Khosla, A. and Lucas, S.G., eds., 2016, Cretaceous Period: Biotic Diversity and Biogeography. New Mexico Museum of Natural History and Science Bulletin 71.

NEW THEROPOD FAUNA FROM THE UPPER CRETACEOUS (HUINCUL FORMATION) OF NORTHWESTERN PATAGONIA, ARGENTINA

MATÍAS J. MOTTA[1], ALEXIS M. ARANCIAGA ROLANDO[1], SEBASTIÁN ROZADILLA[1], FEDERICO E. AGNOLÍN[1, 2], NICOLÁS R. CHIMENTO[1], FEDERICO BRISSÓN EGLI[1, 3] AND FERNANDO E. NOVAS[1, 3]

[1]Laboratorio de Anatomía Comparada y Evolución de los Vertebrados, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Av. Ángel Gallardo 470, C1405DJR Buenos Aires, Argentina; [2]Fundación de Historia Natural “Félix de Azara”, Universidad Maimónides, V. Virasoro 732, 1405 Buenos Aires, Argentina; [3]CONICET, Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina

Abstract—The present contribution describes theropod remains coming from the Huincul Formation (Neuquén Group; Cenomanian-Turonian; Upper Cretaceous) at a single locality located in northwestern Río Negro province, Patagonia, Argentina. This theropod association is composed of abelisauroids, two different-sized carcharodontosaurid allosauroids, a coelurosaur of uncertain relationships, a megaraptoran tyrannosauroid, and a possible unenlagiid paravian. Two new theropod genera and species are here described. The new carcharodontosaurid is based on an isolated postorbital bone bearing a unique prominence above the orbital brow. The new megaraptoran of uncertain affinities is described on the basis of a partially articulated tail and sacral vertebra. A new taxon is characterized by having notably elongate and highly pneumatic sacral and caudal vertebrae. It shows a large number of similarities with the African taxa *Deltadromeus* and *Baharisaurus*. These genera probably constitute a still poorly known clade of megaraptoran tyrannosauroids different from the Megaraptoridae. These findings support that Patagonia is a key place for understanding theropod evolution in Gondwana.

INTRODUCTION

Within South America, Argentina possess the richest record of theropod dinosaurs for the Late Cretaceous, and this is especially true for Patagonia (Novas et al., 2013). Here the group is represented by several clades, such as Noasauridae, Abelisauridae, Carcharodontosauridae, Megaraptoridae, Alvarezauridae, Unenlagiidae as well as basal coelurosaurs (Novas, 2011; Novas et al., 2013). One of the better known Upper Cretaceous formations, for its large and varied record of vertebrate remains, is the Huincul Formation (Neuquén Group; Cenomanian-Turonian; Garrido, 2010), which documents a high number of fishes, dipnoans, turtles, crocodiles and dinosaurs (Leanza et al., 2004; Garrido, 2010). Among the most outstanding members of the latter clade are the titanosaur *Argentinosaurus huinculensis* (Bonaparte and Coria, 1993), the rebbachisaurid *Cathartesaura anaerobica* (Gallina and Apesteguía, 2005), the carcharodontosaurid *Mapusaurus roseae* (Coria and Curie, 2006) and the abelisaurids *Skorpiovenator bustingorryi* and *Ilokelesia aguadagrandensis* (Canale et al., 2008; Coria and Salgado, 1998). These dinosaurs are part of a faunal composition that is characteristic of the lower part of the Upper Cretaceous in western Gondwana (Novas, 2011; Novas et al., 2013). This assemblage is different from the uppermost Cretaceous, where large derived abelisaurids and megaraptorids were the apex predators, and the gigantic titanosaurs were replaced by the smaller saltasaurine sauropods and ornithischians, such as hadrosaurids and ankylosaurids (Leanza et al., 2004; Novas et al., 2011).

In the present contribution, we report new theropod remains from the Violante farm fossiliferous locality (Río Negro province, Patagonia), where the outcrops of the Huincul Formation are exposed. This association shows different theropod clades, including small-sized abelisauroids, large-sized carcharondontosaurids, megaraptoran and paravian coelurosaurs.

LOCALITY AND HORIZON

The Violante farm (39°23’52.37”S, 68°37’4.30”W) is located southeast of the Ezequiel Ramos-Mexía lake, at the northwest of Río Negro province, Argentina (Fig. 1). Here the Huincul Formation (middle Cenomanian-early Turonian; Garrido, 2010) is widely exposed. This formation is composed of yellowish and greenish fine- to medium-grained sandstones that sometimes can be tuffaceous (Leanza et al., 2004). Within the study area, this stratigraphic unit has been characterized by Garrido (2000, 2010) as representing a high sinuosity fluvial system that gradually lowers its sinuosity. Overall, weather conditions were warm with a strong seasonal regimen (Garrido, 2000, 2010; Sanchez et al., 2008).

As mentioned above, the fossil content is highly diverse. Silicified trunks of cycads and conifers have been reported (Leguizamón and Garrido, 2000), the latter group represented by the Araucariaceae and Cupressaceae (Martinez, 2008, 2009b), and some basal angiosperms (i.e., Magnoliophyta; Martinez, 2009a, b). Vertebrate remains consist of turtles, crocodiles and fish teeth (Garrido, 2000, 2010). Among the latter, remains of the dipnoan *Ameghinoceratodus iheringi* (Apesteguía et al., 2007) have been described. The dinosaur record is extensive, including large-sized theropods such as *Mapusaurus rosae* (Coria and Currie, 2006), *Ilokelesia aguadagrandensis* (Coria and Salgado, 1998) and *Skorpiovenator bustingorryi* (Canale et al., 2008). Among sauropods there are titanosaurids and rebbachisaurids (Bonaparte and Coria, 1993; Gallina and Apesteguía, 2005).

Institutional Abbreviations: MPCA PV. Colección Paleontología de Vertebrados, Museo Provincial “Carlos Ameghino”, Rio Negro, Argentina.

SISTEMATIC PALAEONTOLOGY
DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1888
THEROPODA Marsh, 1881
ABELISAUROIDEA Bonaparte and Novas, 1985
Gen. et sp. indet. 1

Referred material: MPCA-Pv 800, distal end of a left quadrate (Fig. 2).

Description and comparisons: The preserved portion of the quadrate is transversely wide, with the medial condyle projected slightly more ventrally than the lateral one, a condition present in some abelisauroids, such as *Abelisaurus comahuensis, Carnotaurus sastrei* and *Masiakasaurus knopfleri* (Bonaparte and Novas, 1985, Bonaparte, 1993; Sampson et al., 2001; Carrano et al., 2002, 2011; Novas et al., 2013). The shaft is anteroposteriorly wider at its medial side and narrows towards the lateral edge. The condyles are subovoidal in contour in ventral view. The external condyle is broader and more anteroposteriorly compressed than the internal one. On the other hand, the inner condyle is transversely narrower, but anteroposterioly elongate. The condyles are separated by a shallow and obliquely oriented intercondylar sulcus. Posteriorly, the dorsal margin of both condyles is delimited by a low, transverse ridge. The quadratojugal contact is represented by a shallow posterolateral concavity. The pterygoid flange was not preserved.

Comments: The morphology of the quadrate closely matches that of other abelisauroids, such as *Carnotaurus, Majungasaurus, Masiakasaurus* and *Noasaurus* (Bonaparte, 1993; Sampson and Krause, 2007; Carrano et al., 2011; Bonaparte and Powell, 1980) in having asymmetrical condyles that are separated by an obliquely oriented sulcus, a medial condyle that is anteroposterioly elongated and transversely narrow, and a lateral condyle that is transversely expanded and anteroposteriorly short. Because of its fragmentary nature, MPCA-

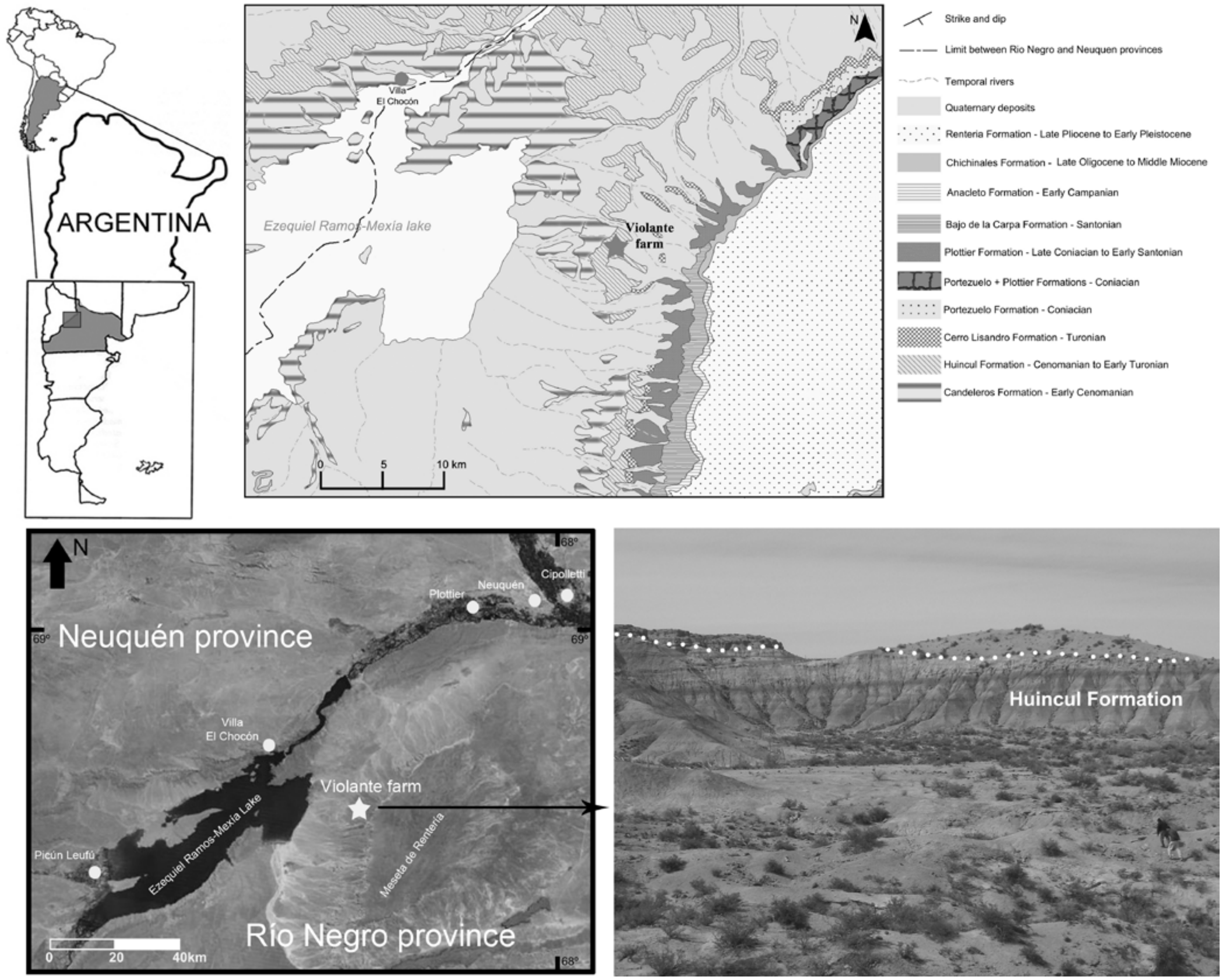

FIGURE 1. Detail of the area of study showing the location of the Violante farm, the geological map of the El Cuy Department (modified from Hugo and Leanza, 2001), and a photograph showing Huincul Formation beds where the fossil specimens were found.

Pv 800 cannot be identified beyond Abelisauroidea indet.

Gen. et sp. indet. 2

Referred material: MPCA-Pv 801, nearly complete right metatarsal IV, with the distal end lacking part of its dorsal margin (Fig. 3).

Description and comparisons: The metatarsal is long and relatively slender. The shaft flares laterally on its distal end. The proximal end has a subtriangular shape in proximal view with an anterior projection, as occurs in other abelisauroids (e.g., *Aucasaurus*; Coria et al., 2003). There is a concavity on the proximomedial surface of the shaft, probably for articulation with metatarsal III. The proximal half of the shaft is subtriangular in cross-section, with conspicuous flat ventral and medial margins, indicating a very strong metatarsal III as occurs in abelisauroids and coelophysoids (Gauthier, 1986). The shaft narrows towards its distal end, as occurs in other abelisauroids (e.g., Brissón et al., 2016). In lateral view, the shaft is nearly straight. The shaft narrows immediately before the distal end, thus defining a subtle neck. Only the lateral condyle of the distal end was preserved. The lateral trochlea is low, and its ventral margin is lateroventrally oriented. Ventrally, there is a wide space separating the condyles, as in *Aucasaurus* and *Masiakasaurus* (Carrano et al., 2002; Coria et al., 2003).

Comments: The isolated metatarsal reported here is very similar to that of *Masiakasaurus* in gross morphology, being long and slender and thus differing from the more massive metatarsals of abelisaurids (Carrano et al., 2002). However, because of the absence of shared derived traits between the material here described and the known metatarsals IV of noasaurids (e.g. *Velocisaurus, Masiakasaurus*; Bonaparte, 1991; Carrano et al., 2002) there is not enough evidence to justify it identification beyond Abelisauroidea.

TETANURAE Gauthier, 1986
ALLOSAUROIDEA Currie and Zhao, 1993
CARCHARODONTOSAURIDAE Stromer, 1931
Taurovenator violantei gen. et sp. nov.

Etymology: The generic name derives from the Latin words “tauro” (Bull) and “venator” (Hunter). The specific name honours Enzo Violante, owner of the farm where the specimen was discovered.

Holotype: MPCA PV 802, isolated right postorbital (Fig. 4).

Diagnosis: Mid-sized carcharodontosaurid having the following autapomorphies: 1) presence of a horn-like prominence in the orbital brow, and 2) presence of a deep excavation in the ventral surface of the postorbital.

Description and comparisons: As in other theropods this bone is heavily constructed and T-shaped in lateral view. This element seems to be more robust than that of *Eocarcharia* and *Mapusaurus* (Coria and Currie, 2006; Sereno and Brusatte, 2008). In lateral view, the orbital brow is stout and short, and, as in most carcharodontosaurids, its posterior half is transversely thicker than the anterior half. On its posterodorsal corner, there is a prominent and rounded process that superficially resembles the orbital boss of *Eocarcharia* (Sereno and

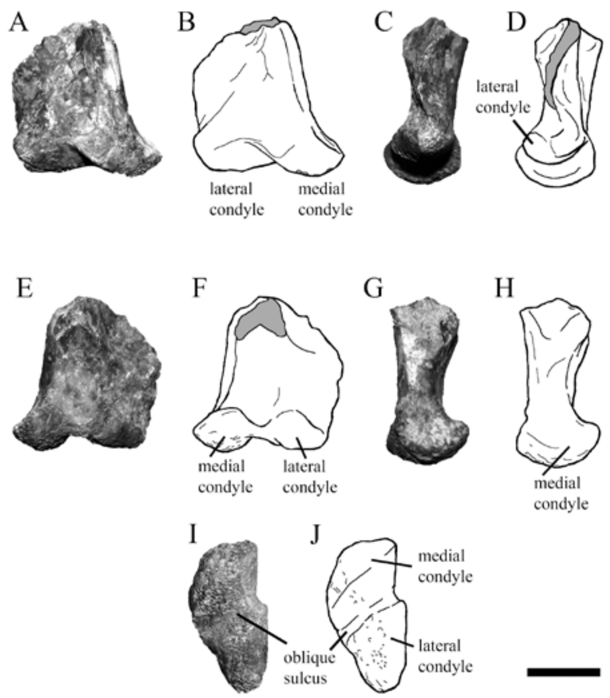

FIGURE 2. Left quadrate of Abelisauroidea indet. **A, B,** posterior view; **C, D,** lateral view; **E, F,** anterior view; **G, H,** medial view; **I, J,** distal view. Scale bar: 1 cm.

Brusatte, 2008), but differs in being more prominent, notably rounded, smaller, and relatively narrower. The lateral wall of the brow is nearly smooth, but it becomes conspicuously rugose closer to its dorsal margin, as also occurs in *Giganotosaurus* and *Carcharodontosaurus* (Sereno and Brusatte, 2008; Fig. 5). The lateral wall is anteroventrally projected, and reaches the orbit, forming a convex ventral margin when viewed anteriorly, a condition reminiscent of that in *Mapusaurus* and *Carcharodontosaurus* (Coria and Currie, 2006; Sereno and Brusatte, 2008; Fig. 5). In lateral view, the ventral margin of the lateral wall is anteroposteriorly sigmoidal and posteriorly contacts the orbital boss. In medial view, on its anterior margin, this brow shows the articular surface with the frontal and posterior to it, there is the crescent-shaped articular surface for the laterosphenoid. Posterior to the brow, this bone shows a robust and rounded bar that is posteriorly projected. This bar together with the squamosal constitutes the supratemporal arch.

The ventral ramus is dorsoventrally short, anteroposteriorly wide, and transversely narrow, resulting in a subtriangular cross-section. This ramus is anteroventrally projected and forms an acute angle with the brow that resembles *Mapusaurus* and *Carcharodontosaurus*, contrasting with the condition exhibited by *Giganotosaurus* (Coria and Currie, 2006; Sereno and Brusatte, 2008). The lateral surface of this ramus is decorated by abundant anastomosed and bifurcate vascular grooves, suggesting that this region was strongly vascularized. The ventral ramus is shorter and wider than *Eocarcharia*, resembling in this aspect *Mapusaurus* and *Carcharodontosaurus* (Coria and Currie, 2006; Sereno and Brusatte, 2008). A large and subtriangular intraorbital process is placed at the distal end of the ventral ramus, a similar process occurs in most derived carcharodontosaurids (e.g., *Mapusaurus, Giganotosaurus, Carcharodontosaurus*; Coria and Currie, 2006; Sereno and Brusatte, 2008; Fig. 5), contrasting with the smaller and rugose process present in *Eocarcharia* (Sereno and Brusatte, 2008) and other allosauroids (e.g., *Sinraptor*; Currie and Zhao, 1993). In posterior view, the articular surface for the squamosal is present in the posterior bar. Below, the posterior surface of the ventral ramus exhibits a shallow vertical groove.

There is a vertical ridge that runs along the ventral ramus becoming rugose posteriorly. A similar ridge is present in *Mapusaurus* and *Carcharodontosaurus*, but absent in *Eocarcharia* (Coria and Currie, 2006; Sereno and Brusatte, 2008). This area probably represents the articular surface for the jugal.

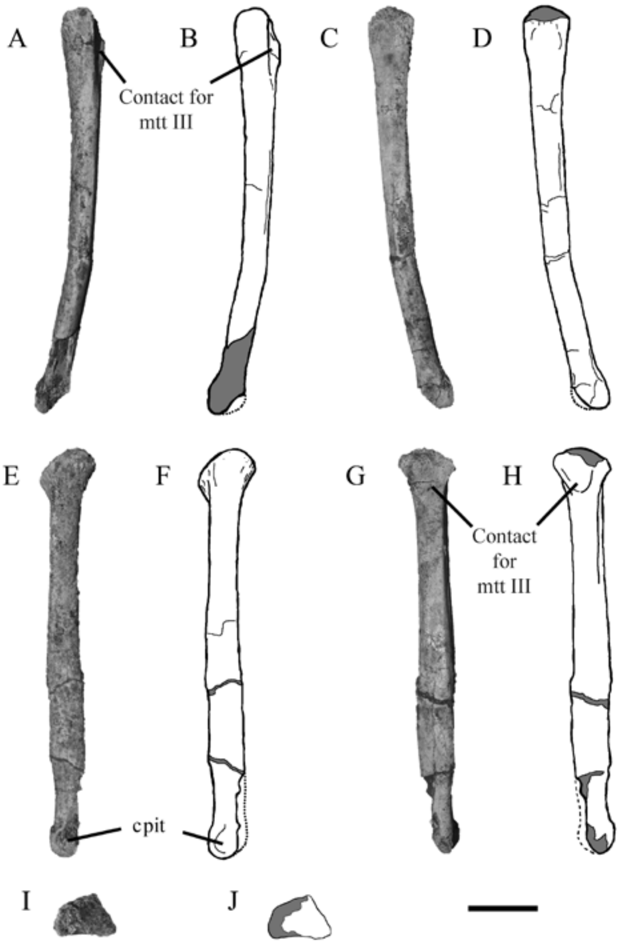

FIGURE 3. Right metatarsal IV of Abelisauroidea indet. **A, B,** anterior view; **C, D,** posterior view; **E, F,** lateral view; **G, H,** medial view; **I, J,** proximal view. Abbreviations: cpit, collateral ligamental pit. Scale bar: 3 cm.

In *Taurovenator*, the postorbital bar seems to be more robust than in *Mapusaurus* and *Eocarcharia* (Coria and Currie, 2006; Sereno and Brusatte, 2008). Nevertheless, the posterior bar is relatively subcircular in cross section, which resembles *Carcharodontosaurus* more than other carcharodontosaurids, in which this bar is subtriangular in cross section (Sereno and Brusatte, 2008).

In anterior view, the articular surface for the frontal can be observed at its medial margin. It is represented by an anteroposteriorly short but strongly rugose surface. Near the lateral margin of the bone there is a notably tall lacrimal articular surface, as occurs in other members of this family (Sereno and Brusatte, 2008). Furthermore, this articulation excludes the frontal from the orbital margin, as occurs in derived Carcharodontosauridae (Sereno and Brusatte, 2008).

In ventral view, a very deep concavity is present in the inner surface of the brow. This concavity is posteriorly delimited by the ventral ramus and laterally by the ventrally projected lateral wall of the brow. At the most posterior portion of this cavity, there is a deep and subrectangular pit that transversely enters the bone, and is here interpreted as a pneumatopore.

In dorsal view, the brow shows a prominent and rounded orbital boss at its posterior margin. The roof of the postorbital is slightly rugose, and the ornamentation increases through the laterodorsal corner of the brow. Posterior to the orbital boss, the bone narrows caudally towards the rounded and short posterior bar. Coria and Currie (2006) describe the brow in *Mapusaurus*, as a “palpebral,” a different ossification that is completely fused with the postorbital. In the present specimen, there is no evidence indicating the presence of such a structure.

Remarks: *Taurovenator* is similar in gross morphology to other derived carcharodontosaurids such as *Giganotosaurus*,

FIGURE 4. Right postorbital (holotype) of *Taurovenator violentei* gen. et sp. nov. **A**, lateral view; **B**, medial view; **C**, posterior view; **D**, dorsal view; **E**, anterior view. Scale bar: 3 cm.

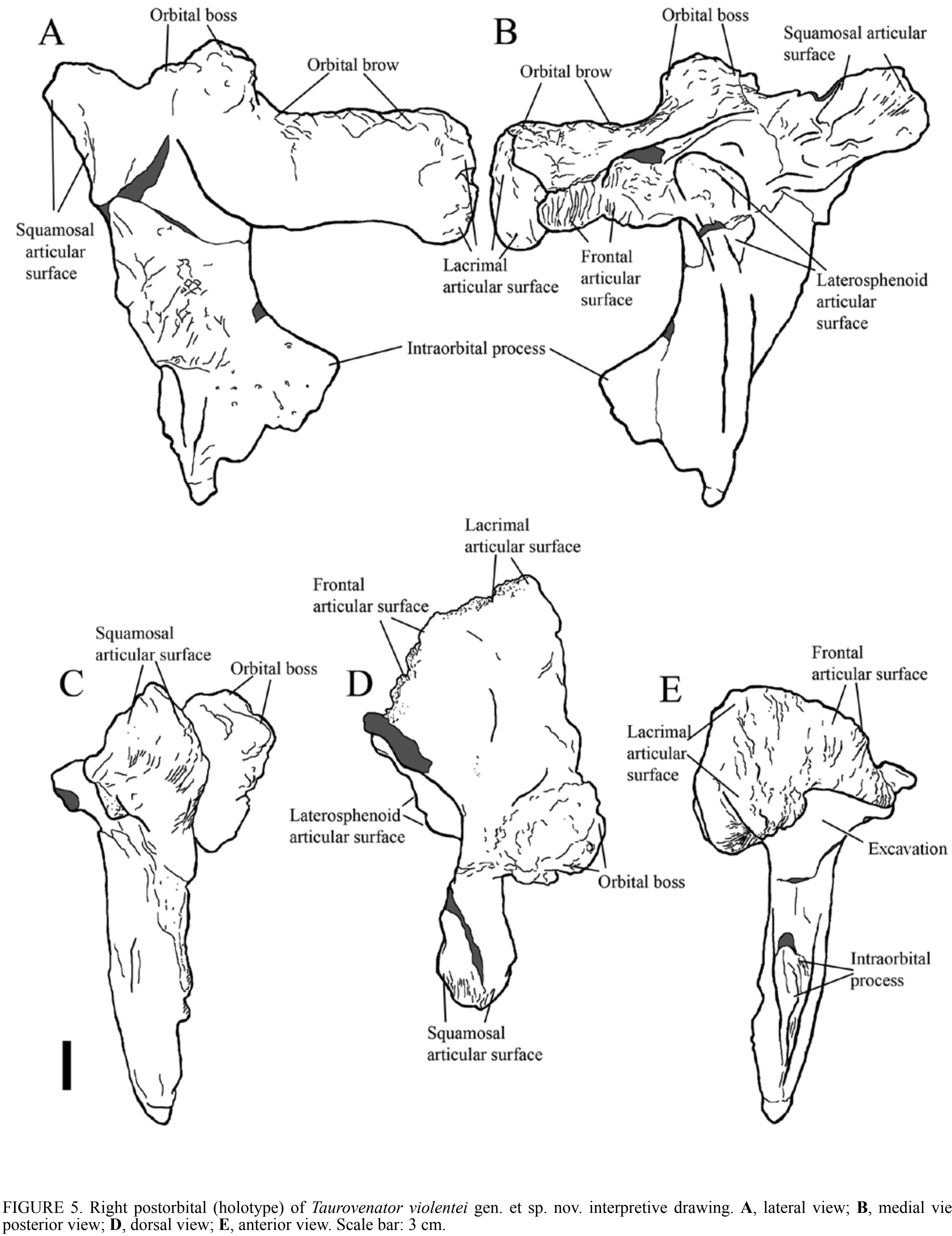

FIGURE 5. Right postorbital (holotype) of *Taurovenator violentei* gen. et sp. nov. interpretive drawing. **A**, lateral view; **B**, medial view; **C**, posterior view; **D**, dorsal view; **E**, anterior view. Scale bar: 3 cm.

Carcharodontosaurus, and *Mapusaurus* (Coria and Currie, 2006; Sereno and Brusatte, 2008)(Fig. 6). In spite of that, the postorbital of *Taurovenator* is notably smaller than that of *Mapusaurus* or *Giganotosaurus* (Coria and Currie, 2006; Sereno and Brusatte, 2008), although it is proportionally more robust and transversely thicker than in the aforementioned species.

Taurovenator shares with derived carcharodontosaurids the following features:

1) Dorsoventrally short and anteroposteriorly wide ventral ramus of the postorbital, that bears a short and dorsally placed subtriangular shaped intraorbital process. A postorbital with a ventral process anteroposteriorly broader than transversely wider is present in most Theropoda (Holtz, 1998). In some large-sized clades, such as abelisaurids, carcharodontosaurids and tyrannosaurids, the ventral process is wide in lateral view and has an intraorbital process (or suborbital flange) that supports the ventral margin of the orbit (Novas, 1997; Rauhut, 2003). This feature was acquired independently in each lineage, according to most phylogenetic hypotheses (Holtz et al., 2004; Fig. 5).

A dorsoventrally short ventral ramus seems to be diagnostic of *Taurovenator, Acrocanthosaurus*, and derived carcharodontosaurids, because allosaurids (e.g., *Allosaurus*), sinraptorids (e.g., *Sinraptor*) and basal carcharodontosaurids (e.g., *Eocarcharia*) have a longer ventral ramus (Fig. 6). This also results in the position of the intraorbital process becoming more dorsally positioned in *Acrocanthosaurus* and derived carcharodontosaurids, such as *Mapusaurus*, *Carcharodontosaurus*, or *Taurovenator*. In a similar way, the width of the ventral process of carcharodontosaurids is greater when compared more basal allosauroids (e.g., *Allosaurus*, *Sinraptor, Eocarcharia*). The above mentioned combination of characters appears to be related with the reinforcement of the orbit and skull roof.

2) The ventral process of the postorbital forms an acute angle with the orbital brow. The ventral ramus of the postorbital is vertical or slightly anteroventrally directed in most theropod groups. In some taxa such as abelisaurids or derived carcharodontosaurids this ramus is strongly anteroventrally oriented (Novas, 1997). In more basal allosauroids, such as allosaurids, sinraptorids, *Eocarcharia,* and *Acrocanthosaurus* (Eddy and Clarke, 2011), the ventral ramus is vertical or forms a 90° angle with the orbital brow. In derived carcharodontosaurids and abelisaurids, the angle between the ventral ramus and the orbital brow is approximately 60°-70° (Sereno and Brusatte, 2008; Fig. 4).

3) A vertical ridge in the medial surface of the ventral process. Presence of a subvertical ridge that represents the articular surface for the laterosphenoid on its dorsal half and the articular surface for the jugal at its ventral half. In abelisaurids (Bonaparte et al., 1990), and selected basal tetanurans, such as spinosaurids, *Allosaurus, Acrocanthosaurus*, and carcharodontosaurids (Carrano et al., 2012), is notably ventrally projected as a rod-like process. Within Carcharodontosauria, this structure is observed in *Acrocanthosaurus, Carcharodontosaurus,* and *Taurovenator* (Eddy and Clarke, 2011). In *Mapusaurus,* the ventral ramus is broken but a well-developed vertical ridge is observed on the dorsal portion of the ventral ramus (Coria and Currie, 2006). In *Eocarcharia,* the medial surface of the ventral ramus is flat, and a vertical ridge is absent (Sereno and Brusatte, 2008). This might indicate that the contact for the jugal was different in derived carcharodontosaurids when compared to the basal *Eocarcharia*.

4) The posterolateral wall of the orbital brow projects ventrally and overhangs the orbit. As indicated by previous authors, the postorbital morphology is highly diverse within Carcharodontosauria, which is very informative taxonomically (Sereno and Brusatte, 2008). The lateral wall of the orbital brow of *Taurovenator* expands ventrally and is medially directed surrounding the orbit. This feature is present in *Taurovenator, Acrocanthosaurus*, and *Mapusaurus* (Coria and Currie, 2006). In other allosauroids, such as *Allosaurus* or *Sinraptor,* this feature is absent, whereas in *Eocarcharia* the brow expands ventrally but does not surround the orbit (Figs. 4-5).

In conclusion, based on the features mentioned above, we assign *Taurovenator* to the Carcharodontosauridae. Among carcharodontosaurids, *Taurovenator* closely resembles the derived members of the group including *Carcharodontosaurus, Giganotosaurus,* and *Mapusaurus*, but not *Acrocanthosaurus* or *Eocarcharia*.

On the other hand, *Taurovenator* shows two unique features that deserve the following comments:

1) Presence of a boss on the posterodorsal margin of the orbital brow (Fig. 4). One of the most striking traits of *Taurovenator* is the presence of a horn-like structure in the orbital brow. Some large-sized theropod groups such as Ceratosauridae, Abelisauridae, Carcharodontosauridae and Tyrannosauridae show ornamental structures in the postorbital region, and these cranial ornamentations are traditionally regarded as indicative of intraspecific competition related with mating (Sereno and Brusatte, 2008). In carcharodontosaurids the cranial ornamentation is widely distributed (Novas, 1997), for example, prominent and rugose lateral brows are common among carcharodontosaurids. (Coria and Currie, 2006; Sereno and Brusatte, 2008). Furthermore, in *Eocarcharia,* a big and rounded orbital boss is present in the laterodorsal margin of the postorbital (Sereno and Brusatte, 2008). A similar but less-developed boss is observed in *Carcharodontosaurus*; furthermore, the ventral ramus of the bone shows a "pitted pyramidal projection" in the lateral margin near the distal end of the element (Sereno and Brusatte, 2008). In spite of such diversity of cranial ornamentation, no other carchardontosaurid shows a horn-like projection of the orbital boss at its posterolateral margin as the one present in *Taurovenator*.

2) Presence of an excavation housed at the posterodorsal surface of the eye socket (Fig. 4). This feature is not mentioned for other carcharodontosaurids or basal tetanurans. In *Majungasaurus* a neurovascular foramen is also present in the spot, but is much smaller in size (Sampson and Witmer, 2007). In *Mapusaurus* (Coria and Currie, 2006) the region in which the fossa should be housed is broken, and, thus, the condition cannot be corroborated. In *Acrocanthosaurus, Carcharodontosaurus,* and *Eocarcharia* a deep excavation or fossa is totally absent. In this way, we conclude that presence of such a structure in *Taurovenator* should be regarded as an autapomorphy of the latter.

Gen. et sp. indet

Referred material: MPCA-Pv 803/1-803/11, associated specimen consisting of a dorsal vertebral centrum (803/1), one fragmentary rib (803/2), incomplete right hindlimb composed of distal tarsals III (803/3) and IV (803/4), metatarsal II (803/5), metatarsal III (803/6) and possible distal fragment of an indeterminate metatarsal (803/7), pedal phalanges IV-1 (803/8) and IV-3 (803/9), and two pedal unguals (803/10-803/11).

Description and comparisons: A single dorsal vertebra is represented by a poorly preserved centrum with the base of the neural arch (Fig. 7). It is interpreted as a posterior dorsal vertebra due to the absence of a parapophysis on the centrum and the amphyplatic condition of the articular surfaces. The centrum is laterally compressed and has its posterior half dorsoventrally higher than the anterior half. The centrum shows a ventral longitudinal keel and exhibits a strong middle constriction as occurs in other allosauroids (e.g., *Allosaurus, Acrocanthosaurus*; Holz et al., 2004). It shows notably laterally expanded rims surrounding the anterior and posterior articular surfaces, resulting in a spool-shaped centrum. On its lateral surface, there is a large and deep, dorsally located pneumatic foramen that is subdivided by an oblique septum, a condition present in posterior dorsal vertebrae of other carcharodontosaurids (including *Acrocanthosaurus* and *Giganotosaurus*; Harris, 1998), *Torvosaurus,* Megaraptoridae, and Tyrannosauridae (Rauhut, 2003; Sereno et al., 2008). In spite of its fragmentary nature, the spool-shaped contour in ventral view, longitudinal ventral keel, and large subdivided pneumatic foramen are a combination of features that indicate that MPCA-Pv 803/1 belongs to a carcharodontosaurid theropod.

Two distal tarsals were also recovered. These elements are rarely preserved or illustrated in the literature, so that, exhaustive comparisons cannot be done.

Distal tarsal III is not entirely preserved and lacks its posterior margin. Its proximal surface is convex, and the distal surface is slightly concave, probably to contact with metatarsal III (Fig. 8). The lateral surface shows a deep and well-defined ovoid depression that is located at its anterior half. This concavity bears several vascular pits. The medial surface shows a wide but shallow depression that bears a broad and low subvertical ridge. The anterior surface shows an obliquely oriented concavity and a laterodistally located suboval pit. The lateral depression probably represents part of the contact with tarsal IV. Over all, the distal tarsal III here described is similar in gross morphology to the distal tarsal III of *Sinraptor* (Currie and Zhao, 1993).

Distal tarsal IV shows similar gross morphology to that of *Allosaurus* and *Sinraptor* (Madsen 1976; Currie and Zhao 1993; Fig. 9). The lateral and distal surfaces are badly preserved. The proximal surface shows a large and obliquely oriented concavity similar to that present in *Sinraptor* (Currie and Zhao, 1993). The distal surface is slightly concave. The medial surface shows a small subcircular pit near its anterior end, and a large posterior concavity. A similar morphology is

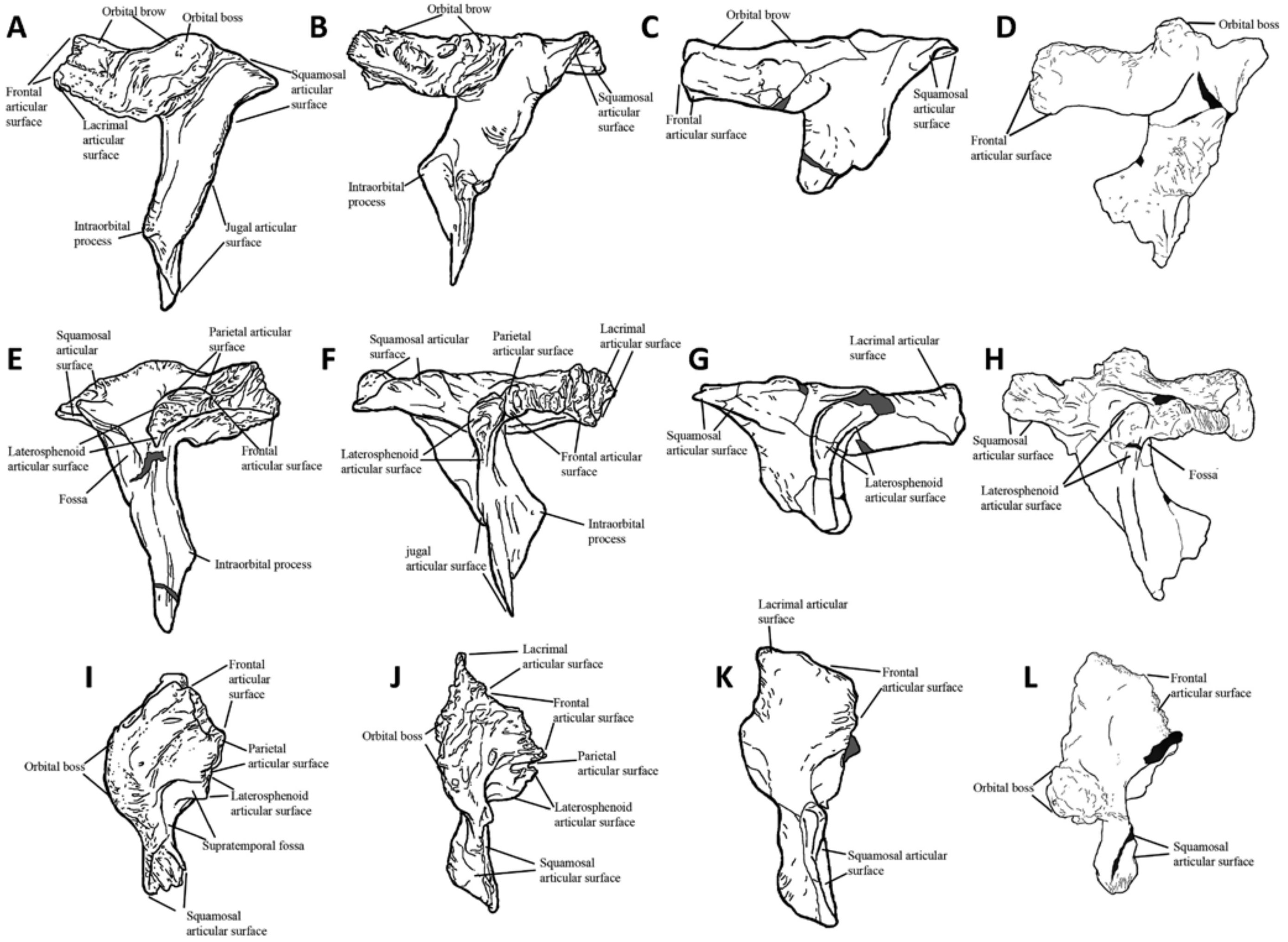

FIGURE 6. Selected carcharodontosaurid left postorbitals in A-D, lateral; E-H, medial; and I-L, dorsal views. **A, E, I,** *Eocarcharia dinops* (modified from Sereno and Brusatte, 2008); **B, F, J,** *Carcharodontosaurus saharicus* (modified from Sereno and Brusatte, 2008); **C, G, K,** *Mapusaurus roseae* (modified from Coria and Currie, 2006); **D, H, L,** *Taurovenator violantei* nov. Not to scale.

present in *Sinraptor* (Currie and Zhao, 1993) and *Allosaurus* (Madsen, 1976).

A well-preserved right metatarsal II was recovered and only lacks part of its distal end (Fig. 10). The bone is 43.5 cm long. This element is robust and almost straight for most of its length, with a lateral curvature near its distal end. In proximal view, the proximal end shows a slightly convex medial margin and a strongly convex lateral margin, giving the metatarsal a “D” contour when viewed proximally, a condition present also in *Sinraptor* and *Mapusaurus* (Currie and Zhao, 1993; Coria and Currie, 2006). As occurs in *Sinraptor,* when viewed proximally, the metatarsal bears a set of rugose grooves along its medial margin, suggesting some kind of cartilage cap. There is a rounded pit in the center of the proximal surface. In medial view, the proximal end is roughly fan-shaped, and more anteroposteriorly expanded than in *Allosaurus* (Madsen, 1976) or *Neovenator* (Brusatte et al., 2008), resembling *Sinraptor* in this aspect (Currie and Zhao, 1993). The shaft is stout and expands distally to form the medial hemicondyle. The distal end shows a deep and rounded collateral pit on its medial side. In anterior view, the distal end is laterally oriented because of the lateral curvature of the shaft. There is a remarkable small protuberance at the middle of the shaft, a trait also present in *Acrocanthosaurus* (Currie and Carpenter, 2000). In lateral view, the proximal end bears a well defined facet to contact metatarsal III. Moreover, there are three longitudinal scars at the distal half of the bone that probably served as the insertion of the *M. gastrocnemius pars lateralis* (Carrano and Hutchinson, 2002). In posterior view, the distal half of the bone bears a suboval concavity that shows a dorsoventrally oriented major axis, probably to contact the first metatarsal, as occurs in *Allosaurus* (Osborn, 1899).

The right metatarsal III is badly weathered (Fig. 11). In gross morphology this element is similar to that *Allosaurus* (Madsen, 1976), *Sinraptor* (Currie and Zhao, 1993), and *Mapusaurus* (Coria and Currie, 2006). In proximal view it is subtriangular in shape, with the anterior half more transversely compressed than the posterior portion. The medial border shows a slightly concave contact for metatarsal II. The lateral border is more concave than the medial one. In gross morphology this element is more transversely compressed and anteroposteriorly shorter than the metatarsal II, which is proportionally more robust, a condition widespread among allosauroids (e.g., *Sinraptor*, *Mapusaurus*, *Allosaurus*).

One right pedal phalanx IV-1 was recovered (Fig. 12). It is a robust and asymmetrical element, being strongly tilted laterally. The lateral condyle is more robust than the medial condyle. In proximal view, the articular surface is dorsoventrally taller than transversely wide and shows an asymmetrical dorsal margin, as occurs in some other allosauroids such as *Neovenator* (Brusatte et al., 2008). The dorsal surface is slightly concave in lateral view and shows a well defined and subcircular extensor pit. The collateral ligamental pits are subcircular, the lateral one being relatively smaller, better defined, and deeper than the medial one. The ventral surface is nearly flat and shows a proximal tubercle on its lateral margin, similar to that of *Neovenator* (Brusatte et al., 2008). The distal surface shows a poorly developed intercondylar groove that separates distal condyles, resulting in a nearly flat ventral margin, whereas in *Neovenator* this groove is deeper.

A pedal phalanx that probably represents phalanx IV-3 was found

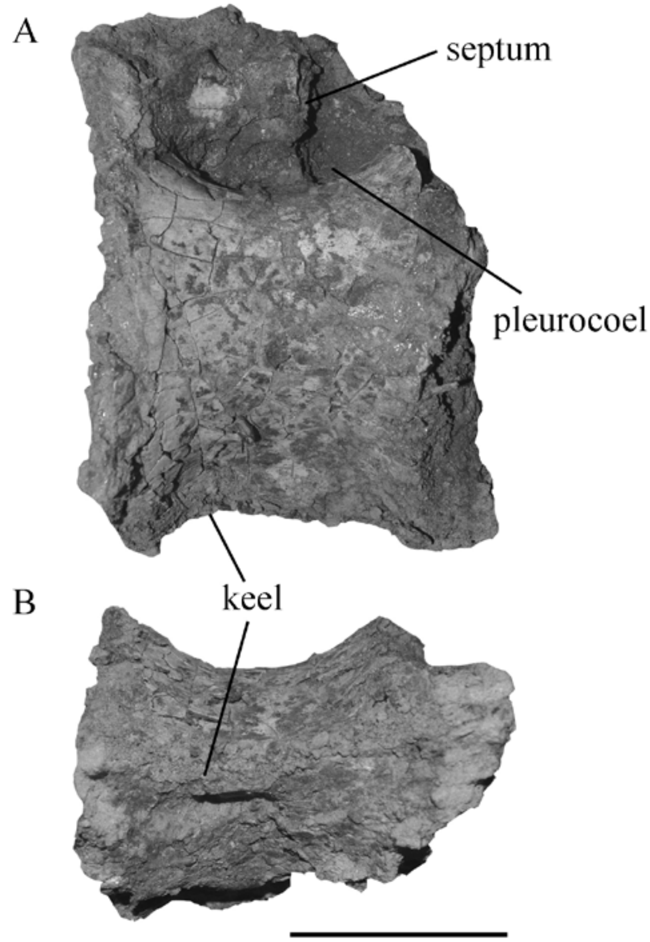

FIGURE 7. Centrum of dorsal vertebra of Carcharodontosauridae indet. **A**, left lateral; and **B**, ventral views. Scale bar: 10 cm.

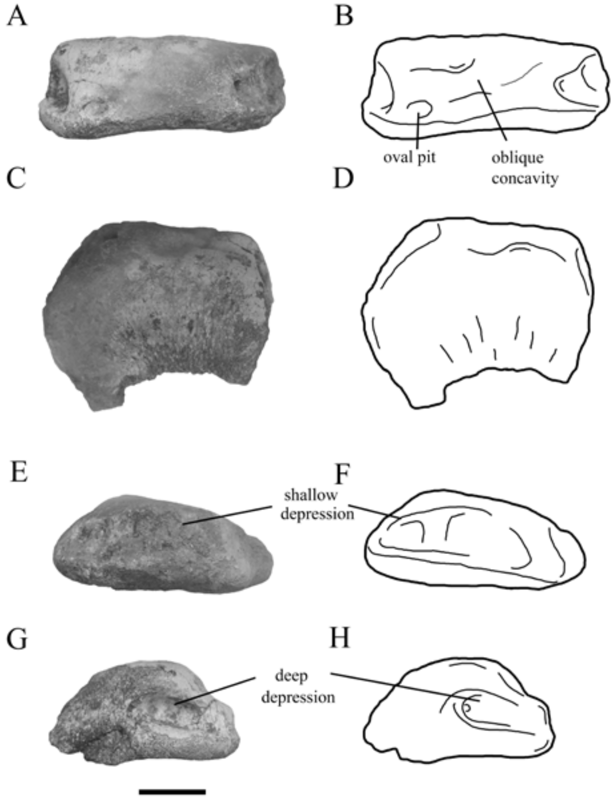

FIGURE 8. Distal tarsal III of Carcharodontosauridae indet. in: **A, B,** anterior view; **C, D,** proximal view; **E, F,** medial view; **G, H,** lateral view. Scale bar: 3 cm.

(Fig. 13). This element is notably short, with a length of approximately 6 cm. In proximal view the articular surface is concave and ovoid in contour, showing a median keel as in other allosauroids, such as *Neovenator* (Brusatte et al., 2008). The ventral surface is flat and wider than the dorsal one, which is slightly concave. In this way, when viewed dorsally, the ventral portion of the phalanx is notably exposed. Both lateral and medial surfaces bear deep and large collateral ligamental pits. There is a wide rim running along the laterodorsal and mediodorsal edges of the phalanx. These rims run along the phalanx and end on the anterior margin of each collateral ligamental pit. Other allosauroids such as *Sinraptor* and *Neovenator* (Currie and Zhao, 1993; Brusatte et al., 2008) show weaker rims at the sides of the phalanx. Both distal condyles are rounded and separated by a deep intercondylar groove.

Two pedal ungual phalanges where recovered. Because they were not found in direct articulation, and because of the homogeneity of carcharodontosaurid claw morphology, we are unable to determine to which digit they pertain.

The available unguals are notably similar to each other (Figs. 14-15). They are robust, and the shaft is almost straight, without a pronounced lateral compression as occurs in the pedal phalanx of many large theropods such as *Neovenator, Tyrannosaurus* and *Allosaurus* (Madsen, 1976; Brochu, 2002; Brusatte et al., 2008). In proximal view the proximal end tapers dorsally, resulting in a subtriangular proximal contour. The proximal articular surface shows two bumps at the ventral margin and lacks the median subvertical crest, in contrast with the pedal unguals of other theropods (e.g., abelisaurids, coelurosaurs; Ostrom, 1969; Carrano et al., 2002), but resembling other allosauroids (e.g., *Neovenator*: Brusatte et al., 2008; *Sinraptor*: Currie and Zhao, 1993) in this regard. The dorsal surface of the claw is rounded and smooth. It is proximally expanded, forming a notable posteriorly expanded dorsal lip. This thick lip has a concave dorsal margin, and is located more ventrally than the dorsal edge of the ungual blade. This condition is uniquely present in allosauroids such as *Neovenator, Allosaurus,* and *Sinraptor,* being absent in other theropods such as *Tyrannosaurus* or *Australovenator* (Brochu, 2003; Hocknull et al., 2009). Presence of such an unique proximal lip may represent a unique feature of allosauroids, a hypothesis that needs to be further studied.

There is a single and deep longitudinal groove along the lateral and medial sides of the claw, the medial one being more dorsally placed, wider, and with less well defined edges than the lateral one. This condition is shared with other theropods, including allosauroids such as *Neovenator, Sinraptor* and *Mapusaurus* (Currie and Zhao, 1993; Coria and Currie, 2006; Brusatte et al., 2008), and contrasts with abelisaurids, which show a distinctive bifurcated groove in each side of the claws that usually delimits a notable lateral bump (Coria and Salgado, 1998; Carrano et al., 2002; Novas et al., 2005).

These phalanges lack a flexor tubercle, a condition shared with abelisaurids and carcharodontosaurids (Currie and Zhao, 1993; Carrano et al., 2002; Coria and Currie, 2006; Brusatte et al., 2008). The specimens MPCA-Pv 810 and 811 show a flat ventral surface, without any sign of a longitudinal groove or keel, in contrast with abelisaurids (e.g., *Masiakasaurus; Noasaurus*; Bonaparte and Powell, 1980; Novas et al., 2005), that have a flexor fossa on their ventral surfaces, but being similar to other allosauroids (e.g., *Neovenator, Sinraptor, Mapusaurus*; Currie and Zhao, 1993; Brusatte et al., 2008). There is a posteroventral rugosity that represents the area for the insertion of *M. flexor digitorum longus*.

In sum, the presence of a very large, dorsally concave and ventrally oriented proximal lip, and ventral surface lacking a flexor tubercle are features that may be useful to diagnose allosauroid pedal unguals. Furthermore, the total absence of a proximal subvertical keel and presence of two proximal ventral bumps may be diagnostic of Carcharodontosauridae. The synapomorphic condition of each trait, as well as its distribution, should be corroborated by future numerical phylogenetic analyses.

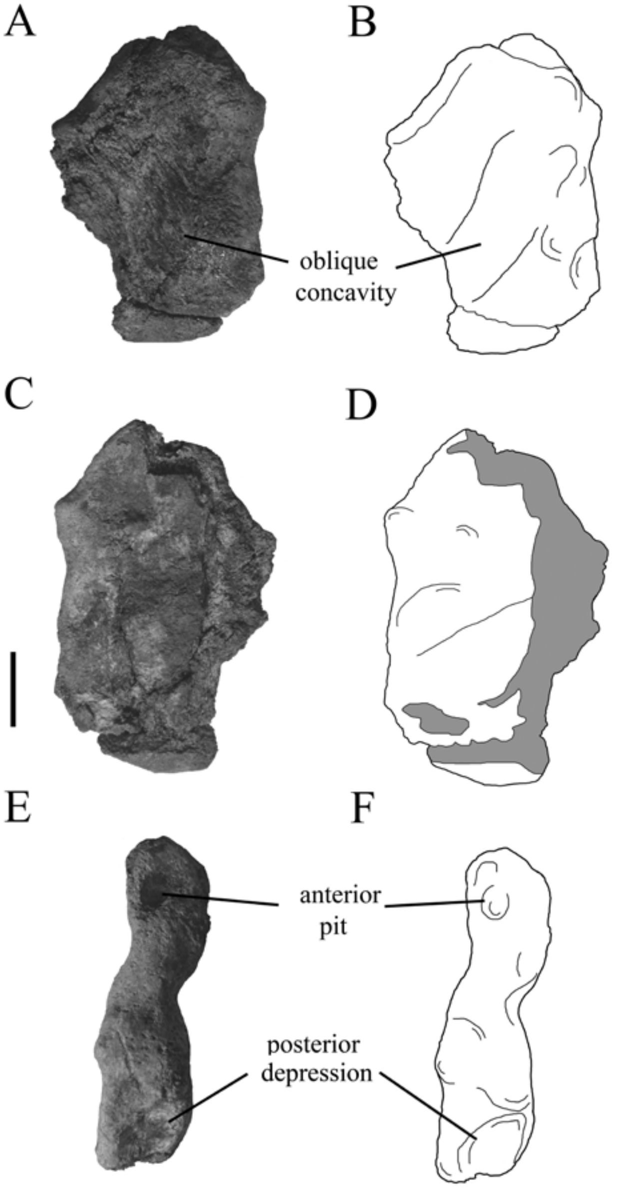

FIGURE 9. Distal tarsal IV of Carcharodontosauridae indet. in: **A, B,** proximal view; **C, D,** distal view; **E, F,** medial view. Scale bar: 3 cm.

COELUROSAURIA Huene, 1914
Gen. et sp. indet.

Referred material: MPCA-Pv 806/1-806/11, associated individual composed of three incomplete caudal vertebral centra (806/1-3), incomplete anterior cervical vertebra (806/4), incomplete distal caudal vertebra (806/5), incomplete distal metapodial (806/6), incomplete proximal ungual phalanges of the hand (806/7-8) (Figure 15).

Description and comparisons: The specimen (Fig. 16) represent a single individual of small-sized coelurosaur having notably slender proportions. In spite of its poor preservation, the fused neural arches indicate that it was probably a skeletally mature individual. The presence of ferruginous covering of the material precludes the detailed description of most recovered bones.

The available cervical vertebra is very poorly preserved. The centrum has a strongly parallelogram-shaped contour, and is ventrally smooth. The neural arch was dorsoventrally low. The neural spine is dorsoventrally low and anteroposteriorly extended.

The caudal vertebrae are long and gracile. They show subovoid anterior and posterior articular surfaces that are wider than tall. The ventral surface is flat, having a shallow longitudinal groove surrounded by two feebly developed ridges that are restricted to the anterior third of the centrum. The neural canal is small. The prezygapophyses are robust, but are too incomplete to allow a more detailed description and comparisons. The neural spine is transversely narrow and anteroposteriorly elongate.

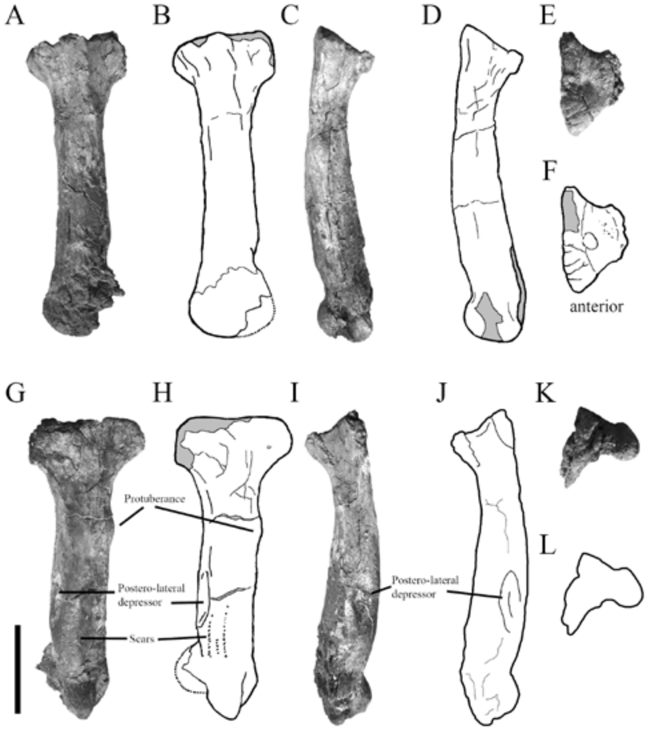

FIGURE 10. Rigth metatarsal II of Carcharodontosauridae indet. in: **A, B**, medial view; **C, D,** anterior view; **E, F,** proximal view; **G, H,** lateral view; **I, J,** posterior view; **K, L,** distal view Scale bar: 15 cm.

The ungual phalanges are poorly preserved. They are notably dorsoventrally tall and transversely compressed, and the proximal end shows an acute and well-developed subvertical ridge. There is no proximodorsal lip. The flexor tubercle is represented by its base; in spite of that is appears to be very well-developed.

Comments: In spite of its fragmentary nature, the present specimen may be referred to Coelurosauria mainly on the basis of elongate cervical vertebrae, lacking ventral grooves or a keel and retaining a relatively well-developed and anteroposteriorly long neural spine (see Agnolin and Martinelli, 2007). Further, the caudal vertebrae show notably small neural spines, a feature considered as typical of coelurosaurs (Rauhut, 2003). In addition, the strongly compressed and acute ungual phalanges are also different from that known in noasaurid abelisauroids (Agnolin and Chiarelli, 2010).

Within coelurosaurs, the affinities of the present specimen are far from certain. In spite of that, it is worth mentioning that it differs from unenlagiids and dromaeosaurids (e.g., *Buitreraptor, Deinonychus*; Ostrom, 1969; Gianechini and Apesteguía, 2010) in having caudal vertebrae lacking strong lateral and ventral grooves and ridges, and in having transversely wide and ovoid anterior and posterior articular surfaces (rather than box-like; Norell and Makovicky, 1997). Further, it differs from troodontids in lacking caudal vertebrae with a dorsally excavated neural arch (Averianov and Sues, 2016). In this way, the present specimen is determined as a non-paravian coelurosaurian of uncertain affinities.

TYRANNOSAUROIDEA Osborn, 1905
MEGARAPTORA Benson, Carrano and Brusatte, 2010
Aoniraptor libertatem gen. et sp. nov.

Etymology: *Aoni* from the Tehuelche language, which means south, and *raptor*, Latin word for thief; *libertatem*, from the Latin, meaning "independence," due to the 200 years anniversary of 9th July 1810, which led to the declaration of independence of Argentina from the Spanish government, thus constituting one of the most important chapters in the history of this South American country.

FIGURE 11. Right metatarsal III Carcharodontosauridae indet. in: **A,** proximal view; and **B,** lateral view. Scale bar: 10 cm.

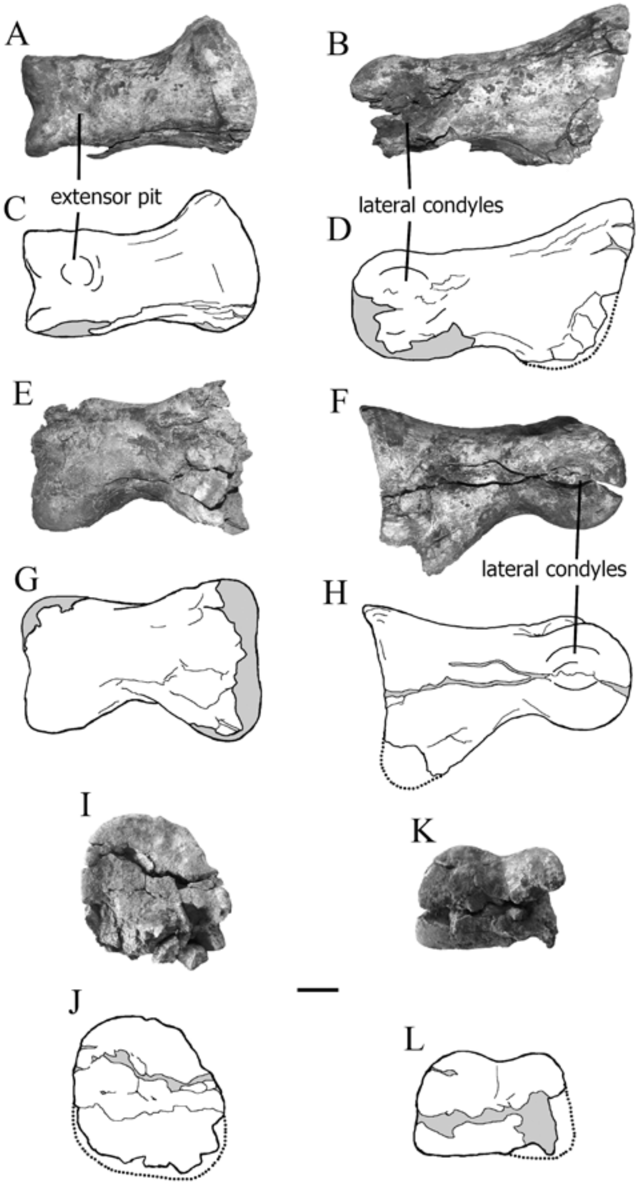

FIGURE 12. Right pedal phalanx IV-1 of Carcharodontosauridae indet. in: **A, C,** dorsal view; **B, D,** medial view; **E, G,** ventral view; **F, H,** lateral view; **I, J,** proximal view; **K, L,** distal view. Scale bar: 3 cm.

Diagnosis: Megaraptoran theropod diagnosable on the basis of the following autapomorphies: (1) anterior mid-caudal vertebrae with fan-shaped prezygapophyses lacking a discernible articular surface for contacting the postzygapophyses; (2) presence of a blunt and thick process on the lateral surface of the prezygapophyses of anterior mid-caudal vertebrae; and (3) mid-posterior caudals with a pair of non-articular flat surfaces located on the posterodorsal corner of the centrum.

Holotype: MPCA-Pv 804/1 to 804/25, incomplete vertebral series represented by the last sacral vertebra, 6 proximal caudal vertebrae, 4 mid-caudal vertebrae, and 5 haemal arches.

Description: The available vertebrae indicate that *Aoniraptor* was a mid-sized theropod with an estimated length of 6 meters. The neural arches are not fused to the centra, indicating a skeletally immature individual. The centra are elongate, amphicoelous, and highly pneumatic.

All available vertebrae that are in articulation show an element separating each other that probably represents the intervertebral disc. These elements approximately represent one tenth the total length of each corresponding vertebra and each is about 1 cm of length.

The first sacral is slightly deformed and has an incompletely preserved neural arch (Fig. 17). The centrum is relatively elongate,

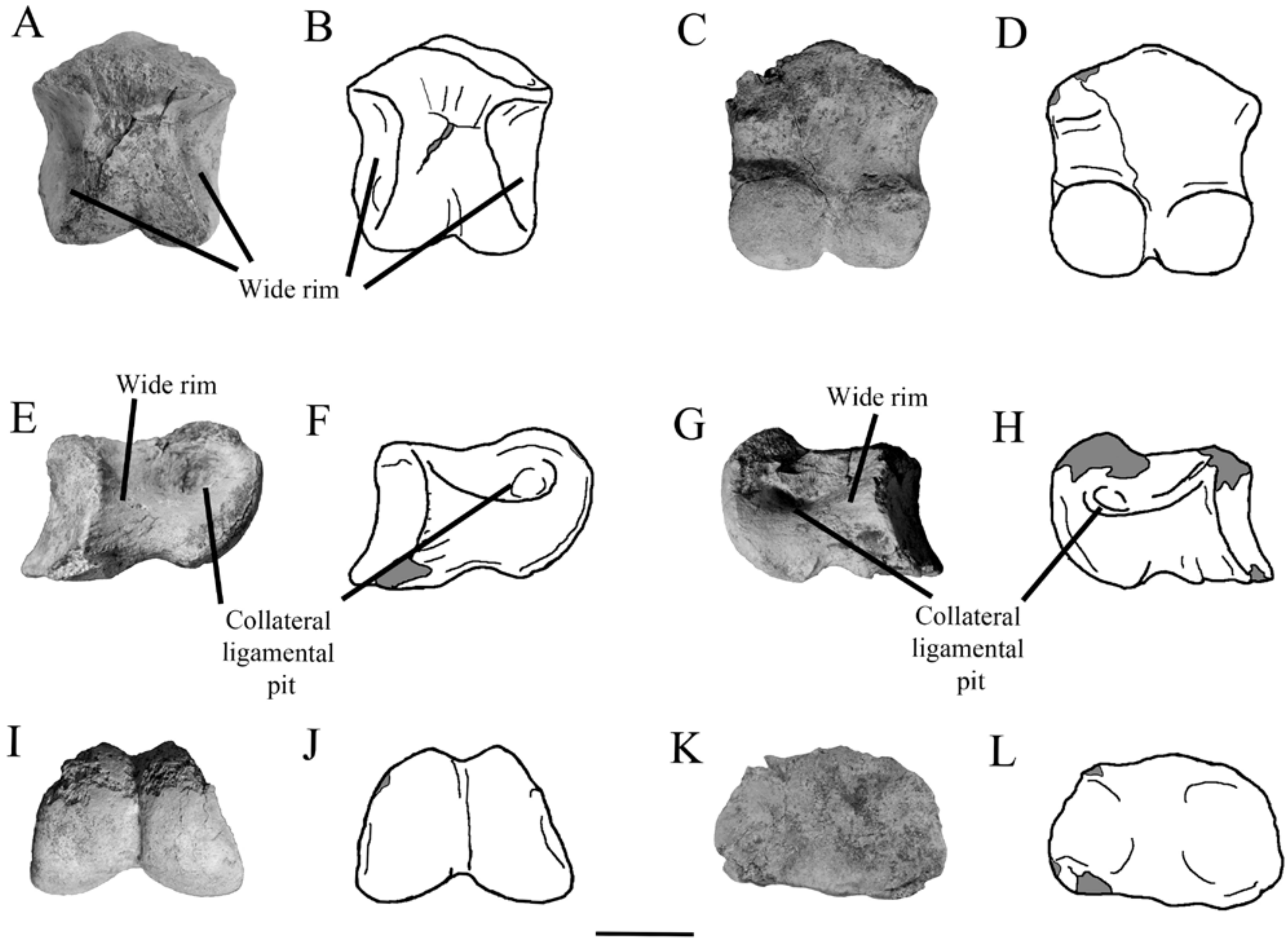

FIGURE 13. Right pedal phalanx IV-3 of Carcharodontosauridae indet. in: **A, B,** dorsal view; **C, D,** ventral view; **E, F,** lateral view; **G, H,** medial view; **I, J,** distal view; **K, L,** proximal view. Scale bar: 3 cm.

transversely narrow, and is highly pneumatized. The anterior articular surface is subcircular in outline, being dorsoventrally lower than the posterior articular surface. This results in a roughly paralellogram-shaped centrum. Its surface is rugose, indicating a strong attachment with a preceding sacral. The posterior surface is suboval, having a dorsoventrally oriented major axis. The articular surface shows a well-developed striated rim of bone along its perimeter. In lateral view, the ventral margin of the centrum is strongly concave, and, in ventral view, is flat, lacking any sign of a keel or groove.

Pneumatic traits along the vertebral series are notably variable within and among vertebrae in *Aoniraptor*. In this regard, the first sacral has at the dorsal half of the centrum a large but shallow fossa, ventrally delimited by a rounded and mound-like shelf of bone. Within this fossa, in right lateral view, there is a large and deep pneumatic foramen that is anteriorly and posteriorly delimited by thin subvertical ridges of bone. These ridges delimit two smaller and shallow fossae. On the left lateral side, the pneumatization is different in that there are four small fossae that are separated by subvertical ridges of bone.

The neural arch is deformed and difficult to interpret, being also posteriorly displaced. However, the main anatomical details are still discernible. The neural arch is strongly pneumatized, showing a camerate internal structure. The neural spine is only represented by its incomplete base, but it shows that it was transversely compressed and anteroposteriorly long. It is laterally bounded by two narrow and acute laminae that are obliquely oriented and diverge posterolaterally. These laminae are separated from the neural spine by deep fossae. The transverse process is strongly pneumatized, being of camerate internal structure. It is strongly anteroposteriorly expanded and shows a roughly subtriangular contour when viewed laterally. It shows a longitudinal shallow groove that is ventrally delimited by an acute ridge. Within this groove there is a large number of longitudinal striations, probably related to its anchoring with the ilium. At the inner surface of the anterior expansion of the sacral articulation the transverse process shows a subtriangular and deep fossa that is anterolaterally delimited by a strong ridge of bone that runs to the base of the neural spine. It is worth mentioning that the transverse process and neural arch show a large number of dispersed pneumatic fossae and foramina.

The first caudal vertebra is very similar to the first sacral (Fig. 17). It differs in that both anterior and posterior articular surfaces are at the same level and are subequal in size and morphology, and in that the vertebral centrum is dorsoventrally taller. In addition, there is a small rugose surface located at the posteroventral corner of the centrum that articulates with the haemal arches. In ventral view the centrum shows a small posteroventral flattened surface that is absent in the sacral vertebra. Further, the posterior margin of the neural arch of the last sacral ends at the same level as the posterior articular surface of the centrum, whereas in the caudal vertebrae the neural arch ends anterior to the posterior margin of the vertebral centrum.

The anterior and posterior articular surfaces are suboval in contour. In right lateral view the centrum lacks any sign of pneumatization, with the exception of a very shallow depression, whereas on the left side there is a large fossa that bears a large pneumatic foramen, delimited by anterior and posterior, small and acute ridges of bone.

The neural arch is highly incomplete and distorted. It shows a camerate internal structure. The right prezygapophysis and the base of the transverse process have been preserved. The prezygapophysis is relatively large, and subvertically oriented. The base of the transverse process shows two well-defined buttresses that bound presumably

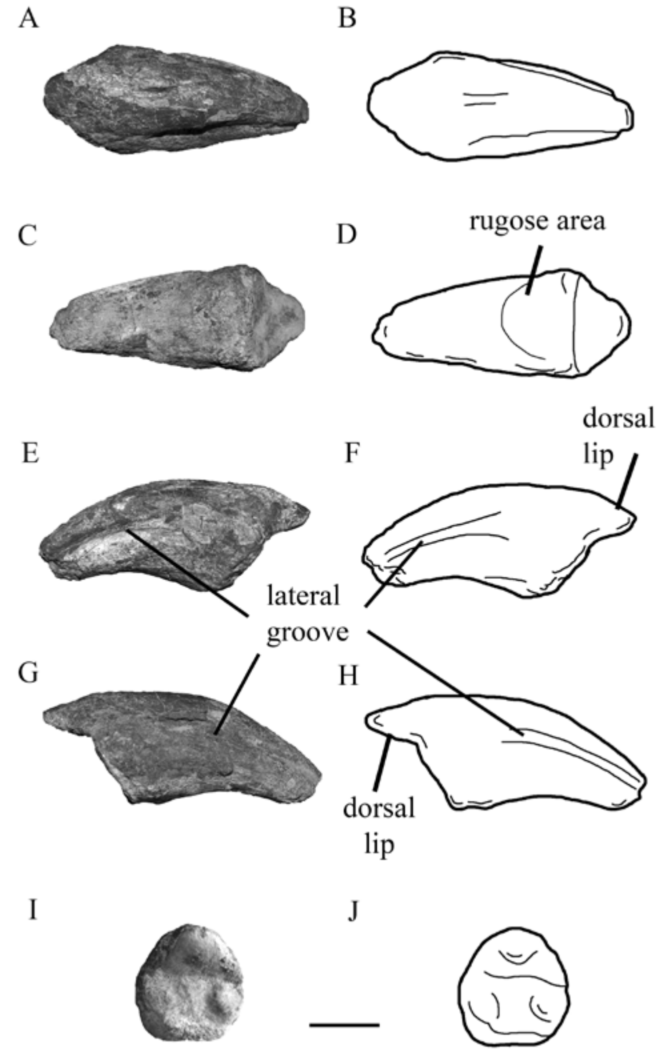

FIGURE 14. Right pedal ungual phalanx of Carcharodontosauridae indet. **A, B,** ventral view; **C, D,** dorsal view; **E, F,** medial view; **G, H,** lateral view; **I, J,** proximal view. Scale bar: 3 cm.

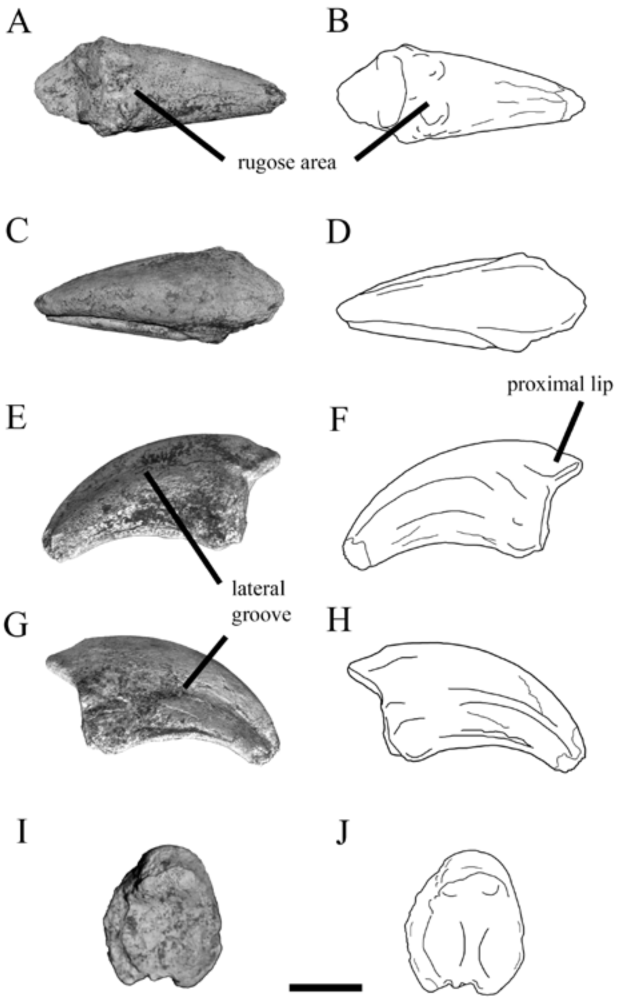

FIGURE 15. Right pedal ungual phalanx of Carcharodontosauridae indet. **A, B,** dorsal view; **C, D,** ventral view; **E, F,** lateral view; **G, H,** medial view; **I, J,** proximal view. Scale bar: 3 cm.

pneumatic fossae. The base of the transverse process indicates that it was laterodorsally oriented.

Other anterior caudal vertebrae are represented by centra and incomplete neural arches. The vertebrae 2 and 3 are represented by the centra, whereas anterior neural arches where found dissarticulated (Figs. 18-19).

The vertebral centra are similar in size, morphology, and proportions to that of the first caudal vertebra (Fig. 17). The anterior articular surface is more deeply excavated than the posterior one. In this regard, the intervertebral disc on these vertebrae is anteroposteriorly thick, and shows a more strongly convex posterior surface. In ventral or dorsal views, the anterior expansion of the articular surface is transversely wider than the posterior one. The centra lack pneumatic fossae. In dorsal view, approximately at the mid-length of the suture between the neural arch and centrum there is a large subcircular internal foramen on each side that penetrates within the centrum. In this way, possibly the pneumatization of the vertebral centrum was probably due to the invasion of the pneumatic system coming from the neural arch.

The ventral surface of the centrum shows a flattened ellipsoidal surface. This surface is larger in the third vertebra than in the first or second.

Regrettably, the only two available anterior neural arches were found disarticulated, incomplete, and weathered (Fig. 18). However, a large number of interesting features may be recognized. The transverse processes are notably elongate and are posterolaterally oriented, having only a subtle dorsal orientation. In dorsal and ventral view they are paddle-shaped, being slightly distally expanded on the anteroposterior axis. The transverse processes are remarkably dorsoventrally low and sublaminar in cross-section. In ventral view, at the proximal half of the centrum there are posterior and anterior laminae that run from the transverse process to the base of the neural arch, probably representing part of the buttresses present in anterior and mid-vertebrae. The anterior margin of the transverse process shows an anterior lamina that connects it with the prezygapophysis, and a shallower posterior one, that contacts with the postzygapophysis. There is a large and deep subtriangular pneumatic fossa delimited laterally by the lamina running from the transverse process to the prezygapophyses and ventrally by the anterior buttress.

The prezygapophyses are relatively robust and short, being dorsomedially oriented. There is a well-developed spinoprezygapophyseal lamina. The postzygapophyses are very small-sized, having a subcircular articular surface. There is a small notch separating the postzygapophyses from the transverse process.

In dorsal view, in the area of contact between the base of the neural spine and the transverse process, there is a shallow, albeit notably wide, blind fossa.

There are eight nearly complete mid-vertebrae preserved. They differ from more anterior vertebrae in having a notably low neural spine and relatively short transverse processes.

Three anterior mid-neural arches were found in articulation. These arches are very poorly preserved, and are represented only by their left lateral half (Figs. 19-20). In gross morphology they resemble anterior caudals. They are notably elongate and probably occupied the entire length of the vertebral centrum. The neural spine has been completely preserved in a single vertebra. It is subrectangular in contour, having an anteroposteriorly elongate main axis. Its dorsal margin is gently

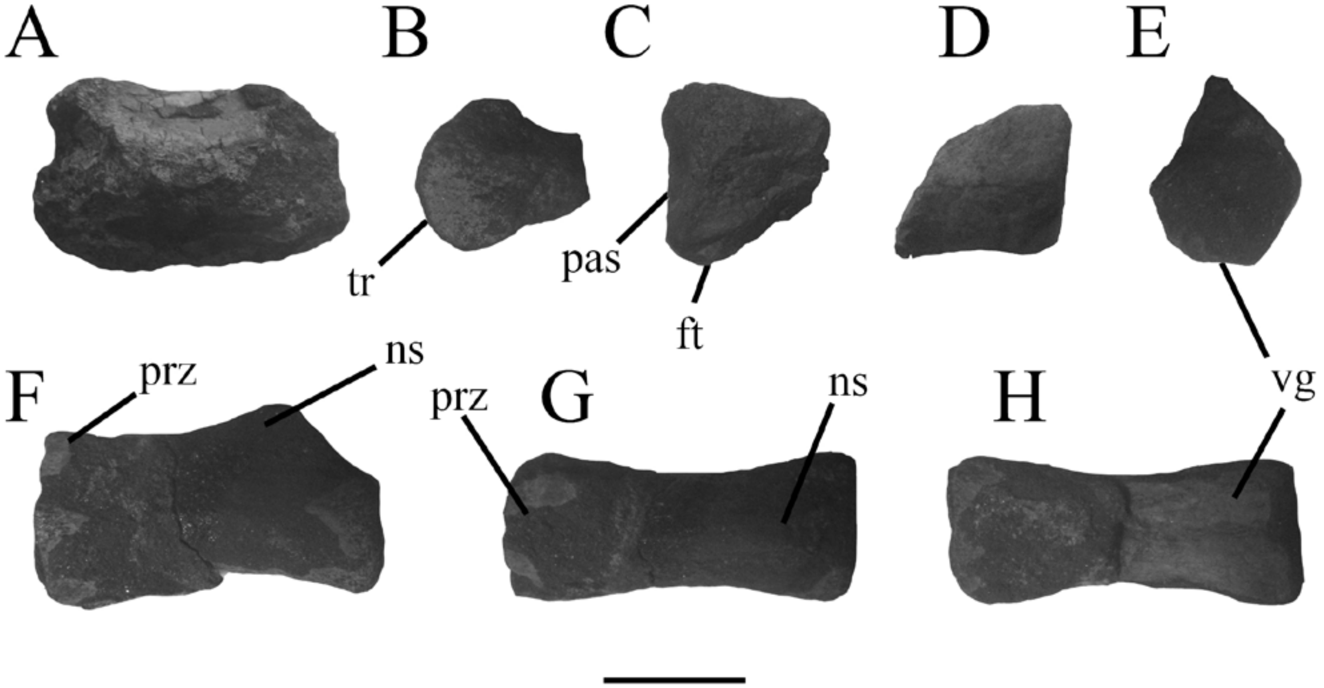

FIGURE 16. Coelurosauria indet. **A,** cervical vertebra in dorsal view; **B,** distal end of indeteminate metapodial; **C,** lateral view of manual ungual phalanx; **D,** lateral view of incomplete vertebral centrum; **E-H,** nearly complete caudal vertebra in: **E**, anterior, **F**, left lateral, **G**, dorsal, and **H**, ventral views. **Abbreviations**: **ft**, flexor tubercle; **ns**, neural spine; **pas**, proximal articular surface; **prz**, prezygapophysis; **tr**, distal trochlea; **vg**, ventral groove. Scale bar: 1 cm.

concave, resulting in a roughly saddle-shaped contour when viewed from the sides. It is located on the posterior half of the vertebral centrum. The posterior margin of the neural spine has preserved a notably expanded ligamentary lamina for interspinal scars. As occurs in anterior caudal vertebrae, there is a wide and well-defined fossa on the area of contact between the neural spine and the transverse process. The spinoprezygapophyseal and the prezygapophyseal/transverse process laminae are present as in the anterior caudal, but in this case, they are more developed and more acute. The spinoprezygapophyseal lamina defines a very wide and deep prespinal fossa. The transverse process are notably posteriorly oriented and are subrectangular in contour when viewed dorsally. They are slightly distally expanded, and are shorter than in more anterior caudals. The base of the laminar transverse process shows two robust and short buttresses that are separated from each other by means of a wide but shallow blind fossa. These buttresses are delimited by anterior and posterior deep and wide pneumatic fossae. The anterior fossa is anteroposteriorly elongate and is bounded posteriorly, anteriorly, and ventrally by a rounded mound-like lamina of bone. The posterior fossa is smaller than the anterior one but is notably deeper and subcircular in contour. The prezygapophyses are anteromedially oriented; they are notably expanded transversely and fan-shaped. The articular surface of the prezygapophyses is not discernible at all in any anterior mid-caudal vertebrae, a condition not known in any other theropod. Laterally, the prezygapophysis shows a blunt and thick process. As in the case of the anterior caudal vertebrae, the postzygapophyses are notably small.

The centra are longer and lower than in more anterior caudals. Furthermore, the centra are much more transversely compressed, especially at mid-length. The ventral surface is narrower and sharper than more anterior vertebrae. Notably these, as well as more posterior mid-caudal vertebrae, lack any sign of pleurocoels or fossae, but show a camerate centrum. It is worth mentioning that a vertebral centrum has an attached crocodyliform tooth that partially penetrates it.

Five articulated and nearly complete posterior mid-caudal vertebrae are preserved (Fig. 22). They are similar in gross morphology to the other described caudals. The anteriormost element of the series retains a robust and anterodorsally facing prezygapophysis. The prezygapophyseal-transverse process lamina is reduced when compared with more anterior caudals. The buttresses below the transverse process are nearly absent, and the fossae delimited by these elements are also reduced, but an anterior small fossa is retained. The transverse processes are notably short and paddle-shaped, having a notable expansion on the posterior margin. They are slightly ventrally oriented. The fossa shared by the base of the neural arch and the transverse process is subtle to nearly absent.

The centrum has a pair of flat surfaces located on its posterodorsal corner, a trait that is present in all other mid-posterior caudals. This surface is not known in any other theropod described to the date. Because the vertebrae are articulated it can be observed that this surface lacks any contact with other osseous structures.

The remaining posterior mid-caudal vertebrae are very similar to that described above (Figs. 22-23). They show even more reduced fossae and buttresses at the base of the transverse process, that disappear in the most posterior element preserved. The transverse processes are slightly more ventrally oriented than in the anterior vertebrae, and, in the case of the last three preserved vertebrae, this process is notably shortened. The distal end of these processes is notably expanded on its anterior and posterior margins. The neural spines are notably dorsally concave and saddle-shaped in contour. The posterior dorsal margin of the neural spines shows a well-developed but blunt process that is posteriorly oriented. The anterior dorsal corner of the neural spine shows a notch. It is possible that both processes were in contact by some kind of soft tissue.

The prezygapophyses are notably different in the last three preserved vertebral elements. They are notably elongate and are not dorsally projected as in more anterior vertebrae. The prezygapophyses show a well-developed and suboval articular surface, that contact with the small postzygapophyses. The prezygapophyses show a well-developed, thick and finger-like anteriorly pointed process that is not present in other vertebrae. The elongation of the prezygapophyses results in a remarkably expanded and elongate prespinal fossa. In all available vertebrae there is a subtle prezygopostzygapophyseal lamina.

In ventral view, in all available posterior mid-caudal vertebrae there is no longitudinal keel, groove or flattened surface. The centra are transversely narrower than anterior ones. In the case of the latter two preserved elements the centrum is notably low and wide, being subequal in width and height.

There are five preserved haemal arches. Three of them belong to anterior vertebrae, and the remaining two come from posterior mid-caudal vertebrae. All haemal arches are relatively elongate and lack a deep posterior curvature. They show a closed haemal canal.

The proximal haemal arches (Fig. 25) are very long and slender. The proximal articular surface is saddle shaped and transversely expanded. The anterior processes are laminar, moderately extended

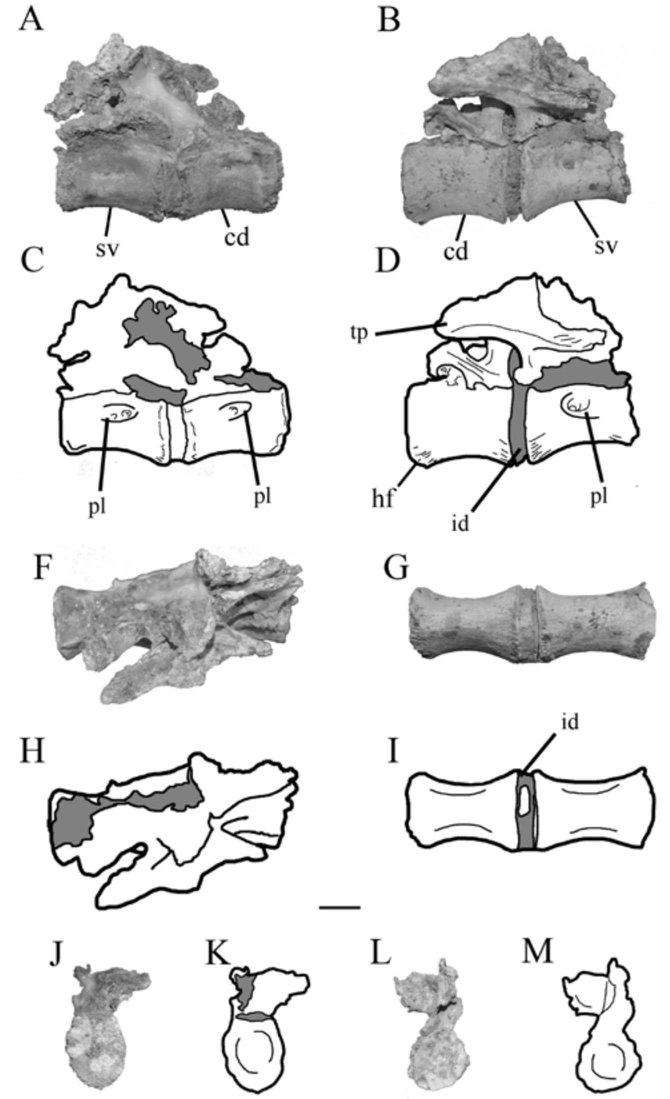

FIGURE 17. *Aoniraptor libertatem* (holotype). Last sacral and first caudal vertebrae in: **A, C,** left lateral; **B, D,** right lateral; **F, H,** dorsal; **G, I,** ventral; **J, K,** posterior; and **L, M,** anterior views. **Abbreviations**: **cd**, first caudal vertebra; **hf**, haemal facet; **id**, possible intervertebral disc; **pl**, pleurocoel; **sv**, last sacral vertebra; **tp**, transverse process. Scale bar: 3 cm.

anteriorly and extend to the ventral level of the haemal canal. The posterior processes are thicker than the anterior ones, and their proximal margins are more clearly separated from the proximal end of the haemal arch. They are notably extended ventrally and distally join each other at approximately half of the haemal arch. The haemal canal is ovoid in contour, with a main dorsoventral axis that becomes narrower distally. In posterior view, the base of the haemal canal is strongly pneumatized. In the anteriormost preserved haemal arch there is a distinct and deep pneumatic foramen that is located immediately below the opening of the canal. In the other preserved proximal haemal arch, this fossa is shallower and smaller. In anterior view the base of the haemal canal shows a small blind concavity of subtriangular contour.

The blade of the haemal arches is strap like, and notably transversely compressed. They are anteroposteriorly narrow and show a slight posterior curvature that is even more evident toward the distal end. The anterior margin is surrounded by two longitudinal and subparallel grooves.

The posterior mid-caudal neural arches (Fig. 26) are very similar to the anterior ones. However, they differ in that the anterior process is proximally located, reaching the level of the proximal articular surface of the haemal arch, and in that the posterior processes are more prominent. The proximal end lacks pneumatic features, as also occurs

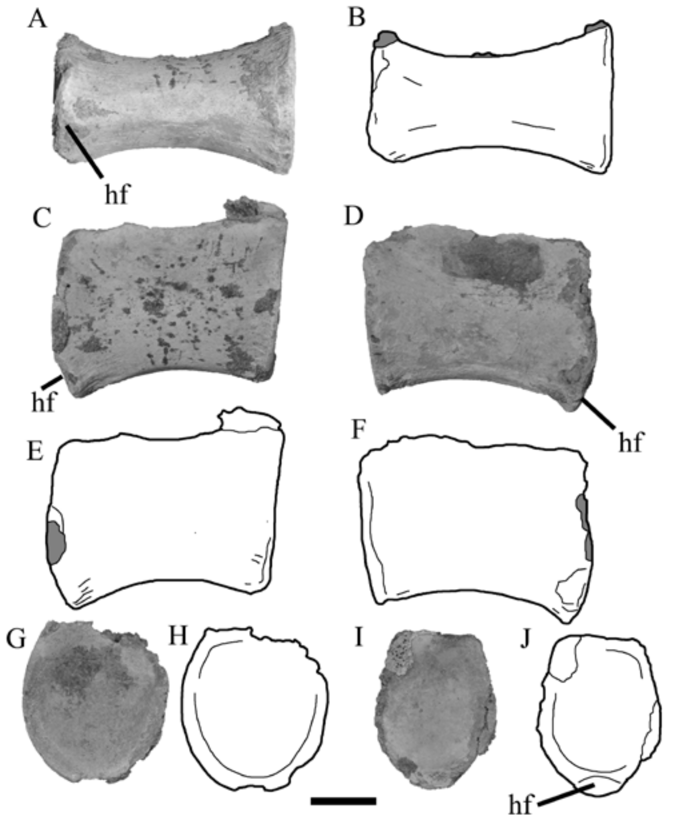

FIGURE 18. *Aoniraptor libertatem* (holotype). Third caudal vertebral centrum in: **A, B,** ventral; **C, E,** right lateral; **D, F,** left lateral; **G, H,** anterior; and **I, J,** posterior views. **Abbreviations**: **hf**, haemal facet. Scale bar: 2 cm.

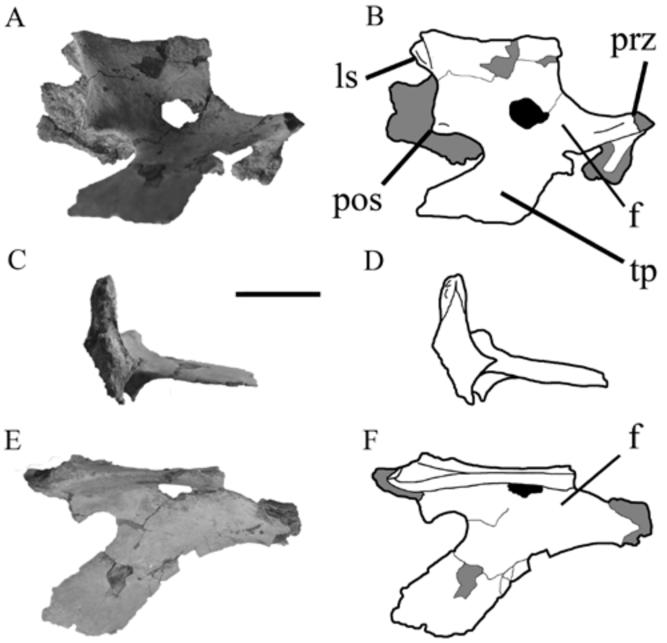

FIGURE 19. *Aoniraptor libertatem* (holotype). Neural arch of anterior caudal vertebra in **A, B,** right lateral; **C, D,** posterior; and **E, F,** dorsal views. **Abbreviations**: **f**, fossa; **ls**, ligamental scar; **pos**, postzygapophysis; **prz**, prezygapophysis; **tp**, transverse process. Scale bar: 2 cm.

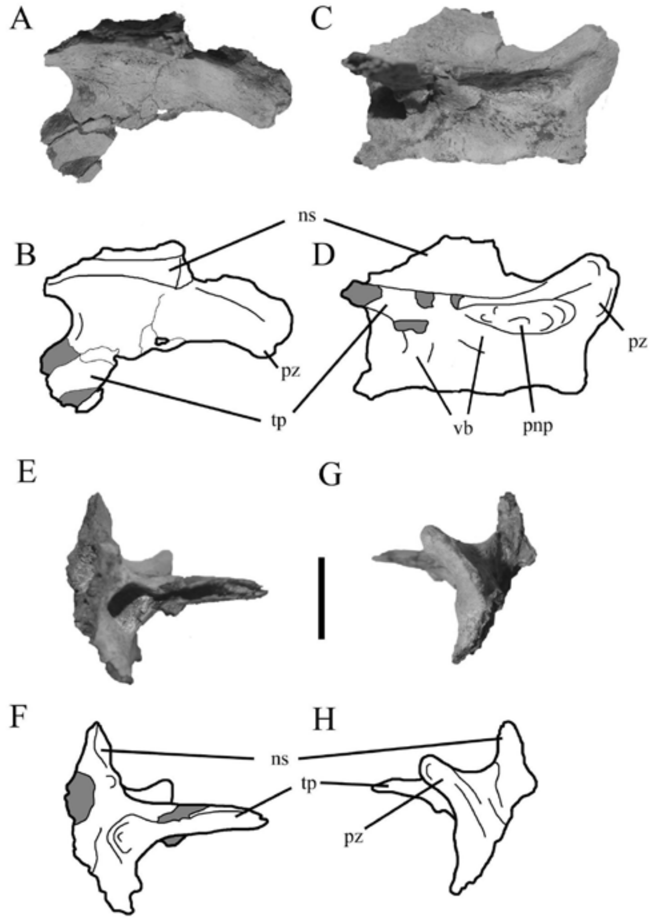

FIGURE 20. *Aoniraptor libertatem* (holotype). Neural arch of anterior mid-caudal vertebra in **A, B,** dorsal; **C, D,** right lateral; **E, F,** posterior; and **G, H,** anterior views. **Abbreviations**: **ns**, neural spine; **pnp**, pneumatic excavation; **pz**, prezygapophysis; **tp**, transverse process; **vb**, ventral buttresses. Scale bar: 3 cm.

in posterior mid-caudal vertebrae. The posterior process is laminar and very well developed. They show a subtriangular contour when viewed from the sides, having a posteriorly located apex. The blade of these haemals is more posteriorly curved than in the most anterior haemal arches.

Discussion and comparisons: In spite of its incomplete nature, *Aoniraptor* shows a large number of traits that allow recognition of its phylogenetic affinities. In *Aoniraptor* the last sacral vertebra and first anterior caudal show large pleurocoels on the sides of the centra, a feature distributed in a handful of theropod groups, namely Carcharodontosauridae (i.e., *Carcharodontosaurus*; South American members of this clade show only shallow blind fossae; Méndez et al., 2012), Therizinosauria; Oviraptorosauria, Tyrannosauridae, *Torvosaurus* and Megaraptora (Stromer, 1931, 1933; Barsbold et al., 1990; Britt, 1993; Brochu, 2002; Calvo et al., 2004; Novas et al., 2005; 2008; 2013; Benson et al., 2011; Brusatte et al., 2012). Among these clades, only the Megaraptora (e.g. *Aerosteon, Megaraptor*; Mendez et al., 2012; Martinelli et al., 2013) show a set of septa dividing the pleurofossae. In members of the Oviraptoridae and Therizinosauria, the pleurofossae are single and extend distally in the caudal series, the neural spines are dorsoventrally taller and the middle to posterior chevrons show a well-developed boat-shaped contour (Barsbold et al., 1990; Xu et al., 2007).

In the same way, *Aoniraptor* resembles megaraptorans (e.g., *Aerosteon, Megaraptor*; Sereno et al., 2009; Porfiri et al., 2014) in the internal structure of its vertebrae (Martinelli et al., 2013). These have a camerate internal structure consisting of a large number of small chambers (Britt, 1993). This condition is present also in some ceratosaurs (Carrano and Sampson, 2008) and some allosauroids (e.g. *Acrocanthosaurus*, *Neovenator*; Harris, 1998; Brusatte et al., 2008). Further, *Aoniraptor* shows a megaraptorid synapomorphy that is the presence of ventral buttresses on each transverse process of the most anterior elements, that delimit a pair of pneumatic fossae (Benson et al., 2010; Novas et al., 2013). In addition, *Aoniraptor* shows notably elongate and subrectangular-shaped neural spines on mid-caudal vertebrae, a derived feature shared by most coelurosaurs (Rauhut, 2003), and absent in allosauroids and abelisaurids.

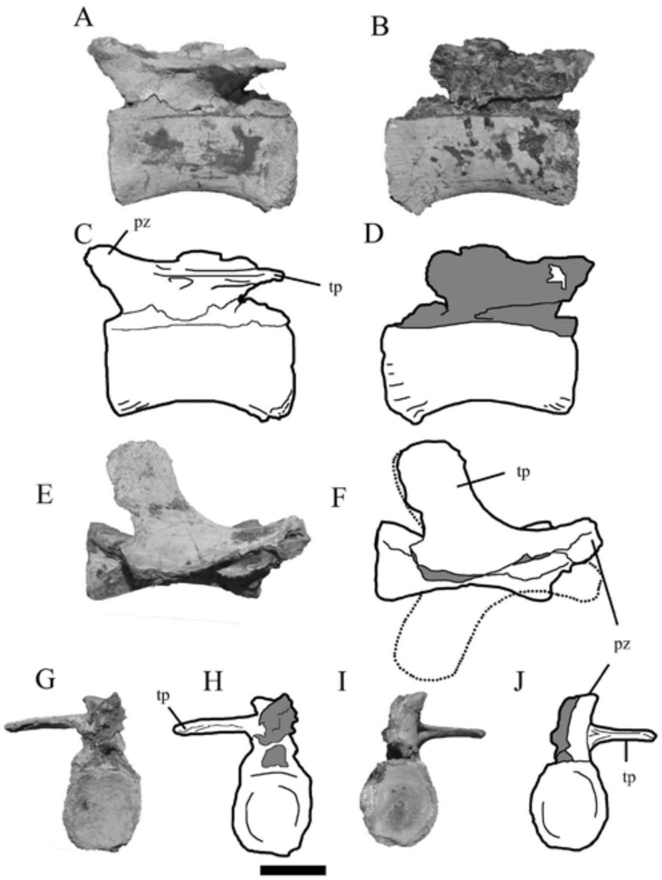

FIGURE 21. *Aoniraptor libertatem* (holotype). Anterior mid-caudal vertebra in **A, C,** left lateral; **B, D,** right lateral; **E, F,** dorsal; **G, H,** posterior; and **I, J,** anterior views. **Abbreviations**: **pz**, prezygapophysis; **tp**, transverse process. Scale bar: 3 cm.

In the present contribution we recognize a set of anatomical features that may help to elucidate the phylogenetic position of *Aoniraptor libertatem*. In this regard, *Aoniraptor* shows several traits that resemble caudal vertebrae of tyrannosaurid theropods (Fig. 27). For example, in *Aoniraptor* the neural spines of mid-caudal vertebrae are strongly saddle-shaped in lateral view. This condition is present in *Tyrannosaurus* and *Alioramus* (Brochu, 2003; Brusatte et al., 2012). This differs from *Ceratosaurus* (Madsen and Welles, 2000) and basal tetanurans such as *Allosaurus* and *Torvosaurus* (Madsen, 1976; Britt, 1991), in which the neural spine is notably elongate and has an anterior spike-like process (Rauhut, 2003). In *Aoniraptor libertatem*, the mid-caudals retain well-developed laminae along the anterior and posterior margins of the neural spines, indicating the anchoring of large interspinous ligaments. Furthermore, the top of the neural spines show small anterior and posterior processes. These conditions are present in some derived tyrannosauroids such as *Tarbosaurus, Tyrannosaurus* and *Alioramus* (Brochu, 2003; Brusatte et al., 2010), and we are unaware of its presence in any other theropod clade. In addition, *Aoniraptor* shows very large and notably elongate and distally spreading prezygapophyses on mid-caudal vertebrae. This combination of features results in a prespinal fossa that is notably wide, deep, and elongate. This derived trait is absent in most theropods, with the exception of derived tyrannosauroids such as *Alioramus* and *Tyrannosaurus* (Brusatte et al., 2012). Further, in *Aoniraptor* the mid-caudals show a thick spinoprezygapophyseal lamina present along the dorsal margin of the prezygapophyses, being continuous with a finger-like non-articular anterior process that curves ventrally in the prezygapophysis. This combination of features is also shared by *Tyrannosaurus, Albertosaurus, Tarbosaurus,* and *Alioramus* (Brusatte et al., 2012). In other theropods these well-developed laminae

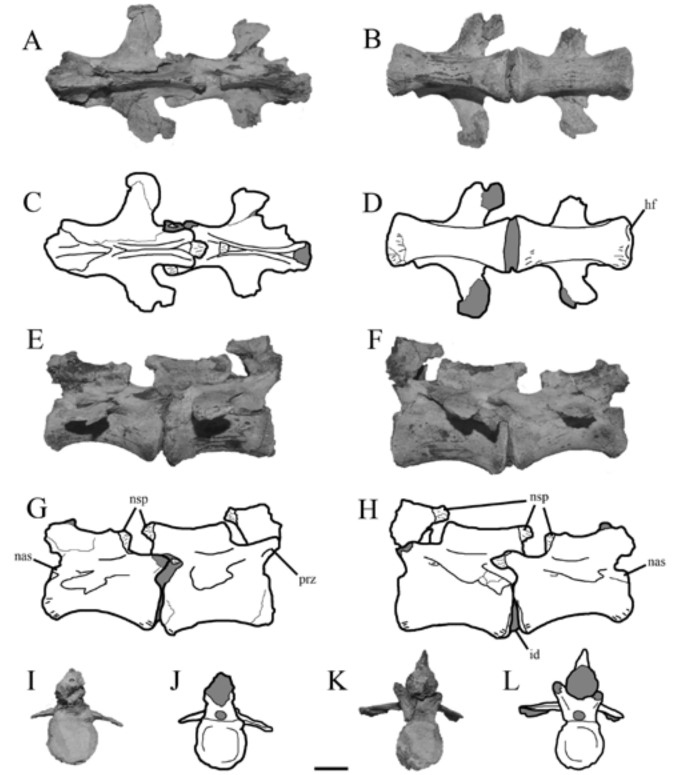

FIGURE 22. *Aoniraptor libertatem* (holotype). Posterior mid-caudal vertebrae in **A, C,** dorsal; **B, D,** ventral; **E, G,** right lateral; **F, H,** left lateral; **I, J,** posterior; and **K, L,** anterior views. **Abbreviations**: **hf**, haemal facet; **id**, intervertebral disc; **nas**, non-articular flat surface; **nsp**, additional anterior and posterior processes of neural spines. Scale bar: 2 cm.

and non-articular process are feebly developed or absent. The presence of a prezygopostzygapophyseal lamina on mid-caudal vertebrae was previously indicated by Brusatte et al. (2010) as a shared derived character of advanced tyrannosauroids.

A conspicuous feature of *Aoniraptor* is the presence of large ovoid pockets located on the posteroventral side of the haemal canal. This condition has been previously reported in the derived tyrannosauroid *Alioramus* by Brusatte et al. (2012), and is also probably present in *Megaraptor* (MCF-PVPH 79). This pocket penetrates the bone and very probably constitutes a pneumatic feature, as expressed by Brusatte et al. (2010). It is worth mentioning that the presence of such a structure may imply that part of the respiratory system, probably the abdominal air sacs, invaded the anterior and mid-portion of the tail in these taxa, a condition unusual among non-avian dinosaurs.

In sum, *Aoniraptor libertatem* has a combination of features that indicates it belongs to Megaraptora, and several traits that indicate it may be well-nested among derived tyrannosauroids. In spite of that, *Aoniraptor* shows several traits that distinguish it from megaraptorids such as *Megaraptor* and *Aerosteon*. First, *Aoniraptor* lacks the ventral, thick longitudinal keel along caudal vertebrae present in these taxa, a feature considered as typical of megaraptorids by Méndez et al. (2012). Further, *Aoniraptor* differs in the different proportions of the centrum, having very elongate anterior caudal centra, whereas in *Aerosteon* and *Megaraptor* proximal caudal vertebrae are nearly as long as tall (Calvo et al., 2004; Sereno et al., 2008). In addition, in *Aoniraptor* the vertebral centrum of all caudals, with the exception of the first one, lacks any sign of pleurocoels or deep penumatic fossae. This differs from the extensive pneumatization seen in megaraptorids such as *Aerosteon* and *Megaraptor*, in which pleurocoels are present in all available anterior and mid-caudal vertebrae (Calvo et al., 2004; Sereno et al., 2008; Méndez et al., 2012; Martinelli et al., 2013). Furthermore, in *Aoniraptor* the buttresses located below the transverse processes of anterior caudals are not so thick and prominent as in *Megaraptor* and *Orkoraptor* (Calvo et al., 2004; Novas et al., 2008).

As indicated above, *Aoniraptor* shares a large number of features with derived tyrannosauroids such as *Alioramus, Tarbosaurus,* and *Tyrannosaurus*. However, it has conspicuous features to differentiate it, including the presence of pleurocoels on its first caudal vertebra, and the straight and long haemal arches, contrasting with the boat-shaped condition of tyrannosauroids (Rauhut, 2003). Aditionally, the elongate proportions of the centrum in *Aoniraptor* are very different from the shorter and more robust elements of tyrannosauroids.

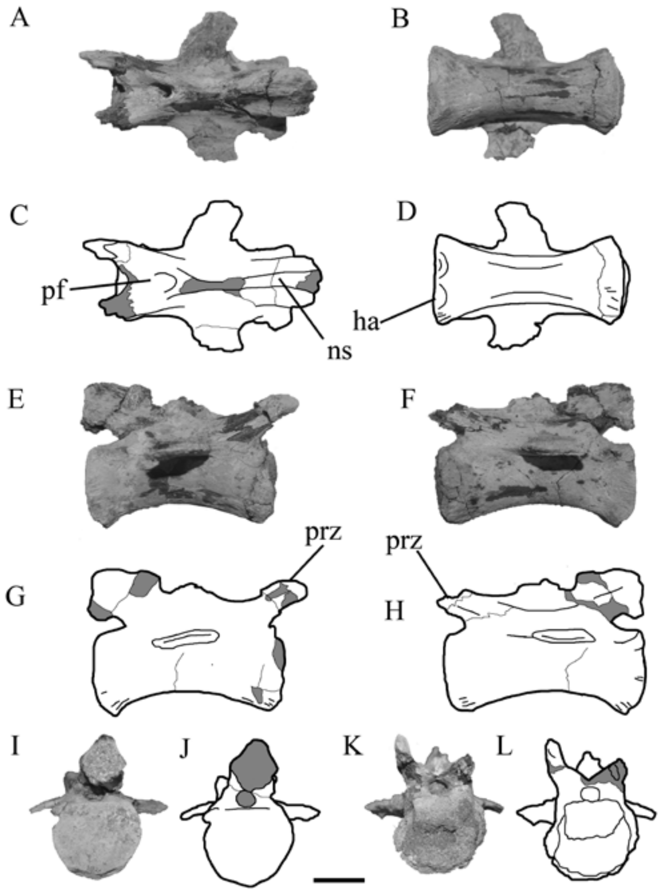

FIGURE 23. *Aoniraptor libertatem* (holotype). Posterior caudal vertebra in **A, B,** right lateral; **C, D,** left lateral; **E, F,** dorsal; **G, H,** ventral; **I, J,** posterior; and **K, L,** anterior views. **Abbreviations**: **ns**, neural spine; **pz**, prezygapophysis; **tp**, transverse process. Scale bar: 3 cm.

In conclusion, based on the aforementioned combination of characters, *Aoniraptor libertatem* is regarded as a non-megaraptorid megaraptoran tyrannosauroid (*sensu* Novas et al., 2013; Porfiri et al., 2014), a hypothesis that should be tested by a numerical phylogenetical analysis.

Comments on isolated remains previously referred to as Megaraptoridae: Based on the recognition of some anatomical features, especially the presence of pleurocoels, several authors sustained the presence of megaraptorids in different South American localities based on isolated caudal vertebral centra. For example, Martinelli et al. (2013) and Méndez et al. (2012) sustained the presence of megaraptorids in Brazil on the basis of isolated caudal elements. Méndez et al. (2012) described an isolated centrum from the Bauru Group (Maastrichtian; Late Cretaceous). As pointed out by Méndez and collaborators, this element differs from megaraptorids such as *Aerosteon* and *Megaraptor* in that the ventral surface lacks a middle longitudinal keel as well as in its more elongate proportions. These features, together with a greatly rugose anterior articular surface, suggest that this vertebra is likely a sacral vertebrae. In the same line, Martinelli et al. (2013) described an isolated centrum from the Bauru Group (Campanian; Late Cretaceous) as belonging to Megaraptoridae. Although the centrum was identified as a caudal vertebra, the rugose texture of its anterior articular surface, as well as the anteroposteriorly expanded transverse processes, indicate that this may represent a posterior sacral vertebra.

As in the case of *Aoniraptor* both elements show pleurocoels and notably elongate and dorsoventrally low centra. This contrasts

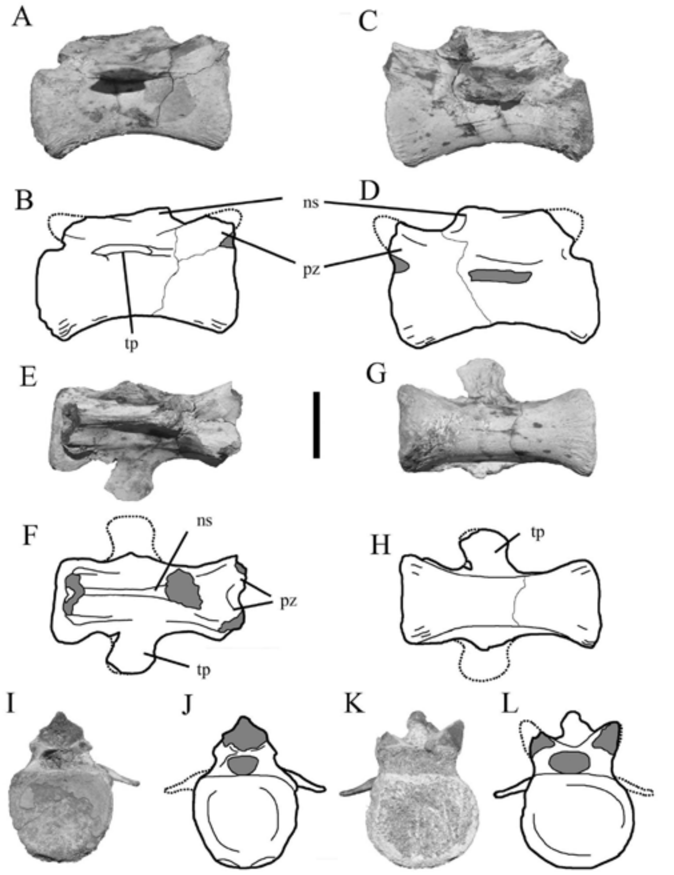

FIGURE 24. *Aoniraptor libertatem* (holotype). Posterior caudal vertebra in **A, C,** dorsal; **B, D,** ventral; **E, G,** right lateral; **F, H,** left lateral; **I,J,** posterior; and **K, L,** anterior views. **Abbreviations**: **ha**, haemal arch; **ns**, neural spine; **pf**, prespinal fossa; **prz**, prezygapophysis. Scale bar: 3 cm.

with *Megaraptor*, which shows notably robust and dorsoventrally tall sacral vertebral centra (Porfiri et al., 2014). In this aspect, the elements reported by Méndez et al. (2012) and Martinelli et al. (2013) may be identified as belonging to a form more nearly related to *Aoniraptor* than to *Megaraptor*, but only more complete elements from Brazil could clarify this.

***Aoniraptor libertatem* and comments on the phylogenetic position of some African theropods:** Resemblances between the tail anatomy of *Aoniraptor* and the Early Cretaceous African taxa *Bahariasaurus ingens* (Stromer, 1934) and *Deltadromeus agilis* (Sereno et al., 1996) are noteworthy. Stromer (1934, 1935) originally described a large number of scattered specimens as referable to *Bahariasaurus,* coming from different localities. Because the specimens were found in different localities and stratigraphic units, the referral to a single taxon should be regarded as problematic. In this way, based on the work of Sereno et al. (1996), the holotype and only known specimen of *Bahariasaurus* only includes two caudal vertebrae (determined as dorsals by Stromer in the original description, but the absence of parapophyses indicates that may be better interpreted as caudal elements), a neural arch, three sacral centra, pubes and a proximal ischium (all illustrated and described by Stromer, 1934, but lost during the Second World War). The remaining specimens were referred by Sereno et al. (1996) to *Deltadromeus*, including pubes, femur, fibula, and proximal tibia (Stromer, 1922, pl. 2, figs. 4,15; pl. 3, figs. 3,5,6). In spite of noticing minor differences between both taxa, Sereno et al. (1996) did not deny the close similarities between the materials of *Deltadromeus* and *Bahariasaurus*, as originally pointed out by Stromer (1934, 1935).

The then poor knowledge of theropod Gondwanan faunas, together with the incomplete and peculiar nature of the available specimens of *Bahariasaurus* and *Deltadromeus*, as well as the loss of the former's holotype during the Second World War, conspired against recognizing the phylogenetic affinities of both taxa. Because of these, *Bahariasaurus* was considered as Ceratosauria (Bonaparte, 1991), as Carnosauria of uncertain affiliation (Molnar et al., 1990), as Allosauria (Paul, 1984; Rauhut, 1995), and as possible Tyrannosauridae (Chure, 2000). On the other hand, *Deltadromeus* was proposed as having coelurosaurian (Sereno et al., 1996; Rauhut, 2003) or ceratosaurian (Wilson et al., 2003; Carrano and Sampson, 2008) affinities. In spite of these opinions, we were not able to find clear derived ceratosaurian or allosauroid features shared with *Bahariasaurus* or *Deltadromeus*.

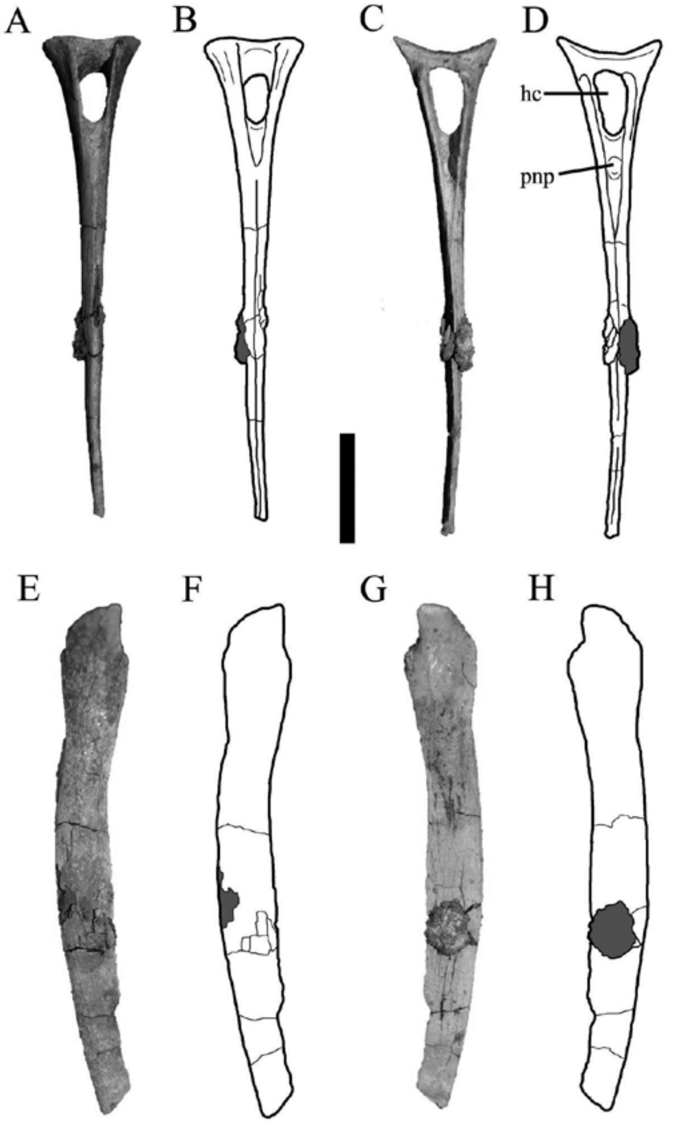

FIGURE 25. *Aoniraptor libertatem* (holotype). Anterior haemal arch in **A, B,** anterior; **C, D,** posterior; **E, F,** left lateral; **G, H,** right lateral views. **Abbreviations**: **hc**, haemal canal; **pnp**, pneumatic pocket. Scale bar: 3 cm.

In the case of *Bahariasaurus*, the caudal anatomy is highly reminiscent of *Aoniraptor* in several features. For example, elongate anterior caudal centra, anterior caudals with buttresses at the base of neural arch, anterior caudals (and also sacral vertebrae) with deep pneumatic fossae on the sides of its centrum, whereas these are absent in more posterior caudals, subrectangular elongate neural spines with deep laminae indicating the anchoring of interspinal ligaments, deep and wide prespinal fossa, and a well-developed lamina contacting the prezygapophyses with the transverse processes (see illustrations and description in Stromer, 1934) are derived features shared by both taxa.

The same seems to be true also for *Deltadromeus*. Available illustrations of the original description of the specimen (Sereno et al., 1996) indicate that this taxon shares with *Aoniraptor* subrectangular, elongate and robust rectangular neural spines on anterior mid-caudal

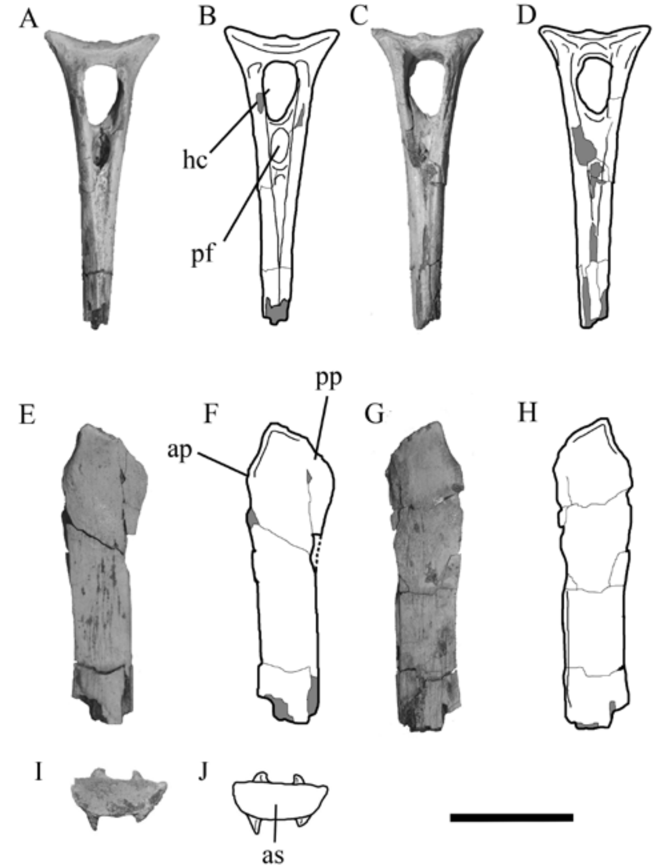

FIGURE 26. *Aoniraptor libertatem* (holotype). Mid-haemal arch in **A, B,** posterior; **C, D,** anterior; **E, F,** left lateral; **G, H,** right lateral; and **I, J,** proximal views. **Abbreviations**: **ap**, anterior process; **as**, proximal articular surface; **hc**, haemal canal; **pf**, pneumatic pocket; **pp**, posterior process. Scale bar: 3 cm.

vertebrae (considered as autapomorphic for this taxon by Sereno and collaborators in the original description), strong ligamental scars in anterior neural spines, presence of a prezygopostzygapophyseal lamina on mid-caudal vertebrae, anterior mid-caudals having a fossa in the area of contact between the neural arch and the transverse processes, and thick spinoprezygapophyseal laminae. This latter feature is absent in remaining theropods, including the tyrannosauroids *Alioramus* and *Tyrannosaurus*, and appears to be a character exclusively shared by *Deltadromeus* and *Aoniraptor*.

Wilson et al. (2003) cited the reduction of distal condyles of metatarsal IV in *Deltadromeus* as indicating that this genus should be included within noasaurid ceratosaurians. However, this condition is widely present in basal coelurosaurs, such as ornithomimids and tyrannosaurids, as early noted by Rauhut (2003), and is also present in the megaraptorans *Megaraptor* and *Australovenator* (Calvo et al., 2004; Hocknull et al., 2009). In this way, the presence of reduced condyles of distal metatarsal IV is an ambiguous trait uniting *Deltadromeus* with Noasauridae, and no clear synapomorphic features may include this genus among abelisauroid theropods. Based on strong anatomical similarities of vertebral elements, we consider that *Aoniraptor*, *Deltadromeus agilis,* and *Bahariasaurus ingens*, conform to a clade of non-megaraptorid megaraptoran theropods.

In spite of the strong similarities noted above, important differences between *Deltadromeus* and *Bahiasaurus,* on one hand, and megaraptorids, including *Megaraptor* and *Aerosteon*, on the other, exist. For example, the African taxa show a complex distal end of the femur having an additional anterior expansion of the medial distal condyle, a narrow and poorly expanded distal pubic boot, and a notably narrow pubic shaft. On the other hand, the megaraptorid *Australovenator* has a simpler distal end of the femur (Hocknull et al., 2009), and *Megaraptor* and *Aerosteon* have robust pubes with a notably anteroposteriorly expanded pubic boot (Benson et al., 2010). Additional distinctive features, noted solely for *Deltadromeus,* include humerus with reduced deltopectoral crest and bulbous head, and radius and ulna proximally featureless (Sereno et al., 1996). In contrast, megaraptorids such as *Megaraptor* and *Australovenator* have robust forelimbs, a humerus with flattened humeral head and large deltopectoral crest, and a proximal end of the ulna complex and with an enlarged olecranon (Agnolin et al., 2010; White et al., 2012). In this way, *Aoniraptor*, *Deltadromeus* and *Bahariasaurus* differ from megaraptorids in a large number of features, which may indicate the presence of another, still poorly known megaraptoran clade in Southern landmasses. If this hypothesis is corroborated, the name Bahariasauridae Huene, 1936 may be employed to group these taxa, highlighting the distinctiveness of its members.

Finally, Apesteguía et al. (2013) reported the presence of a *Deltadromeus*-like theropod having a bulbous humeral head in the Late Cretaceous of Patagonia, which reinforces the idea that this clade was probably diverse and widespread in Gondwana. The presence of two fingers in this unpublished specimen (Apesteguía et al., 2013) adds an additional similarity between these taxa and tyrannosaurids.

MANIRAPTORA Gauthier, 1986
PARAVES Sereno, 1997
?UNENLAGIIDAE Bonaparte, 1999
Gen. et sp. indet.

Referred materials: MPCA-Pv 805/1-805/6, non-articulated, associated specimens including three caudal vertebrae (805/1-3); a distal end of a right metacarpal I (805/4); and fragmentary right pedal digit ungual II (805/5).

Description and comparisons: Two of the preserved vertebrae are likely mid-caudals (Fig. 28). These elements are anteroposteriorly long and laterally compressed, with feebly developed neural spines and transverse processes. The transverse processes are posterolaterally oriented and subtriangular in contour in dorsal view. In addition, the transverse processes are located on the posterior half of the centrum. A posteriorly positioned transverse process is present in *Buitreraptor* (Makovicky et al., 2005), *Rahonavis* (Forster et al., 1998) and *Mahakala* (Turner et al., 2011). The ventral surface of the centrum is transversely compressed, bearing a ventral longitudinal ridge. This ventral ridge is

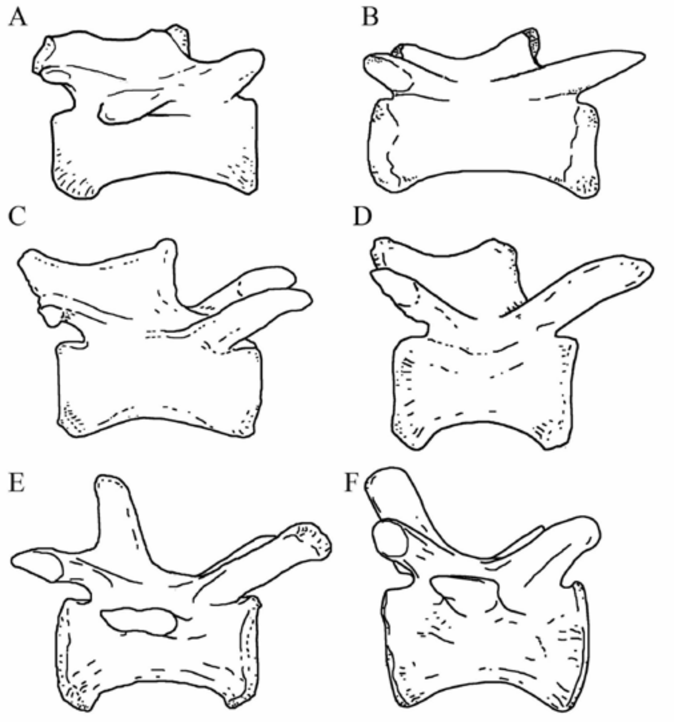

FIGURE 27. Comparissons of mid caudal vertebrae of selected theropods in right lateral view. **A,** *Aoniraptor libertatem* nov.; **B,** *Deltadromeus agilis* (redrawn from Sereno et al., 1996); **C,** *Alioramus altai* (redrawn from Brusatte et al., 2012); **D,** *Tyrannosaurus rex* (redrawn from Brochu, 2003); **E,** *Ceratosaurus nasicornis* (redrawn from Madsen and Welles, 2000); and **F,** *Allosaurus fragilis* (redrawn from Madsen, 1976). Not to scale.

also present in *Buitreraptor* (Makovicky et al., 2005) and *Rahonavis* (Forster, *et al.* 1998) mid caudals, but not in *Deinonychus* (Ostrom, 1996) and *Velociraptor* (Norell and Makovicky, 1997).

Another caudal vertebra is likely a posterior caudal (Fig. 29). It is anteroposteriorly long and dorsoventrally low, with concave lateral surfaces when viewed ventrally. As in distal caudals of most paravians (e.g., *Buitreraptor, Deinonychus, Rahonavis, Mahakala* and *Microraptor* (Ostrom, 1996; Makovicky et al., 2005; Hwang et al., 2002; Turner et al., 2011) the transverse processes are represented by smooth and long lateral ridges (Ostrom, 1969). The articular surfaces are rounded and slightly platycoelous, as in other paravians such as *Deinonychus* (Ostrom, 1969). Ventrally, the centrum presents two longitudinal ridges that define a medial longitudinal groove. This feature is common among paravians, such as *Deinonychus* (Ostrom, 1996) and *Buitreraptor* (Gianechini and Apestguía, 2010). The distal vertebrae lack any pneumatic features, as in other paravians (Ostrom, 1969).

A right metacarpal one is preserved, but lacks most of its proximal end (Fig. 30). The metacarpal exhibits some interesting features, including a stout and notably asymmetric shaft, which contrasts with most paravians (e.g., *Deinonychus*, *Velociraptor*; Ostrom, 1969; Norell and Makovicky, 1999), which have slightly and poorly asymmetric shafts. The proximal end possesses a sub-triangular cross-section that results in three different surfaces (lateral, dorsomedial and ventral) that constitute the main body of the metacarpal, a widespread condition among theropods. The metacarpal has a laterodorsal ridge that originates on the dorsal margin of the lateral condyle and extends proximally probably until the (not preserved) proximodorsal end of the bone. The laterodorsal ridge forms a smooth edge that probably overlapped metacarpal II laterally. A laterodorsal ridge is present in *Buitreraptor*, albeit less developed, whereas it is absent in *Deinonychus* or *Velociraptor* (Ostrom, 1969; Norell and Makovicky, 1999). The distal end bears well-developed distal condyles separated by a deep groove, thus this element is strongly ginglymoid as in other paravians (e.g., *Velociraptor*; Norell and Makovicky, 1999). In distal view the condyles diverge ventrally, contrasting with other paravian theropods such as *Deinonychus* or *Buitreraptor* (Ostrom, 1969; Makovicky et al., 2005) in which both condyles are subparallel to each other. This divergence is due to the ventral portion of the medial condyle, which is strongly flaring medially. The medial condyle is stouter and more posterodorsally positioned than the lateral one. In medial view, there is a strong ventral rim that contacts the trochlea of the medial condyle and projects proximally along the medioventral surface of the bone, resulting in a continuous flange of bone, not present in other theropods. In distal view the lateral condyle has a small depression on its laterodorsal portion that probably served for articulation with the metacarpal II. The lateral condyle lacks any trace of a ligamental pit, whereas the medial condyle bears a small, albeit well-defined ligamental pit on the ventral portion of the condyle, a condition shared with *Buiteraptor*. Dorsally, the two condyles are united by a transverse ridge of bone.

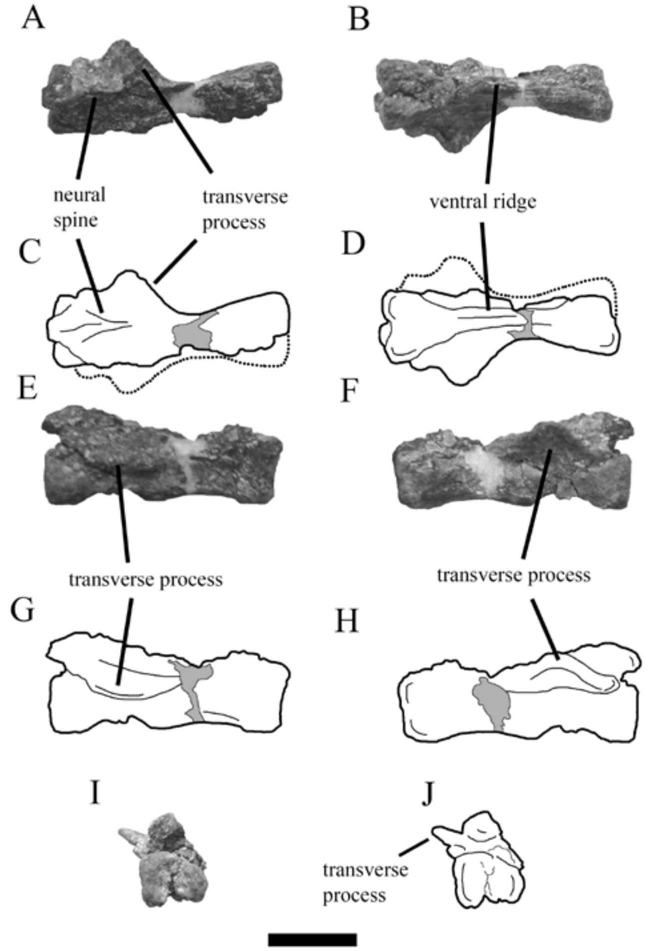

FIGURE 28. Mid-caudal vertebra of ?Unenlagiidae indet. in: **A, C,** dorsal view; **B, D,** ventral view; **E, H,** lateral view; **I, J,** anterior view; **K, L,** posterior view. Scale bar: 1 cm.

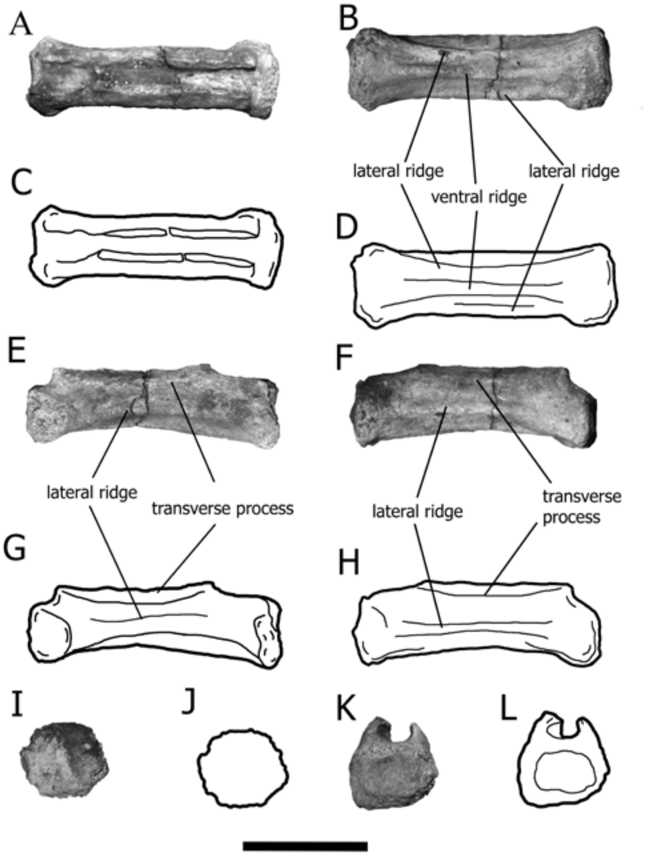

FIGURE 29. Posterior caudal vertebra of ?Unenlagiidae indet. in: **A, C,** dorsal view; **B, D,** ventral ridge; **E, H,** lateral view; **I, J,** posterior view. Scale bar: 1 cm.

A right pedal ungual phalanx of digit II was found (Fig. 31). It is well preserved, missing only the distal tip. As in most theropods, the claw is laterally compressed and ventrally curved. The proximal articular surface is large and ovoid, with a median keel separating the two articular concavities, as is typical in deinonychosaurian sickle-claws (Werner and Rauhut, 1995). On the proximodorsal corner of the claw, there is a well-developed, proximally projected process, which is continuous with the dorsal margin of the blade. This morphology resembles the pedal unguals of paravians such as *Deinonychus* and *Buitreraptor* (Ostrom, 1969; Senter, 2007). As in these taxa, the medial articular concavity is larger than the lateral one, indicating that this element pertains to the right pes. A well-developed flexor tubercle projects ventral to the proximal articular surface. As in paravians such as *Deinonychus* and *Buitreraptor*, the flexor tubercle is placed immediately distal to the articular surface (Ostrom, 1969). The ventral surface of the ungual is represented by a ventromedial sharp ridge that runs along the entire ventral surface of the claw. This feature is

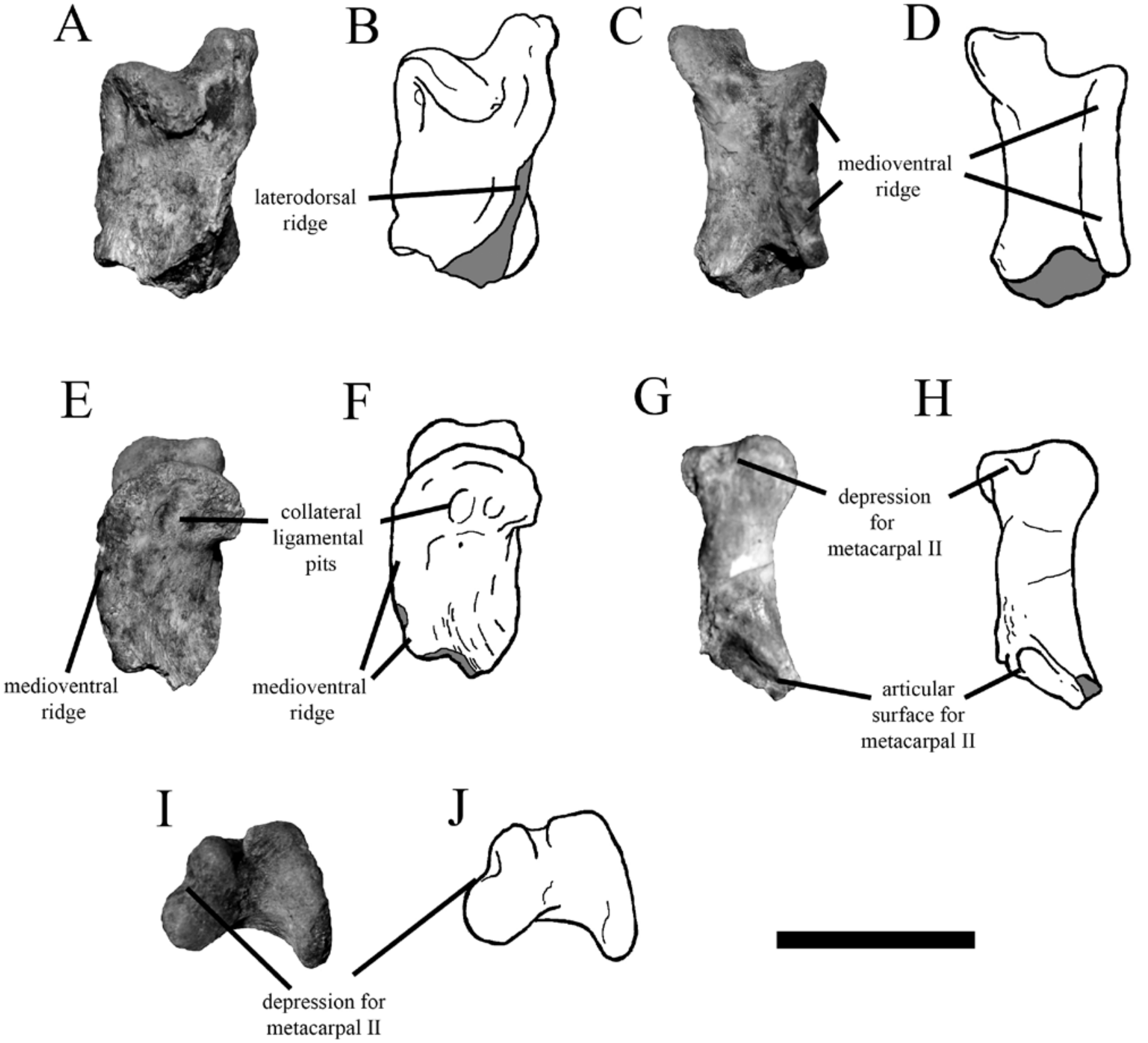

FIGURE 30. Right metacarpal one of ?Unenlagiidae indet. in: **A, B,** dorsal view; **C, D,** ventral view; **E, F,** lateral view; **G, H,** medial view; **I, J,** distal view. Scale bar: 1 cm.

present in other paravians, for example *Deinonychus, Velociraptor* and *Buitreraptor* (Ostrom, 1969; Norell and Makovicky, 1999; Makovicky et al., 2005). The lateral and medial sides show shallow longitudinal grooves; the lateral one is placed in a higher position than the medial one, as in other paravians (Kirkland et al., 1993; Rauhut and Werner, 1995).

Discussion: Although fragmentary, the recovered materials bear some features that are worth discussion. The specimens show a combination of characters shared with other paravians (e.g., transverse processes of the distal caudals represented by slight and long ridges; rounded and slightly platycoelous articular faces on caudal vertebrae; two longitudinal grooves separated by a ridge in the ventral surface of caudal centra; proximal end of metacarpal I with a triradiate contour; sickle-claw ungual II, having well-developed flexor tubercle, a ventromedialy located sharp edge, and asymmetrical longitudinal grooves on medial and lateral sides of the blade) that are indicative of the paravian affinities of the specimens.

The position of MPCA-Pv 805/1- 805/6 within paravians is more difficult to assess due to the fragmentary and isolated nature of the specimens; however, some features might indicate unenlagiid affinities. In this regard, the vertebral centra show a series of lateral grooves and ridges, that, together with the presence of a ventral ridge on the mid-caudal centra, are traits that are also recorded in *Buitreraptor* (Makovicky et al., 2005), *Mahakala* (Turner et al. 2011) and *Rahonavis* (Forster, et al. 1998), and are absent in troodontids and dromaeosaurids (e.g., *Gobivenator, Deinonychus, Velociraptor, Linheraptor*; Osborn, 1924; Ostrom, 1969; Xu et al., 2010; Tsuihiji et al., 2014) in which the lateral surface is smooth, and the ventral surface shows a longitudinal medial groove. On the other hand, the preserved metacarpal bears a well-developed laterodorsal ridge that is not present in troodontids or derived dromaeosaurids (e.g., *Sinornithoides, Deinonychus;* Ostrom, 1969; Currie and Dong, 2001) but is present in a yet undescribed *Buitreraptor* specimen (Agnolin and Novas, 2013) and might turn out to be an unenlagiid synapomorphy. Based on the above mentioned traits, geographic and temporal location, MPCA-Pv 805/1-805/6 is likely to represent an unenlagiid theropod, but this should be considered

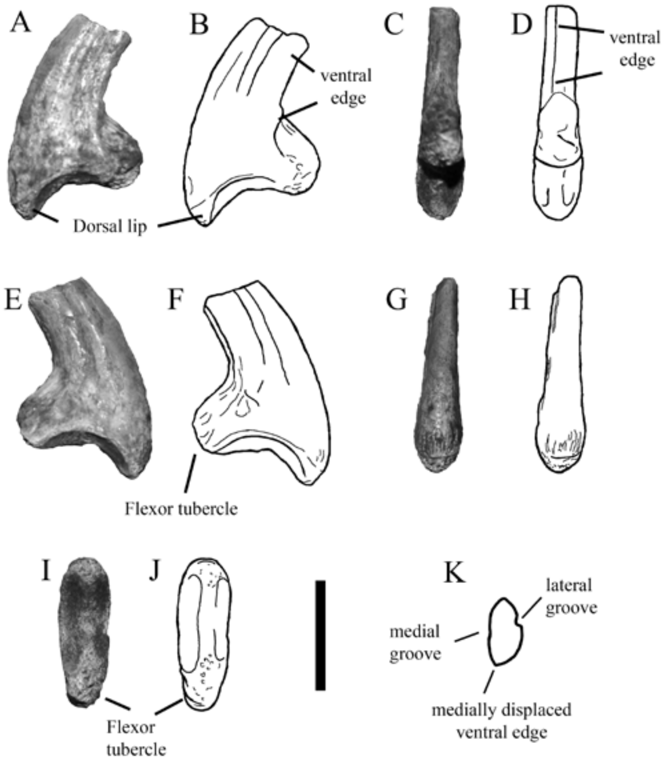

FIGURE 31. Right pedal ungual phalanx II of ?Unenlagiidae indet. in: **A, B,** medial view; **C, D,** ventral view; **E, F,** lateral view; **G, H,** dorsal view; **I, J,** proximal view; **K,** cross-section at mid-length. Scale bar: 1 cm.

cautiously, due to the fragmentary nature of the specimens.

CONCLUSIONS

Present findings provide insights about the Upper Cretaceous theropod diversity in northwestern Patagonia. The abelisauroids here described are reminiscent of the poorly known group Noasauridae, but due to the isolated nature of these elements, a precise determination was not possible. Nevertheless, the only previously reported abelisauroids from the Huincul Formation were large-sized abelisaurids (see Canale et al., 2006). The new abelisauroid material allows us to recognize the presence of small abelisauroids together with large abelisaurids.

Among the newly collected material, large elements pertaining to two carcharodontosaurid individuals were found. A partial right foot represents a gigantic sized theropod that is comparable in size with *Mapusaurus roseae,* known from the same stratigraphic unit. Due to the incomplete nature of the specimens here described a referral to *Mapusaurus* cannot be sustained, although it cannot be dismissed as well. The new material improves the knowledge of carcharodontosaurid foot anatomy. Moreover, an isolated postorbital is the basis for recognition of the new medium-sized carcharodontosaurid *Taurovenator violantei,* which increases the diversity of the clade. This new species shows some conspicuous features such as a horn-like orbital boss and a pneumatic foramen in the ventral side of the orbital brow that are unique for this taxon and distinguish it from other carcharodontosaurids. Furthermore, it indicates the coexistence of very large and medium sized carcharodontosaurids at the same fossiliferous locality.

Here we report for the first time the presence of megaraptoran and paravian theropods from the Huincul Formation. In this regard, the new megaraptoran, namely *Aoniraptor libertatem*, constitutes the oldest member of this clade known in South America. It represents the most complete caudal remains for this group and thus sheds light on megaraptoran caudal anatomy. A large number of traits present in *Aoniraptor* are found in derived tyrannosauroid taxa and support the hypothesis that megaraptorans are members of Tyrannosauroidea (Novas et al., 2013; Porfiri et al., 2014). Further, the shared features of *Aoniraptor* with African taxa such as *Bahariasaurus* and *Deltadromeus* indicate that these three forms may constitute a still poorly known clade of derived Gondwanan tyrannosauroids.

Finally, the paravian remains show a caudal vertebral morphology with features similar to some unenlagiid taxa. However, the metacarpal shows some anatomical peculiarities that may indicate it belongs to a new, unnamed form.

The presence of at least six theropod species in a single fossiliferous locality, belonging to abelisauroids, allosauroids, tyrannosauroids, and paravians, probably represents the taxonomically richest theropod association found in Patagonia. Furthermore, it supports the idea that Patagonia is a key place (Novas et al., 2013) that provides important information for the understanding of theropod evolution in Gondwana.

ACKNOWLEDGMENTS

We thank Gabriel Lio for useful comments and support during the making of this work. We also thank the technicians Marcelo P. Isasi, Carlos H. Alsina, Ricardo Stoll and Germán Stoll for helping with the preparation of the materials. Ariel Méndez kindly lent photographs and information on Brazilian specimens. Special thanks to Mr. Enzo Violante, who allowed field trips and paleontological investigation on his own farm. We are indebted to the comments and corrections to the manuscript made by the reviewers, A.G. Martinelli and A.H. Méndez.

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