Journal Pre-proof

A new medium-sized abelisaurid (Theropoda, Dinosauria) from the late cretaceous (Maastrichtian) Allen Formation of Northern Patagonia, Argentina

Mauro Aranciaga Rolando, Mauricio A. Cerroni, Jordi A. Garcia Marsà, Federico I. Agnolín, Matías J. Motta, Sebastián Rozadilla, Federico Brisson Eglí, Fernando E. Novas

Please cite this article as: Aranciaga Rolando, M., Cerroni, M.A., Garcia Marsà, J.A., Agnolín, F.I., Motta, Matí.J., Rozadilla, Sebastiá., Brisson Eglí, F., Novas, F.E., A new medium-sized abelisaurid (Theropoda, Dinosauria) from the late cretaceous (Maastrichtian) Allen Formation of Northern Patagonia, Argentina, *Journal of South American Earth Sciences* (2020), doi: https://doi.org/10.1016/j.jsames.2020.102915.

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

A New Medium-sized Abelisaurid (Theropoda, Dinosauria) from the late Cretaceous (Maastrichtian) Allen Formation of Northern Patagonia, Argentina.

Mauro Aranciaga Rolando, [1,2*]; Mauricio A. Cerroni[1,*]; Jordi A. Garcia Marsà[1]; Federico l. Agnolín[1,2]; Matías J. Motta[1]; Sebastián Rozadilla [1]; Federico Brisson Eglí [1]; *and* Fernando E. Novas[1].

[1] Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Consejo Nacional de Investigaciones Científicas y Técnicas – CONICET, Buenos Aires, Argentina;

e-mails: mauro.a_guido@hotmail.com, mauricio.cerroni@gmail.com, jagmdarwinista@gmail.com, fedeagnolin@yahoo.com.ar, matiasjmotta@gmail.com, sebastianrozadilla@gmail.com, fedebe@gmail.com, fernovas@yahoo.com.ar

[2] Museo Municipal de Ciencias Naturales "Carlos Ameghino", Mercedes, Argentina.

e-mails: mauro.a_guido@hotmail.com, fedeagnolin@yahoo.com.ar

*Corresponding authors

Short title: A new medium-sized abelisaurid from Patagonia

Abstract: Abelisaurid theropods are well known in Cretaceous beds along South America, particularly Patagonia. However, the record of latest Cretaceous abelisauroids is still far from satisfactory. Until recently, few taxa were described from Maastrichtian beds: *Carnotaurus sastrei* and *Quilmesaurus curriei*, but also perhaps *Abelisaurus comahuensis*. In this contribution, we describe a new genus and species (*Niebla antiqua* gen. et sp. nov.), of medium-sized abelisaurid coming from Late Cretaceous (Maastrichtian) beds from Río Negro province, northern Patagonia, Argentina. The paleohistological analysis shows that this individual has reached the somatical maturity and that it represents an adult of a mid-sized abelisaurid. The specimen is represented by a nearly complete braincase, fragmentary jaw and teeth, relatively complete scapulocoracoid, dorsal ribs and incomplete vertebrae. The new taxon is relatively small, much smaller than other coeval abelisaurids such as *Carnotaurus* and *Abelisaurus*. The braincase shows autapomorphic features such a dorsoventrally tall basal tuber and postemporal foramen enclosed by parietal and exoccipitals. The scapulocoracoid is notably similar to that of *Carnotaurus* in having a posterodorsally oriented glenoid, a dorsoventrally expanded and wide coraco-scapular plate, and a very narrow and straight scapular blade. These features are very different from those of other abelisaurids, which may indicate a unique conformation of the pectoral girdle among these South American theropods.

THE Cretaceous record of abelisaurid theropods in Patagonia is by far the richest of the Southern Hemisphere when compared with other Gondwana landmasses (Novas *et al.* 2013; Delcourt 2018). Patagonia badlands have yielded a high number of informative abelisaurid specimens, including *Abelisaurus* (Bonaparte & Novas, 1985), *Carnotaurus* (Bonaparte 1985), *Aucasaurus* (Coria *et al.* 2002), *Ekrixinatosaurus* (Calvo *et al.* 2004), *Skorpiovenator* (Canale *et al.* 2009), and *Viavenator* (Filippi *et al.* 2016). Despite the fact that most of these records come from Neuquén province, abelisaurids have also been reported for from Chubut, Santa Cruz, and Río Negro provinces. Particularly, Rio Negro province has yielded few named taxa, such as *Abelisaurus* (Bonaparte & Novas, 1985), *Quilmesaurus* (Coria, 2001) and the recently described *Tralkasaurus* (Cerroni *et al.* 2020). Among them, relatively complete cranial material is restricted just to *Abelisaurus*.

Here we report a new species of abelisaurid theropod from the Late Cretaceous of Rio Negro province, Patagonia, Argentina. The new taxon is a medium-sized specimen with a well-preserved braincase as well as pectoral and axial elements. The aim of present contribution is to describe the new taxon and compare it with coeval abelisaurids.

MATERIAL AND METHODS

Locality and age. The only known specimen here described comes from the Matadero Hill (67°23'22.13"W; 39°30'27.08"S; Fig. 1), located within the Arriagada Farm, at 70 km south from General Roca city, Río Negro province, Argentina. The specimen was found associated in an area of 2 m^2 approximately. The bones of the specimen were found intermingled and not in articulation.

The specimen comes from the top of the Allen Formation, Late Cretaceous (Maastrichtian) of the Neuquén Group (Garrido 2010). This stratigraphic unit is composed by sandstones, mudstones and pelites reaching about 70 meters thickand represents shallow water courses, bearing freshwater and brackish vertebrates and mollusks (Casadío 1994; Martinelli & Forasiepi, 2004). Dinosaurs are well-known in Allen Formation, and include non-avian theropods such as the abelisaurid *Quilmesaurus curriei* (Coria, 2001), indeterminate tetanurans (Coria and Salgado 2005), the alvarezsaur *Bonapartenykus ultimus* (Agnolin *et al.* 2012), the large-sized unenlagiid *Austroraptor cabazai* (Novas *et al.* 2009), as well as the birds *Limenavis patagonica* (Clarke and Chiappe 2001) and *Lamarqueavis australis* (Agnolin 2010).

The abelisaurid *Abelisaurus comahuensis* was long thought to come from the Anacleto Formation, from sedimentary beds near Pellegrini Lake (Heredia & Salgado 1999; Leanza *et al.* 2004). However, a recent communication referred *Abelisaurus* to the lower member of the Allen Formation (Delaloye & Garrido 2017). Nonetheless, Giannechini *et al.* (2015), following information from local farmers, raised the possibility that the *Abelisaurus* holotype does not come from Pellegrini Lake, and instead, belongs to a farm close to Salitral Moreno in which continental sediments from Allen Formation outcrops; however, as pointed out these authors there is no record or field notes to assert this line of evidence. Thus, until more evidence becomes published, we regard the stratigraphic position of *Abelisaurus* as uncertain.

CT scanning. The holotype braincase of *Niebla antiqua* (MPCN-PV-796) was CT-scanned at the TCba Centro de Diagnostico Salguero (Buenos Aires, Argentina) using a CT 64 Ingenuity Core medical tomographer. The slice thickness was of 0.8 mm and the scan

energy parameters were of 219 mA and 140 kV. The virtual three-dimensional cranial endocast and inner ear were obtained and visualized using the software 3DSlicer v4.10 (Fedorov *et al.* 2012). The resultant 3D models were exported (.stl) and coloured using DesignSpark Mechanical 4.0 (see Supplementary 3D Material). Final modifications were made with Adobe Photoshop CS6.

Anatomical terminology. We follow the terminology of braincase anatomy employed by Paulina-Carabajal (2011*a, b*). Due to the lack of a clear neutral position of the pectoral girdle among theropods, we describe it with the long axis of the scapular blade vertically oriented (Brochu 2003). For descriptive purposes, we follow Burch & Carrano (2012) and Burch (2017) regarding the position of the scapulocoracoid and nomenclature of muscles.

Palaeohistology. Palaeohistological analysis was conducted on the basis of a transverse section of a dorsal rib of the holotype of the new taxon. Thin section was prepared following the method outlined by Chinsamy & Raath (1992). The bone was embedded in a clear epoxy resin (Araldite© GY 279, catalyzed with Aradur® hY 951) and left for 24 hours to set. This bone was divided in smaller resin blocks perpendicular to the long axis of the bone, using a cut diamond tipped saw within a Ken 9025 grinding machine. A single surface of each resin block was then affixed to a frosted petrographic glass slide using the same resin used for embedding and left to set for a further 24 hours. The sections were wet-ground to approximately 60 µm thick and polished using a Prazis APL-S polishing machine with abrasive papers of increasing grit size (P80, P120, P320, P400, P600, P1200, P1500, P2000, P3000). The histological sample was studied using a Nikon E400 petrographic polarizing microscope under normal, polarized, and lambda types of light.

Histological nomenclature, including growth marks, follows Francillon-Vieillot *et al.* (1990). Following the later authors, the lines of arrested growth (LAGs) are a type of cementing line that represents temporary but complete cessation of appositional growth. The annulae consist on narrow layers of parallel fibered or lamellar bone that reflect periods of relatively slow growth rates. The term growth mark is here used for both LAGs and annulus.

Phylogenetic analysis. We scored *Niebla* in the data matrix of Filippi *et al.* (2016). To the original data matrix, we add four scapulocoracoid characters (see SI): orientation of the glenoid (Ch. 417); scapular blade length/width ratio (Ch. 418); size of coracoid (Ch. 419); and position of scapulocoracoid suture (Ch. 420). However, we removed several fragmentary and uninformative taxa as well as those specimens of uncertain ceratosaur affinities, such as *Caramillasaurus* (Sanchez Hernandez & Benton 2012), Cerro Bayo taxon (Coria *et al.* 2006), *Genusaurus* (Accarie *et al.* 1995), La Bouchard taxon (Allain & Pereda-Suberbiola 2003), *Kryptops* maxilla (Farke & Sertich 2013), *Laevisuchus* (Rauhut & Carrano 2016), *Tarascosaurus* (Le Loeuff & Buffetaut 1991), Porcieux specimen (Buffetaut *et al.* 1988), and the postcranium of *Kryptops* (Novas *et al.* 2013).

The data matrix was analyzed here under equally weighted parsimony using TNT 1.5 (Goloboff *et al.* 2008; Goloboff & Catalano 2016). In both cases, a new technologies search of 50000 replicates of Wagner trees followed by TBR branch-swapping algorithm (holding 100 trees per replication) was performed. The best trees obtained at the end of the replicates were subjected to a final round of TBR branch swapping. Branches with a maximum possible length of zero among any of the recovered most parsimonious trees were collapsed (rule 3 of Swofford & Begle 1993; Coddington & Scharff 1994). Characters

3, 6, 15,19, 23, 24, 25, 26, 43, 48, 56, 58, 59, 60, 63, 72, 76, 79, 87, 88, 96, 97, 98, 101, 102, 124, 126, 127, 132, 154, 163, 174, 179, 183, 198, 201, 202, 206, 207, 225, 237, 245, 248, 256, 261, 268, 272, 282, 293, 297, 314, 319, 329, 370, 371, 372, 376, 378, 383, 388, 395, 400, 408, 413 were treated as additive (=ordered) following the original settings. As a measure of branch support, decay indices (=Bremer support) were calculated (Bremer 1988, 1994), and as a measure of branch stability, a bootstrap resampling analysis (Felsenstein 1985) was conducted. Both absolute and GC (i.e., difference between the frequency whereby the original group and the most frequent contradictory group are recovered in the pseudoreplications; Goloboff *et al.* 2003) bootstrap frequencies are reported. Both consistency and retention indexes were obtained. Regarding *Aucasaurus*, the holotype material is not available for its study and, for this reason, all the comparisons were made from the original publication of this taxa.

***Institutional abbreviations.* MACN-CH:** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Chubut Collection, Ciudad Autónoma de Buenos Aires, Argentina; **MMCh-PV**: Museo Municipal Ernesto Bachmann, Villa El Chocón, Neuquén province, Argentina; **MPCN**: Museo Patagónico de Ciencias Naturales, General Roca, Río Negro Province, Argentina.

SYSTEMATIC PALAEONTOLOGY

Theropoda Marsh, 1881

Ceratosauria Marsh, 1884

Abelisauroidea Bonaparte, 1991

Abelisauridae Bonaparte and Novas, 1985

Niebla antiqua gen. et sp. nov.

Zoo bank registration: urn:lsid:zoobank.org:pub:9664B915-0C4F-445D-8507

552AC8484DB2

Derivation of name. Niebla, from the Spanish "mist" in reference to the foggy days during the excavation of the specimen; *antiqua*, comes from the Latin "old" and makes reference to the age of the specimen.

Holotype. MPCN-PV-796 is comprised by complete braincase, incomplete left dentary, isolated teeth, dorsal vertebral centra and ribs, and right scapulocoracoid (Fig. 1). The specimen was found associated but not in articulation.

Diagnosis. Abelisaurid theropod diagnosable on the basis of the following combination of characters (autapomorphies marked by an asterisk): 1) strongly thickened and heavily sculptured frontals, 2) frontals with deep longitudinal groove surrounding the supraorbital swelling*, 3) frontals with short bony platform for the contact with the nasal, 4) anteroposteriorly elongate supratemporal fenestra *, 5) parietal with posterolaterally oriented parietal alae*, 6) nuchal wedge of supraoccipital bone subequal in dorsoventral depth to the dorsoventral height of the occipital condyle*, 5) associated groove of the postemporal foramen completely enclosed by parietal and exoccipital-opisthotic bones*, 6) bony plate below the occipital condyle subrectangular in contour and dorsoventrally taller

than transversely wide*, 7) forebrain with large olfactory tract and bulbs, and 8) paired laminae over the mesethmoid.

Type locality. Cerro Matadero (67°23'22.13"W; 39°30'27.08"S; Fig. 1), Arriagada Farm, located70 km south from General Roca city, Río Negro province, Argentina.

DESCRIPTION

The type specimen of *Niebla antiqua* is represented by two incomplete dorsal centra, weathered dorsal ribs, a scapulocoracoid and fragmentary skull bones including a nearly complete braincase and the tip of the right dentary (Fig. 1).

Skull

The braincase of *Niebla* it is exquisitely preserved and shows little deformation, evidenced by some lateral compression (Fig. 2). The only missing portions correspond to the distal end of the paroccipital processes, most of the nuchal crest and the distal tips of the basipterygoid processes. The interorbital septum is slightly broken and pushed to the left lateral side. The cultriform process is complete but isolated from the skull. The excellent preservation of the braincase allows the recognition of most cranial nerves (CNs) exits and vascular foramina. The bones of the skull are tightly fused and sutures are not clear.

Frontal. The frontal bones are firmly fused into a single element that preserves well-defined sutures with neighbouring bones (Fig. 2). The frontals are strongly thickened, being dorsoventrally thicker on the supraorbital flange, forming supraorbital bulges or swellings. The dorsal surface of the bulges is convex (Fig. 3), and between both supraorbital bulges,

there is a concave median depression which is also found in some abelisaurids such as *Abelisaurus* and *Aucasaurus* (Paulina-Carabajal 2011*a*). In dorsal view, the frontals are subquadrangular in contour, and show a strong ornamentation composed by anastomosed grooves, small and irregular tubercles, and shallow pits. The ornamentation is well marked on the posterior half of the frontal, in which the tubercles are variable in size and shape, some being relatively large. At the central concave surface of the frontals, there are some longitudinally oriented grooves that differ from the randomly distributed anastomosed grooves present in the remaining frontal surface. The anterior half of the frontals is less sculptured, with few tubercles and some anastomosed grooves. Particularly, the supraorbital bulges are bordered medially by a deep and irregular groove that begins in the frontolacrimal contact and ends over the anterior margin of the supratemporal fossa; such groove also exhibits few and relatively large pits.

The anterior end of the frontal shows an anteroposteriorly short and transversely wide, tongue-shaped platform for the contact with the nasal (Fig. 4). The posterior margin of the platform exhibits an interdigitate suture for the nasals whereas the remaining articular surface shows longitudinal grooves. The bony platform roofs the sphenethmoids and would extend ventral to the nasals. This surface is notably anteroposteriorly short when compared with the relatively longer surface present in *Majungasaurus* (Sampson & Witmer 2007) and *Arcovenator* (Tortosa *et al.* 2013: Fig. 2). The contact for the lacrimal is characterized by a deep and broad notch which houses a socket that would house a prefrontal prong, as reported for *Masiakasaurus* (Carrano *et al.* 2011) and *Majungasaurus* (Sampson & Witmer 2007).

Posteriorly, the frontal is deeply excavated by the supratemporal fossae (Fig. 2); the anterior margin of the supratemporal fossa is strongly curved backwards and forms a marked step between the fossa and the frontal roof (Fig. 2A). Each supratemporal fossa is transversely wide and deep, being transversely wider than anteroposteriorly long, a condition shared by *Viavenator* (Filippi *et al.* 2017) and *Majungasaurus* (Sampson & Witmer 2007). The limit between frontal and parietal is marked by a transverse and subtle suture, at the level of a wide and rhomboidal-shaped shallow fossa. The limit between these bones is also marked by a change in ornamentation: the part corresponding to the frontal is highly sculptured, whereas that corresponding to the parietal is almost smooth.

In ventral view, the frontal roofs the lateral walls of the braincase; the sutures between both are clearly visible (Fig. 2). The ventral surface of the frontals is almost smooth, with exception of some vascular foramina and grooves. These become more abundant towards the orbital rim, close to the postorbital-frontal contact; the vascular furrows run from the medial surface and are laterally oriented towards the orbital rim. Several vascular foramina are also visible along the suture between frontals and the lateral walls of the braincase.

Parietal. The parietal bone is incompletely preserved and is almost represented by the sagittal crest and part of the parietal alae (Fig. 2). As the frontal bones, the parietals are fused to each other. The suture with the frontals is evidenced by a faint and irregular suture, which is almost transversely oriented. In dorsal view, parietal ornamentation is almost smooth.

The sagittal crest is transversely wide and becomes posteriorly narrow, resulting in a subtriangular contour with a posteriorly directed apex. The broad sagittal crest separates the supratemporal fossae. Posteriorly, the connection with the parietal eminence is not preserved. The sagittal crest is relatively flat and sub-horizontally oriented in lateral view; this condition resembles that present in *Aucasaurus*, *Ekrixinatosaurus*, and *Rugops* (Sereno *et al.* 2004; Paulina-Carabajal 2011*a*), contrasting with the narrow and posteriorly inclined crest of *Abelisaurus*, *Carnotaurus* and *Majungasaurus* (Paulina-Carabajal 2011*b*). The poorly preserved parietal ala is represented by its ventral portion reduced to a thin bony sheet. The ala is posterolaterally directed, a plesiomorphic trait also present in *Ceratosaurus* and *Eoabelisaurus* (Madsen & Welles 2000; Pol & Rauhut 2012), but contrasting with most abelisaurids in which the parietal alae are strongly laterally projected (Paulina Carabajal 2011*a,b*).

Supraoccipital. Only the ventral part of the supraoccipital has been preserved (Fig. 4). The supraoccipital crest is sub-vertically oriented and it is transversely thick, being broader than the supraoccipital crest of *Carnotaurus* and *Majungasaurus* (Sampson & Witmer 2007; Paulina-Carabajal 2011*b*). It is not clear if the supraoccipital forms part of the dorsal margin of the foramen magnum because of its complete fusion with the exoccipital-opisthotic. The large opening representing the exit foramen for the middle caudal cerebral veins are located lateral to the supraoccipital, as occurs in *Majungasaurus* and *Arcovenator* (Tortosa *et al.* 2013). Between the middle cerebral veins exit and the parietal ala, there is a narrow groove that runs dorsomedially and ends in a foramen (Figs 4, 5A), which probably corresponds to the postemporal foramen as occurs in other theropods such as *Majungasaurus*, *Carnotaurus* and *Allosaurus* (Sampson & Witmer 2007; Paulina Carabajal

2011*b*); further, the postemporal foramen takes course into the supratemporal fenestra. In *Niebla*, the groove associated to the postemporal foramen is exclusively delimited by the parietal and exoccipital-opisthothic bones, whereas in many theropods this groove is delimited by parietal, exoccipital-opisthothic and squamosal bones (Sampson & Witmer 2007).

Exoccipital-opisthothic. As in most theropods, the sutures of the exoccipital-opisthothic bones are obscured by fusion, resulting in an otoccipital complex (Currie 1997). These bones delimit the lateral and probably the dorsal margins of the foramen magnum (Fig. 4). This foramen is subcircular contour and is transversely narrower than the occipital condyle. The exoccipital-opisthothic forms the neck of the occipital condyle, excluding the basioccipital from the participation of the foramen magnum. The paracondylar recesses are relatively deep excavations placed lateral to the occipital condyle. At the bottom of the paracondylar recesses there are three foramina: two small and posteriorly facing foramina which correspond to separate exit of the metotic foramen (which houses the exit passages for the CN IX-XI), whereas a larger and medially facing foramen corresponds to the exit of the hypoglossal cranial nerve (CN XII) (Fig. 5B).

The ventral surface of the exoccipital-opisthothic is fused to the basisphenoid, forming the crista tuberalis (Fig. 2). In posterior view, the crista tuberalis is sub-vertically oriented (Fig. 4) and is nearly straight as in *Abelisaurus* and *Carnotaurus* (Paulina-Carabajal 2011*a, b*).

Only the proximal portion of the paroccipital processes is preserved (Fig. 4). The preserved portion indicates that the dorsoventral depth of the paroccipital processes is

subequal in height relative to the foramen magnum. The paroccipital processes exhibit a sub-horizontally oriented and sharp crest, below level of the parietal alae. This crest is ventrally arched, similar to that present in *Majungasurus* and *Viavenator* (Sampson & Witmer 2007; Paulina-Carabajal & Filippi 2017). The posterior surface of the paroccipital process is slightly concave. Anteriorly, the base of the paroccipital process continues with the prootic through the otosphenoidal crest (Fig. 3). This crest extends anteroposteriorly from the paroccipital process to the dorsal level of the CN V (trigeminal nerve) exit; also, the otosphenoidal crest overhangs the collumelar recess.

Basioccipital. The basioccipital forms the body of the occipital condyle and the basal tubera (Fig. 4). The occipital condyle is slightly posteroventrally directed, as in other abelisaurids (Wilson *et al.* 2003; Sampson & Witmer 2007). It has a hemispherical contour and is slightly wider than the foramen magnum (Fig. 4). The dorsal groove for the spinal cord is wide, as occurs in some abelisaurids such as *Majungasaurus* and *Arcovenator* (Tortosa *et al.* 2013), and differs from the narrower groove of *Carnotaurus* (MACN-PV 894). The ventral edge of the occipital condyle is well-developed ventrally and forms a bony lip. The condylar neck ventral surface shows a faint median longitudinal crest, less prominent than in *Carnotaurus*, *Abelisaurus* and *Majungasaurus* (Sampson & Witmer 2007; Paulina-Carabajal 2011*a*).

The basal tubera are completely fused to the crista tuberalis of the exoccipital-opisthotic and form a sub-rectangular plate extending below the occipital condyle (Fig. 4), as in other abelisaurids (e.g., *Abelisaurus*, *Carnotaurus*, Paulina-Carabajal 2011*a,b*; *Majungasaurus*, Sampson & Witmer 2007; *Viavenator*, Filippi *et al.* 2017). The bony plate in *Niebla* is remarkably dorsoventrally taller than transversely wide, being two and half

times taller than the occipital condyle, and with a transverse width that barely exceeds twice the width of the occipital condyle. This differs from the broader platforms of the basioccipital seen in the abelisauroids *Abelisaurus*, *Majungasaurus*, *Carnotaurus* and *Masiakasaurus* (Carrano *et al.* 2011; Paulina-Carabajal 2011*a, b*). A faint and wrinkled subvertical crest that diverges towards the basal tubera is present at the midline. The sub-condylar recesses, located at both sides of the midline crest, are represented by a poorly defined and almost flat surface covered by scars probably for the insertion of craniocervical muscles (Snively & Russell 2007). The ventral margin of the bony plate shows a median notch, similar to the condition present in *Arcovenator* and *Majungasaurus* (Tortosa *et al.* 2013), and differs from the straight margin present in *Carnotaurus* (Paulina-Carabajal 2011*a, b*).

Basisphenoid. The basisphenoid delimits the ventral surface of the braincase; it is almost completely preserved and lacks the distal tip of the basipterygoid processes (Figs. 2,3). The basisphenoid is tightly fused to the surrounding bones (basioccipital, opisthothic, prootic, and laterosphenoid). In ventral view, there is a faint suture represented by a shallow groove located between the basisphenoid and basal tubera (Fig. 2B). The aperture of the basisphenoidal recess is teardrop-shaped in contour and deeply excavates the ventral aspect of the bone as in other abelisauroids (Carrano & Sampson 2008; Paulina-Carabajal 2011*a, b*; Filippi *et al.* 2017). This recess does not invade the condylar neck as shown by CT scans. The bony lateral walls delimiting the basisphenoidal recess are thick and anteroposteriorly short. The anterior bony wall of the basisphenoidal recess is thick and joins the base of the basipterygoid processes. Anterior to this bony wall (Fig. 2), the subsellar recess is

represented by a relatively large and blind cavity ventral to the cultriform process, as occurs in several abelisaurids (Paulina-Carabajal 2011*a,b*).

In lateral view, the basiphenoid is excavated by the lateral tympanic recess (Fig. 3). This recess is partially overhanged by a thin-walled preotic pendant. The lateral tympanic recess is represented by a single and uniform excavation, lacking bony septa and accessory depressions or sub-recesses as those present in *Abelisaurus* (Paulina-Carabajal 2011*a*), *Masikasaurus* (Carrano *et al.* 2011), and some basal tetanurans (e.g., *Piatnizkysaurus* Bonaparte, 1979; Rauhut 2004; *Allosaurus*; Chure & Madsen 1996; Chure & Loewen 2020). Anterior to the preotic pendant, and below the CNs III and IV openings, there is a large foramen that probably transmitted the sphenoidal artery.

The cultriform process is almost complete (Fig. 3), though it is broken from its original position. It is represented by a transversely narrow bony sheet (~2 mm) that is anterodorsally projected and is totally fused to the interorbital septum. The smooth surface of the cultriform process contrasts with the highly striated surface of the interorbital septum (Fig 3B).

Prootic. The prootic is strongly fused to the surrounding bones (Fig. 3). The contact between the prootic and opisthothic-exoccipital is represented by the collumelar recess. This recess is shallow and delimited posteriorly by the crista tuberalis, dorsally by the otosphenoidal crest and anteriorly by a subvertical bar; the latter extends from the otosphenoidal crest to the dorsal end of the lateral tympanic recess (Fig. 3). Anterior to the subvertical bar there is a small foramen which represents the facial nerve (CN VII) exit. The relatively shallow collumelar recess of *Niebla* differs from the deep recess present in

Majungasaurus (MACN-PV 19770, cast). A well-defined stapedial groove is present along the dorsolateral surface of the bone and ends in a large oval fenestra. A small foramen is placed posterior to the oval fenestra and below the collumelar recess (within the stapedial groove). Such foramen may correspond to the tympanic branch exit of the glossopharyngeal nerve (CN IXty) (Fig. 5), as occurs in the megaraptoran *Murusraptor* (Paulina-Carabajal & Currie 2017). A large foramen located just anterior to the oval fenestra and separated by a weak septum, would corresponds to the cochlear fenestra as in *Majungasaurus* (Sampson & Witmer 2007).

Dorsal to the preotic pendant, there is a large and oval foramen (7 mm) surrounded by a large fossa (Figs. 3A, 5C), that corresponds to the maxilla-mandibular nerve (CN $V_{2,3}$); this foramen marks the boundary between prootic and laterosphenoid (Fig. 3). The CN $V_{2,3}$ foramen is aligned with the nuchal crest, as occurs in some abelisaurids such as *Carnotaurus* and *Majungasaurus* (Paulina-Carabajal 2011*b*). The foramen for the ophthalmic branch of the trigeminal nerve (CN V_1) is not well preserved, but its corresponding groove is well-defined (Fig. 5C). This groove is sub-horizontally oriented and runs anterior from the CN $V_{2,3}$. In the left side of the skull (Figs. 3A, 5D), there is a subvertical bony bar which extends from the laterosphenoid to the dorsal margin of the preotic pendant, and partially delimits the CN V_1. Similar bony bars were interpreted as the external separation of the CN V_1 from the CN $V_{2,3}$ in the laterosphenoid of *Abelisaurus* and *Majungasaurus* (Sampson & Witmer 2007; Paulina-Carabajal 2011*a*), whereas in *Niebla* and *Carnotaurus* this separation is clear (Paulina-Carabajal 2011*b*). Curiously, at the right side of the skull (Fig. 3B) such bony bar seems to be lost, which could indicate that the bony bar is usually poorly ossified.

Laterosphenoid. The postorbital process is dorsally projected and slightly laterally surpasses the level of the lateral margin of the frontals (Fig. 3). The ventral end is marked by a broad and oval contact for postorbital. The ventral surface of the laterosphenoid exhibits a wide groove that runs along the antotic crest towards the dorsal margin of the furrow for the CN V_1. The above mentioned groove (probably related to the circumorbital membrane; Sampson and Witmer 2007) is partially visible in lateral view; it widens towards the CN V_1, and appears to be broader than in *Majungasaurus* (MACN-PV 19770, cast), whereas other abelisaurids it is totally absent (e.g., *Carnotaurus*, *Abelisaurus*). As mentioned above, the ophthalmic branch of the trigeminal nerve (CN V_1) faces anteriorly and is partially separated from the CN $V_{2,3}$ by a subvertical bar.

Orbitosphenoid. The sutures of the orbithosphenoid with surrounding elements (frontal, ethmoidal complex, laterosphenoid and interobital septum) are not discernible (Fig. 3). The limit between orbithosphenoid and laterosphenoid is marked by the foramina of the oculomotor and trochlear cranial nerves (CN III and IV, respectively) that innervated extraocular muscles. Anterior to the preotic pendant and posteroventral to the optic nerve (CN II) there is a deep incisure and a shallow fossa, each one separated by a thin-walled septum; close to these incisures there is a small fossa. The small fossa faces laterally and houses a foramen, probably for the abducens nerve (CN VI). On the other hand, a medially placed and deep incisure corresponds to the exit for the CNs III and IV, whose foramina are not visible because this space is filled with matrix (Fig. 5 C, D). A large and subcircular foramen, located just below the CN II and anterior to the deep incisure, probably corresponds to the exit of the sphenoidal artery. Similar large openings are present in

Majungasaurus (Sampson & Witmer 2007) and *Carnotaurus* ("fenestra rostral to the pituitary fossa", Paulina-Carabajal 2011*b*).

The optic nerve (CN II) exit is represented by a large and sub-oval foramen (10 mm in dorsoventral height). Posterodorsal to the CN II exit, within the orbitosphenoid-frontal contact, there is a vascular foramen probably correlated with the exit of the orbitocerebral vein.

Interorbital septum. The interorbital septum of *Niebla* is almost complete (Fig. 2). It is entirely fused to the orbithosphenoid posteriorly, to the mesethmoid dorsally and to the cultriform process ventrally, although the latter is broken due taphonomical breakage. The interorbital septum is represented by a median longitudinal wall that is transversely thin and dorsoventrally extended. The external surface of the septum is sculptured by subparallel striations, whereas the cultriform process and the sphenethmoid are almost smooth. The interorbital septum was probably the result of the calcification of a cartilaginous sheet, as occurs in extant archosaurs (Sampson & Witmer 2007). An ossified interorbital septum is present in ceratosaurs (e.g., *Carnotaurus*, *Ceratosaurus*, *Viavenator*, *Indosaurus, Eoabelisaurus*; Novas *et al.* 2004; Paulina-Carabajal 2011*a, b*; Pol & Rauhut 2012; Filippi *et al.* 2017), and carcharodontosaurid tetanurans (e.g., *Giganotosaurus*; Coria & Currie 2002).

A large and long interorbital window within the interobital septum communicates both orbital spaces, as occurs in *Abelisaurus*, *Majungasaurus* and *Arcovenator* (Tortosa *et al.* 2013), whereas in *Carnotaurus* and *Viavenator* the interorbital septum is complete (Filippi *et al.* 2017).

Ethmoidal complex. The ossified ethmoidal complex is exquisitely preserved (Figs. 2, 4, 5) and is composed by the sphenethmoids and mesethmoid. As occurs in other ceratosaurs, this complex is coosified with the interorbital septum (Sampson & Witmer 2007). The sphenethmoids encloses the olfactory bulbs and tracts, whereas the mesethmoid is a median septum that bisects the anterior part of the olfactory bulbs (Ali *et al.* 2008; Paulina-Carabajal 2011*a, b*). Both sphenethmoids and mesethmoid delimitate the olfactory nerve foramina (CN I) which are relatively large, subtriangular in contour and faces rearward.

The sphenethmoids contact the frontals dorsally but its suture remains visible. Some vascular foramina are present along the sphenethmoids-frontals contact. Otherwise, the suture between orbithosphenoid and interorbital septum cannot be discerned. Along its lateral surface the mesethmoid shows two longitudinally oriented, narrow and well-defined laminae delimiting almost enclosed grooves of uncertain nature. Sampson and Witmer (2007) reported similar bony ossifications in *Majungasaurus* and argued that such bony structures formed canals to accommodate branches of the olfactory and ophthalmic nerves, and the ethmoidal artery as well. However, such paired laminae may be better regarded as olfactory turbinales due its laminar and symmetrical condition, as well as its position within the nasal cavity, as hypothesized for tyrannosaurs (Witmer & Ridgely 2009, 2010).

Endocranial anatomy. The cranial endocast and the right inner ear were partially reconstructed (Fig. 6). The cranial endocast has a total length of 144 mm from the foramen magnum to the anterior end of the olfactory bulb and has an approximate volume of 64.2 cm^3; however, the endocast is not completely reconstructed. The overall conformation of the endocast is similar to that reported for other abelisaurids (e.g., *Majungasaurus*, Sampson & Witmer 2007; *Aucasaurus*, Paulina-Carabajal & Succar 2015; *Viavenator*,

Paulina-Carabajal & Filippi 2017), in which forebrain and hindbrain are sub-horizontally oriented, whereas the midbrain is angled between both regions. *Carnotaurus* may be an exception due its anteroventrally directed olfactory tract and bulbs (Cerroni & Paulina-Carabajal 2019). The dural expansion is not markedly projected dorsally, being almost aligned with the level of the forebrain.

The olfactory tract is straight in lateral view, and the olfactory bulbs are large and suboval in contour. The cerebral hemispheres are well-defined and aligned with the olfactory bulbs when viewed laterally, as occurs in many large-sized non-avian theropods (Sampson & Witmer 2007; Witmer & Ridgely 2009). Ventrally, the narrow infundibular stalk connects with a rounded pituitary body. None of the internal carotids or sphenoidal arteries passages is visible in the CT scans. The roots of the CN II are poorly defined but the reconstructed part shows that they are anteriorly divergent. The separate passages for the CNs III and IV are not clearly observed. The root of the CN V shows its base represented by a narrow stalk that is laterally expanded; this expansion probably corresponds with the Gasserian ganglion (Sampson and Witmer 2007). The CN VI extends from the hindbrain and reaches the posterior face of the pituitary body. The flocculus is a large blade-like and posterolaterally projected prominence that invades the space of the anterior semicircular canal. It is unclear in the CT scans if the flocculus reached the posterior semicircular canal, as occurs in *Viavenator* (Paulina-Carabajal & Filippi 2017). The relatively large size of the flocculus of *Niebla* resembles that present in South-American abelisaurids (e.g., *Aucasaurus*, *Carnotaurus*, *Viavenator*) in contrast with the smaller flocculus exhibited by *Majungasaurus*. The metotic passage of the CNs IX-XI (glossopharyngeal, vagus, and accessory nerves, respectively) and the CN XII

(hypoglossal) has a single trunk each one; however, the metotic passage has two separate exits (metotic foramina) within the paracondylar recess.

The inner ear was partially identified in the CT scans (Fig. 6D), with the semicircular canals incompletely reconstructed due are hardly identified in the scans; but in contrast, the vestibular region is well-defined. The lateral and anterior semicircular canals are relatively slender. Regarding the vestibule, the lagena is conical and short, as occurs in most theropods (Sampson & Witmer 2007); the ovalis and cochlea fenestrae are visible.

Dentary. Some incomplete fragments of the left dentary have been recovered, including a partial symphyseal portion (Fig. 7 A-C). The dentary shows wide alveoli that are ovoidal in contour. The lateral surface of the dentary is nearly smooth, and two nutritive foramina are located at its ventral third. Anteriorly, the bone becomes transversely thicker and shows a slightly rugose lateral surface. There is no well-defined chin, and the anterior end of the dentary becomes dorsoventrally narrower towards its tip. It shows a nearly flat ventral surface. In spite of being eroded, the symphysis was anterodorsally oriented as occurs in most abelisaurids (Canale *et al.* 2009).

Teeth. Some isolated teeth have been recovered (Fig. 7 D). The better-preserved tooth is relatively tall (2.5 times apicobasally taller than mesiodistally long), with a curved mesial margin and a straight distal one, as usually occurs in abelisaurids (Smith 2007). This tooth is asymmetrical with its mesial carina slightly medially displaced with respect to the mesiodistal axis of the element, indicating that it belongs to the anterior third of the dentary. The denticles cover the entire height of the crown, are obliquely oriented and

chisel-like, being larger towards the base and progressively decrease in size apically. The teeth are suboval in cross-section.

Postcranium

Dorsal vertebrae. Two isolated and deformed vertebral centra belonging to the dorsal region are present (Fig. 8 B). The parapophyses are absent, indicating that the vertebrae pertain to the mid- or posterior region of the backbone. The inner structure of the centrum is camerate, as occurs in other ceratosaurs (Britt 1993). The centrum is amphyplatyan; the posterior articular surface is slightly dorsoventrally taller than transversely wide. In lateral view, the centra are very elongate, and show a concave and poorly delimited blind pleurofossa. This fossa runs along almost over the entire length of the centrum, a condition observed in anterior and mid- dorsal vertebrae of *Majungasaurus*, but absent in more posterior elements (O´Connor 2007). The neural canal is transversely wide and deep, being deeper at the mid-length of the vertebral centrum.

Dorsal ribs. Incomplete dorsal ribs were recovered (Fig. 8 A, C). None of the elements preserved complete proximal or distal ends. The most complete element represents a mid-dorsal rib. In spite of being incompletely preserved, the base of large pneumatic foramina is observed. The proximalmost cross-section shows large internal chambers as occurs in other abelisaurids (O´Connor 2007; Filippi *et al.* 2017). The rib shaft is subtriangular in cross-section and is strongly medially curved. It shows a longitudinal ridge of bone.

Scapulocoracoid. The right scapulocoracoid is almost completely preserved with exception of the anterior margin and the posteroventral sternal process (Fig. 9). The scapular blade is

fragmented in three pieces and the anterior margin of its proximal end is somewhat damaged. Scapula and coracoid are totally fused and the suture is almost obliterated. The remnant of this suture is represented by an anteroposteriorly oriented ridge.

The scapular blade of *Niebla* is anteroposteriorly narrow, straight and notably elongate, its total length representing six times the anteroposterior length of its proximal third. In spite of having a subequal width almost along all its length, it shows a subtle distal expansion. In anterior view its blade is strongly medially curved. The morphology and proportions of the scapula of *Niebla* are very similar to that of *Carnotaurus* with excepttion that there is no distal expansion of the blade in the latter (Burch & Carrano 2012). In other ceratosaurs, such as *Ceratosaurus, Majungasaurus* and the preserved portion of *Masiakasaurus*, the scapular blade is anteroposteriorly wider and shows a sigmoidal curvature when it is observed in lateral view. This may be consequence of a well-developed flange for the anchoring of the *m. triceps brachii scapularis* (Burch 2017).

The lateral surface of the scapular blade is gently convex. On the other hand, the medial surface of the scapula is proximally convex and becomes concave distally. The medial surface of the blade shows a longitudinal thickening along its anterior margin. This thickening becomes shallower distally and is totally absent towards the distal tip. The thickening shows some longitudinal striations that may constitute the correlates for the *m. subscapularis* origin (Burch 2017). The posterior margin of the blade in medial view shows a deep longitudinal groove along its proximal half. Near the proximal end of the scapula this groove is transversely wide and rugose, and becomes progressively narrower and smooth towards the distal end of the blade. This groove probably represents the origin of the *m. scapulohumeralis posterior* (Burch 2017). Posteriorly, the blade becomes notably

sharp and shows rugosities that probably represent the area of insertion for the *m. subscapularis* (Burch 2017). The distal tip of the blade shows some striations are visible over the medial surface at the anterior and posterior corners, which could represent the insertion of the *m. rhomboideus* and *m. serratus profundus*, respectively (Burch 2017).

The acromion is sub-rectangular in contour and it is proximodistally low. The dorsal margin of the acromion is gently concave towards the scapular blade, and forms an obtuse angle with the main axis of the scapular blade. The lateral surface of the acromion is concave and shows, along its dorsal margin the rugosities for attachment of the *m. deltoideus clavicularis* (Burch 2017). Ventrally, the subacromial depression is shallow but anteroposteriorly wide resembling *Carnotaurus* (MACN-CH 894) and *Masiakasaurus* (Carrano *et al.* 2011), whereas in *Majungasaurus* it is notably narrow and deep (Burch & Carrano 2012). The surface of the scapular fossa is rugose, representing the origin of the *m. supracoracoideus accesorius* (Burch 2017).

Burch & Carrano (2012) pointed out that some osteological traits could be size- or ontogeny-related, as for example, the notch between acromion and coracoid blade present in *Majungasaurus* (and *Niebla* as well) is more pronounced in younger and smaller individuals than in adult and bigger specimens. The presence of this notch in the small, but somatically mature *Niebla*, contrasts with its total absence in larger ceratosaurs, such as *Ceratosaurus* and *Carnotaurus*, reinforcing the idea that presence or development of this notch is a size-related feature.

As in other abelisaurids the glenoid is relatively wide, deep and subcircular in contour (Filippi *et al.* 2017). If the scapular blade is oriented at 45° with respect to the

horizontal plane, the glenoid results posteriorly oriented, as occurs in *Carnotaurus*. On the other hand, in other basal theropods, including *Ceratosaurus, Masiakasaurus* and *Majungasaurus* the glenoid is posteroventrally oriented (Madsen & Welles 2000; Carrano *et al.* 2011; Burch & Carrano 2012). A shallow and poorly defined supraglenoid excavation is present, as in *Carnotaurus*, *Elaphrosaurus* and *Masiakasaurus* (Rauhut & Carrano 2016). This excavation shows some obliquely oriented ridges that may represent the origin of *m. triceps brachii scapularis* (Burch 2017). There is no evidence of a well-developed tubercle, indicating a reduced origin of the *m. triceps brachii scapularis*, as hypothesized for other abelisaroids (Burch 2017).

The coracoscapular plate is notably wide and its lateral surface is nearly flat. The coracoid shows a gently convex lateral surface. The surface is badly preserved but its dorsal portion shows slight striations that could be the origin of the *m. supracoracoideus* (Burch 2017). A large and suboval-shaped coracoidal foramen is present and close to the glenoid. The subglenoid cavity is shallow, as observed in *Carnotaurus* (Bonaparte *et al.* 1990) and *Viavenator* (Filippi *et al.* 2017). The ventral process is poorly preserved but it is relatively wide and ventrally projected, surpassing in height the width of the scapular blade, a condition that resembles *Carnotaurus* and contrasts with *Viavenator, Majungasaurus* and *Masiakasaurus,* in which the ventral process is ventrally short and hooked, and its dorsoventral height does not surpass the anteroposterior width of the scapular blade. The posteroventral process has a well-developed proximal concavity that represents a correlate for origin of *m. coracobrachialis* (Burch 2017). In *Niebla*, there is not a biceps tubercle or a clear muscle scar for the m. *biceps brachii* attachment, as in the case of other abelisauroids such as *Carnotaurus* and *Majungasaurus* (Burch & Carrano 2012; Burch 2017). The

coracoid below the glenoid is extensive, as in *Carnotaurus,* and represents more than two and half times the proximodistal height of the glenoid, whereas in other ceratosaurs as *Majungasaurus, Viavenator, Masiakasaurus* and *Ceratosaurus* the glenoid height represents only one and a half times the coracoidal extension below the glenoid. Medially, the coracoid has a convex surface. Dorsal to the coracoid foramen, there is a small and rugose concavity that would represent the origin of the *m. subcoracoideus* (Burch 2017).

Histological analysis

The dorsal rib employed by the histological analysis suffered some distortion due to diagenetic processes. Some fractures match with the lines of arrested growth (LAGs). These growth marks generate planes of weakness in the specimen, which result in postmortem fractures (Fig. 9: A, B). However, this has not affected the main features of the cortex of compact bone and the medullary cavity. The medullary cavity is reduced, infilled by trabeculae and delimited by a thin inner circumferential layer (ICL). The ICL and trabeculae are composed by lamellar layers of secondary endosteal bone with scarce osteocyte lacunae (Fig. 10: C). The cortex is well-vascularized by primary and secondary osteons which are longitudinally oriented. The cortex has been strongly remodeled and is mainly composed of dense Haversian bone tissue (Fig. 10: C, D). Secondary osteons of more than one single generation are observed in the inner cortex, but also in the middle cortex, although in the latter are scarcer. There are some Volkman's canals located between secondary osteons. Non-remodeled primary bone is observed in some spaces between the secondary osteons in the middle cortex, but especially in some areas of the outer cortex, and is totally present in the subperiosteum. The presence of rounded osteocyte lacunae,

randomly organized around the cortex, indicates that the matrix consists of woven fibered bone in the middle and outer cortex. The subperiosteum is constituted by a parallel-fibered bone tissue. It is avascular in almost all the sample, but in some areas, there are still primary osteons and Volkman's channels, although scarcer with respect to the outer cortex, which is not affected by the Haversian system. The LAGs were probably present around the cortex, but have been obliterated by the Haversian system. The LAGs open dorsally in the rib, increasing the space between them (Fig. 10: B). In the outer cortex and the subperiosteum at least nine LAGs are observed. In the subperiosteum, the LAGs are closely spaced between them, comprising a well-defined external fundamental system (EFS).

DISCUSSION

Phylogenetic position of *Niebla antiqua*

The phylogenetic analysis resulted in a relatively well-resolved strict consensus tree (Fig. 11). In such analysis, 176 more parsimonious trees (MPTs) of 865 steps were recovered, with a consistency index (CI) of 0,610 and a retention index (RI) of 0,723. The topology obtained is consistent with those of some previous works (Tortosa *et al.* 2013; Filippi *et al.* 2016; Cerroni *et al.* 2020), in which *Ligabueino* (Bonaparte 1996) is obtained as the sister taxa of Abelisauroidea, and *Eoabelisaurus* as the sister taxa of the clade comprising *Ligabueino* + Abelisauroidea. The enigmatic *Austrocheirus* (Ezcurra *et al.* 2010) nests within Noasauridae (Fig. 11), a phylogenetic relationship that is supported by a single character**:** presence of a flat surface in the anterior face of the tibia (Ch. 383:1). This

morphology is shared by diverse basal abelisauroids (Ezcurra *et al.* 2010) and thus, we consider the phylogenetic position of *Austrocheirus* as tentative.

Niebla has nine autapomorphies: supratemporal fenestra anteroposteriorly elongated (Ch. 95:0); parietal with posterolaterally oriented parietal alae (Ch. 99:0); length of the nuchal wedge of supraoccipital subequal to the vertical diameter of the occipital condyle (Ch. 105:0); presence of prootic with tuberosity on the margin of the crista prootica (Ch. 125:1); pneumaticity of the neural arch of presacral vertebrae moderate (Ch. 173:0); centrum of posterior presacral vertebra as high as long (Ch. 256:1); posteroventral process of coracoid reaching the glenoid facet (Ch. 295:0); posterior margin of scapular blade curves over full length (Ch. 301:0); and acromion process abruptly expanded dorsally (Ch. 304:0).

The phylogenetic analysis nested *Niebla* and derived abelisaurids (Fig. 11) within Abelisaurinae, together with *Carnotaurus, Aucausaurus* and *Abelisaurus*. The position of *Niebla* within Abelisauridae is supported by the following two synapomorphies: tooth with straight or very slightly curved distal carina (Ch. 170:1); and scapula with a concavity on its ventral margin and above the glenoid (Ch. 302:1). The Bremer support of Abelisauridae is minimal and the absolute and relative frequencies are 38% and 34%, respectively. 32 extra steps are needed to place *Niebla* outside Abelisauridae.

The Indo-Madagascan taxa *Rahiolisaurus* (Novas *et al.* 2010) and *Dahaloleky* (Farke & Sertich 2013) are recovered in a natural clade (Fig. 11) as the sister group of Brachyrostra (as occurs in Filippi *et al.* 2016, but contra Tortosa *et al.* 2013). The node *Rahiolisaurus + Dahaloleky* is supported by the presence of two pneumatic foramina in the

postaxial cervical centra (Ch. 223:0) and the absence of an anterior process on the epipophyses (Ch. 216:0).

The clade (*Rahiolisaurus* + *Dahalokely*) + Brachyrostra is supported by several synapomorphies, including presence of posterior projections on the cervical epipophyses (Ch. 217:1); anterior caudal vertebrae with circular-shaped articular surfaces (Ch. 284:1); preacetabular process of ilium with a slight angle on its dorsal margin (Ch. 338:2); postacetabular process of ilium with a marked angle on its posterior third (Ch. 344:2); and metatarsal III strongly backwards the other metatarsals (Ch. 408:2). 3 extra steps are needed to nest *Rahiolisaurus* + *Dahaloleky* with other Indo-Madagascan taxa.

Niebla is included within a polytomy including all Abelisaurinae genera by the presence of three synapormorphies (Fig. 11): lateral margin of frontals forms a slight bulge or a swell with the postorbital (Ch. 60:1); narrow scapulocoracoid (Ch. 418:1); and expanded coraracoid below the glenoid articulation (Ch. 419:1). The Bremer support of Abelisaurinae is minimal and the absolute and relative frequencies of bootstrap are 12% and -5%, respectively. 32 extra steps are needed to place *Niebla* outside Abelisaurinae. The clade Furileusauria (Filippi *et al.* 2017) was not recovered because of the low resolution among Patagonian abelisaurids.

Growth dynamics and age of *Niebla antiqua*

Previously published histological studies in Patagonian abelisaurids are restricted to *Aucasaurus* (Cerda 2015), an unnamed abelisaurid MMCh-PV 69 (Canale *et al.* 2016), and *Quilmesaurus* (Baiano & Cerda 2017). An extensive Haversian system is present in the

dorsal ribs of *Niebla*, as well as in MMCh-PV 69 and *Aucasaurus* (Cerda 2015; Canale *et al.* 2016). As in other non-avian theropods (e.g. Chinsamy-Turan 1990; Bybee *et al.* 2006; Lee & O'Connor 2013; Evans *et al.* 2015), including abelisaurids (Cerda 2015; Canale *et al.* 2016; D´Emic *et al.* 2016) the growth marks deposited in the dorsal rib identified in *Niebla* indicate that this specimen had a cyclical growth strategy, with periodic cessation of growth. However, in *Niebla* only LAGs were recorded, whereas no annulus is present, in contrast to other abelisaurids. The presence of LAGs in the outer cortex suggests an extended slowdown of the growth rate during the ontogeny of the specimen (D´Emic *et al.* 2016). The presence of LAGs very close to each other in an almost avascular matrix, results in an EFS, which suggests that the specimen has been reached its somatic maturity at time of death (Chinsamy-Turan 2005). Based on the number of growth cycles in the dorsal rib, a minimum age of nine years may be estimated for *Niebla*. This together with its anatomical traits shows us that *Niebla* represents a new species, but also a body plan more common than the previously thought for Abelisauridae (may be with a different ecological niche and hunt strategies). This leads us to think that the size diversity of abelisaurids during Cretaceous times was more complex (see below)and the histology is a necessary tool in determining the maximum size of these theropods.

Comparisons between *Niebla*, *Abelisaurus* and *Quilmesaurus* and the size diversity of abelisaurids

Abelisaurus was originally described by Bonaparte & Novas (1985) as coming from sedimentary beds of the Allen Formation (Maastrichtian), near Pellegrini Lake, Río Negro

province, Argentina. However, subsequent works indicate that Pellegrini Lake deposits may be referred to the Anacleto Formation (Campanian; Heredia & Salgado 1999; Leanza *et al.* 2004), whereas other authors referred the same beds to the lower member of Allen Formation (Delaloye & Garrido 2017). Gianechini *et al.* (2015) even cast doubts on the original geographical provenance of *Abelisaurus* holotype, but still maintained it belongs to the Allen Formation. If this is true, *Abelisaurus* may come from beds of the same age to those that yielded *Niebla*. Because of this, we made detailed comparisons between both taxa.

In dorsal view of the skull, the most remarkable feature shared by both taxa is the presence of thickened frontals at the orbital level forming marked supraorbital bulges, each one being demarked laterally by a median depression (also present in *Aucasaurus*; Paulina-Carabajal 2011*a*). Further, the ornamentation of the frontals is markedly similar, in which numerous tubercles of varying size and anastomosed grooves are scattered over the frontal surface. Another similarity includes the interdigitating suture between nasal and frontals (also shared with *Arcovenator* and *Viavenator*, Tortosa *et al.* 2013; Filippi *et al.* 2017). The supratemporal fossae in *Abelisaurus* and *Niebla* are wider than long, however the latter differs in that the fossa strongly excavates its anterolateral margin, resulting in narrow fossae, whereas in *Abelisaurus* the anterior margin of the supratemporal fossa conform a wide "U"-shape in contour.

In posterior view, *Abelisaurus* and *Niebla* share an overall morphology of the foramen magnum and occipital condyle. *Abelisaurus* shows a ventral keel on the condylar neck (Paulina-Carabajal 2011*a*), whereas in *Niebla* this keel is poorly developed. The most outstanding difference between both genera rests on the morphology of the bony plate of

the basioccipital below the occipital condyle. In *Niebla* it is distinctly dorsoventrally taller than transversely wide, whereas in *Abelisaurus*, as occurs in other abelisaurids (e.g. *Carnotaurus*, *Majungasaurus*, *Arcovenator*) the basioccipital plate are relatively low and transversely expanded. *Niebla* and *Abelisaurus* show slightly divergent basal tubera and a ventral notch; this notch is notably deep in *Niebla*.

In lateral view, the braincase of *Niebla* and *Abelisaurus* are very similar in most features (e.g., ossified interorbital septum with large interorbital window, bony bar of the laterosphenoid separating CN V_1 and CN $V_{2,3}$ exits, CN $V_{2,3}$ exit slightly anteriorly located with respect to the nuchal crest). However, as indicated in the diagnosis and in the comparative section, *Niebla* exhibits several features that are absent in *Abelisaurus* (e.g., associated groove of the postemporal foramen completely enclosed by parietal and exoccipital-opisthotic, frontals with deep longitudinal groove surrounding the supraorbital swelling).

In addition to the anatomical features that differentiate *Niebla* from *Abelisaurus*, the histological analysis revealed that *Niebla* acquired its somatical maturity at a size significantly smaller than that of *Abelisaurus*. For example, the width of the skull roof at the level of the mid-postorbital contact is considerably smaller in *Niebla* (115 mm) relative to that of *Abelisaurus* (189 mm, Paulina-Carabajal 2011*a*). Moreover, the skull of *Niebla* is even smaller than that of contemporary abelisaurids from Patagonia (Fig. 12), such as *Aucasaurus* (140 mm, Paulina-Carabajal 2011*a*) and *Carnotaurus* (200 mm, MACN-CH 894). Also, it must be noted that *Aucasaurus* it is known by being somatically mature (Cerda, 2015), whereas in *Carnotaurus* the histology has not yet conducted but strong fusion of numerous bones indicates, at least, a subadult specimen. In sum, the anatomical

and histological information provided here, confirm that *Niebla* and *Abelisaurus* were two clearly distinctive taxa, different both in size and morphology.

A more difficult task is to differentiate *Niebla* from the certainly coeval *Quilmesaurus curriei*, coming from beds of the Allen Formation in Salitral Moreno (a locality very close to the Arriagada Farm that yielded *Niebla*; Coria 2001). Because *Quilmesaurus* is only known by a partially preserved tibia and distal femur some authors doubted about its validity (Juárez Valieri *et al.* 2004). Aside from the status of *Quilmesaurus* and in spite of the absence of overlapping material with *Niebla*, the tibia and femur of the former indicate that it was a relatively medium-sized theropod (*ca.* 5.3 m, Grillo & Delcourt, 2016) which was actively growing at time of death (Baiano & Cerda 2017); indicating that *Quilmesaurus* had not yet reached the maximum size. In this way, the maximum size of *Quilmesaurus* (Fig. 12) would be longer and would achieve a size perhaps more similar to that exhibited bylarger forms from Patagonia such as *Abelisaurus* (*ca.* 7.3 m), *Aucasaurus* (*ca* .6.10 m) and *Carnotaurus* (*ca.* 7.75 m) (see Grillo and Delcourt, 2016). The body lengths of these abelisaurids are much larger than that of *Niebla* (Fig. 12), whose size range would be between 4-4.5 meters, based on the scapulocoracoid length (measurement that appear to be a reliable proxy to estimate body length; Grillo & Delcourt, 2016). The roughly coeval presence of the relatively large-sized *Quilmesaurus* and *Abelisaurus* (if it comes from Allen Formation beds), together with the small- to medium-sized *Niebla* indicate the coexistence of at least two different-sized abelisaurids in the maastrichtians enviroments of North Patagonia. Furthermore, *Niebla* constitutes the smallest abelisaurinae (Fig. 12), since *Abelisaurus*, *Aucasaurus* and *Carnotaurus* are notably larger (ranging between 6-8 m). In a more inclusive context of size diversity within

South America in the Late Cretaceous, *Niebla* remains as the smallest abelisaurid when compared with other abelisaurids such as *Xenotarsosaurus* (*ca.* 5.4 m) and *Carnotaurus* (named above) from central Patagonia, and even with much larger taxa such as *Pycnonemosaurus* (*ca.* 9 m) from Brazil (Grillo & Delcourt, 2016). Because body size is usually employed as an indirect proxy of ecological niche, it is very probable that *Niebla* occupied a different ecological role from that of coeval abelisaurids. Similarly, the finding of relatively small abelisaurids cohabiting with relatively large taxa was recently reported for Cenomanian-Turonian beds in Patagonia (Canale *et al.* 2016; Cerroni *et al.* 2020).

Moreover, cretaceous assemblages from Northern Hemisphere shed similar evidence of size diversification in different theropod groups. This occurs for tyrannosaur-dominated assemblages, in which larger tyrannosaurs coexisted with smaller taxa in Asia (Nemegt Formation, *Tarbosaurus* and *Alioramus*) and North America (Hell Creek Formation, *Tyrannosaurus* and *Nanotyrannus*), as for example (Carr et al., 2011; Brusatte & Carr, 2015). Further, other theropod families from northern hemisphere experimented similar niche diversification such as dromaeosaurids (Yixian Formation, *Microraptor* and *Tianyuraptor* Xu & Qin, 2017) and caenagnathids (Hell Creek Formation, Lamanna et al., 2014). This reinforces recent proposals suggesting that abelisaurids exhibited a wide size-based niche partitioning, including the coexistence of small-, medium- and large-sized forms (Canale *et al.*, 2016; see Cerroni *et al.* 2020). The high diversification of body sizes of abelisaurids in the Maastrichtian age may be a consequence of the absence of carcharodontosaurids, since they became extinct at that geological time (Novas et al., 2013); leading abelisaurids to take on the role of dominant predators in north Patagonia for the Late Cretaceous. However, in spite of recent discoveries that showed that

megaraptorans reached Maastrichtian times, at least for south Patagonia (Novas et al., 2019), an assemblage of large theropods composed exclusively by abelisaurids for north Patagonia remains uncertain, until new discoveries shed light regarding this issue.**Scapulocoracoid morphology of *Niebla antiqua***

As indicated in the text, the pectoral girdle of *Niebla* is very similar in gross morphology to that of *Carnotaurus* and *Aucasaurus* (however as the scapulocoracoid of this latter is not available for its study more detailed comparison could not been made) and differs from other ceratosaurs, including closely related abelisaurids such as *Viavenator* and *Majungasaurus* in several features. As indicated in the description, *Niebla* and *Carnotaurus* share a very long, narrow, and straight scapular blade, as well as an enlarged scapulocoracoidal plate due to the widened coracoid below the glenoid articulation. These features contrast with basal ceratosaurs (e.g., *Limusaurus, Elaphrosaurus, Ceratosaurus*) and remaining abelisauroids (e.g., *Majungasaurus, Viavenator*, *Rahioliosaurus*, *Masiakasaurus*) which exhibit anteroposteriorly wider and proximodistally shorter scapular blades, more ventrally oriented glenoids, low acromion, and relatively smaller coraco-scapular plates and a very low and long coracoid (Madsen & Welles 2000; Novas *et al.* 2010; Carrano *et al.* 2011; Burch & Carrano 2012; Rauhut & Carrano 2016). The derived morphology exhibited by *Niebla, Carnotaurus* and also probably *Aucasarus* may be indicative of correlated changes on soft anatomy.

Further, when the scapulacoracoid of *Niebla* and *Carnotaurus* is positioned in the "neutral pose" of Burch & Carrano (2012) some differences are observed with respect to other ceratosaurs. The "neutral pose" consists in locating the main axis of the acromion in horizontal position, resulting in that the scapular blade is in an approximate angle of about

45° with respect to the horizontal plane. In "neutral pose" the scapulocoracoid glenoid of *Majungasaurus* and *Ceratosaurus*, as occurs in other basal averostrans, is posteroventrally oriented (Carpenter 2002). However, in the case of *Niebla* and *Carnotaurus* the neutral pose results in that the glenoid orientates directly posteriorly, lacking an important ventral component. This is in agreement with the proposal of Bonaparte *et al.* (1990) who indicate that the lack of twisting of humerus and the uncrossed condition of ulna and radius in *Carnotaurus* resulted in a very unusual position of the hand, with the palmar side dorsally oriented.

In contrast to other dinosaurs, in abelisaurids the extreme reduction of the forelimb is associated with an enlarged scapulocoracoid. Burch (2017) proposed that the enlargement of the scapulocoracoid in abelisaurids may be related to a close association between the scapula and the axial skeleton (Burch 2017, and references therein). Some of the muscles attaching to the scapular blade have an important role during other activities like feeding, respiration and neck movement in extant archosaurs (Meers 2003; Codd *et al.* 2008; Otero 2018). Burch (2017) indicated for *Majungasaurus* that scapular muscles involved in respiration and feeding (e.g. *m. levator scapulae*, *m. trapezius*, and *m. serratus superficialis*) were predominantly attached to the ventral and dorsal margins of the scapulocoracoid. As we indicated previously, *Niebla* has a narrow and elongate scapular blade when is compared with that of *Majungasarus*. Some traits on the scapulocoracoid of *Niebla*, including the narrow scapular blade, glenoid surface posteriorly oriented and the lack of well-developed muscle correlates (e.g., bicep tubercle and bump for the *m. triceps brachii scapularis* origin) may be indicative of a reduced range of motion or, with respect

Majungasaurus. However, caution is needed when size estimation of soft tissues is based only on osteological correlates (Bryant and Seymour 1990).

CONCLUSIONS

Niebla antiqua represents a new abelisaurid characterized by highly derived braincase and pectoral girdle morphology. The histological analysis indicates that in spite of its relatively small size, the holotypic specimen of *Niebla* represents a somatically mature individual. The count of LAGs suggests a minimum age of nine years for *Niebla* and increases the histological evidence for these theropods. The presence of a small to middle-medium sized abelisaurid in the Upper Cretaceous shows that there is a higher diversity of derived abelisaurids in Patagonia that previously thought.

The anatomy of the scapulocoracoid of *Niebla* shows a particular morphology of the scapular girdle that departs from that known in most other ceratosaurs. The significance of this scapulocoracoid morphology is not clear yet, but may be indicative of important changes on soft anatomy. Finally, the comparison with the probably coeval *Abelisaurus* shows that both are different and distinctive taxa. It corroborates previous thoughts suggesting that we are far from satisfactorily known the diversity of South American ceratosaurs.

References

ACCARIE, H., BEAUDOIN, B., DEJAX, J., FRIES, G., and MICHARD, J. G. 1995. Découverte d'un dinosaure théropode nouveau (Genusaurus sisteronis ng, n. sp.) dans l'Albien marin de Sisteron (Alpes de Haute-Provence, France) et extension au Crétacé inférieur de la lignée cératosaurienne. *Comptes rendus de l'Académie des sciences. Série 2. Sciences de la terre et des planètes*, **320**, 327334.

AGNOLIN, F. L. 2010. An avian coracoid from the Upper Cretaceous of Patagonia, Argentina/Un coracoides de ave del Cretacico Superior de Patagonia, Argentina. *Studia Geologica Salmanticensia*, **46**, 99–120.

—, POWELL, J. E., NOVAS, F. E. and KUNDRÁT, M. 2012. "New alvarezsaurid (Dinosauria, Theropoda) from uppermost Cretaceous of north-western Patagonia with associated eggs". *Cretaceous Research*, **35**, 33–56.

ALLAIN, R., and SUBERBIOLA, X. P. 2003. Dinosaurs of France. *Comptes Rendus Palevol*, **2**, 27–44.

ALI, F., ZELENITSKY, D., THERRIEN, F. and WEISHAMPEL, D. B. 2008. Homology of the "ethmoid complex" of tyrannosaurids and its implications for the reconstruction of the olfactory apparatus of non-avian theropods. *Journal of Vertebrate Paleontology,* **28**, 123–133.

BAIANO, M. A. and CERDA I. A. 2017. Bone microstructure of *Quilmesaurus curriei* (Theropoda; Abelisauridae). *PeAPA,* **18**, R10.

BONAPARTE, J. F. 1979. Dinosaurs: a Jurassic assemblage from Patagonia. *Science*, **205**, 1377–1379.

—. 1985. "A horned Cretaceous carnosaur from Patagonia." *National Geographic Research*, **1**, 149–151.

— and NOVAS F. E. 1985. «*Abelisaurus comahuensis*, n.g., n.sp., Carnosauria del Cretácico Tardío de Patagonia». *Ameghiniana,* **29**, 259–265.

—. 1991. The Gondwanian theropod families Abelisauridae and Noasauridae. Historical Biology 5:1–25. BONAPARTE, J. F., NOVAS, F. and CORIA, R. 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. *Natural History Museum Contributions to Science,* **416**, 1–42.

—. 1996. Cretaceous tetrapods of Argentina; pp. 73–130 in G. ARRATIA (ed.), Contributions of Southern South America to Vertebrate Paleontology. Münchner Geowissenschaftliche Abhandlungen (A)30, Verlag Dr. Friedrich Pfeil, Münchner

BREMER, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution*, **42**, 795–803.

BREMER, K. R. 1994. Branch support and tree stability. *Cladistics*, **10**, 295–304.

BRITT, B. B. 1993. Pneumatic postcranial bones in dinosaurs and other archosaurs. (Unpublished doctoral thesis). University of Calgary, Calgary, AB.

BROCHU, C. A. 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Journal of Vertebrate Paleontology*, **22**, 1–138.

BRUSATTE, S. L., and CARR, T. D. The phylogeny and evolutionary history of tyrannosauroid dinosaurs. *Scientific Reports* **6**, 20252.

BRYANT, H. N., and SEYMOUR, K. L. 1990. Observations and comments on the reliability of muscle reconstruction in fossil vertebrates. *Journal of Morphology*, **206**, 109–117.

BUFFETAUT, E., MECHIN, P., and MECHIN-SALESSY, A. 1988. Un dinosaure théropode d'affinités gondwaniennes dans le Crétacé supérieur de Provence. *Comptes rendus de l'Académie des sciences. Série 2, Mécanique, Physique, Chimie, Sciences de l'univers, Sciences de la Terre*, **306**, 153–158.

BURCH, S. H., and CARRANO, M. T. 2012. An articulated pectoral girdle and forelimb of the abelisaurid theropod *Majungasaurus crenatissimus* from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology*, **32**, 1–16.

—. 2017. Myology of the forelimb of *Majungasaurus crenatissimus* (Theropoda, Abelisauridae) and the morphological consequences of extreme limb reduction. *Journal of Anatomy*, **231**, 515–531.

BYBEE, P. J., LEE, A. H. and LAMM, E. T., 2006. Sizing the Jurassic theropod dinosaur *Allosaurus*: assessing growth strategy and evolution of ontogenetic scaling of limbs. *Journal of Morphology*, **267**, 347–359.

CALVO, J. O., RUBILAR-ROGERS, D. and MORENO, K., 2004. A new abelisauridae (Dinosauria: Theropoda) from northwest Patagonia. *Ameghiniana*, **41**, 555–563.

CANALE, J. I., SCANFERLA, C. A., AGNOLÍN, F. L. and NOVAS, F. E., 2009. New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisauroid theropods. *Naturwissenschaften*, **96**, 409–414

—, CERDA, I., NOVAS, F. E. and HALUZA, A. 2016. Small-sized abelisaurid (Theropoda: Ceratosauria) remains from the Upper Cretaceous of northwest Patagonia, Argentina. *Cretaceous Research*, **62**, 18–28.

CARPENTER, K. 2002. Forelimb biomechanics of nonavian theropod dinosaurs in predation. *Senckenbergiana lethaea*, **82**, 59–75.

CARR, T. D., WILLIAMSON, T. E., BRITT, B. B., and STADTMAN, K. 2011. Evidence for high taxonomic and morphologic tyrannosauroid diversity in the Late Cretaceous (Late Campanian) of the American Southwest and a new short-skulled tyrannosaurid from the Kaiparowits formation of Utah. *Naturwissenschaften*, **98(3)**, 241-246.

CARRANO, M. T. and SAMPSON, S. D. 2008. The phylogeny of Ceratosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology*, **6**, 183–236.

—, LOEWEN, M. A. and SERTICH, J. J. W., 2011. New materials of *Masiakasaurus knopfleri* Sampson, Carrano, and Forster, 2001, and implications for the morphology of the Noasauridae (Theropoda: Ceratosauria). Smithson. *Contributions in Paleobiology*, 95.

CASADÍO, S., 1994. Estratigrafía y paleontología del intervalo Maastrichtiano-Daniano en el occidente de la provincia de La Pampa, Argentina. Tesis Doctoral Universidad Nacional de Córdoba, 420 pp. Córdoba. (Inédita).

CERDA, I. A. 2015. Estudio paleohistologico del holotipo de *Aucasaurus garridoi* (Theropoda: Abelisauridae), aspectos paleobiologicos inferidos. *Ameghiniana*, **52**, 6.

CERRONI, M. A., and PAULINA-CARABAJAL, A. 2019. Novel information on the endocranial morphology of the abelisaurid theropod *Carnotaurus sastrei*. *Comptes Rendus Palevol,* **18**, 985–995.

—, MOTTA M. J., AGNOLÍN F. L., ARANCIAGA ROLANDO A. M., BRISSÓN EGLI F. and NOVAS F. E. 2020. A new abelisaurid from the Huincul Formation (Cenomanian-Turonian; Upper Cretaceous) of Río Negro province, Argentina. *Journal of South American Earth Sciences*, **98**, 102–445.

CHINSAMY-TURAN, A. 1990. Physiological implications of the bone histology of *Syntarsus rhodesiensis* (Saurischia: Theropoda). *Palaeontologia Africana*, **27**, 77–82.

—. 2005. The Microstructure of Dinosaur Bone: Deciphering Biology with Fine-Scale Techniques. Johns Hopkins University Press, Baltimore, 195 pp.

—. and RAATH, M. A. 1992. Preparation of fossil bone for histological examination. *Paleontologia Africana*, **29**, 39–44.

CHURE D. J. and MADSEN J. H. 1996. Variation in aspects of the tympanic pneumatic system in a population of *Allosaurus fragilis* from the Morrison Formation (Upper Jurassic). *Journal of Vertebrate Paleontology*, **16**, 63–66.

— and LOEWEN M. A. 2020. Cranial anatomy of *Allosaurus jimmadseni*, a new species from the lower part of the Morrison Formation (Upper Jurassic) of Western North America. *PeerJ*, **8**, e7803.

CLARKE, J. A. and CHIAPPE, L. M. 2001. A new carinate bird from the Late Cretaceous of Patagonia (Argentina). *American Museum Novitates*, **3323**, 1–23.

CODD, J. R., MANNING, P. L., NORELL, M. A., and PERRY, S. F. 2008. Avian-like breathing mechanics in maniraptoran dinosaurs. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 157–161.

CODDINGTON, J., and SCHARFF, N. 1994. Problems with zero□length branches. *Cladistics*, **10**, 415–423.

CORIA, R. A. 2001. A new theropod from the Late Cretaceous of Patagonia. In: Tanke, D. H. et Carpenter, K. (eds). *Mesozoic Vertebrate Life*, Indiana University Press: p. 3–9.

— and CURRIE, P. J. 2002. The braincase of *Giganotosaurus carolinii* from the Upper Cretaceous of Argentina. *Journal of Vertebrate Paleontology*, **22**, 802–811.

— and SALGADO, L. 2005. Last Patagonian theropods. in Carpenter, K. 2005. The Carnivorous Dinosaurs, Indiana University Press: 153–160.

—, CHIAPPE, L. M. and DINGUS, L., 2002. A new close relative of *Carnotaurus sastrei* Bonaparte 1985 (Theropoda: Abelisauridae) from the Late Cretaceous of Patagonia. *Journal of Vertebrate Paleontology*, **22**, 460–465.

—, CURRIE, P. J., and CARABAJAL, A. P. 2006. A new abelisauroid theropod from northwestern Patagonia. *Canadian Journal of Earth Sciences*, **43**, 1283–1289.

CURRIE, P. J. 1997. Braincase anatomy. In: P.J. Currie y K. Padian (Eds.), Encyclopedia of Dinosaurs. Academic Press, New York, p. 81–83.

DELALOYE, A.P. and GARRIDO, A. C. 2017. Unidad de procedencia de *Abelisaurus comahuensis* Bonaparte y Novas (Dinosauria, Theropoda, Abelisauridae) y su paleoambiente, Lago Pellegrini, provincia de Río Negro, Argentina. *Ameghiniana,* **54 (6)**, R3.

DELCOURT, R. 2018. Ceratosaur palaeobiology: new insights on evolution and ecology of the southern rulers. *Scientific Reports,* **8**, 9730.

D´EMIC, M., CURRY ROGERS, K. and O´CONNOR, P. 2016. Bone histology reveals unusual life history in the theropod dinosaur M*ajungasaurus crenatissimus* from the latest Cretaceous of Madagascar. SVP meeting Journal of Vertebrate Paleontology, program and abstracts, 124.

EVANS, D., BARRET, P., BRINK, K. S. and CARRANO, M., 2015. Osteology and bone microstructure of new, small theropod dinosaur material from the early Late Cretaceous of Morocco. *Gondwana Research*, **27**, 1034–1041.

EZCURRA, M. D., AGNOLIN, F. L., and NOVAS, F. E. 2010. An abelisauroid dinosaur with a non-atrophied manus from the Late Cretaceous Pari Aike Formation of southern Patagonia. *Zootaxa*, **2450**, 1–25.

FARKE, A. A., and SERTICH, J. J. 2013. An abelisauroid theropod dinosaur from the Turonian of Madagascar. *PloS one*, **8**.

FEDOROV, A., BEICHEL, R., KALPATHY-CRAMER, J., FINET, J., FILLION-ROBIN, J. C., PUJOL, S., and BUATTI, J. 2012. 3D Slicer as an image computing platform for the Quantitative Imaging Network. *Magnetic resonance imaging*, **30**, 1323–1341.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, **39**, 783–791.

FILIPPI, L. S., MÉNDEZ, A. H., JUÁREZ VALIERI, R. D. and GARRIDO, A. C 2016. A new brachyrostran with hypertrophied axial structures reveals an unexpected radiation of latest Cretaceous abelisaurids. *Cretaceous Research,* **61**, 209–219.

—, MÉNDEZ, A. H., GIANNECHINI, F. A., JUÁREZ VALIERI, R. D. and GARRIDO, A. C. 2017. Osteology of *Viavenator exxoni* (Abelisauridae; Furileusauria) from the bajo de la Carpa formation, NW patagonia, Argentina. *Cretaceous Research*, **83**, 95–119.

FRANCILLON-VIEILLOT, H., DE BUFFRENIL, V., CASTANET, J., GERAUDIE, J., MEUNIER, F. J., SIRE, J. Y., ZYLBERBERG, L. and DE RICQLES, A. 1990. Microstructure and mineralization of vertebrate skeletal tissues. In: CARTER, J.G. (Ed.), Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends. Van Nostrand Reinhold, New York, pp. 471–548.

GARRIDO, A. C. 2010. Estratigrafia del Grupo Neuquén, Cretácico Superior de la Cuenca Neuquina (República Argentina): nueva propuesta de ordenamiento litoestratigráfico. *Revista del Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'*, Nueva Serie **12**, 121–177.

GIANECHINI, F. A., APESTEGUÍA, S., LANDINI, W., FINOTTI, F., JUAREZ-VALIERI, R. AND ZANDONAI, F. 2015. New abelisaurid remains from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina. *Cretaceous Research*, **54**, 1–16.

GOLOBOFF, P. A., FARRIS, J. S., KÄLLERSJÖ, M., OXELMAN, B., RAMIACUTE; REZ, M. N. J., and SZUMIK, C. A. 2003. Improvements to resampling measures of group support. *Cladistics*, **19**, 32–332.

—, FARRIS, J. S., and NIXON, K. C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics*, **24**, 774–786.

—, and CATALANO, S. A. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics*, **32**, 221–238.

GRILLO, O. N., and DELCOURT, R. 2017. Allometry and body length of abelisauroid theropods: Pycnonemosaurus nevesi is the new king. Cretaceous Research, 69, 71-89

HEREDIA, S. E. and SALGADO, L. 1999. Posición estratigráfica de los estratos supracretácicos portadores de dinosaurios en Lago Pellegrini, Patagonia septentrional, Argentina. *Ameghiniana*, **36**, 229–234.

JUÁREZ VALIERI, R. D., FIORELLI, L. E., and CRUZ, L. E. 2004. *Quilmesaurus curriei* Coria, 2001. Su validez taxonómica y relaciones filogenéticas. Jornadas Argentinas de Paleontología de Vertebrados, Libros de Resúmenes.

LAMANNA, M.C., SUES, H-D., SCHACHNER, E.R., and LYSON, T.R. 2014. A New Large-Bodied Oviraptorosaurian Theropod Dinosaur from the Latest Cretaceous of Western North America. *PLoS ONE* **9(3)**, e92022.

LEANZA, H.A., APESTEGUIA, S., NOVAS, F.E., and DE LA FUENTE, M.S. 2004. Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages. *Cretaceous Research*, **25**, 61–87.

LEE, A. H. and O'CONNOR, P. M., 2013. Bone histology confirms determinate growth and small body size in the noasaurid theropod *Masiakasaurus knopfleri*. *Journal of Vertebrate Paleontology,* **33**, 865–876.

MADSEN, J. H., and WELLES, S. P. 2000. *Ceratosaurus* (Dinosauria, Theropoda): a revised osteology. Utah Geological Survey.

MARSH, O. 1881. Principal characters of American Jurassic dinosaurs, part V. *American Journal of Science*, **125**, 417–423.

—. 1884. Principal characters of American Jurassic dinosaurs; Part VIII, the order Theropoda. *American Journal of Science*, **160**, 329–340.

MARTINELLI, A. G. and FORASIEPI, A. M. 2004. Late Cretaceous vertebrates from Bajo de Santa Rosa (Allen Formation), Rio Negro province, Argentina, with the description

of a new sauropod dinosaur (Titanosauridae). *Revista Museo Argentino de Ciencias Naturales,* nueva serie, **6**, 257–305.

MEERS, M. B. 2003. Crocodylian forelimb musculature and its relevance to Archosauria. *The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology: An Official Publication of the American Association of Anatomists*, **274**, 891–916.

NOVAS, F. E., POL, D., CANALE, J. I., PORFIRI, J. D. and CALVO, J. O. 2008. "A bizarre Cretaceous theropod dinosaur from Patagonia and the evolution of Gondwanan dromaeosaurids". *Proceedings of the Royal Society B: Biological Sciences*. **276**, 1101–7.

—, CHATTERJEE, S., RUDRA, D. K., and DATTA, P. M. 2010. *Rahiolisaurus gujaratensis*, n. gen. n. sp., a new abelisaurid theropod from the Late Cretaceous of India. In *New aspects of Mesozoic biodiversity* (pp. 45-62). Springer, Berlin, Heidelberg.

—, AGNOLIN, F. L., EZCURRA, M. D., PORFIRI, J. and CANALE, J. I. 2013. Evolution of the carnivorous dinosaurs during the Cretaceous: the evidence from Patagonia. *Cretaceous Research*, **45**, 1–74.

—, AGNOLIN, F.L., ROZADILLA, S., ARANCIAGA ROLANDO, A.M. , BRISSON EGLI, F., MOTTA, M.J., CERRONI, M.A., EZCURRA, M. D., MARTINELLI, A., D´ANGELO, J., ALVAREZ HERRERA, G., GENTIL, A., BOGAN, S., CHIMENTO, N., GARCIA MARSA, J.A., LO COCO, G., MIQUEL, S., BRITO, F., VERA, E., PEREZ LONAIZE, V., FERNANDEZ M.S., y SALGADO, L. 2019. Paleontological discoveries in the Chorrillo Formation (upper Campanian-lower Maastrichtian, Upper Cretaceous), Santa Cruz Province, Patagonia, Argentina. *Revista del Museo Argentino de Ciencias Naturales nueva serie* **21**, 217 - 293.

O'CONNOR, P. M. 2007. The postcranial axial skeleton of *Majungasaurus crenatissimus* (Theropoda: abelisauridae) from the late cretaceous of Madagascar. Journal of Vertebrate Paleontology, **27**, 127–162.

OTERO, A. 2018. Forelimb musculature and osteological correlates in Sauropodomorpha (Dinosauria, Saurischia). *PloS one*, **13(7)**, e0198988.

PAULINA-CARABAJAL, A. 2011*a*. Braincases of abelisaurid theropods from the Upper Cretaceous of north Patagonia. *Palaeontology*, **54**, 793–806.

—. 2011*b*. The braincase anatomy of *Carnotaurus sastrei* (Theropoda: Abelisauridae) from the Upper Cretaceous of Patagonia. *Journal of Vertebrate Paleontology*, **31**, 378–386.

—, and SUCCAR, C. 2015. Endocranial morphology and inner ear of the theropod *Aucasaurus garridoi*. *Acta Palaeontologica Polonica,* **60**, 141–144.

—, and CURRIE, P. 2017. The braincase of the theropod dinosaur *Murusraptor*: Osteology, neuroanatomy and comments on the paleobiological implications of certain endocranial features. *Ameghiniana*, **54**, 617–640.

—. and FILIPPI, L. 2017. Neuroanatomy of the abelisaurid theropod *Viavenator*: The- most complete reconstruction of brain and inner ear for a South American representative of the clade. *Cretaceous Research*, **83**, 84–94.

POL, D. and RAUHUT, O. W. M. 2012. A Middle Jurassic abelisaurid from Patagonia and the early diversification of theropod dinosaurs. *Proceedings of the Royal Society of Biological Sciences*, **279**, 3170–3175.

RAUHUT, O. W. M. 2004. Braincase structure of the Middle Jurassic theropod dinosaur *Piatnitzkysaurus*. *Canadian Journal of Earth Sciences*, **41**, 1109–1122.

—, and CARRANO, M. T. 2016. The theropod dinosaur Elaphrosaurus bambergi, from the Late Jurassic of Tendaguru, Tanzania. *Zoological Journal of the Linnean Society*, **178**, 546–610.

SAMPSON, S. D. and WITMER, L. M. 2007. Craniofacial anatomy of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Society of Vertebrate Paleontology Memoirs*, **8**, 32–102.

SÁNCHEZ-HERNÁNDEZ, B. and BENTON, M. J. 2012. Filling the ceratosaur gap: A new ceratosaurian theropod from the Early Cretaceous of Spain. *Acta Palaeontologica Polonica*, **59**, 581–600.

SERENO, P. C., WILSON, J. A., and CONRAD, J. L. 2004. New dinosaurs link southern landmasses in the Mid–Cretaceous. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**, 1325–1330.

SMITH, J. B., 2007. Dental morphology and variation in *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the late Cretaceous of Madagascar. In: Sampson, S.D., Krause, D.W. (Eds.), *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar, *Society of Vertebrate Paleontology Memoir,* **8**, 103–126.

SNIVELY, E. and RUSSELL, A. P. 2007. Functional Variation of Neck Muscles and Their Relation to Feeding Style in Tyrannosauridae and Other Large Theropod Dinosaurs. *The Anatomical Record*, **290**, 934–957.

SWOFFORD, D. L., and BEGLE, D. P. 1993. PAUP User's Manual. *Center for Biodiversity, Illinois Natural History Survey, Champaign, Illinois*.

TORTOSA, T., BUFFETAUT, E., VIALLE, N., DUTOUR, Y., TURINI, E. and CHEYLAN, G., 2013. A new abelisaurid dinosaur from the Late Cretaceous of southern France: Palaeobiogeographical implications. *Annals of Paleontology*, **100**, 63–86.

WILSON, J. A., SERENO, P. C., SRIVASTAVA, S., BHATT, D. K., KHOSLA, A., and SHANI, A. 2003. A new abelisaurid (Dinosauria, Theropoda) from the Lameta Formation (Cretaceous, Maastrichtian) of India.

WITMER, L. M. and RIDGELY, R. 2009. New insights into the brain, braincase, andear region of tyrannosaurs (Dinosauria, Theropoda), with implicationsfor sensory organization and behavior. *The Anatomical Record*, **292**, 1266–1296.

—, and RIDGELY, R.C. 2010. The Cleveland tyrannosaur skull (*Nanotyrannus* or *Tyrannosaurus*): new findings based on CT scanning, with special reference to the braincase. *Kirtlandia*, **57**, 61–81.

XU, X., and QIN, Z.C. 2017. A new tiny dromaeosaurid dinosaur from the Lower Cretaceous Jehol Group of western Liaoning and niche differentiation among the Jehol dromaeosaurids. *Vertebrata PalAsiatica* **55** (**2**), 129–144

Figure captions

Figure 1. A, Map showing the site of Arriagada Farm. **B**, silhouette of *Niebla antiqua* showing the preserved bones in white. Scale bar: 0.5 meters.

[Planned for full page width]

Figure 2. Braincase of *Niebla antiqua* in dorsal (**A, A´**) and ventral views (**B, B´**). Grey zones indicate sediment or broken areas. ***Abbreviations***: **bs,** basisphenoid; **bpt,** basipterygoid process; **bsr,** basisphenoidal recess; **bt,** basal tubera; **eth,** ethmoidal complex, **fr,** frontal**; gsob,** groove of supraorbital bulge; **lc,** lacrimal contact; **ls,** laterosphenoid; **mf,** median fossa; **nc,** nasal contact; **nc,** nuchal crest; **oc,** occipital condyle **pa,** parietal; **pcr,** paracondylar recess; **p,** parietal; **sc,** sagittal crest; **sob,** supraorbital bulge; **stf,** supratemporal fossa; **ssr,** subsellar recess; **vg,** ventral groove of laterosphenoid; **XII,** cranial nerve XII. Scale bar: 10 cm.

[Planned for full page width]

Figure 3. Braincase of *Niebla antiqua* in right lateral (**A, A´**) and left lateral views (**B, B´**). Grey parts are sediment. Cranial nerves are pointed with numbers. ***Abbreviations***: **bb,** bony bar; **bt,** basal tubera; **btp,** basipterygoid process; **cap,** capitate process of laterosphenoid; **col,** collumelar recess; **cul,** cultriform process; **eth,** ethmoidal complex; **fo,** fenestra ovalis; **inc,** incisures of CN III+IV; **iof,** interorbital fenestra; **ios,** interorbital septum; **ls,** laterosphenoid; **ltr,** lateral tympanic recess; **nc,** nuchal crest; **osc,** otosphenoidal crest; **pa,** parietal; **pro,** prootic pendant; **sg,** stapedial groove; **sph,** sphenoidal artery exit; **ssr,** subsellar recess; **vgl,** ventral groove of laterosphenoid; **II-XII,** cranial nerves II-XII. Scale bar: 10 cm

[Planned for full page width]

Figure 4: Braincase of *Niebla antiqua* in posterior (**A, A´**) and anterior views (**B, B´**). Grey parts are sediment. ***Abbreviations*: ac,** arched crest**; bt,** basal tubera; **bsr,** basisphenoid recess; **bo,** basiocciptal; **cap** capitate process of laterosphenoid; **ct,** crista tuberalis**; fm,** foramen magnum; **fr,** frontal; **ios,** interorbital septum; **ls,** laterosphenoid; **mc,** median crest; **mcv**, middle cerebral veins exit; **mth,** mesethmoid; **nc,** nuchal crest; **ob,** olfactory bulbs; **oc**, occipital condyle; **pa,** parietal; **pcr,** paracondylar recess; **pop,** paroccipital process; **pro,** prootic pendant; **ptf,** postemporal fenestra; **soc,** supraoccipital crest; **sph,** sphenoidal artery exit; **ssr,** subscelar recess; **t,** turbinates; **vgl,** ventral groove of laterosphenoid; **VI?,** exit for cranial nerve VI?; **XII,** cranial nerve XII. Scale bar: 10 cm.

[Planned for full page width]

Figure 5. Details of the braincase of *Niebla*. **A,** Close up of the posterior region showing the postemporal fenestra. **B**, Detail of cranial nerve foramina of the occital region in posterolateral view. **C**, Neurovascular foramina in detail on the right and; **D**, left sides. Not to scale. ***Abbreviations*: bb,** bony bar; **bs,** basisphenoid; **col,** columellar recess, **fc?,** fenestra cochlear? **fm**, foramen magnum; **fo,** fenestra ovalis; **gptf,** groove associated to postemporal fenestra; gV_1, groove for ophthalmic ramus of trigeminal nerve; **inc,** incisures for III+IV; **ios,** interorbital septum; **mcv,** middle cerebral vein; **met,** metotic; **pro,** prootic pendant; **ptf**, postemporal fenestra; **soc**, supraoccipital crest; **sph**, sphenoidal artery exit; **IXty**, tympanic branch exit of glossopharyngeal nerve; **II-XII,** cranial nerves II-XII.

[Planned for half height width]

Figure 6. Digital reconstruction of the braincase of *Niebla antiqua* in right lateral (**A**), dorsal (**B**), and posterior (**C**) views. Bone is rendered solid (above) and semitransparent (below). Cranial endocast (blue) and inner ear (green) in lateral (**D**), dorsal (**E**) and posterior (**F**) views. *Abbreviations*: **asc**, anterior semicircular canal; **cer**, cerebral hemispheres; **ct**, common trunk; **ds**, dorsal sinus; **fpr**, fenestra pseudorotunda; **la**, lagena; **lsc**, lateral semicircular canal; **met**, metotic passage; **ob**, olfactory bulbs; **ot**, olfactory tracts; **pit**, pituitary; **pmcv**, posterior middle cerebral veins; **I-XII,** cranial nerves. Scale bar equals 10 cm (A-C) and 5 cm (D-F).

[Planned for half height width]

Figure 7. Anterior tip of right dentary (**A-C**) of *Niebla antiqua* in lateral (A), medial (B) and dorsal (C) views. Isolated dentary teeth in labial view (**D**). *Abbreviations***: al**, alveolus; **f,** foramina; **rt**, replacement tooth; **t,** teeth. Scale bars: 5 cm (dentary) and 1 cm (tooth).

[Planned for half height page]

Figure 8. Incomplete dorsal ribs (**A, C, C´**) and dorsal vertebrae (**B**) of *Niebla antiqua*. Dorsal rib in anterior view (A). Isolated mid- or posterior dorsal centrum in right lateral view (B). Close-up and interpretative drawing of isolated dorsal rib (C, C´). *Abbreviations***: cap,** capitulum; **lr,** lateral ridge; **pc,** pleurocoel; **tub,** tuberculum. Scale bars: 10 cm the vertical one and 2 cm the horizontal one.

[Planned for half-width page]

Figure 9. Scapulocoracoid of *Niebla antiqua* in dorsal (**A**), medial (**B**), lateral (**C**) and ventral (**D**) views. ***Abbreviations***: **acr**, acromion; **sf,** scapular fossa; **f,** coracoid foramen; **gl**, glenoid; **sb,** scapular blade; **sgf,** subglenoid fossa (=posteroventral fossa); **spf,** supraglenoid fossa; **pvp,** posteroventral process. Scale bars: 10 cm.

[Planned for full page width]

Figure 10: Rib cross-section of *Niebla antiqua* (**A-D**). Partial view showing the external fundamental system constituted by 8 LAGs (white arrowheads) (A). Another partial view, showing the section dorsally oriented and the change in the LAGs (black arrowheads) distribution (B). Detail of the inner circumferential layer and the trabeculae infilled in the medullary cavity (C). Detail of the Haversian system (D). ***Abbreviations***: **efs**; external fundamental system; **hs**; haversian system; **icl**; inner circumferential layer; **tb**: trabecular bone. Scale bar: A =0.7 mm; B, C =0.5 mm; D =0.3 mm.

Figure 11. Strict consensus tree of the phylogenetic relationships of *Niebla antiqua* and palaeobiogeographically framework. Small numbers in the nodes are the absolute (left) and relative (right) bootstrap frequencies. Dark bars are the know temporal duration of the species. ***Abbreviations***: **Noa**; Noasauridae; **Mjn**; Majungasaurinae.

[Planned for full page width]

Figure 12. Simplified version of the consensus tree showing the sizes of some contemporaneous abelisaurids to *Niebla.*

[Planned for full page width]

Table 1: Measurements of selected materials of *Niebla antiqua*. Measurements marked with * represent estimated values due damaged bone.

- A description of a new abelisaurid species from the Maastrichtian of Patagonia
- The publication of the mid-sized abelisaurid that represents one of the smallest of the group
- This specimen represents an adult specimen
- Phyllogenetically represents one of the most derived of the group
- *Niebla* reveals a more complex scenario for the abelisaurid evolution from the cretaceous of Patagonia.

MUSEO ARGENTINO DE CIENCIAS NATURALES

"BERNARDINO RIVADAVIA"

Av. Ángel Gallardo 470 C1405DJR

Buenos Aires, Argentina

Telephone: 54-11- 4982-6595

18/09/2020

Dear Editor of *Journal of South American Earth Sciences*

We the authors of "**A New Medium-sized Abelisaurid (Theropoda, Dinosauria) from the late Cretaceous (Maastrichtian) Allen Formation of Northern Patagonia, Argentina.**" declare that have not submitted this article in another journal and that all the data is available to be published here.

Yours sincerely,

Alexis M. Aranciaga Rolando

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: