar equals 1 cm.

in cross-section, as noted by Carrano et al. (2002). Because highly reduced rod-like metatarsals II and IV are not known in any other abelisauroid, this feature may be regarded as unique to *Velocisaurus*.

Pedal phalanx IV-1 anteroposteriorly short, dorsoventrally tall, medially tilted, and with transversely narrow dorsal surface—In agreement with the transversely compressed and dorsoventrally tall distal condyle of metatarsal IV, phalanges of this digit in *Velocisaurus* are transverse1y narrow and dorsoventrally deep. This feature contrasts with non-abelisauroid theropods, such as *Sinraptor, Allosaurus, Acrocanthosaurus, Buitreraptor*, and *Deinonychus*, in which the phalanges of digit IV are proportionally dorsoventrally lower and transversely wider (Novas et al., 2004).

Phalanx IV-1 exhibits a subtriangular proximal end with the long axis oriented dorsoventrally. The medial surface is subvertically oriented with a slightly concave profile when viewed dorsally, which results in a medial tilting of the bone. It has an asymmetrically developed distal ginglymous with the medial arc wider and deeper than the lateral one. This combination of characters is absent in most known abelisauroids, e.g., the robust foot of abelisaurids such as *Aucasaurus* and *Majungasaurus* (Coria et al., 2002; Carrano, 2007).

The combination of features mentioned above are reminiscent of that of some indeterminate pedal phalanges from the Maastrichtian of India (Novas et al., 2004), suggesting that some kind of *Velocisaurus*-like abelisauroid might have been present in that continent. In sum, the presence of at least four autapomorphic traits allows us to recognize the taxonomic validity of *Velocisaurus unicus*.

The Phylogenetic Position of *Velocisaurus unicus*

With the aim of determining the phylogenetic affinities of *Velocisaurus*, we carried out a phylogenetic analysis of Abelisauroidea based on the data matrix of Pol and Rauhut (2012). The analysis resulted in six most parsimonious trees (MPTs) of 395 steps in length, which are summarized in a strict consensus tree (Fig. 11). With the aim of testing the robusticity of tree topology, we calculated Bremer support for each node. A monophyletic Noasauridae is very poorly supported (Bremer support = 1), whereas Abelisauroidea is relatively well supported (Bremer support = 3).

The presence of ‘Y’-shaped vascular grooves on pedal unguals is the only unambiguous synapomorphy sustaining the abelisauroid affinities of *Velocisaurus* (character 203(1) of Pol and Rauhut, 2012; see details in Novas and Bandyopadhyay, 2001). However, other features of the available skeletal elements are congruent with abelisauroid affinities: (1) the femoral head is anteromedialy directed as in non-tetanuran theropods, and the lesser trochanter is separated by a deep cleft from the femoral head as occurs in abelisauroids (Bonaparte, 1991b); (2) the accessory trochanter is not connected with the lesser trochanter, so a continuous trochanteric shelf is absent as is the case in abelisaurids and *Masiakasaurus* (Carrano, 2007); (3) the fourth trochanter is represented by a thin and low ridge, as in abelisauroids (Novas et al., 2004); (4) the tibial crest for the attachment of the fibula with the tibia is connected with the proximal articular surface, as occurs in non-tetanuran theropods (Rauhut, 2003); (5) the distal end of the tibia exhibits a midline ridge, as occurs in some selected abelisauroids (Rauhut, 2005;

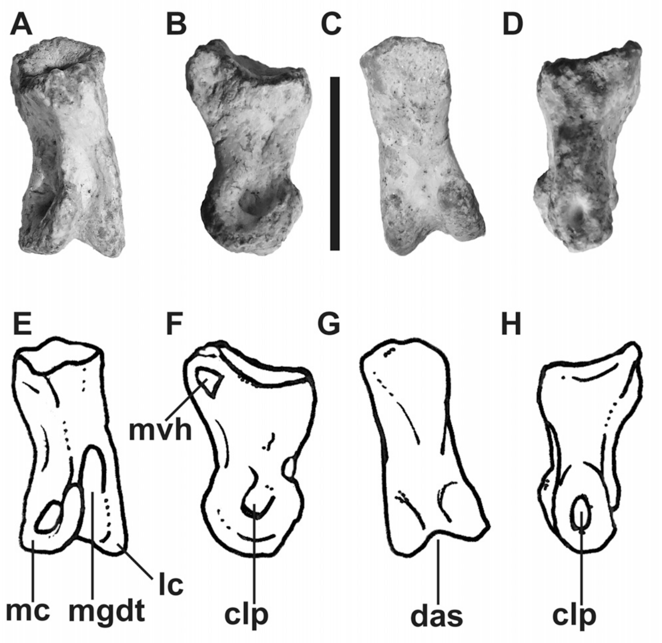

FIGURE 9. Left pedal phalanx IV-1 of *Velocisaurus unicus* (MPCN-PV-370) in dorsal (**A**), medial (**B**), ventral (**C**), and lateral (**D**) views. Line drawings of MPCN-PV-370 in dorsal (**E**), medial (**F**), ventral (**G**), and lateral (**H**) views. **Abbreviations**: **clp**, collateral ligament pit; **das**, distal articular surface; **hp**, hyperextensor pit; **lc**, lateral condyle; **mc**, medial condyle; **mgdt**, medial groove of distal trochlea; **mvh**, median ventral heel; **pas**, proximal articular surface. Scale bar equals 1 cm.

Ezcurra et al., 2010); (6) a very large iliofibularis tubercle is present on the proximal end of the fibula, as diagnostic of Ceratosauria (Rauhut, 2003); (7) presence of a tall posterior process along the posterior margin of the astragalus, as occurs in some abelisauroids (present in the holotype of *Velocisaurus*; Ezcurra et al., 2010); (8) an antarctometatarsal metatarsus, as occurs in non-tetanuran theropods (Rauhut, 2003); and (9) the ungual phalanx lacking a ventral tubercle, which is replaced by a ventral fossa (Novas and Bandyopadhyay, 2001). This extensive set of traits provides strong evidence that *Velocisaurus* belongs to Abelisauroidea.

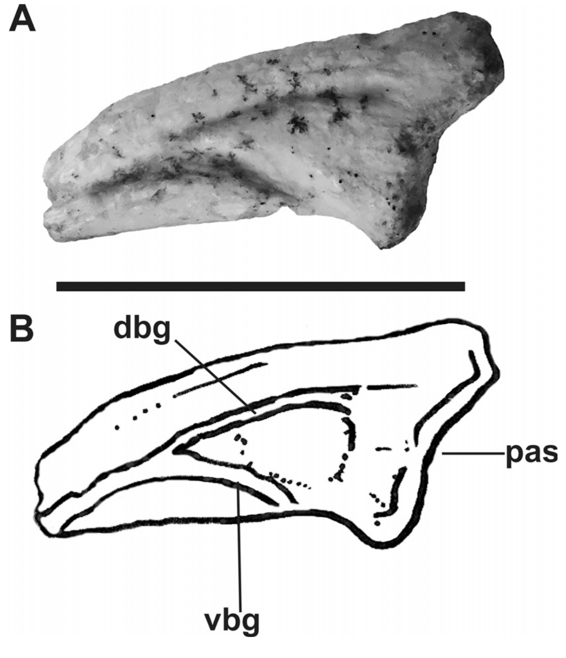

FIGURE 10. Left pedal phalanx IV-5 of *Velocisaurus unicus* (MPCN-PV-370) in lateral (**A**) view. Line drawing of MPCN-PV-370 in lateral (**B**) view. **Abbreviations**: **dbg**, dorsal blood groove; **pas**, proximal articular surface; **vbg**, ventral blood groove. Scale bar equals 1 cm.

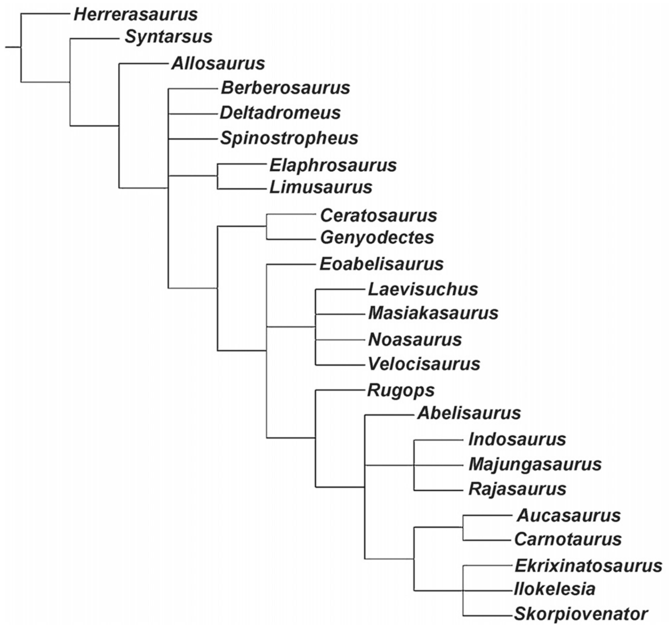

FIGURE 11. Strict consensus cladogram of six MPTs of length 395 steps, CI 0.55, and RI 0.70, depicting phylogenetic relationships of *Velocisaurus unicus* within Abelisauroidea.

The phylogenetic position of *Velocisaurus* within Abelisauroidea is more difficult to assess. In the present analysis, it is included within a monophyletic Noasauridae clade, as previously supported by several authors (Agnolín et al., 2003, 2004; Brissón Egli and Apesteguía, 2008; Carrano and Sampson, 2008; Agnolín and Chiarelli, 2010; Carrano et al., 2011). Three unambiguous synapomorphies (below, in bold) sustain such relationship.

Flat anterior distal tibia (character 190(1); Rauhut, 2005)—This character was considered by Rauhut (2005) as possibly diagnostic of Abelisauroidea or probably Noasauridae. Later, Ezcurra et al. (2010) also suggested that a flat distal end of the tibia was a feature present in basal abelisauroids (e.g., *Austrocheirus, Masiakasaurus, Velocisaurus*) and abelisaurids (e.g., *Skorpiovenator, Aucasaurus*), and might be diagnostic of Abelisauroidea. Rauhut (2012) analyzed in detail this set of characters and concluded that its distribution was very problematic because it was also present in a variety of theropod lineages, such as most coelurosaurs. Thus, the patchy occurrence of this character among different basal and derived abelisauroid taxa, suggests that it is a problematic feature and thus may be diagnostic of a more inclusive clade (i.e., Abelisauroidea).

Metatarsal II with reduced width of shaft, and proximal articular surface 2/3 or less the width of metatarsals III and IV (characters 200(1), 201(1); Carrano and Sampson, 2008; Pol and Rauhut, 2012)—In the original description, *Noasaurus* was distinguished from other lightly built theropods by its transversely narrow metatarsal II (Bonaparte and Powell, 1980). Bonaparte (1991b) also included a metatarsal II with its upper half much thinner than its distal end in the diagnosis of Noasauridae (at that time including only *Noasaurus*). Later, Carrano et al. (2002) considered this reduction of metatarsal II as a synapomorphy uniting *Noasaurus* and *Masiakasaurus* in a monophyletic Noasauridae, a criterion followed by most recent authors (e.g., Sampson et al., 2001; Wilson et al., 2003; Canale et al., 2009; Carrano et al., 2011; Pol and Rauhut, 2012). However, in several abelisaurids, such as *Rahiolisaurus, Skorpiovenator*, and *Aucasaurus*, the proximal half of metatarsal II is transversely narrow and sublaminar (Coria et al., 2002; Novas et al., 2010), resembling the condition of *Noasaurus*. Therefore, Novas (2009) considered that the narrow metatarsal II may be diagnostic of the more inclusive clade Abelisauroidea. Nonetheless, in some abelisaurids, such as *Majungasaurus* and *Rajasaurus* (Wilson et al., 2003; Carrano, 2007), the proximal end of metatarsal II is not reduced at all. The equivocal distribution of this feature among Abelisauroidea indicates a more complex distribution of the character than previously thought.

In *Velocisaurus*, metatarsal II is strongly reduced both transversely and anteroposteriorly, with a rod-like shaft that is different from the laminar condition of *Noasaurus, Masiakasaurus*, and other abelisauroids. The differences in gross morphology between the metatarsus of *Velocisaurus* and those of *Masiakasaurus* and *Noasaurus* lead us to be cautious in regarding this trait as a unique synapomorphy of Noasauridae.

In sum, the reduction of metatarsal II in *Velocisaurus* may not be an unambiguous trait sustaining its inclusion within Noasauridae, thereby blurring the taxonomic meaning of this character, which is in need of revision. The absence of pedal elements in basal abelisaurids (e.g., *Rugops, Abelisaurus*) also cautions against considering this trait as diagnostic of any abelisauroid clade.

CONCLUSIONS

Herein we describe a new specimen of the small enigmatic abelisauroid *Velocisaurus unicus* Bonaparte, 1991, which was previously known by a single incomplete specimen coming from Neuquén City, Neuquén Province, Patagonia. The new material allows us to define several autapomorphies for this taxon and confirms the taxonomic validity of *Velocisaurus*. Furthermore, analysis of features supporting the inclusion of *Velocisaurus* within Noasauridae indicates that this grouping is very weakly supported, and that the phylogenetic relationships of *Velocisaurus* within abelisauroids are far from certain.

The unique combination of characters and the coelurosaur-like distal tibia of *Velocisaurus* indicate that it belongs to a still poorly understood radiation of gracile-limbed abelisauroids. Isolated material of small theropods from Africa and India suggest that the distribution of *Velocisaurus*-like abelisauroids may be more widespread than currently known.

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APPENDIX 1. Scoring for *Velocisaurus unicus*.

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