A new ornithopod dinosaur from the Santonian of Northern Patagonia (Rincón de los Sauces, Argentina)

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ABSTRACT

In recent decades, the Argentinian ornithopod record — which includes eight species that have been described — has increased as a result of the discovery of diverse new bone remains from the Upper Cretaceous. The area near the town of Rincón de los Sauces (Neuquén Province) presents rich fossiliferous outcrops that have provided new ornithopod remains. These bones are from two units: the Plottier and Bajo de la Carpa formations. In the latter, several isolated postcranial bones and a partial articulated skeleton (MAU-Pv-CO-596) have been found. The holotype of *Mahuidacursor lipanglef* gen. et sp. nov. (MAU-Pv-CO-596) comes from the Cerro Overo site (Santonian, Upper Cretaceous). The skeleton preserves elements from the cervical and dorsal series, the pectoral girdle and the right forelimb. It corresponds to a medium-bodied ornithopod with a gracile general appearance. Histological analysis suggests that the specimen was a sexually mature but not fully grown individual. Some distinctive characters present in *Mahuidacursor*, such as the strongly bowed humeral shaft and the weakly developed deltopectoral crest, are shared with other South American basal ornithopods. A phylogenetic analysis including *Mahuidacursor* within a large ornithischian dataset was performed. The results show *Mahuidacursor* to be a basal ornithopod recovered within a polytomy along with *Notohypsilophodon* and the clade Elasmaria (*Talenkauen + Macrogryphosaurus*).

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1. Introduction

The South American record of non-hadrosaurid ornithopod dinosaurs is composed of some partial skeletons and numerous isolated remains, most of them from the Argentinian Patagonia (see tables 1—3 in Cruzado-Caballero et al., 2018). As a result, several species have been defined (i.e. *Gasparinisaura cincosaltensis* Coria and Salgado, 1996; *Notohypsilophodon comodorensis* Martínez, 1998; *Anabisetia saldiviai* Coria and Calvo, 2002; *Talenkauen santacrucensis* Novas et al., 2004; *Macrogryphosaurus gondwanicus* Calvo et al., 2007).

The phylogenetic relationships between these taxa are poorly resolved due largely to the scarcity of cranial material and the incompleteness of the specimens, limiting the presence of overlapping material. In 2007 Calvo and collaborators defined Elasmaria, the first endemic clade of non-hadrosaurid ornithopods from South America. Later, Boyd (2015) reported *Notohypsilophodon* within the clade Elasmaria but relocated this clade within Thescelosaurinae and outside Ornithopoda. More recently, Rozadilla et al. (2016) performed a new phylogenetic analysis comprising a greater number of Argentinian and Antarctic non-hadrosaurid ornithopod taxa. As a result, the location of the clade Elasmaria changed again, appearing as a member of the group Ornithopoda, and the Argentinian and Antarctic non-hadrosaurid ornithopods formed an unresolved polytomy, with *Gasparinisaura* as the sister group of the polytomy. There is some evidence that points to a large set of Gondwanan basal

ornithopods that are closely related and may be part of a common clade (i.e. Rozadilla et al., 2016; Herne et al., 2018), but up to now we are far from providing a robust phylogenetic framework. This can only be resolved with the contribution of new fossil discoveries.

Here we describe a new ornithopod with clear affinities to certain other ornithopod taxa previously related to the clade Elasmaria. The new specimen was found near the town of Rincón de los Sauces (Neuquén Province, Argentina; Fig. 1). In recent years the area around Rincón de los Sauces has added numerous remains to the dinosaur record, including *Rinconsaurus caudamirus* Calvo and González Riga, 2003, *Bonitasaura salgadoi* Apesteguía, 2004, *Petrobrasaurus puestohernandezi* Filippi et al., 2011, *Overosaurus paradasorum* Coria et al., 2013, and *Viavenator exxoni* Filippi et al., 2018. As regards the ornithopod record this area has added new remains in sedimentary deposits aged between late Coniacian and Campanian (see references in Cruzado-Caballero et al., 2016a, 2018 and Jimenez-Gomis et al., in press). The new ornithopod is a partial skeleton discovered in the Cerro Overo fossil locality. Previous reports from the same locality include isolated remains belonging to several individuals of different ontogenetic stages, which exhibit affinities with the elasmarians *Macrogryphosaurus* and *Talenkauen* (Cruzado-Caballero et al., 2018; Jimenez-Gomis et al., in press). However, these fragmentary remains could not be assigned to a new taxon or to any other known species. On the basis of the new specimen, in this paper we erect a new basal ornithopod genus and species and evaluate its phylogenetic relationships. This research highlights the remarkable diversity of basal ornithopods present in the Upper Cretaceous of Argentina and reinforces the phylogenetic hypothesis that recovers an endemic clade of South American ornithopods.

Institutional Abbreviations— **MAU**, Museo Municipal Argentino Urquiza (Rincón de los Sauces, Neuquén, Argentina); **FMNH,** the Field Museum, Chicago, USA; **MACN**, Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Buenos Aires, Argentina); **MPCA-Pv**, Museo Provincial Carlos Ameghino, Paleovertebrate Collection (Cipolletti, Río Negro, Argentina).

2. Geological setting

The Neuquén Group (Cenomanian − lower Campanian) consists of a 1,200 m-thick red-bed succession that characterizes the Upper Cretaceous succession of the Neuquén Basin (North Patagonia). These deposits were accumulated in a fluvial setting, with minor intercalations of aeolian and shallow lacustrine sediments (Cazau and Uliana, 1973). The outcrops of the group are those with the greatest exposure outside the Andean area of the Basin, bearing a rich and varied fauna of fossil reptiles whose presence has been known to the scientific community since the end of the nineteenth century (Leanza et al., 2004; Garrido, 2010).

The fossil remains studied here were recovered from the Bajo de la Carpa Formation (Río Colorado Subgroup), a lithostratigraphic unit included in the upper part of the Neuquén Group with an age estimated to be Santonian (Legarreta and Gulisano, 1989; Bonaparte, 1991; Hugo and Leanza, 2001; Garrido, 2010). Indeed, this unit brought the first vertebrate remains known for the Upper Cretaceous of the Neuquén Basin, comprising crocodiles and fossil snakes found by Roth (1898) and studied by Smith Woodward (1896, 1901).
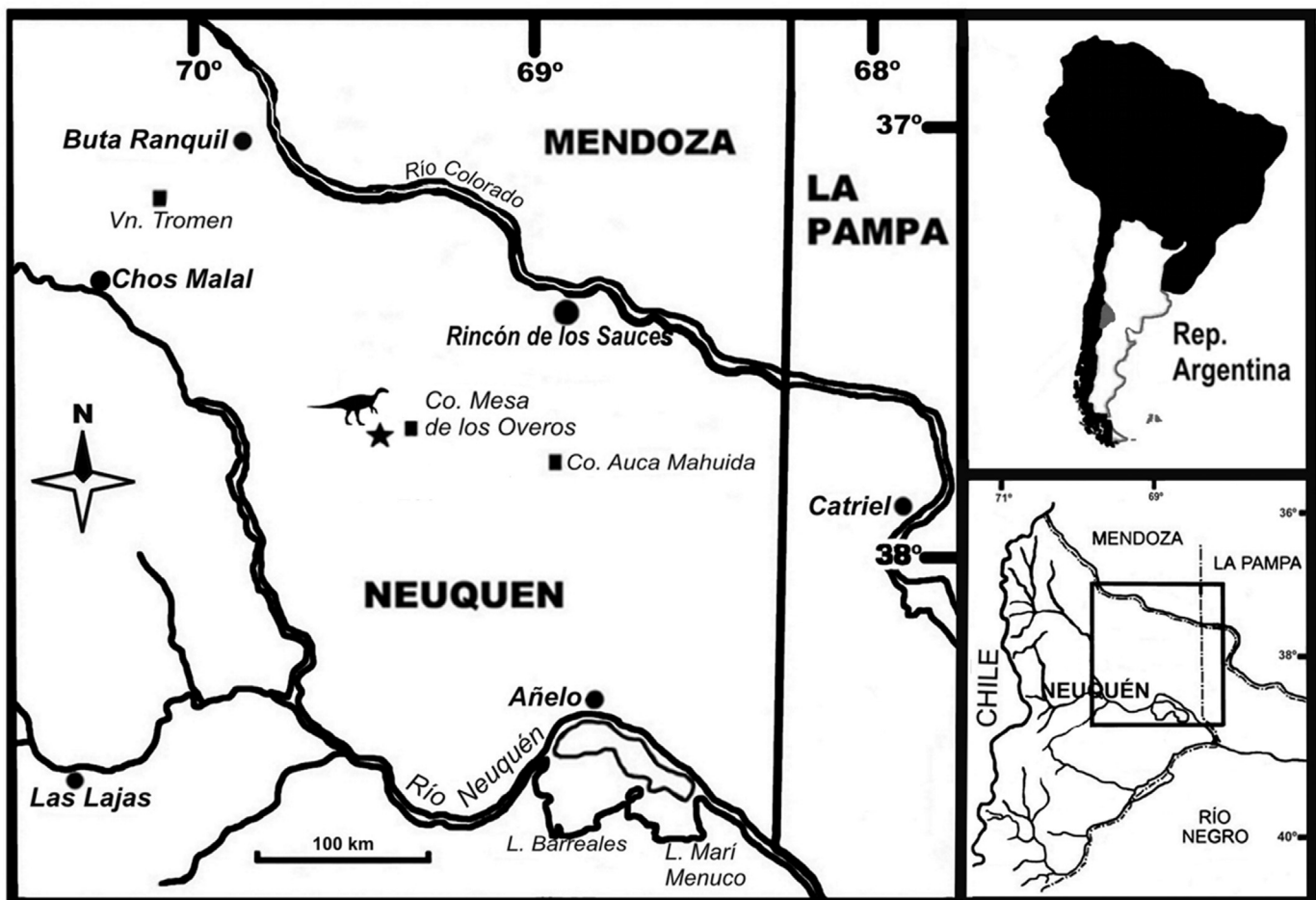

Fig. 1. Map showing the location of the Cerro Overo site (Rincón de los Sauces, Neuquén, Argentina). (1 column/80 mm wide).

The site where these remains were first found is located in what is currently the university campus of the Universidad Nacional del Comahue in Neuquén, the capital city of the province of Neuquén. Over the decades, a great variety of fossils have been recovered from this location, noteworthy among which are the remains of small abelisaurids and alvarezsaurids (Bonaparte, 1991; Martinelli and Vera, 2007), crocodiles (Bonaparte, 1991; Fiorelli and Calvo, 2007; Martinelli and Pais, 2008), snakes (Caldwell and Albino, 2001), as well as bird remains and bird eggs (Alvarenga and Bonaparte, 1992; Chiappe and Calvo, 1994; Schweitzer et al., 2002; Fernández et al., 2013). A similar faunal association was also found in deposits of this unit outcropping near the locality of Paso Córdoba, Río Negro Province, located approximately 42 km from the city of Neuquén (Gazzera and Calvo, 1991).

However, in spite of the rich faunal association recovered from the Bajo de la Carpa Formation in the decades from 1890 to 2000, remains of medium to large-sized dinosaurs were not known for this unit, with the exception of the titanosaur *Bonitasaura* and the later relocation of *Rinconsaurus* and *Overosaurus* within the fluvial deposits of the unit (Filippi, 2015). Since the discovery in 2013 of a new fossiliferous site belonging to the Bajo de la Carpa Formation in the northwestern area of Neuquén Province, located approximately 40 km southwest of the town of Rincón de los Sauces, the number of known species has increased substantially, including a new faunal association composed of sauropod, theropod and ornithopod dinosaurs, as well as a wide variety of turtles and fishes (Filippi et al., 2015, 2016, 2018; Cruzado-Caballero et al., 2016b, 2018).

The presence of two different faunal associations in the Bajo de la Carpa Formation is consistent with variations in the palaeoenvironmental conditions of these deposits according to their location within the palaeogeographic context of the basin (Filippi et al., 2015). An association of aeolian and low-sinuosity to braided fluvial deposits thus characterizes the Bajo de la Carpa Formation at the city of Neuquén and the locality of Paso Córdoba (Heredia and Calvo, 1997, 2002; Garrido and Calvo, 2004; Caldwell and Albino, 2001; Sánchez et al., 2006; Garrido, 2010), whereas a thick succession of muddy floodplains associated with anastomosed fluvial deposits distinguishes this unit in the area southwest of the town of Rincón de los Sauces (Cruzado-Caballero et al., 2018).

The bone remains identified as *Mahuidacursor* are from the latter locality. They were recovered from the upper third of the Bajo de la Carpa Formation, which in this area exhibits a total thickness of 108 m. The fossiliferous bed is composed of sandy siltstone interbedded with thin massive mudstone levels. The sandy siltstone shows a faint horizontal stratification, associated with an intense bioturbation developed on top of the bed. Within the palaeoenvironmental context, dominated by the development of an anastomosed fluvial system (Cruzado-Caballero et al., 2018), this fossiliferous level has been interpreted as levee deposits.

The preservational features of the *Mahuidacursor* holotype (i.e. an articulated specimen with unabraded and little-weathered bone elements) suggest relatively short subaerial body exposure, which prevented the total disarticulation and dispersion of bones. Because at the time of the discovery the bone remains were partially exposed on the surface, it is possible that the missing pieces of the skeleton have been lost due to recent erosion. However, the action of scavengers prior to the final burial of the body cannot be ruled out.

3. Material and methods

3.1. Phylogenetic analysis

In this paper, we follow the definition of Sereno (1986, emended) for the clade Iguanodontia, which is 'the most inclusive group containing *Parasaurolophus walkeri* Parks, 1922 but not *Hypsilophodon foxii* Huxley, 1869 or *Thescelosaurus neglectus* Gilmore, 1913' (see discussion in Sereno, 2005), and the definition of Calvo et al. (2007) for Elasmaria, which is '*Talenkauen santacrucensis, Macrogryphosaurus gondwanicus*, their most recent common ancestor *plus* all the descendants'. However, we will not consider the clade Elasmaria to be within the clade Euiguanodontia as in the original publication, due to the status of the clade Euiguanodontia, which was defined by Coria and Salgado (1996) as '*Gasparinisaura cincosaltensis*, Dryosauridae, Ankylopollexia (= *Camptosaurus* + Styracosterna) and all descendants of their common ancestor', but is inactive, *Gasparinisaura* being positioned among the hypsilophodontids (see discussion in Sereno, 2005).

3.2. Palaeohistology

Histological thin sections from a dorsal rib, an ossified tendon and an intercostal plate were prepared by one of us (IAC) at the Museo "Carlos Ameghino" (Cipolletti, Río Negro Province, Argentina). The slices were prepared using standard methods outlined by Chinsamy and Raath (1992) and studied using a petrographic polarizing microscope (Nikon E200 pol). The nomenclature and definitions of structures used in this study are derived from Francillon-Vieillot et al. (1990) and Chinsamy (2005). The thin sections are deposited in the Museo Municipal Argentino Urquiza (Rincón de los Sauces, Neuquén, Argentina).

4. Systematic palaeontology

Dinosauria Owen, 1842
Ornithischia Seeley, 1887
Ornithopoda Marsh, 1881

Mahuidacursor gen. nov.

Derivation of genus name: The generic name *Mahuidacursor* is from the Mapuche word 'mahuida', which means mountain, in reference to the various mountains of volcanic origin that stand out in the landscape around the town of Rincón de los Sauces, with the suffix '-cursor,' from the Latin for runner.
Diagnosis: As for the type and only known species.

Mahuidacursor lipanglef sp. nov.

Derivation of species name: The specific name *lipanglef* is from the Mapuche, in reference to the gracile nature of the specimen, in particular the slender architecture of its forelimbs; the word 'lipang' means arm, and 'lef', lightly.
Holotype: MAU-Pv-CO-596 consists of a partial articulated postcranial skeleton (Fig. 2). The fossil remains are kept within a plaster jacket, in which the left side of the dinosaur skeleton is prepared and well-exposed. By contrast, the right side − which is the side that was cropping out − remains hidden. The skeleton preserves the last four cervical vertebrae (the most anterior of them extracted outside the plaster jacket) and the corresponding ribs, an additional posterior cervical centrum, the most anterior six vertebrae and seven left ribs of the dorsal series, the two scapulae, coracoids and sternal plates, four intercostal plates (those located between the second and sixth dorsal ribs), as well as the right forelimb (also articulated but recovered outside the plaster jacket) including humerus, radius, ulna and almost complete manus (excluding some distal phalanges).
Type locality and Horizon: The Cerro Overo site, near the town of Rincón de los Sauces (Neuquén Province, Argentina); Bajo de la Carpa Formation, Santonian, Upper Cretaceous (Fig. 1).
Diagnosis: Species as for the genus. Medium-sized ornithopod dinosaur diagnosable by the presence of dorsal ribs not distally thickened and bearing a surface restricted to the most
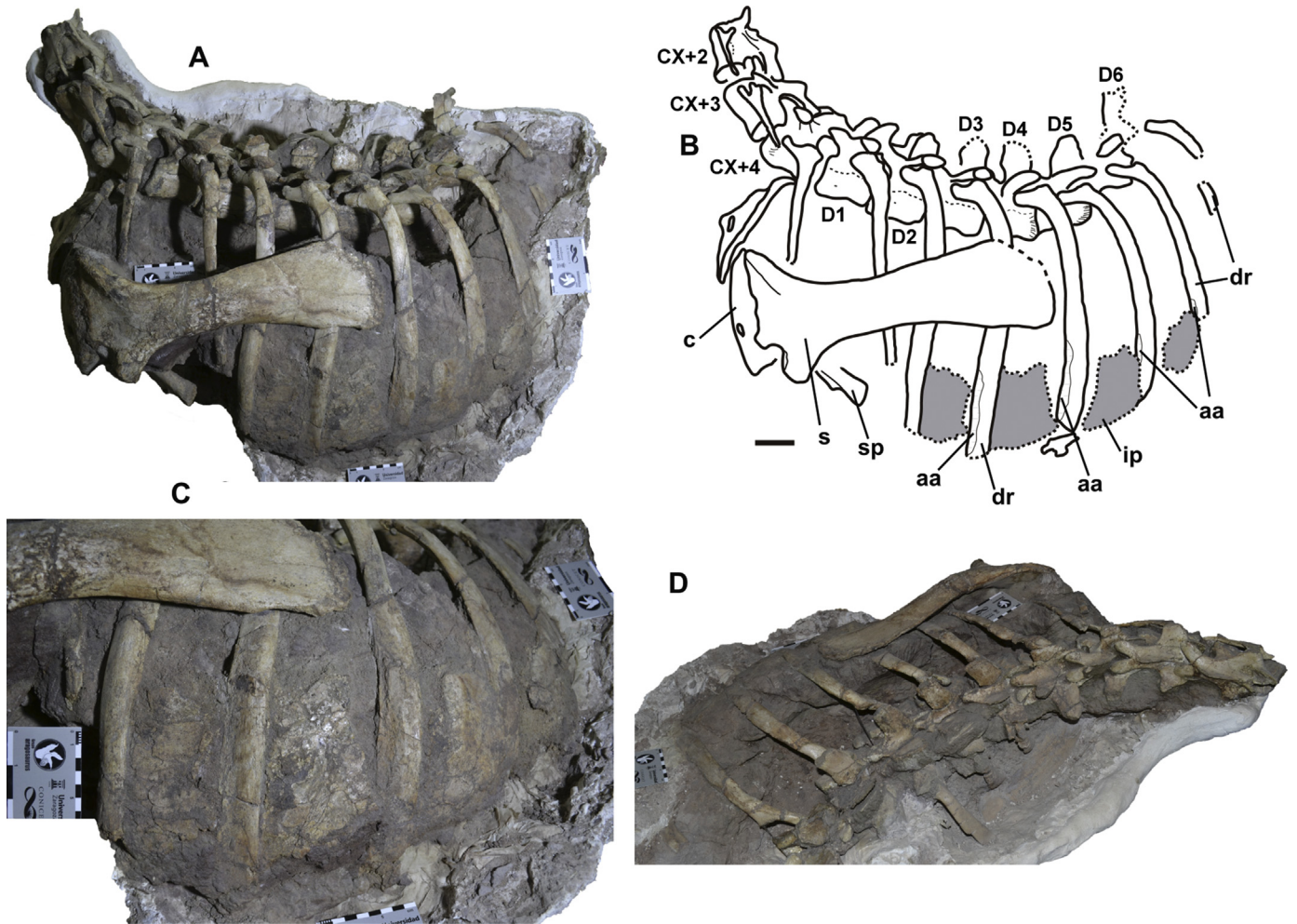
Fig. 2. Holotype of *Mahuidacursor lipanglef* gen. et sp. nov. (MAU-Pv-CO-596) in left lateral (A—B) and dorsal (D) views. Detail of the intercostal plates in (C). Abbreviations: aa, articulation area; dr, dorsal rib; ip, intercostal plate. Scale bar: 5 cm. (2 columns/166 mm wide).

anterolateral margin for contact to the preceding intercostal plate (potentially autapomorphic) and the following combination of synapomorphic characters: first dorsal vertebra with rectangular dorsal neural spine; first and second dorsal centra as long as the last cervical centrum; dorsal centra relatively long, and increasing in length only moderately throughout the dorsal sequence; posterior process of the coracoid scarcely developed; humerus length subequal to the scapular length; long and slender scapula; posterior end of the scapular blade narrower than the proximal end of the bone; poorly developed humeral head, rudimentary deltopectoral crest and humeral shaft strongly bowed.

Differential diagnosis: *Mahuidacursor* differs from *Macrogryphosaurus* in the concave profile of the ventral side of the cervical centra in *Macrogryphosaurus* as well as in the proportions of the cervical centra (i.e., wider than high in Macrogryphosaurus. as wide as high in Mahuidacursor) and the neural spine of the last cervical (i.e., height significantly increasing in *Macrogryphosaurus* and remaining low in *Mahuidacursor*); it differs from *Talenkauen* in the humerus (i.e. the scapula length ratio, which is clearly greater in *Talenkauen*), in the scapula (the ratio of the distal width of the scapular blade to the proximal width being clearly greater in *Talenkauen* than in *Mahuidacursor*), and also in the neural spine of the last cervical (i.e. *Talenkauen* displaying the same condition as *Macrogryphosaurus*); it differs and from *Notohypsilophodon* in the bowing of the humeral shaft, which is gentler in the latter.

4.1. Description and comparison

4.1.1. Cervical vertebrae

Five cervical vertebrae are preserved (Figs. 2-3). One of them is an eroded centrum found isolated but near the rest of the skeleton. The four most posterior ones were found in anatomical connection even though the first of them was extracted apart from the plaster jacket containing the main body of the individual. The cervical centra are anteroposteriorly elongated whereas they are almost as wide as high (see Supporting Information 2). The latter is a different condition from that of Macrogryphosaurus whose cervical centra are wider than high (Calvo et al., 2007). The anteroposterior length increases posteriorly except for the last vertebra, in which it decreases, this pattern being similar to *Talenkauen*, *Macrogryphosaurus* and *Gasparinisaura* (see Supporting Information 2; Cambiaso, 2007). The length:height ratio of the most anterior cervical centrum is more than 1.5, as in the anterior cervical centra of *Thescelosaurus*, *Parksosaurus*, *Talenkauen*, *Macrogryphosaurus* and *Dryosaurus altus* Marsh, 1894 (Boyd, 2015; Han et al., 2017) and unlike those of most ornithischians (i.e. *Lesothosaurus diagnosticus* Galton, 1978; *Haya* Makovicky et al., 2011; *Zalmoxes robustus* Nopcsa, 1899; *Yinlong downsi* Xu et al., 2006; Boyd, 2015; Han et al., 2017). The centra are spool-shaped and bear a well-defined ventral keel, as in basal ornithopods (i.e. *Haya*, *Hypsilophodon*, *Macrogryphosaurus*, *Notohypsilophodon*; Calvo et al., 2007; Makovicky
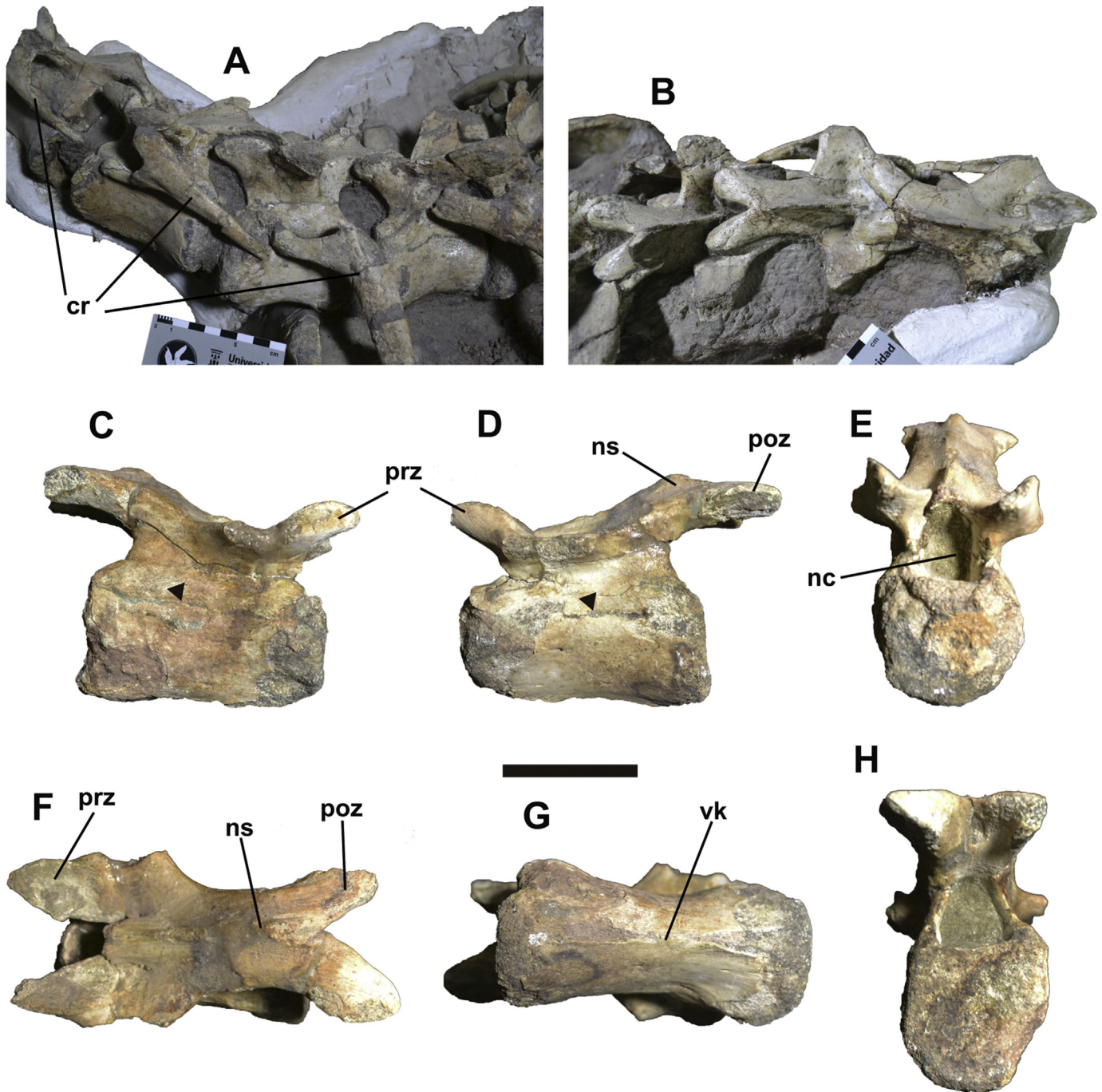
Fig. 3. *Mahuidacursor lipanglef* gen. et sp. nov. (MAU-Pv-CO-596) articulated cervical vertebrae in left lateral (A) and dorsal (B) views. Isolated cervical vertebra in right and left lateral (C—D), anterior (E), dorsal (F), ventral (G) and posterior (H) views. Abbreviations: cr, cervical rib; nc, neural canal; ns, neural spine; poz, postzygapophyseal process; prz, prezygapophyseal process; vk, ventral keel. Scale bar: 5 cm. (2 columns/166 mm wide).

et al., 2011; Ibiricu et al., 2014; Boyd, 2015) and the iguanodontian *Valdosaurus canaliculatus* Galton, 1977 (Barrett et al., 2011). This keel is sharper in its anterior part than in the posterior part, like in other basal ornithopods (i.e. Butler et al., 2011). In lateral view, the ventral border of the centra is almost straight, as in other basal ornithopods (i.e. *Thescelosaurus, Talenkauen*; Gilmore, 1915; Novas et al., 2004) and unlike the concave border of *Changchunsaurus parvus* Zan et al., 2005 and *Macrogryphosaurus* (Calvo et al., 2007; Butler et al., 2011). The articular surfaces are heart-shaped and amphicoelous, as in most ornithischians (i.e. *Thescelosaurus,*

Gasparinisaura, Macrogryphosaurus, Talenkauen, Notohypsilophodon; Calvo et al., 2007; Cambiaso, 2007), this differs from the slightly opisthocoelous cervical vertebrae of iguanodontians (Galton, 1974; Norman et al., 2004). In lateral view, all the centra show an open neurocentral suture indicating an immature stage (Irmis, 2007; see discussion below; Figs. 2 B, 3 C-D). The neural spines are dorsoventrally low, lateromedially narrow and triangle-shaped in lateral view. The dorsoventral development of the neural spines is rudimentary, as in most ornithischians, and differs from the prominent neural spines of *Thescelosaurus, Tenontosaurus tilletti*

Ostrom, 1970, *Heterodontosaurus tucki* Crompton and Charig, 1962, *Scelidosaurus harrisonii* Owen, 1861 and *Stegosaurus stenops* Marsh, 1887 (Han et al., 2017). The last neural spine is low as in other basal ornithopods (i.e. *Thescelosaurus*) and unlike in *Macrogryphosaurus* and *Talenkauen* where it increases significantly in height (Novas et al., 2004; Cambiaso, 2007). The transverse processes are located dorsally to the neural arch, as in *Macrogryphosaurus* and in the most posterior cervical vertebra of *Talenkauen* (Cambiaso, 2007). They are dorsoventrally narrow and laterally oriented. The prezygapophyses are located anteriorly to the base of the neural spine, and their articular surface is oval-shaped, flat and is directed upwards and inwards. The postzygapophyseal processes are long and are curved backwards and outwards. They extend well above the level of the neural canal. The angle formed by this paired process is between approximately 45° and 30°. The postzygapophyseal processes are gently arched, as in most ornithischians (i.e. *Hypsilophodon*, *Talenkauen*, *Notohypsilophodon*; Galton, 1974; Novas et al., 2004; Ibiricu et al., 2014) and unlike iguanodontians (Norman, 1986; Weishampel et al., 2003). The articular surface of the postzygapophyses is located at the end of that process; it is oval-shaped, flat and faces ventrolaterally.

4.1.2. Cervical ribs

Three posterior cervical ribs are well preserved and articulated (Fig. 3 A-B). The two most anterior ribs are anteroposteriorly projected, exceeding posteriorly the end of their corresponding centrum. They are parallel to the anteroposterior axis of the centrum, sharpening posteriorly, and are dorsoventrally narrow. In the first rib, the *capitulum* and *tuberculum* form a right angle whereas in the second one the *capitulum* and *tuberculum* are anteriorly directed. By contrast, the last cervical rib is similar to the dorsal ribs but its length is approximately half that of the first dorsal rib. It is ventrally directed, lateromedially narrow and anteroposteriorly widened.

4.1.3. Dorsal vertebrae

The dorsal series preserves the first six vertebrae in articulation (Fig. 2 and 4). The centra are spool-shaped, constricted at mid-length and rectangular in lateral view. The dorsal centra show ventral keels, but they are less prominent than in those of the cervicals. A similar ventral keel is also seen in *Yueosaurus tiantaiensis* Zheng et al., 2012, *Changchunsaurus*, *Talenkauen*, *Notohypsilophodon*, *Macrogryphosaurus*, *Hypsilophodon*, *Trinisaura santamartaensis* Coria et al., 2013, *Hexinlusaurus multidens* Barrett et al., 2005 and *Jeholosaurus shangyuanensis* Xu et al., 2000, unlike in *Koreanosaurus boseongensis* Huh et al., 2011, *Orodromeus makelai* Horner and Weishampel, 1988 and *Oryctodromeus cubicularis* Varricchio et al., 2007 (Novas et al., 2004; Calvo et al., 2007; Huh et al., 2011; Ibiricu et al., 2014). Their ventral surfaces are concave in lateral view. All dorsal vertebrae have amphiplatyan centra with heart-shaped articular surfaces, as in *Thescelosaurus*, *Talenkauen*, *Notohypsilophodon* and *Macrogryphosaurus* (Galton, 1974; Novas et al., 2004; Calvo et al., 2007; Ibiricu et al., 2014). The first and second dorsal vertebrae are similar in anteroposterior length to the last cervical vertebra (measurements in Supporting Information 2). Afterwards, the dorsal centra increase in length posteriorly, as in basal ornithopods and the parksosaurid *Thescelosaurus* (Norman et al., 2004; Brown et al., 2011). This contrasts with *Talenkauen* and *Macrogryphosaurus*, in which the first dorsal vertebra is shorter than the last cervical and posteriorly the length decreases, and with the parksosaurid *Orodromeus*, in which the dorsal series decreases in length posteriorly (Scheetz, 1999; Cambiaso, 2007). As the vertebrae are included in the matrix and are articulated, it is not possible to observe the right side and measure their lateromedial width and dorsoventral height. As in the case of the cervical vertebrae, the dorsal centra have neurocentral sutures that are not

entirely fused (Fig. 4 A and D). The dorsal vertebrae bear parapophyses above the neurocentral suture. The height of the dorsal neural arch pedicels is low, as in most ornithischians and unlike in stegosaurians (Han et al., 2017). The dorsal neural spines are short, rectangular and lateromedially narrow; the dorsoventral height and anteroposterior width are roughly similar, as in basal ornithopods but unlike in iguanodontians, where the dorsoventral height is more than twice the anteroposterior width (Han et al., 2017). By contrast, in *Talenkauen* and *Macrogryphosaurus* the neural spine has a greater anteroposterior width than dorsoventral height (Cambiaso, 2007). The second neural spine is rectangular in lateral view, unlike *Macrogryphosaurus*, which does not show this shape until the third vertebra, and *Talenkauen*, until the fifth vertebra (Cambiaso, 2007). The anteroposterior width increases posteriorly. The last neural spine increases significantly in height, so it is almost as dorsoventrally high as anteroposteriorly wide. This spine, though somewhat eroded, shows a widening on its left side at the dorsal end that may be similar to the sixth dorsal vertebra of *Thescelosaurus,* the last seven dorsal of *Hypsilophodon* and the posterior vertebrae of *Talenkauen* (Galton, 1974; Cambiaso, 2007; Brown et al., 2011). The transverse processes are short, robust and anteroposteriorly elliptical in cross-section. They lie at the level of the zygapophyses, as is characteristic of basal ornithopods (Norman et al., 2004). They are oriented laterally and slightly dorsally, as in most ornithischians and unlike in thyreophorans, whose transverse processes are dorsolaterally oriented (i.e. more than 40° above the horizontal; Han et al., 2017). The prezygapophyses are located anteriorly to the base of the neural spine and the postzygapophyses are located in the base. Articulation between the zygapophyses of the dorsal vertebrae is flat and smooth, with a rounded outline, as is common in ornithischians (i.e. *Orodromeus* and *Thescelosaurus*; Han et al., 2017) and unlike some ceratopsians (i.e. *Auroraceratops rugosus* Youet et al., 2005; Han et al., 2017). The articular faces of the prezygapophyses are upward and inward, whereas those of the postzygapophyses are downward and outward. Finally, ossified epaxial tendons are present along the vertebral column, as in other ornithopods (Han et al., 2017).

4.1.4. Dorsal ribs

Seven dorsal ribs are preserved in anatomical articulation (Fig. 2). The *tuberculum* is greatly reduced and is represented only as a boss on the angle of the rib, as in *Macrogryphosaurus* and *Thescelosaurus*, and unlike *Talenkauen*, whose most anterior ribs have a well-developed *tuberculum* (Calvo et al., 2007; Cambiaso, 2007; Brown et al., 2011). The third rib is the most complete, with a length of 425 mm (see Supporting Information 2). In the third to fifth ribs, the anterior edge bears a lateral surface marked with slight rugosities in the distal third (Fig. 2 A-C). This area is associated with the articulation or juxtaposition of the intercostal plates (Fig. 2 A-C). The location of this area differs with respect to other basal ornithopods (*Hypsilophodon*, *Parksosaurus*, *Talenkauen*), in which the area is located on the posterior margin (Brown et al., 2011). By contrast, this surface has not been observed in *Macrogryphosaurus* (Calvo et al., 2007). The shafts of the dorsal ribs are anterolaterally to posteromedially compressed. Unlike the dorsal ribs of *Macrogryphosaurus* and *Talenkauen*, in *Mahuidacursor* the ribs do not present an anteroposterior thickening of their ventral half or end (Calvo et al., 2007).

4.1.5. Intercostal plates

Mahuidacursor bears intercostal plates, as in *Lesothosaurus*, *Othnielosaurus consors* Galton, 2007, *Parksosaurus*, *Thescelosaurus*, *Hypsilophodon*, *Talenkauen* and *Macrogryphosaurus* (see Boyd et al., 2011). There are four intercostal plates preserved, which are in articulation with the contiguous dorsal ribs (Fig. 2 C). The anterior
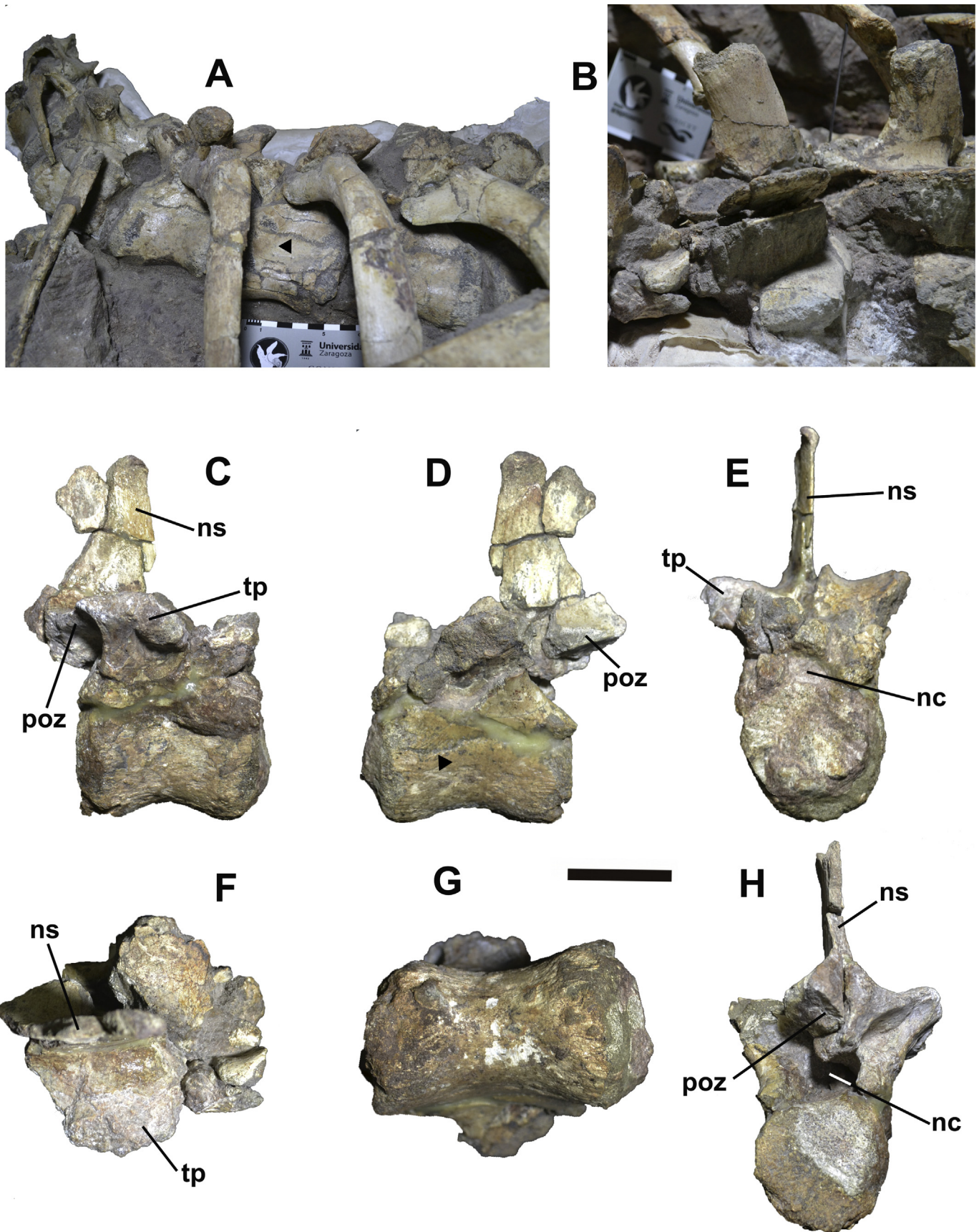
Fig. 4. *Mahuidacursor lipanglef* gen. et sp nov. (MAU-Pv-CO-596) articulated dorsal vertebrae in left lateral (A) and dorsal (B) views. Isolated dorsal vertebra in right and left lateral (C–D), anterior (E), dorsal (F), ventral (G) and posterior (H) views. Abbreviations: nc, neural canal; ns, neural spine; poz, postzygapophysis; tp, transverse process. Scale bar: 5 cm. (2 columns/166 mm wide).

edge of the intercostal plate is below the posterior edge of the dorsal rib, and the posterior edge of the intercostal plate lies above the anterior edge of the dorsal rib. The posterior and ventral edges of the plates are broken. These are lateromedially narrow and have a rectangular outline, unlike the diamond-shaped plates of *Talenkauen* or the subcircular plates of *Macrogryphosaurus* (Calvo et al., 2007; Cambiaso, 2007; measurements in Supporting Information 2).

4.1.6. Scapula

Both scapulae are preserved and are fused with the coracoids (Fig. 5 A-B). Only the left scapula is visible, due to the right scapula being hidden by the matrix. The left scapula is anteroposteriorly straight and lateromedially narrow. It is slightly convex in lateral view. It has a length of 410 mm, slightly shorter than the length of the humerus (440 mm; see Supporting Information 2). The condition of a humerus subequal to the scapula, as present in *Mahuidacursor*, is common among ornithischians, but differs from *Agilisaurus louderbacki* Peng, 1990, *Hexinlusaurus*, *Gasparinisaura* and *Talenkauen* (Cambiaso, 2007; Han et al., 2017). The scapula of *Mahuidacursor* is 30% longer than that of *Talenkauen* and is half as wide at its anterior end as in *Talenkauen* (Cambiaso, 2007). The ratio between the humerus length and scapula length is 1.07, which is similar to other North American ornithopods (*Thescelosaurus neglectus* USNM7757 = 1.06–1.14; *Parksosaurus* ROM84 = 1.02; *Scutellosaurus* P1.175 = 1.1) and *Anabisetia* (1.03), but diverges from *Talenkauen* (1.26; Cambiaso, 2007). The anterior end is expanded, as in basal ornithopods and basal iguanodontians (Ibiricu et al., 2014). The posterior end is clearly narrower than the anterior end as in basal styracosterns (e.g. *Mantellisaurus*, Norman, 1986) and unlike *Talenkauen* (Cambiaso, 2007), where the posterior end is only slightly narrower, and other basal ornithopods, where the posterior end of the scapula is wider (e.g. *Hypsilophodon, Tenontosaurus*; Galton, 1974; Tennant, 2010). The posterior end is asymmetrical and finishes between the third and fourth dorsal vertebrae. The dorsal and ventral borders are divergent towards the distal end, and as in *Dryosaurus* and all the more derived non-hadrosaurid iguanodontians the scapula is flared distally (Norman, 2004). The posterior border is relatively straight, similar to *Eocursor parvus* Butler et al., 2007, *Zalmoxes*, *Mantellisaurus* and *Yinlong* and unlike basal ornithopods (i.e. *Hypsilophodon* or *Haya*), *Dryosaurus*, *Tenontosaurus* and *Camptosaurus*; Han et al., 2017).

The scapula has an acromial process that is very well developed, as in *Talenkauen*, *Anabisetia*, *Thescelosaurus*, *Camptosaurus* and some basal ornithopods (Galton 1974; Cambiaso, 2007; Carpenter and Wilson, 2008). It has a dorsoventrally narrow neck that is approximately 60.7% of the maximum width of the blade. This is different from the robust scapula of *Talenkauen*, in which the width of the neck is approximately 41.25% of the maximum width of the blade (Cambiaso, 2007).

4.1.7. Coracoid

Both coracoids are preserved and are co-ossified with the scapula (Fig. 5 A and C-D). They are robust and subrectangular in shape, as in most of the basal ornithopods (Norman et al., 2004). They are anteroposteriorly wide and lateromedially narrow, similar to those in *Talenkauen* but not as wide as in the latter (Cambiaso, 2007; Supporting Information 2). The lateral side is flat and the posterior border is strongly convex, unlike the slightly sinuous border of *Talenkauen* (Cambiaso, 2007). A circular coracoid foramen and an ellipsoidal concave area below are observed in the lateral side as in *Talenkauen*, in which the concave area is slightly smaller and shallower. The foramen does not directly contact the scapulocoracoid suture. Unlike in *Talenkauen*, *Trinisaura*, *Thescelosaurus*, *Parksosaurus*, *Hypsilophodon*, *Haya*, *Changchunsaurus* and

Orodromeus, the posterior border of the coracoid is weakly concave between the glenoid and the posteroventral tip of the coracoid (Gilmore, 1915; Parks, 1926; Galton, 1974; Scheetz, 1999; Cambiaso, 2007; Butler et al., 2011; Makovicky et al., 2011; Coria et al., 2013). The posterior process of the coracoid is weakly hooked, unlike *Talenkauen* and *Trinisaura*, which have a strongly developed hook, and like *Heterodontosaurus*, *Stormbergia dangershoeki* Butler, 2005 and *Notohypsilophodon* (Butler, 2005; Cambiaso, 2007; Coria et al., 2013; Ibiricu et al., 2014), in which the posterior process of the coracoid is more rounded. The glenoid is smaller than the area of the suture with the scapula.

4.1.8. Sternum

The two sternal plates are present and fused (Fig. 5 E-F). They are almost complete, except for a small part of the posterior margin of both sternal plates and the end of the posterior process of the left sternum (measurements in Supporting Information 2). These plates are triradiate and hatchet-shaped, as in *Macrogryphosaurus*, *Lurdusaurus arenatus* Taquet and Russell, 1999 and derived iguanodontians, and unlike the kidney-shaped sternal plates of other basal ornithopods (i.e. *Hypsilophodon*, *Parksosaurus*, *Tenontosaurus*; Galton, 1974; Taquet and Russell, 1999; Norman, 2004; Norman et al., 2004; Calvo et al., 2007; Han et al., 2017). The main body is projected anteroposteriorly and is V-shaped. The anterior end of the main body is lateromedially narrower than the posterior border, unlike *Lurdusaurus* and the more derived iguanodontians, where the width of the main body is almost constant (Taquet and Russell, 1999; Norman, 2004). The mid-posterior edges are markedly curved backward unlike in styracosterns, where they curve forward and inward (i.e. *Iguanodon bernissartensis* (Boulenger, 1881), *Mantellisaurus atherfieldensis* (Hooley, 1925); Norman, 1980, 1986). Due to this curvature, there are two deep concave zones, unlike the gentle concavities present in *Iguanodon* and *Mantellisaurus* (Norman, 1980, 1986).

The anterior side is thick and rounded. The posterior processes curve backward and outward. These are short and rod-shaped, unlike in *Lurdusaurus* and more derived iguanodontians (Norman, 2004). As the two sternal plates are in anatomical connection with the rest of the bones, only the ventral side can be observed. On this side, there is a sagittal ridge in the fusion between the plates. The parascapular spine is absent, as is common in ornithischians and unlike in *Huayangosaurus taibaii* Dong, Tang and Zhou 1982 (Dong et al., 1982).

4.1.9. Humerus

A complete right humerus was found in articulation with the ulna and radius (Fig. 6). It is slender and long, and the shaft is relatively straight in anterior view, whereas it is slightly sigmoid in profile. However, the humeral shaft is strongly laterally bowed (Fig. 6 A-B), as in *Talenkauen*, *Trinisaura*, *Anabisetia* and *Notohypsilophodon* (see Rozadilla et al., 2016: Fig. 7) and unlike in most cerapodans, which usually have a rather straight humeral shaft (i.e. *Hypsilophodon*, Galton, 1974: Fig. 28; *Haya*, Makovicky et al., 2011: Fig. 3A).

The humerus is longer than the ulna, as is typical in basal ornithopods (the ulna is about 80% as long as the humerus; Norman et al., 2004; see Supporting Information 2). The shaft is more slender than the humerus of *Talenkauen* (Novas et al., 2004). The anterior and posterior borders are divergent at the proximal end. The anterior border is almost straight whereas the posterior border is concave in lateral view. The proximal end is anteroposteriorly wide and lateromedially flattened. The head of the humerus is in the middle of the proximal end of the shaft in lateral view. It has a smooth and subspherical articular surface that is poorly developed, in contrast to the strongly developed articular surface in *Talenkauen* (Fig. 6 E). The deltopectoral crest is weakly developed, in the form
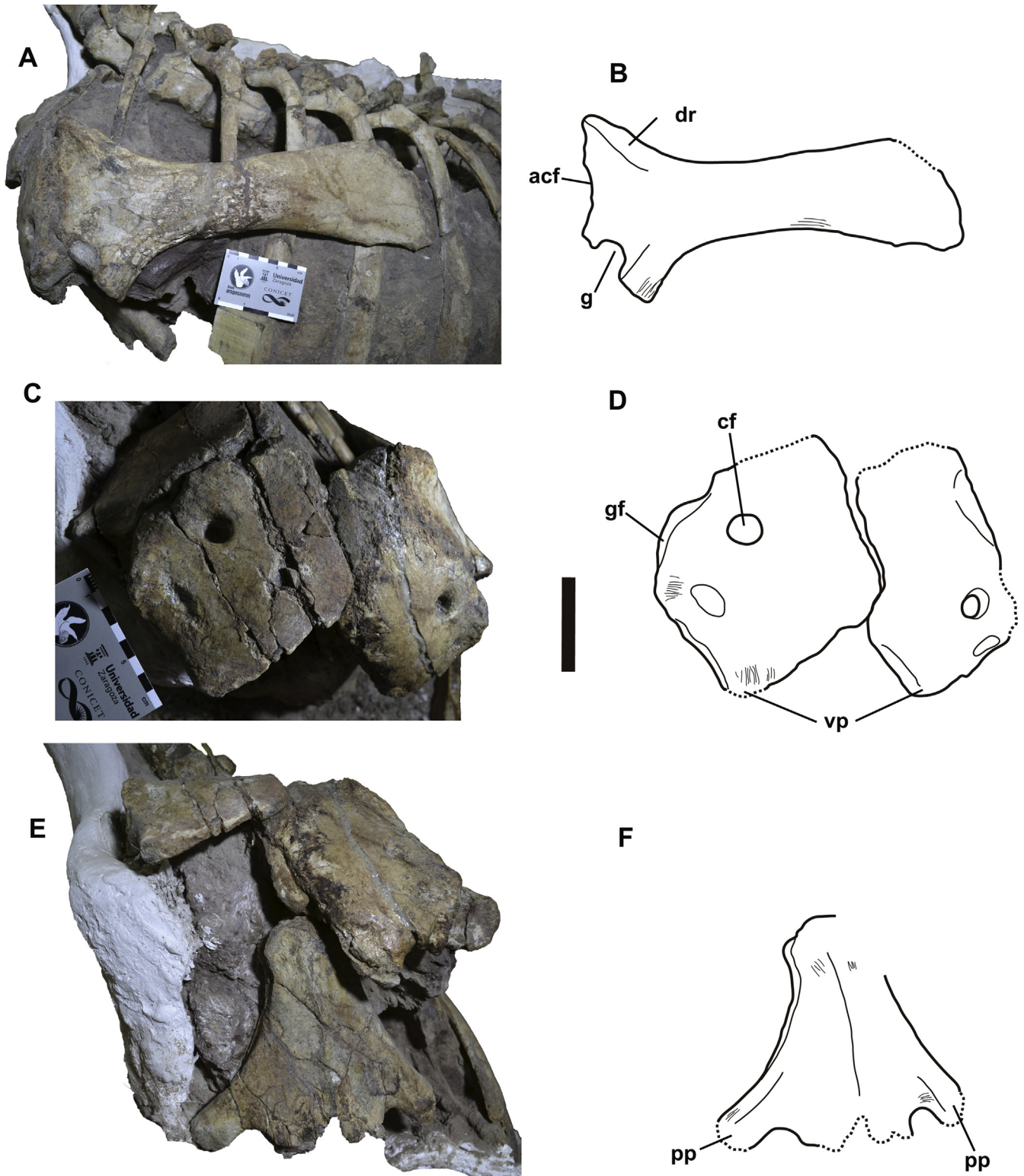
Fig. 5. *Mahuidacursor lipanglef* gen. et sp. nov. (MAU-Pv-CO-596) pectoral girdle. Left scapula in lateral (A−B) view. Right and left coracoids in anterior (C−D) view. Right and left sternal plate in anterior (E−F) views. Abbreviations: acf, articular coracoid facet; cf, coracoid foramen; dr, deltoid ridge; g, glenoid; gf, glenoid fossa; pp, posterior process; sr, sagittal ridge; vp, ventral process. Scale bar: 5 cm. (2 columns/166 mm wide).

of an elongated, thickened edge that extends for approximately half the total length of the humerus (Fig. 6 A-B). This is a feature that it shares with the members of the clade Elasmaria *Talenkauen* and *Notohypsilophodon* and the iguanodontians *Anabisetia* and *Gasparinisaura* but not with more developed ornithopods (i.e. *Thescelosaurus, Dryosaurus, Camptosaurus, Iguanodon*; Novas et al., 2004). Distally, the crest merges smoothly with the shaft and does not form a prominent angle on the humeral shaft. The bicipital

Fig. 6. *Mahuidacursor lipanglef* gen. et sp. nov. (MAU-Pv-CO-596) right humerus in medial (A), lateral (B), posterior (C), anterior (D), proximal (E) and distal (F) views. Abbreviations: hh, humeral head; rc, radial condyle; uc, ulnar condyle. Scale bar: 5 cm. (2 columns/166 mm wide).

groove is shallow and wide in its proximal part. Below the crest the shaft is subcircular in cross-section. The distal condyles are subequal in size, with a prominent intercondylar groove.

4.1.10. Radius

The radius is complete and was found in articulation with the humerus, the ulna and the carpals (Fig. 7). The radius is straight but the distal end appears to be weakly twisted about its longitudinal axis. It is gracile, as in *Talenkauen*, *Anabisetia*, *Dryosaurus* and basal ornithopods (Cambiaso, 2007). The length of the radius is about 70% that of the humerus, as is typical in basal ornithopods (Norman et al., 2004; see Supporting Information 2). It is slightly shorter than the ulna. Distally, the radial shaft is somewhat twisted. Proximally, the shaft is ellipsoidal in cross-section; it is circular in the middle and becomes more triangular distally. The proximal articular surface is slightly concave and rugose. The distal articular surface has two concave areas for the articulation of the carpal bones. As is characteristic of basal ornithopods, a shallow sulcus occupies the proximal surface for articulation with the humerus (Norman et al., 2004). The medial side of the shaft is convex and presents a ridge along almost all its length. The lateral side of the shaft is flat, with an elongate facet for attachment to the ulna.

4.1.11. Ulna

A complete right ulna was found in articulation with the humerus, the radius and the carpals (Fig. 8). In proximal view, the ulna is triangular in cross-section, with a regularly convex lateral border, a concave medial border and a slightly concave anterior articular

border for the radius. The diaphysis is mediolaterally bowed in anterior view and straight in medial view, similar to the iguanodontians *Zalmoxes*, *Iguanodon*, *Ouranosaurus nigeriensis* Taquet, 1976 and *Camptosaurus* and unlike *Haya* and *Tenontosaurus* (Galton, 1974; Taquet, 1976; Norman, 1980; Weishampel et al., 2003; Tennant, 2010; Makovicky et al., 2011). It is slightly longer than the radius. The shaft is roughly triangular in cross-section, with a concave medial surface. The proximal end is anteroposteriorly wider than the distal end. The anterior process develops into a rounded triangular crest that progressively merges with the ulnar shaft. The lateral process is less developed. Between the anterior process and the lateral coronoid process there is a shallow triangular depression into which the head of the radius fits in lateral view.

On the proximodorsal surface of the ulna, the articular facet for the proximal part of the radius is large, triangular in shape and concave. The ulna progressively tapers distally. The ulna has a weak olecranon process, a feature seen in *Notohypsilophodon* but not in basal euornithopods (Martínez, 1998; Makovicky et al., 2011; Fig. 9A-B and E). The distal surface articulates with the carpus and is moderately smooth and convex.

4.1.12. Hand

The right wrist and hand are preserved articulated and moderately complete, but partially masked by sediment and dorsally collapsed (Fig. 8 and 9); the wrist is slightly displaced from its anatomical contact with the ulna and radius.

Fig. 7. *Mahuidacursor lipanglef* gen. et sp. nov. (MAU-Pv-CO-596) right radius in anterior (A), posterior (B) and medial (C) views. Scale bar: 5 cm. (1 column/80 mm wide).

4.1.12.1. Carpals. The carpals are ovoid, as in basal neornithischians (i.e. *Hexinlusaurus*, *Hypsilophodon*, *Haya*; Galton, 1974; Barrett et al., 2005; Makovicky et al., 2011) and unlike the block-shaped carpals of ankylopollexians (i.e. *Camptosaurus*, *Mantellisaurus*; Norman, 1986; Carpenter and Wilson, 2008) and stegosaurians (i.e. *Stegosaurus*; Han et al., 2017). The intermedium-ulnare articulation is free, as is common in ornithischians and unlike in stegosaurs, where it is fused (i.e. Han et al., 2017). The articulation between the carpals and metacarpal I is free, as in other basal ornithopods (i.e. *Hypsilophodon*; Galton, 1974) and unlike in ankylopollexians, where it is co-ossified as two blocks (i.e. *Mantellisaurus*; Norman, 1986).

4.1.12.2. Metacarpals. Metacarpals of digits I to IV are preserved. The metacarpals are slender and morphologically close to those of other basal ornithopods (i.e. *Hypsilophodon*; Galton, 1974), whereas they clearly differ from the metacarpals with block-like proximal ends of ankylopollexians and heterodontosaurids (Butler et al., 2008; Han et al., 2017). The metacarpals are sub-rounded in cross-section and lack extensor pits. Metacarpal I is elongated and is more than 50% the length of metacarpal II, and metacarpal II is subequal to metacarpal III in length (see Supporting Information 2), as is common in ornithischians but unlike in ankylopollexians (Han et al., 2017).

4.1.12.3. Phalanges. The total phalangeal count of the digits cannot be determined, due to the loss of the distal phalanges. The preserved phalanges lack extensor pits, as is common in ornithischians (Han et al., 2017).

5. Histological analysis

In order to assess the minimum age and ontogenetic growth stage of *Mahuidacursor*, histological thin sections were made from one dorsal rib. Although the ontogenetic stages of non-avian dinosaur specimens have usually been inferred from long bone histology (i.e. Canale et al., 2016; Novas et al., 2018), dorsal ribs have recently been demonstrated to be useful for at least minimum age estimation when long bones are not available (i.e. Waskow and Sander, 2014; Waskow and Mateus, 2017). Since *Mahuidacursor* preserves intercostal plates, we also include one of these in our histological analysis. Its inclusion provides a good opportunity to study the histology of these particular structures, allowing comparison with other taxa and testing previous hypotheses about their origin (Boyd et al., 2011). An ossified tendon was also sampled for histological analysis.

A total of five slides were analysed in the present study, one from the ossified tendon and two from each of the other elements. The slides from the dorsal rib correspond to transverse sections obtained from the proximal portion of the shaft and from the *capitulum*. For the intercostal plate, two transverse (i.e. perpendicular to the rib axis) sections were obtained.

5.1. Histological description

Dorsal rib: The rib has a compact cortex that surrounds a marrow cavity filled with cancellous bone (Fig. 10 A-B). The cortical thickness is markedly reduced in the *capitulum*. The transition between the perimedullary cortex and the cancellous bone is rather distinct. The cancellous bone is secondary in origin, comprising different layers of lamellar bone formed during different episodes of remodelling. The inner cortex is also highly remodelled, exhibiting several generations of secondary osteons. This remodelling is not homogeneous, being more pronounced in some areas than in others where secondary osteons reach the outer cortex. The primary bone in the shaft consists of well-vascularized fibrolamellar bone tissue (Fig. 10 B-C). The primary osteons are longitudinally arranged, and their density tends to decrease in the outermost portion of the cortex. The cortical bone exhibits Sharpey's fibres (Fig. 10 D), which are more abundant and densely grouped in some areas (i.e. the anterolateral region in the shaft) than in others. Lines of arrested growth (LAGs) and in some instances annuli are recorded in both sections (Fig. 10 D). Whereas six LAGs are preserved in the shaft, only four are recorded in the *capitulum*. Whereas the two innermost preserved LAGs in the shaft are well spaced, the outer four are more closely grouped. Unlike those observed in the shaft, the outermost preserved LAGs in the *capitulum* are formed in a layer of almost avascular tissue, very similar to a thick annulus (Fig. 10 E). Immediately before the outermost preserved LAG, a layer of well-vascularized fibrolamellar bone is present (Fig. 10 F).

Intercostal plate: The cross-sections reveal a thin structure composed of two thin layers of compact bone enclosing a thick band of cancellous bone (Fig. 10 G). The boundaries between compact and cancellous bone are distinct. The bony trabeculae of the cancellous bone are thin and formed by secondarily deposited lamellar tissue. The cortical bone is formed by poorly vascularized parallel-fibred bone (Fig 10 H-I). Some regions of the lateral cortex exhibit a degree of variation with regard to the intrinsic fibre orientation. Although these fibres are mostly oriented in parallel to the outer surface, they change their orientation from parallel to perpendicular to the anteroposterior axis of the plate (Fig. 10 I).
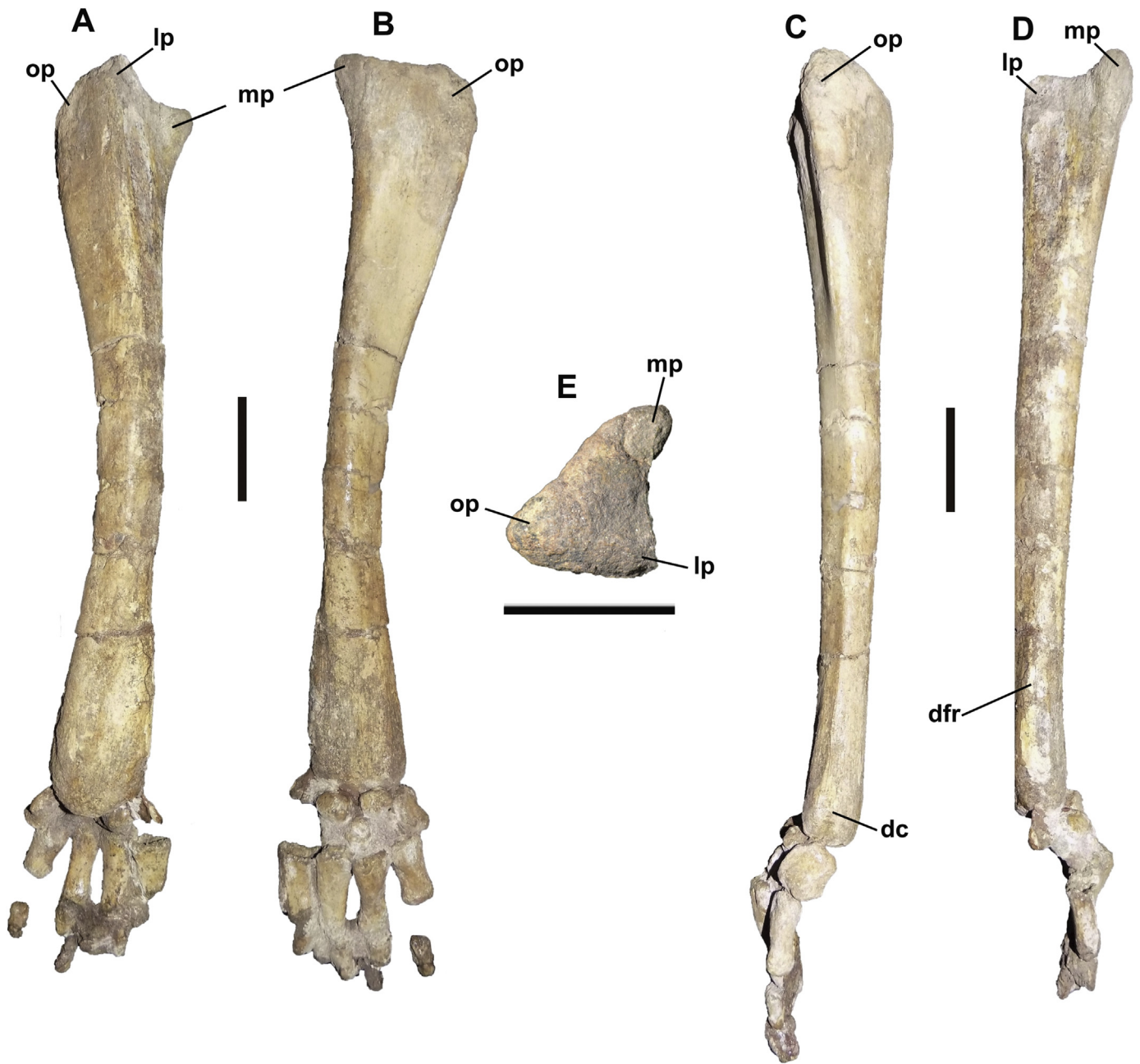
Fig. 8. *Mahuidacursor lipanglef* gen. et sp. nov. (MAU-Pv-CO-596) right ulna and hand in posterior (A), anterior (B), lateral (C), medial (D) and proximal (E) views. Abbreviations: dc, distal condyle; dfr, distal face for radius; lp, lateral process; mp, medial process; op, olecranon process. Scale bar: 5 cm. (2/3 columns/110 mm wide).

Secondary osteons are abundant in the compacta (Fig. 10 J). At least three closely spaced LAGs are preserved. No noticeable histological differences are found between the two cortices.

Ossified tendon: The only sampled tendon exhibits a compact appearance in cross-section, which mostly corresponds with dense Haversian bone (Fig. 10 K). Several superimposed generations of secondary osteons are longitudinally oriented. Remains of primary bone tissue are preserved in the outermost region of the compacta (Fig. 10 L). The primary bone is avascular and monorefringent under polarized light. The bone cell lacunae are rounded or elongated, and circumferentially arranged. Poorly defined growth marks are also discernible (Fig. 10 L).

6. Phylogenetic analysis

To assess the phylogenetic relationships of *Mahuidacursor* and other Argentinean ornithopods, we analysed the dataset proposed by Han et al. (2017), with the addition of the taxa *Mahuidacursor*, *Macrogryphosaurus*, *Talenkauen*, *Notohypsilophodon* and *Diluvicursor* as well as a new character in the matrix (see Supporting Information 1). At present, *Mahuidacursor* can be coded for 9.5% of the morphological characters included in the dataset (i.e. 37 out of 381 characters).

The character distribution was analysed with Mesquite 2.75 (Maddison and Maddison, 2010). The resulting matrix included 77 species-level taxonomic units (73 ingroup taxa and 4 outgroups) coded across 381 characters which were treated as equally weighted, and it was run with TNT v1.5 (Goloboff et al., 2008). Twenty-one characters (2, 23, 31, 39, 125, 163, 196, 203, 204, 222, 227, 238, 243, 247, 268, 292, 296, 302, 306, 320, 361) were treated as ordered (additive) because they form transformation series. A new character (381) was added: intercostal plates; 0, absence or 1, presence.
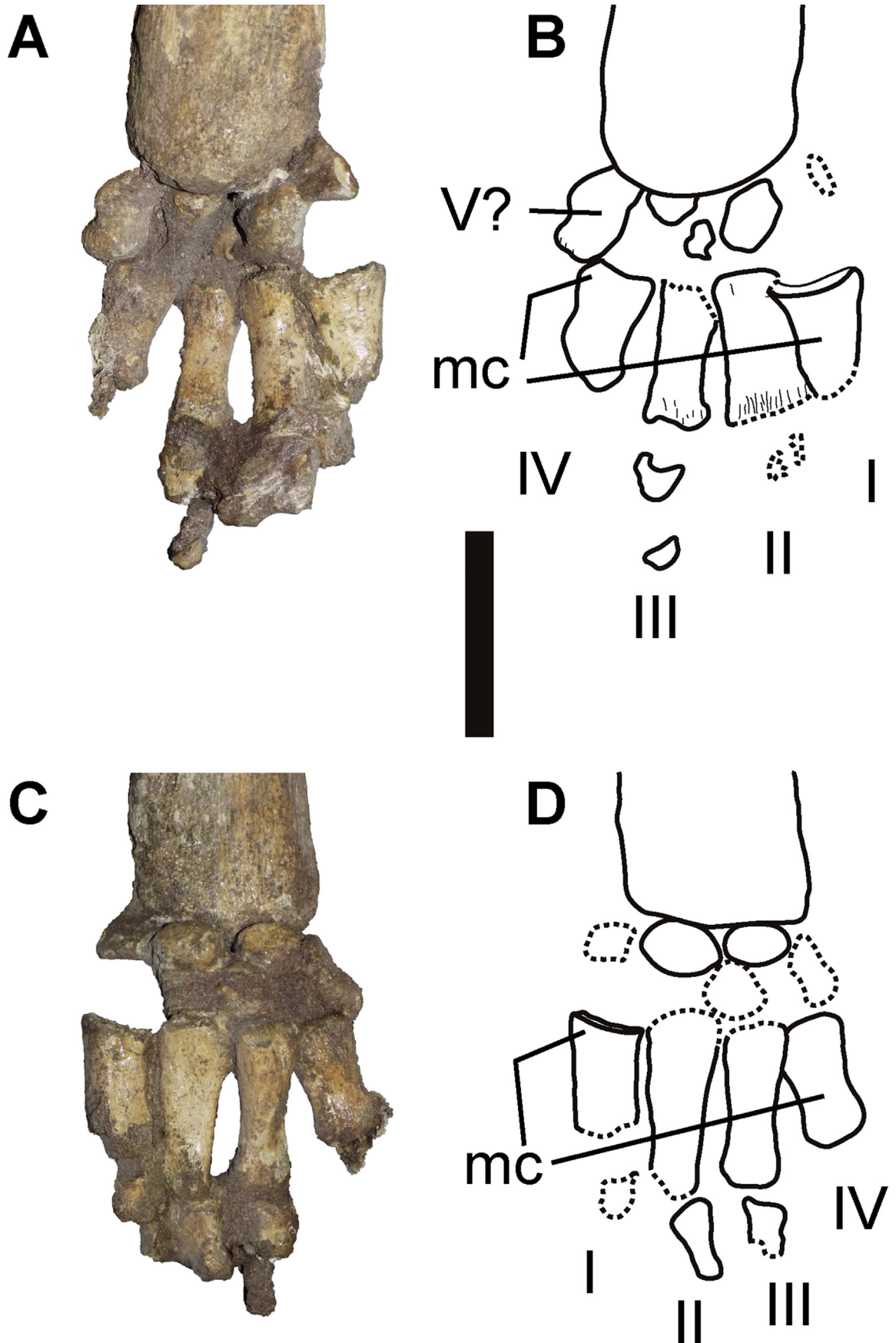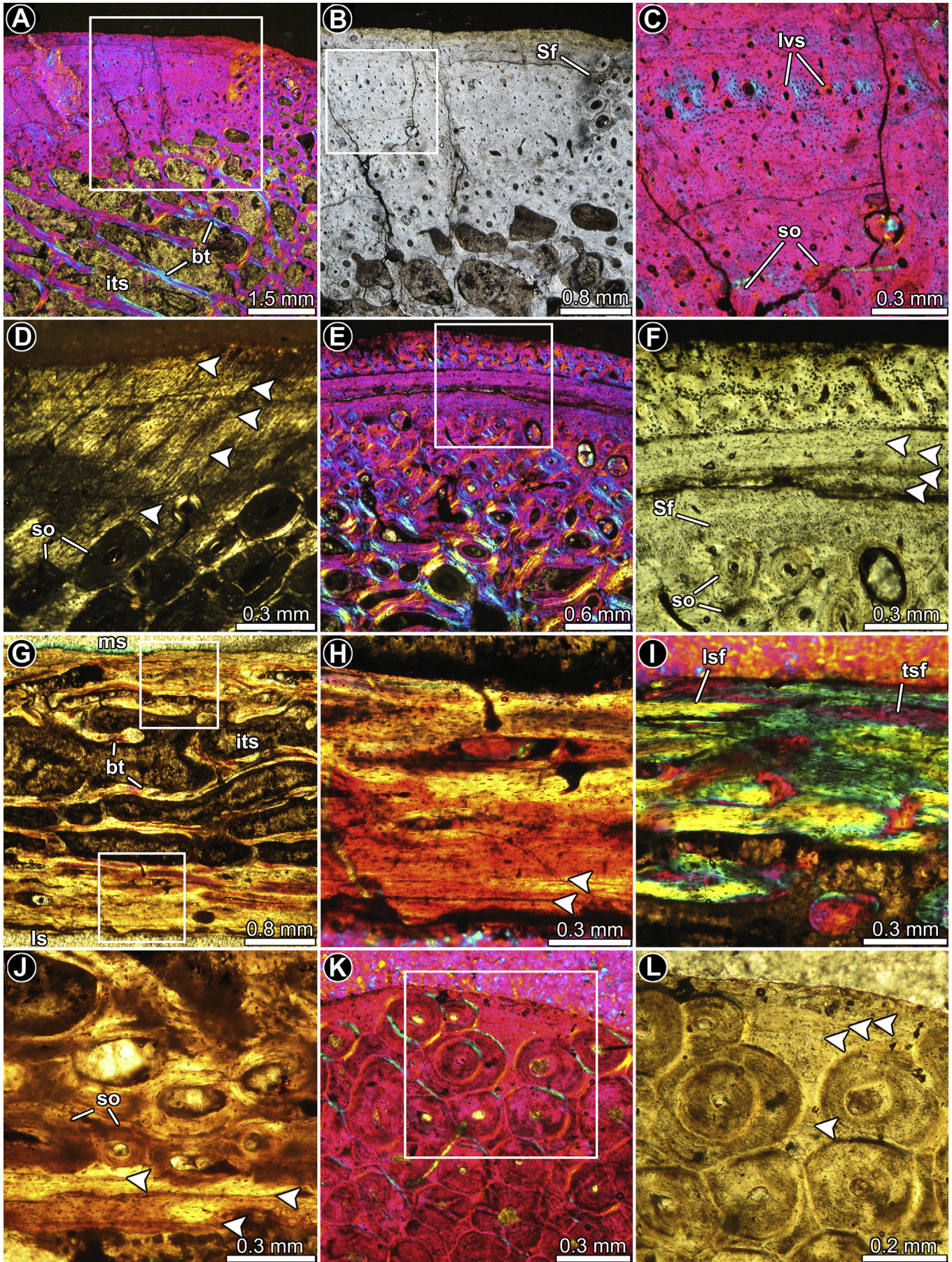
Fig. 9. *Mahuidacursor lipanglef* gen. et sp. nov. (MAU-Pv-CO-596) right manus in dorsal (A–B) and ventral (C–D) views. Abbreviations: mc, metacarpal; I, II, III, IV, V, digits I, II, III, IV, V. Scale bar: 5 cm. (1 column/80 mm wide).

The most parsimonious trees were sought using the 'New Technology Search' option with the 'Sectional Search', 'Rachet', 'Drift' and 'Tree Fusing' options. The maximum number of trees stored in memory was set to 10,000. Bremer support values were calculated using a Bremer Support script made by Goloboff et al. (2008) with the default setting (1000 replicates). The bootstrap values were calculated using the resampling function of TNT, with the standard (sample with replacement) and traditional search options and 1000 replicates, and the results were expressed as absolute frequencies.

166 most parsimonious trees were obtained with a tree length of 1232 steps, a consistency index (CI) of 0.364 and a retention index (RI) of 0.706. The strict consensus tree is presented in Fig. 11. As in Han et al. (2017), the strict consensus tree shows poor resolution in some areas (Fig. 11).

The resulting topology resembles previously published hypotheses, with the exception of the appearance of *Gideonmantellia amosanjuanae* Ruiz-Omeñaca et al., 2012 as the closest outgroup taxon to the taxa *Notohypsilophodon* and *Mahuidacursor* in polytomy and to the sister clade Elasmaria (*Macrogryphosaurus* + *Talenkauen*), which is located as the sister group to the clade Iguanodontia.

In our analysis, the group composed of the South American ornithopods *Notohypsilophodon* + *Mahuidacursor* + [*Macrogryphosaurus* + *Talenkauen*] is defined by the presence of two unambiguous synapomorphies in all trees: a rudimentary deltopectoral crest that is at most a thickening on the anterolateral margin of the humerus (character 277:1) and a humeral shaft that is strongly bowed laterally along its length (character 280:1). There are also four unambiguous synapomorphies in some trees: the anterior cervical centra with a ratio of length to height greater than 1.5 (character 234:0); sternal plates shafted or hatchet-shaped (rod-like posterolateral process, expanded anterior end) (character 265:1); anterior trochanter that is broadened, prominent, 'wing' or 'blade'-shaped, and subequal in anteroposterior width to the greater trochanter (character 353:1); and the presence of intercostal plates (character 381:1). All of them are coded for *Mahuidacursor* except character 353.

7. Discussion

The phylogenetic relationships among the basal members of Ornithopoda remain tangled, as none of the recent hypotheses shows strong support values (Boyd, 2015; Rozadilla et al., 2016; Baron et al., 2017; Herne et al., 2018). The conservative anatomy shown by basal ornithopods, as well as the presence of large number of homoplasies among most taxa (Butler et al., 2009; Rozadilla et al., 2016), makes it difficult to clarify the presence of subclades. However, the special features observed in the forelimbs of *Mahuidacursor* and certain other South American ornithopods (i.e. *Notohypsilophodon*, *Talenkauen* and *Macrogryphosaurus*) help bring to light the existence of a monophyletic clade.

The diversity of ornithopods in South America is not as great as in the northern hemisphere but it is still possible to differentiate two distinct groups: a first group formed by small-sized ornithopods such as *Gasparinisaura* and *Anabis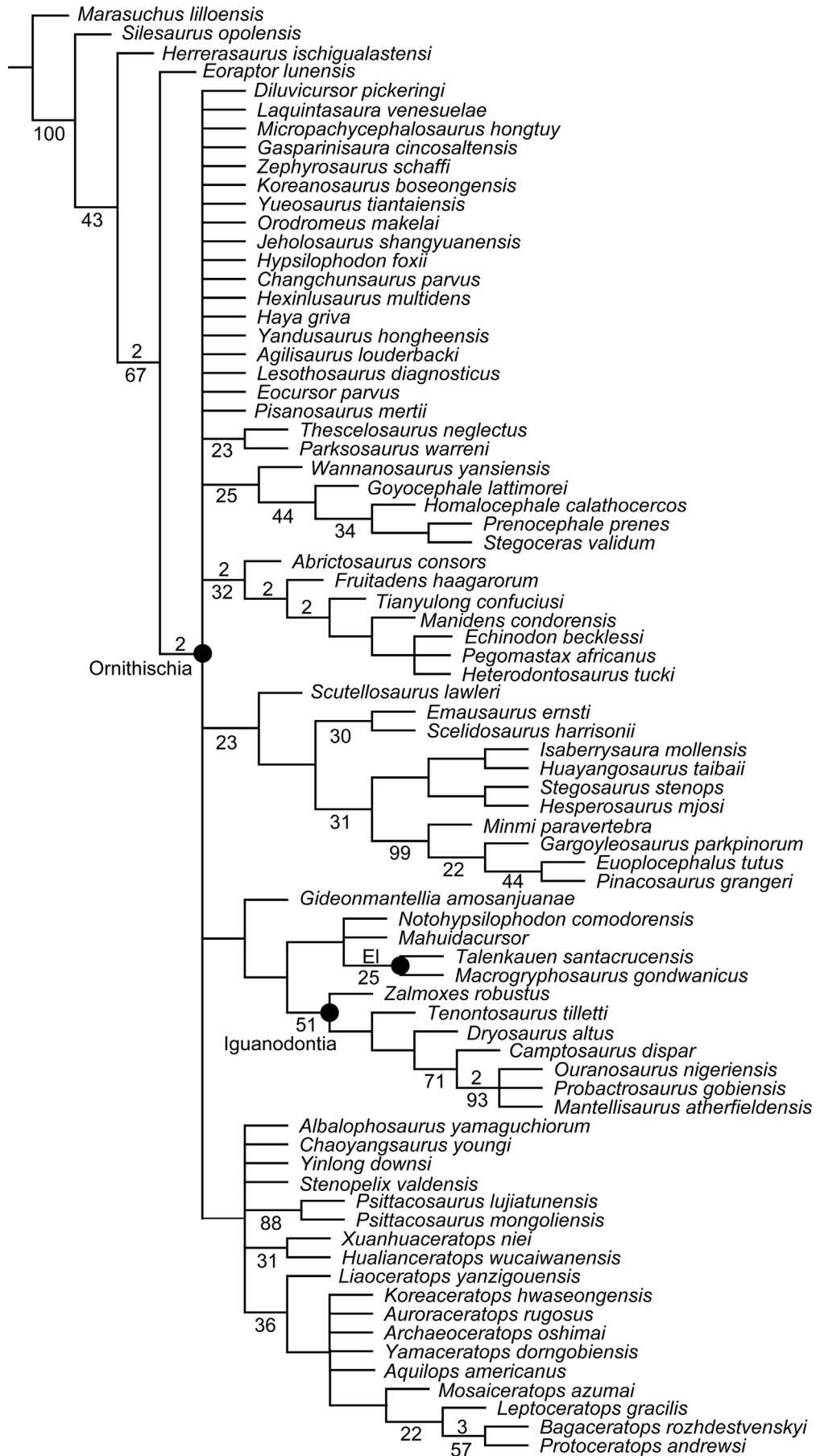etia*, and a second group composed of medium-sized ornithopods such as *Notohypsilophodon* and the clade Elasmaria. It is with the latter group that *Mahuidacursor* shows the greater affinity. *Mahuidacursor* is a medium-sized ornithopod, with a morphotype that is more slender than *Macrogryphosaurus* and *Talenkauen*, as can be observed in its longer cervical and dorsal vertebrae. The elongation of the dorsal vertebrae entails an increase in the length of the thorax and an increase in the space between the dorsal ribs, which is uniquely covered by rectangular intercostal plates. This is unlike *Macrogryphosaurus* and *Talenkauen*, which present an anteroposterior thickening of the dorsal ribs that helps cover the space between the ribs. Moreover, *Mahuidacursor* has a deltopectoral crest of the humerus and lateral process of the ulna that are weakly developed, which may suggest a partial loss of forelimb movement or poor musculature. This would imply a tendency to adopt a bipedal or poorly quadrupedal posture (Maidment et al., 2012; Rozadilla et al., 2016). It would be in accordance with the presence of a slender forelimb and a small hand, as in other medium-sized ornithopods considered bipedal (*Notohypsilophodon*, *Parksosaurus*, *Talenkauen*, *Thescelosaurus*; Parks, 1926; Galton, 1974; Cambiaso, 2007; Ibiricu et al., 2014).

Furthermore, it has been proposed that the Argentinian elasmarians, along with other closely related ornithopods from Gondwana, exhibit adaptations for a specialized cursorial mode of life (Rozadilla et al., 2016; Herne et al., 2018). Of these anatomical features, those located in the forearms (the bowed humerus and the poorly developed deltopectoral crest) can be observed in *Mahuidacursor*. The absence of a tail or hind limbs in the holotype of *Mahuidacursor* precludes the verification of additional cursorial features (i.e. a slender and bunched foot with a narrow metatarsal IV, expanded chevrons; Herne et al., 2018).

In addition to the above mentioned features, *Mahuidacursor* is well differentiated from other ornithischians as well as from all other members of the South American ornithopod clade by a wide set of anatomical features (i.e. dorsal ribs not distally thickened and bearing a surface restricted to the most anterolateral margin for contact to the preceding intercostal plate; first dorsal vertebra with rectangular dorsal neural spine; first and second dorsal centra as long as the last cervical centrum; dorsal centra relatively long, and increasing in length only moderately throughout the dorsal sequence; posterior process of the coracoid scarcely developed; humerus length subequal to the scapular length; long and slender scapula; posterior end of the scapular blade narrower than the proximal end of the bone; poorly developed humeral head).

In the light of the histological analysis, the absence of an External Fundamental System (i.e. a peripheral band of lamellar or parallel-fibred bone with closely packed growth lines) in the sampled rib indicates that the individual was not somatically mature at the time of death (Chinsamy, 2005). Microstructural changes in the compacta close to the outer cortex (i.e. a reduction in the spacing between LAGs and a reduction in the density of vascular spaces) suggest that the individual represented by the specimen had nevertheless reached sexual maturity (Chinsamy, 2005). This combination of microstructural features suggests that the individual corresponds to a sexually mature subadult specimen. On the basis of the number of preserved LAGs, we infer a minimum age

Fig. 10. Bone histology of *Mahuidacursor lipanglef* gen. et sp. nov. (MAU-Pv-CO-596) dorsal rib (A–F), intercostal plate (G–J) and ossified tendon (K, L). Arrowheads in all the pictures indicate the presence of lines of arrested growth. A, C, E, H, I, K: cross-polarized light with lambda compensator; B, F, G, L: plane-polarized light; D: cross-polarized light; J: normal transmitted light. (A) General view of the proximal shaft of the rib in cross-section showing the distribution of the compact and cancellous bone. (B) Detail of compact bone (square inset in A). (C) Detail of the primary tissue composed of fibrolamellar bone (square inset in B). Scattered secondary osteons in different stages of development are observed toward the inner region. (D) Abundant Sharpey's fibres in the outer cortex. (E) General view of the compact and cancellous bone of the rib at the level of the *capitulum*. (F) Detailed view (square inset in E) of the external cortex. Note the major histological variation in the compact bone tissue. (G) General view of the intercostal plate in transverse section. (H) Detail of the cortical bone in the lateral cortex (square inset at the bottom of G). (I) Detail of the cortical bone in the medial cortex (square inset at the top of G). Note the variable orientation of the intrinsic fibres. (J) Detail of the secondary osteons in the cortical bone. (K) General view of the highly remodelled tissue of the ossified tendon. (L) Remains of primary bone preserved in the outer cortex (square inset in K). Abbreviations: bt, bony trabeculae; its, intertrabecular space; ms, medial surface; ls, lateral surface; lsf, longitudinally sectioned fibres; lvs, longitudinally oriented vascular spaces; Sf, Sharpey's fibres; so, secondary osteons; tsf, transversally sectioned fibres. (2 columns/166 mm wide).

of six years. The histological data are congruent with the presence of scars of the neurocentral suture on the dorsal vertebrae, which indicates that skeletal maturity had not been achieved at the moment of death.

Regarding the histological data from the intercostal plate, calcified cartilage is entirely absent in *Mahuidacursor*. This contrasts with the data provided by Boyd et al. (2011) for two specimens of *Thescelosaurus* sp. and *Hypsilophodon*. Such an absence was also reported for *Talenkauen* (Boyd et al., 2011). The presence of calcified cartilage in the intercostal plates of *Thescelosaurus* and *Hypsilophodon* was interpreted by Boyd et al. (2011) as evidence for endochondral ossification in these elements. Although our data do not support an endochondral origin for the intercostal plates, the absence of calcified cartilage does not refute this hypothesis. As reported for *Talenkauen*, the high amount of secondary cancellous bone in the intercostal plate reveals that the primary bone formed in the element has been eroded.

In the case of the ossified tendon, the most noticeable feature reported in *Mahuidacursor* is related to the nature of its primary bone. Unlike what is reported for other ornithopod dinosaurs (i.e. Adams and Organ, 2005; Cerda et al., 2015), the primary bone does not appear to be formed by coarse bundles of mineralized collagenous fibres oriented in parallel to the main axis of the tendon. Such fibres can be easily individualized under polarized light because they are delineated by thin bright lines. Although the primary extracellular matrix in the *Mahuidacursor* tendon is also monorefringent in cross-section, it is not possible to recognize individual mineralized fibres. The unexpected histological variation observed in the *Mahuidacursor* tendon with regard to other ornithopod dinosaurs may be attributed to various, not mutually exclusive causes (i.e. the pattern of formation, ontogenetic stage). Given the high degree of secondary remodelling in the sample, it is not possible at the moment to determine the causes of the observed histological variations.

8. Conclusion

The articulated fossil remains of an ornithopod found in the Santonian Cerro Overo site near Rincón de los Sauces (Neuquén Province, Argentina) reveal the presence of a new taxon, *Mahuidacursor lipanglef*.

Mahuidacursor is a gracile, medium-bodied ornithopod with a slender forelimb. Judging by the histological data, the holotype specimen corresponds to a sexually mature but not fully grown individual. *Mahuidacursor* is a member of an unnamed clade together with the South American ornithopods *Notohypsilophodon*, *Macrogryphosaurus* and *Talenkauen*. This clade is defined by two unambiguous synapomorphies in all trees and four unambiguous synapomorphies in some trees. Furthermore, *Mahuidacursor* is well differentiated from other South American basal ornithopods by a broad set of characters.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2019.02.014.