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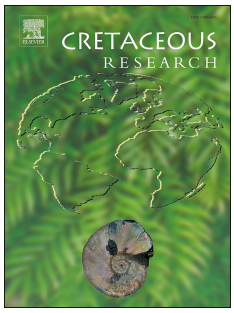

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TESTING THE PERSISTENCE OF CARCHARODONTOSAURIDAE (THEROPODA) IN THE UPPER CRETACEOUS OF PATAGONIA BASED ON DENTAL EVIDENCE

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Abstract

The deposits corresponding to the Upper Cretaceous Neuquén and San Jorge Gulf basins from northern and central Patagonia have provided two of the most complete sequences of terrestrial vertebrate faunas of all Gondwanan landmasses. Among the carnivorous components, the carcharodontosaurid theropods appeared as common elements during the Early Cretaceous and the earliest Late Cretaceous in northern and central Patagonia. Although recorded mostly in the lower Turonian, isolated teeth suggest their presence in younger strata in northern and central Patagonia, reaching the clade in the region as late as the early Maastrichtian. Here, we verify the assignment of such isolated teeth previously identified as belonging to Carcharodontosauridae from the Upper Cretaceous strata of northern and central Patagonia. Using three different

methods, namely a cladistic analysis performed on a dentition-based data matrix, and discriminant and cluster analyses conducted on a large dataset of theropod crown measurements, we assign a tooth from Candeleros Formation to carcharodontosaurid theropods and teeth from Cerro Lisandro, Bajo Barreal, Portezuelo, Plottier and Allen formations to abelisaurid theropods. These new reappraisals provide additional evidence about the extinction of Carcharodontosauridae in South America at about the late Turonian–earliest Coniacian as part of a general faunistic turnover event, with the last clear evidence of this lineage in Patagonia coming from the early–middle Turonian.

Keywords. Shed teeth, taxonomic identification, Late Cretaceous, Patagonia, South America, Carcharodontosauridae.

1. Introduction

Carcharodontosauridae is a clade of medium to large sized cretaceous theropod dinosaurs, with a wide paleogeographic distribution. They are present in both Laurasian (Asia, Europe and North America) and western Gondwanan landmasses (Africa and South America) (Brusatte *et al*., 2009; Novas *et al*., 2013; Csiki-Sava *et al*., 2016; Cuesta *et al*., 2018a, b). The clade represents an important radiation within allosauroid theropods that ranged from the Late Jurassic to the mid-Cretaceous (Brusatte and Sereno, 2008; Rauhut, 2011). Although the monophyly of Carcharodontosauridae is widely accepted, its phylogenetic relationships amongst other theropods, are far to be conclusive (Benson *et al*., 2010; Carrano *et al*., 2012; Porfiri *et al*., 2014; Apesteguía *et al*., 2016), as are their internal relationships (Brusatte and Sereno, 2008; Novas *et al*., 2013; Canale *et al*., 2014; Cuesta *et al*., 2018a,b).

At present, the South American record of Carcharodontosauridae, which comes entirely from Argentine Patagonia, is undisputedly from the Lower to lower Upper Cretaceous; however, previous identifications of fragmentary materials carry their biochron to the Maastrichtian (e.g., Martinelli and Forasiepi, 2004). The record includes the basal *Lajasvenator ascheriae* from the Valanginian Mulichinco Formation (Coria *et al*., 2020); the highly derived *Tyrannotitan chubutensis* from the Aptian Cerro Barcino Formation (Novas *et al*., 2005); *Giganotosaurus carolinii* from the lower Cenomanian Candeleros Formation (Coria and Salgado, 1995); and *Mapusaurus roseae* and *Taurovenator violentei* from the upper Cenomanian to lower Turonian Huincul Formation (Coria and Currie, 2006; Motta *et al*., 2016). These last two taxa have been recently proposed as likely synonyms (Coria *et a*l., 2020: p. 18).

In addition to these nominated taxa, several isolated teeth from Argentina have been considered as belonging to Carcharodontosauridae. Examples include teeth coming from the middle Turonian Cerro Lisandro Formation (Salgado *et al*., 2009), upper Turonian to lower Coniacian Portezuelo Formation (Calvo and Veralli, 2004), and the upper Campanian to lower Maastrichtian Allen Formation (Martinelli and Forasiepi, 2004). These latter records together with very fragmentary cranial material and isolated teeth from the Bauru Group in southeastern Brazil (see Delcourt *et al*., 2020), were utilized as evidence of a long persistence of the clade in South America. The assignation of some of these Patagonian teeth to Carcharodontosauridae has been previously questioned by their resemblance to some abelisaurid teeth (*i.e.,* Canale *et al.*, 2009) or by the distributions of features previously considered as diagnostic of Carcharodontosauridae (*i.e.,* Brusatte *et al*., 2007).

The aim of this contribution is to describe and analyze, with qualitative and quantitative techniques, the systematic of isolated teeth from Patagonia originally

considered as belonging to Carcharodontosauridae from the middle Turonian to lower Maastrichtian. We also include an undescribed shed tooth from the Candeleros Formation. With this review we seek to evaluate the persistence of the clade in southern South America later than the confirmed occurrence of the Carcharodontosauridae in the middle Turonian.

1.1. Institutional Abbreviations. **AMNH FARB**, American Museum of Natural History (fossil amphibian reptiles and bird specimens), New York, USA; **AODF**, Australian Age of Dinosaurs Fossil, Winton, Queensland, Australia; **BP**, Evolutionary Studies Institute (formerly "Bernard Price Institute for Palaeontological Research"), University of the Witwatersrand, Johannesburg, South Africa; **DGM**, Museu de Ciências da Terra, Rio de Janeiro, Brazil; **ENDEMAS-Pv**, Ente de Desarrollo para la Margen Sur, Paleontología de Vertebrados, Cipolletti, Argentina **FMNH PR**, Field Museum of Natural History, Chicago, USA; **FPDM-V**, Fukui Prefectural Dinosaur Museum, Muroko, Terao, Katsuyama, Fukui, Japan; **GSI-IM**, Geological Survey of India, Indian Museum, Kolkata, India; **GZG**, Geowissenschaftliches Zentrum der Universität Göttingen, Göttingen, Germany; **ISIR**, Indian Statistical Institute, Reptiles, Kolkata, India; **IVPP**, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MACN-Pv-RN**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Paleontología de Vertebrados (Pv), Colección Provincia de Río Negro (RN), Buenos Aires, Argentina; **MAU-Pv-LI**, Museo Municipal "Argentino Urquiza", Rincón de los Sauces, Argentina; **MCNA**, Museo de Ciencias Naturales y Antropológicas "Juan Cornelio Moyano", Mendoza, Argentina; **MCF-PVPH**, Museo Municipal "Carmen Funes", Paleontología de Vertebrados, Plaza Huincul, Argentina; **MDPA-Pv**, Museo del Desierto Patagónico, Añelo, Argentina; **MGUP**, Museo di

Geologia e Paleontologia, Universita di Palermo, Italy; **MHNA-PV**, Muséum d'Histoire Naturelle d'Aix-en-Provence, France; **MIWG**, Dinosaur Isle, Isle of Wight Museum Services, Sandown, UK; **MLP**, Museo de La Plata, La Plata, Argentina; **MMCH-PV**, Museo Municipal "Ernesto Bachmann", Villa El Chocón, Argentina; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **MNN**, Musée National du Niger, Niamey, Niger; **MPCA**, Museo Provincial "Carlos Ameghino", Cipolletti, Argentina; **MPCM**, Museo Paleontológico Cittadino di Monfalcone, Gorizia, Italy; **MPCN**, Museo Patagónico de Ciencias Naturales "Juan Carlos Salgado", General Roca, Argentina; **MPM-Pv**, Museo "Padre Molina", Paleontología de Vertebrados, Río Gallegos, Argentina; **MPUR**, Museo di Paleontologia of the Sapienza Universtà di Roma, Rome, Italy; **MUCPv**, Museo de Ciencias Naturales de la Universidad Nacional de Comahue, Paleontología de Vertebrados, Neuquén, Argentina; **NHFO**, Natural History Fossil Collection, Qatar Museum Authority, Doha, Qatar; **NHMUK**, The Natural History Museum, Palaeontology Vertebrates, London, United Kingdom; **NMB**, Naturhistorisches Museum Braunschweig, Braunschweig, Germany; **OCP**, Office Chérifien des Phosphates, Khouribga, Morocco; **PVL**, Fundación 'Miguel Lillo,' San Miguel de Tucumán, Argentina; **PVSJ**, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; **RTMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; **SMA**, Sauriermuseum Aathal, Aathal, Switzerland; **UA**, Université d'Antananarivo, Antananarivo, Madagascar; **UCMP**, University of California Museum of Paleontology, Berkeley, USA; **UNPSJB-PV**, Universidad Nacional de la Patagonia San Juan Bosco, Paleontología de Vertebrados, Comodoro Rivadavia, Argentina; **USNM**, United States National Museum, Washington, USA; **YPM**, Yale Peabody Museum of Natural History, Yale, USA; **WDC-CCPM**, Wyoming Dinosaur Center, Thermopolis, USA.

1.2. Anatomical abbreviations. **AL**, apical length; **CA**, crown angle; **CBL**, crown base; **CBR**, crown base ratio; **CBW**, crown base width; **CH**, crown height; **CHR**, crown height ratio; **CTU**, crown transverse undulation density; **DA**, distoapical denticle density; **DAVG**, average distal denticle density; **DB**, distobasal denticle density; **DC**, distocentral denticle density; **DDT**, dentine thickness distally; **DLAT**, dentine thickness labially; **DLIT**, dentine thickness lingually; **DMT**, dentine thickness mesially; **DSDI**, denticle size density index; **FABL**, fore-aft basal length; **LAF**, number of flutes on the labial surface of a crown; **LIF**, number of flutes on the lingual surface of a crown; **MA**, mesioapical denticle density; **MAVG**, average mesial denticle density; **MB**, mesio-basal denticle density; **MC**, mesiocentral denticle density; **MCE**, mesial carina extent; **MCL**, mid crown length; **MCR**, mid-crown ratio; **MCW**, mid-crown width; **MDE**, mesiobasal denticles extent.

2. Material and Methods.

2.1. Materials included in the present study

The analysis presented here is based on datasets published by Hendrickx *et al*. (2020). Additionally, we include nine new specimens from different stratigraphic units of Patagonia, namely the Neuquén and San Jorge Gulf basins. The specimens incorporated in the current study are listed in Table 1. This table includes the stratigraphic provenance and previous assignments of the material referred to Carcharodontosauridae.

***2.2. Comparative methodology and terminology*.** For the studied teeth, we measured eleven variables (i.e., CBL, CBW, CH, AL, MCL, MCW, CTU, MA, MC, DC, DA;

Table 1) with a digital caliper of 150 mm (6"), with an accuracy of 0.01 mm. Each tooth was described using the dental nomenclature and protocol proposed by Hendrickx *et al*. (2015a) and then compared to the dentition of 155 non-avian theropod species-level taxa (Young *et al*., 2019; Hendrickx *et al*., 2020). We used a binocular loupe to observe denticles, crown ornamentations and enamel surface texture.

The terminology consering anatomical orientation follows the recommendation of Smith and Dodson (2003) and Hendrickx *et al.* (2015a). For the morphometric and anatomical terms and abbreviations, we follow Smith *et al*. (2005) and Hendrickx *et al*. (2015a). Similarly, we follow/adopt phylogenetic definitions by Hendrickx *et al*. (2015a, 2020).

2.3. Cladistic analysis. With the objective to explore their phylogenetic affinities, dental material was first explored by performing a cladistic analysis on an updated version of the data matrix created by Hendrickx and Mateus (2014), which focus on the dentition of non-avian theropods. The most updated version of this data matrix was published by Hendrickx *et al*. (2020) and includes 146 dental characters scored across 105 theropod genera. We recognized six dental morphotypes among the sample of theropod teeth (Table 1), which we scored as separated operational taxonomic units (OTUs).

We followed the methodology by Young *et al*. (2019) and Hendrickx *et al*. (2020) and conducted the cladistic analysis with TNT 1.1 (Goloboff *et al*. 2008) using a backbone tree topology and the positive constraint command, setting the three dental morphotypes as floating terminals (supplementary information 1.2). As in Young *et al.* (2019) and Hendrickx *et al*. (2020), the topological tree was built based on the results of the phylogenetic analyses of Müller *et al*. (2018) for non-neotheropod saurischians, Ezcurra (2017) for non-averostran neotheropods, Rauhut and Carrano (2016) and Wang

et al. (2017) for Ceratosauria, Carrano *et al*. (2012) and Rauhut *et al*. (2012, 2016) for non-coelurosaurian tetanurans, Brusatte and Carr (2016) for Tyrannosauroidea, and Cau *et al*. (2017) for other coelurosaurs. As the search strategy, we used a combination of the tree-search algorithms Wagner trees, TBR branch swapping, sectorial searches, Ratchet (perturbation phase stopped after 20 substitutions) and Tree Fusing (5 rounds) until 100 hits of the same minimum tree length were reached. Then, the trees were subjected to a final round of TBR branch swapping (Hendrickx *et al*., 2020: p. 4). We also performed two additional cladistic analyses as did Young *et al*.'s (2019) and Hendrickx *et al*.'s (2020). One analysis used the dentition-based dataset without constraints, and the second one used a data matrix restricted to crown-based characters (Hendrickx *et al*., 2020: p. 11).

***2.4. Discriminant analysis*.** We included each of the nine shed teeth of theropods to classify them and predict their optimal classifications inside 'family-level' groupings based on quantitative data, performing a discriminant function analysis (DFA) on the dataset of theropod crown measurements published by Hendrickx *et al*. (2020). This dataset includes fifteen measurements (i.e., CBL, CBW, CH, AL, CBR, CHR, MCL, MCW, MCR, MSL, LAF, LIF, CA, MDL, DCL) taken in 1335 teeth belonging to 89 taxa (84 species and five indeterminate family-based taxa) separated into 20 monophyletic or paraphyletic groups. Because many researchers measure dinosaur crowns differently (Hendrickx *et al*., 2020), a second analysis was conducted on a dataset restricted to measurements taken by Christophe Hendrickx (see Hendrickx *et al*., 2020). Finally, given that most of the isolated theropod teeth under study belonged to relatively large sized animals, a third analysis was performed on a dataset restricted to theropod taxa with crowns of more than 20 mm. These two datasets include 725 and

400 teeth belonging to 53 and 46 theropod taxa each separated into 13 groups, respectively.

The discriminant function analysis was performed following the protocol detailed by Young *et al*. (2019), in which, all variables were log-transformed to normalize the quantitative variables. The DFA was run in Past 3 version 3.19 (Hammer *et al*. 2001) using the Discriminant analysis (LDA) function. Each tooth included in the present study (Table 1) was treated as the unknown taxon so that they could be classified at genus and group level in each analysis.

2.5. Cluster analysis. A cluster analysis was performed in Past3 on the different datasets using the Paired group algorithm and a Neighbour joining clustering; we chose Euclidean distances for the Similarity Index (see Young *et al*., 2019; Hendrickx *et al*., 2020).

4. Systematic Paleontology

4.1. Candeleros Formation

Theropoda Marsh, 1881

Tetanurae Gauthier, 1986

Allosauroidea Currie and Zhao, 1993

Carcharodontosauridae Stromer, 1931

Gen. and sp. indet.

Material. MDPA-Pv 005 (Figure 3).

Locality and Horizon. Aguada Pichana area (38°20'30"S; 69°10'4"W), located in the center of Neuquén province, Argentina; upper section of the Candeleros Formation, lower Cenomanian, Upper Cretaceous (Garrido, 2010).

State of preservation and general morphology. The tooth is almost complete with most of the crown preserved (i.e., interpreted here as a shed tooth). MDPA-Pv 005 is quite damaged, with the labial surface highly eroded while the lingual side is less damaged. Nevertheless, the enamel of the crown is well observable in many parts of both faces. Additionally, a horizontal fracture of post-mortem type is observed in the middle of the crown, which attributed to the fall of the tooth and/or to processes that occurred later. Likewise, the tooth lacks its tip and most basal sector (i.e., sector of the cervix). The denticles are much worn both in the mesial and the distal carinae, although very few of them show their original shape.

Crown overall morphology. Due to its labiolingually compressed crown with a distal curvature, and serrated carinae, this element is considered as ziphodont type. While it is not possible to calculate the exact value of the labiolingual compression of the crown (CBR), said ratio is considered to be important to normal. This quantification is based on the preserved proportions of the crown where the ratio is equal to 0.48. Given that the missing basal sector is negligible, it is possible to infer that this value should be close to 0.5. A similar inference can be done regarding baso-apical elongation of the crown. Thus, based on parameters provided by Hendrickx and Mateus (2014), this ratio is normal (CHR=2.2).

In apico-basal sense the mesial margin of the crown is strongly convex in lateral view with a serrated carina. The distal margin of the crown is slightly concave in lateral

view, also presenting a serrated carina. Although both labial and lingual surfaces are mesiodistally convex in apical view, the lingual surface is concave in apico-basal orientation. In basal view, both lingual and labial surfaces are strongly convex, and their faces converge mesially and distally in conspicuous carinae.

The cross-section is lenticular at near the level of the cervix, while on apical view its cross-section is parlinon-shaped. In the mesial view, the mesial carina is diagonally oriented to the labial face, and although its basalmost portion is missing, it must have extended to the cervix or just above it based on the size of denticles observed on the basalmost region. In the distal view, the distal margin is centrally positioned and appears to be lingually displaced weakly. On each side of both faces there is a concave surface adjacent to the distal carina.

Denticles. The mesial carina bears 10 denticles per 5 mm at mid-crown, and 15 denticles per 5 mm close to the apex. The distal carina possesses 15 denticles per 5 mm at mid-crown and 17 denticles per 5 mm at its base. However, the density of denticles close to the cervix is unknown since the carina is eroded and damaged. Similarly, the apical distal denticles density could not be calculated because this margin is highly eroded. In both carinae, denticle densities increase apically and basally from mid-height (DSDI = 1.5). Although in several portions of both carinae the denticles are partially eroded, both mesial and distal denticles are symmetrical to slightly asymmetrically convex with a biconvex external margin. The interdenticular space is narrow, less than one-third of the denticles width.

Crown surface and ornamentation. The crown of the tooth possesses arcuate marginal undulations on both surfaces about the distal margin. These are well compacted, abundant and horizontally oriented in mesial sense. Transverse undulations, flutes,

longitudinal grooves, or ridges are absent. The enamel texture is braided (i.e., oriented enamel texture in alternating with interweaving grooves and sinuous ridges *sensu* Hendrickx *et al*., 2015).

4.2. Cerro Lisandro Formation

Theropoda Marsh, 1881

Ceratosauria Marsh, 1884

Abelisauroidea Bonaparte, 1991

Abelisauridae Bonaparte and Novas, 1995

Gen. and sp. indet.

***Material*.** Endemas-Pv 2 (Figure 4).

***Locality and Horizon*.** El Anfiteatro area, la Bajada Sector (39°17’44”S; 68°27’33”W), located at the center-west of the Río Negro province, Argentina; upper section of the Cerro Lisandro Formation, middle to upper Turonian, Upper Cretaceous (Salgado *et al.*, 2009; Garrido, 2010).

***State of preservation and general morphology*.** Endemas-Pv 2 is an almost complete tooth that lacks a very basal sector of the crown. Some denticles are worn out, although it is possible to observe the density along both carinae. A horizontal fracture of type post-mortem (i.e., attributed to the fall of the tooth and/or to processes that occurred later) located in the close to the apex of the crown is observable.

Crown overall morphology. The tooth is interpreted as a mesial tooth of the series. The preserved height is 31.75 mm, the labiolingual compression of the crown (CBR) is equal to 0.77, and the baso-apical elongation of the crown (CHR) is 2.35. In lateral view, the mesial and distal margins are strongly convex baso-apically with the apex positioned centrally on the crown. In both carinae, the denticles are well developed. Both in apical and basal views, the lingual and labial surfaces are strongly convex and their faces converge mesially and distally in well visible carinae. In cross-section almost at the level of the cervix, the tooth is salinon-shaped. The mesial and distal carinae are strongly displaced lingually. On each side of both faces there is a concave surface adjacent to the distal carina, as there is a lingual surface adjacent to the mesial carina.

Denticles. The mesial carina bears 12 denticles per 5 mm at mid-crown and close to the apex, whereas it possesses 13 denticles per 5 mm close to the cervix. The distal carina bears 11 denticles per 5 mm at mid-crown and close to the apex, and possesses 13 denticles per 5 mm close to the cervix. The denticles are rectangular, chisel-like and slightly inclined apically (Salgado *et al.*, 2009). The interdenticular space is narrow, less than one-third of the denticles width.

Crown surface and ornamentation. The crown of the tooth possesses arcuate marginal undulations on both surfaces about the distal margin. These are well compacted, abundant and horizontally oriented in mesial sense. Transverse undulations, flutes, longitudinal grooves, or ridges are absent. The enamel texture is smooth.

4.3. Bajo Barreal Formation

Theropoda Marsh, 1881

Ceratosauria Marsh, 1884

Abelisauroidea Bonaparte, 1991

Abelisauridae Bonaparte and Novas, 1995

Gen. and sp. indet.

***Material*.** UNPSJB-PV 969 (Figure 5).

***Locality and Horizon*.** Western flank of Sierra de San Bernardo area, Estancia Ocho Hermanos locality (45°17'37"S; 69°35'29"W), located at the center-south of the Chubut province, Argentina; uppermost levels of the Lower Member of the Bajo Barreal Formation, lower Cenomanian to upper Turonian, Upper Cretaceous (Casal *et al*., 2009, 2016).

***State of preservation and general morphology*.** The tooth consists of a fragment of crown with well-preserved labial and lingual surfaces and including the enamel layer. It lacks its most apical apex, whereas the most basal sector of the crown is strongly eroded at level of the cervix. The mesial carina is well-preserved, although lacks the apical tip. The distal carina lacks its basal and apical sectors. In both carinae, the denticles are well preserved and show their original shape.

Crown overall morphology. The shed tooth from Bajo Barreal Formation described originally by Casal *et al*. (2009) possesses a crown labiolingually compressed, anteroposteriorly bent, and both carinae serrated. These are features of a ziphodont crown type. Despite its deficient preservation at the level of the cervix, it is possible to estimate its labiolingual compressed (CBR) with a range that varies between 0.48 to 0.5, whereas the ratio CHR is equal to 2.25. In the lateral view, the distal margin is straight, whereas the mesial margin is convex with its apex located centrally in the crown. In

mesial and distal views, both carinae are centrally positioned along its margins. Based on the size denticles, they could have extended to the cervix, at least in the mesial carina. In basal view, both lingual and labial surfaces are strongly convex and their faces converge mesially and distally in carinae well visible. Besides, in the cross-section almost at the level of the cervix is lenticular.

***Denticles*.** The mesial and distal carinae bear 13 denticles per 5 mm at mid-crown. However, the denticle density in the apex of both carinae could not be calculated because these are highly eroded. The same is true for most basal denticles of the mesial carina. The all denticles are symmetrical with its external margin convex. Interdenticular spaces are narrow, measuring less than a third of the width of the denticles.

***Crown surface and ornamentation*.** In lateral view, the crown has enamel marked wrinkles separated by sulci that traverse continuously the labial and lingual surface. These surfaces are concave towards the base of the tooth on both margins and straight and perpendicular to the major axis of the tooth in the middle of the surface. In the apical area, three denticles are observed between two wrinkles, while in the middle part five denticles are observed between two wrinkles. The relationship between mesial denticles vs. distal (DSDI) obtained in UNPSJB-PV 969 is equal to 1.

4.4. Portezuelo Formation

Theropoda Marsh, 1881

Ceratosauria Marsh, 1884

Abelisauroidea Bonaparte, 1991

Abelisauridae Bonaparte and Novas, 1995

Gen. and sp. indet.

***Locality and Horizon*.** Northern coast of Los Barreales lake area, Futalognko site (38°27'8"S; 68°43'31"W), located at the center of the Neuquén province, Argentina; upper levels of Portezuelo Formation, upper Turonian–lower Coniacian, Upper Cretaceous (Veralli and Calvo, 2004; Garrido, 2010).

***State of preservation and general morphology*.** All teeth are almost complete and are interpreted as isolated shed tooth crowns. Specimens MUCPv 384, MUCPv 386 and MUCPv 387 are the best preserved teeth, although all lack the basalmost sector of the crown; specimens MUCPv 381 and MUCPv 391 are the most damaged ones. MUCPv 381 lacks most of its basal portion, a large portion of the distal margin close to the mid-crown, and its apicalmost sector. MUCPv 391 is represented by a large apical portion of the crown.

Morphotype I

***Material*.** MUCPv 381, 384, 386, and 387 (Figure 6).

***Crown overall morphology*.** Crowns studied here, which integrate the Morphotype I, are considered lateral teeth. They are characterized by an important to normal labiolingual compression at the crown base ($0.48 \leq CBR \leq 0.55$; Table 1). Basoapically, the mesial margin is strongly convex, whereas the distal margin is straight to slightly concave in lateral view, with the apex almost at the same level of the distal carina. In apical or basal view, both labial and lingual surfaces are mesiodistally convex. The four crowns show well-developed mesial and distal carinae. In the mesial view, the mesial carina is centrally positioned on the mesial margin on some teeth, whereas in MUCPv

384 is slightly curved lingually towards the base. In the distal view, the distal carina is straight in almost all crowns, except in MUCPv 384 whose distal carina is strongly bowed labially. The crowns are lenticular to lanceolate in cross-section at the level of the cervix.

Denticles. On all crowns, the mesial carina bears 11 denticles per 5 mm at mid-crown, whereas the distal carina bears between ten to 12 denticles per 5 mm at mid-crown. The mesial denticles are slightly larger than the distal denticles at the mid-crown and about the same size at the mid-crown (DSDI = 0.9 to 1.09). Both the mesial and distal denticles are chisel-shaped, sub-quadrangular at the base and inclined apically, and their external margin is symmetrically convex. Additionally, the denticles are longer mesiodistally than wide baso-apically. The interdenticular space is narrow and there are not interdenticular sulci between the denticles.

Crown surface and ornamentation. Marginal undulations, and transverse undulations are present. The texture is irregular and not oriented in any preferential direction.

Morphotype II

Material. MUCPv 391 (Figure 6).

Crown overall morphology. Both the mesial and distal margin is strongly apicobasally convex, with the apex positioned almost at the middle of the crown. Both labial and lingual surfaces are mesiodistally convex and the lingual surface is strongly apicobasally concave. The tooth shows well-developed mesial and distal carinae, with well visible denticles and displaced lingually. The crown is salinon-shape (i.e., with labial margin convex and lingual margin biconcave) in cross-section at the mid-crown.

Denticles. The mesial carina bears 12 denticles per 5 mm at mid-crown, whereas the distal carina bears 11 denticles per 5 mm at mid-crown. The mesial denticles are slightly larger than the distal denticles at the mid-crown to roughly the same size at the mid-crown (DSDI = 0.9). Both the mesial and distal denticles are chisel-shaped, sub-quadrangular at the base and inclined apically, and their external margin is symmetrically convex. The denticles are longer mesiodistally than wide baso-apically. The interdenticular space is narrow and there are not interdenticular sulci between the denticles.

Crown surface and ornamentation. Marginal undulations are present and well-developed. The texture is irregular and not oriented in any preferential direction.

4.5. Plottier Formation

Theropoda Marsh, 1881

Ceratosauria Marsh, 1884

Abelisauroidea Bonaparte, 1991

Abelisauridae Bonaparte and Novas, 1995

Gen. and sp. indet.

Material. Endemas-Pv 16 (Figure 7).

Locality and Horizon. El Anfiteatro area, northern of Parrita post locality (39°18’13”S; 68°24’35”O), located at the center-west of the Río Negro province, Argentina; Lisandro Formation, upper Coniacian-lowermost Santonian?, Upper Cretaceous (Salgado *et al*., 2009; Garrido, 2010).

***State of preservation and general morphology*.** Endemas-Pv 16 consists of an almost complete tooth that lacks part of the crown base. Although all denticles are worn, some of them present their original form fairly well preserved.

Crown overall morphology. Based on its general morphology, this tooth is considered as a lateral shed tooth. While it is not possible to calculate the exact value of the labiolingual compression of the crown (CBR), said ratio is inferred to be normal (close to 0.52) given that the missing basal sector is negligible. Similar inferences (CHR = 2.4) can be done regarding the baso-apical elongation of the crown based on the parameters provided by Hendrickx and Mateus (2014). The mesial margin of the crown is strongly convex in lateral view with observable serrated carina. The distal margin of the crown is slightly concave in lateral view, also with observable serrated carina. Both in apical and basal view, lingual and labial surfaces are convex and their faces converge mesially and distally in well visible carinae. In cross-section almost at the level of the cervix, the tooth is lenticular to slightly oval. As mentioned by Salgado *et al*. (2009), the mesial carina is straight and located centrally in the mesial margin, whereas distal carina is slightly displaced lingually. Unlike previously reported observations (Salgado *et al*., 2009), the distal carina is not extended to the cervix and it is impossible to determine due to its missing most basal sector. Regarding the mesial carina, this is extended to the cervix.

Denticles. The mesial carina bears 15 denticles per 5 mm at mid-crown, and 18 denticles per 5 mm close to the cervix. Since the carina is eroded, the density of denticles close to the apex is unknown. The distal carina possesses 14 denticles per 5 mm at mid-crown, 15 denticles per 5 mm close to the apex, and 15 denticles per 5 mm close to the base of the crown. In both carinae, the density of denticles increases apical and basally from mid-crown (DSDI = 0.9). The denticles are chisel-like in shape and

slightly inclined towards the apex, and the interdenticular space is narrow, less than one-third of the denticle width.

Crown surface and ornamentation. The enamel texture is smooth, lacking transverse undulations, marginal undulations, flutes, longitudinal grooves, or ridges are absent.

4.6. Allen Formation

Theropoda Marsh, 1881

Ceratosauria Marsh, 1884

Abelisauroidea Bonaparte, 1991

Abelisauridae Bonaparte and Novas, 1995

Gen. and sp. indet.

***Material*.** MACN-Pv-RN 1085 (Figure 8).

***Locality and Horizon*.** Bajo de Santa Rosa area, Cerro Bonaparte locality (40°03’25”S; 66°47’53”W), located at the center of the Río Negro province, Argentina; lower subunit of the Allen Formation, middle Campanian to lower Maastrichtian, Upper Cretaceous (Martinelli and Forasiepi, 2004; Salgado *et al.*, 2007).

***State of preservation and general morphology*.** MACN-Pv-RN 1086 consists of a fragment of the middle and apical sector of the crown. Both enamel labial and lingual surfaces of the shed tooth are well preserved, as are the denticles.

Crown overall morphology. The crown studied here is interpreted as a mesial tooth based on its general morphology. Given that it lacks the basal sector (i.e., at level of the

cervix), it is not possible to measure the crown height, labiolingual compression of the crown, and/or the ratio baso-apical height. Apicobasally, the mesial margin of the crown is slightly convex in lateral view with a present and serrated carina. The distal margin of the crown is straight to slightly convex. Likewise, the carina is present and serrated in the mesial margin. Regarding to apex, is located centrally in the crown. In the apical view, the labial and lingual surfaces are mesiodistally convex, but the lingual surface also is concave apicobasally. In basal view, both lingual and labial surfaces are strongly convex, and their faces converge mesially and distally in well visible carinae. In cross-section at level mid-crown, the tooth is salinon-shaped. In the mesial view, the mesial carina is oriented to the lingual surface. In the distal view, the distal carina is centrally positioned on the crown.

Denticles. The mesial carina bears ten denticles per 5 mm at mid-crown, and nine denticles per 5 mm close to the apex. The distal carina possesses nine denticles per 5 mm at mid-crown, and nine denticles per 5 mm close to the apex. The mesial denticles increase toward mid-crown, whereas the distal denticles have the same density (DSDI = 0.9). Both mesial and distal denticles are symmetrical to slightly asymmetrically convex with a biconvex external margin. The interdenticular space is narrow, less than one-third of the denticles width. The interdenticular sulci are clearly visible, being long and well-developed.

Crown surface and ornamentation. The crown of the tooth possesses arcuate marginal undulations on the lingual surface about the mesial and distal margin. These are well compacted, abundant and horizontally oriented in mesial sense. Transverse undulations, flutes, longitudinal grooves, or ridges are absent. The enamel texture is smooth to irregular.

5. Analysis

***5.1. Cladistic analysis*.** The cladistic analysis of the dentition-based yielded 100 most parsimonious trees (MPT) when using the constrained search (namely, CI = 0.198; RI = 0.465; L = 1319; strict consensus tree: CI = 0.196; RI = 0.458; L = 1333). The shed tooth CdM (see Table 1) was either recovered within Carcharodontosauridae, as the sister taxon of *Mapusaurus*, or as the sister taxon of a small clade formed by *Giganotosaurus* and *Mapusaurus* in the strict consensus tree (Figure 9). In all of the most parsimonious trees, CLM and PoM2 was either recovered within a small subclade formed by *Skorpiovenator* and *Aucasaurus*, where each operational taxonomic unit is located in different positions between the different more parsimonious trees. Regarding PlM, BBM, PoM1and AlM was either recovered within a small subclade conformed by *Arcovenator*, *Majungasaurus*, and *Indosuchus*, whose OTUs also variate their positions along the different more parsimonious trees. In this sense, in the strict consensus tree, these specimens were recovered within Abelisauridae and on a polytomy together with *Skorpiovenator*, *Aucasaurus*, *Majungasaurus*, *Indosuchus*, *Chenaniasaurus*, and *Arcovenator* (Figure 9).

The cladistic analysis conducted from the dentition-based data matrix without constraints found 100 most parsimonious trees (CI = 0.254; RI = 0.583; L = 1024). The strict consensus tree (CI = 0.178; RI = 0.346; L = 1458) recovered the tooth CdM within clade Carcharodontosauridae, essentially in a polytomy together with *Mapusaurus*, *Carcharodontosaurus*, and *Giganotosaurus* (Figure 10). CLM and PoM2 were recovered in a polytomy with *Skorpiovenator*, whereas PlM, BBM, and PoM1 were recovered closely related to *Indosuchus*. Respect AlM is resolved in a polytomy

together with *Aucasaurus*, *Abelisaurus*, *Majungasaurus*, *Rugops*, and *Kryptops* (Figure 10).

Regarding the cladistic analysis conducted of the tooth-crown-based data matrix without constraints found a poorly resolved strict consensus tree from 100 most parsimonious trees (namely, CI = 0.245; RI = 0.633; L = 652; strict consensus tree: CI = 0.112; RI = 0.05; L = 1433). Even though strict consensus tree yielded great polytomy, a better-resolved tree was obtained by pruning a *posteriori Limusaurus* (juvenile and adult). In this study, the tooth shed CdM was recovered in a polytomy within Carcharodontosauridae together with *Carcharodontosaurus*, and Giganotosaurini (*Mapusaurus* + *Giganotosaurus*), whereas PlM, BBM, and PoM1 were recovered in a small subclade that contains the abelisaurid *Indosuchus*. CLM and PoM2 were recovered close to the base of Abelisauridae but more derived than *Arcovenator* and *Chenaniasaurus*, whereas AlM was nested in a small polytomy together with *Aucasaurus*, *Majungasaurus*, *Abelisaurus*, *Rugops*, and *Kryptops* (Figure 11).

5.2. Discriminant analysis. The DFA conducted on the whole dataset classified the shed teeth MDPA-Pv 005 and MACN-Pv-RN 1085 as tyrannosaurids; MUCPv 381, MUCPv 384, MUCPv 386, MUCPv 387 and Endemas-Pv 2 as megalosaurids, and MUCPv 391 and UNPSJB-PV 969 as non-abelisauroid ceratosaurians; and Endemas-Pv 16 as a non-tyrannosauroid tyrannosaurid (clade-level analysis; PC1 and PC2 account for 38.19% and 30.88% of the total variance, respectively; Figure 12). MDPA-Pv 005 was classified to taxon-level as the carcharodontosaurid *Mapusaurus*; MUCPv 381, MUCPv 391, and MACN-Pv-RN 1085 as abelisaurid *Chenaniasaurus*; MUCPv 384 and MUCPv 386 as the ceratosaurid *Genyodectes*; MUCPv 387 as the abelisaurid *Skorpiovenator*; UNPSJB-PV 969 as the ceratosaurian *Berberosaurus*; Endemas-Pv 2 as

the allosaurid *Allosaurus*; and Endemas-Pv 16 as indeterminate abelisaurid (PC1 and PC2 account for 35.7% and 27.78% of the total variance, respectively).

Reclassification rate (RR) was relatively high (59.25% to clade-level and 56.55% to taxon-level). When the discriminant function analyses were conducted if absence of denticles was inapplicable, the RR at the group-level was slightly better (61.88%), whereas at taxon-level was roughly the same (57.46%, see supplementary information). In this analysis, the crowns were classified the same as in previous analysis (clade level; PC1 39.15% and PC2 30.96%). Similarly, all shed crowns were classified the same as in previous analysis at taxon-level (PC1 36.43% and PC2 22.58%).

In so far as to DFA based on the whole datasets of Hendricks´s first-hand measurements (i.e., datasets restricted to taxa with teeth larger than two centimeters), MDPA-Pv 005 was classified as tyrannosaurid; MUCPv 381, MUCPv 384, MUCPv 386, MUCPv 387 and MACN-Pv-RN 1085 as megalosaurids; MUCPv 391 and Endemas-Pv 2 as allosaurids, and UNPSJB-PV 969 and Endemas-Pv 16 as metriacanthosaurids (clade level; PC1 47.43% and PC2 27.57%; Figure 13). At, taxon-level, MDPA-Pv 005 was classified as the carcharodontosaurid *Mapusaurus*; MUCPv 391 and Endemas-Pv 2 as the allosaurid *Allosaurus*; MUCPv 384 and MUCPv 386 as the megalosaurid *Duriavenator*; MUCPv 381 and MACN-Pv-RN 1085 as the megalosaurid *Torvosaurus*; MUCPv 387, UNPSJB-PV 969 and Endemas-Pv 16 as indeterminate abelisaurids (PC1 and PC2 account for 54.22% and 18.47% of the total variance, respectively). RR are much better at taxon-level than at clade-level (i.e., 61.65% and 58.25%, respectively), however, it are low when compared to the RR when the absence of denticles was considered as inapplicable (61.75% and 60.4%, respectively). In this analysis, the shed tooth MDPA-Pv 005 was classified as a

carcharodontosaurid at clade-level, whereas the remaining teeth were classified the same as in the previous analysis (PC1 56.13% and PC2 23.98%). At taxon-level, MUCPv 381 was classified as the megalosaurid *Dubreuillosaurus*, and the crowns remaining were classified the same as in the previous analysis (PC1 45.25% and PC2 21.14%).

In both analyses, the PC1 summarized a major contribution of the variables CBL, CBW, CH, AL, MCL, MCW, MSL and minor contributions from MDL and DDL. The high positive PC1 scores identified taxa with high and wide teeth, whereas the more negative PPC1 scores set apart taxa with teeth that are short and narrow. The PPC2 summarized a major contribution of the variables LAF and LIF. High positive PC2 scores identified mainly taxa with a major number of flutes on the labial and lingual surfaces of the crown, whereas negative scores characterized taxa with non-number of flutes in both surfaces of the crown.

5.3. Cluster analysis. The cluster analysis using hierarchical clustering option found the tooth MDPA-Pv 005 as the sister taxon of *Acrocanthosaurus*; MUCPv 384 closely related to *Berberosaurus*; MUCPv 386 as *Chenaniasaurus*; MUCPv 387 as *Duriavenator*; UNPSJB-PV 969 as *Ceratosaurus*; Endemas-Pv 2 as *Majungasaurus*; and Endemas-Pv 16 as *Monolophosaurus*. When using the Neighbour-joining clustering option, recoveries MDPA-Pv 005 closely related to *Mapusaurus*, *Giganotosaurus*, *Ceratosaurus* or *Acrocanthosaurus*, MUCPv 384 to *Gorgosaurus*, *Berberosaurus*, *Majungasaurus* or *Carnotaurus*; MUCPv 386 to *Chenaniosaurus* or *Duriavenator*; MUCPv 387 to *Carnotaurus* or *Majungasaurus*; UNPSJB-PV 969 to *Ceratosaurus*, Endemas-Pv 2 to *Carnotaurus* or *Majungasaurus*, and Endemas-Pv 16 to *Raptorex* (see

supplementary information 2.1). The cluster analysis based on the datasets restricted to taxa with teeth larger than two centimeters. MDPA-Pv 005 was then classified as *Mapusaurus*, *Giganotosaurus*, *Acrocanthosaurus* or *Ceratosaurus*; MUCPv 381 as *Carnotaurus*; MUCPv 384 as *Megalosaurus* or *Duriavenator*; MUCPv 386 as *Duriavenator*; MUCPv 387 as *Megalosaurus* or *Duriavenator*; MUCPv 391 as *Carnotaurus*; UNPSJB-PV 969 as *Ceratosaurus*; Endemas-Pv 2 as *Carnotaurus* or *Majungasaurus*; Endemas-Pv 16 as *Monolophosaurus*; and MACN-Pv-RN 1085 as *Carnotaurus* or *Dubreuillosaurus*. When using the Neighbour-joining clustering option, recoveries of MDPA-Pv 005 were classified as *Acrocanthosaurus*; MUCPv 381 to *Majungasaurus* or *Dubreuillosaurus*; MUCPv 384 as *Berberosaurus* or *Arcovenator*; MUCPv 386 as *Duriavenator*; MUCPv 387 as *Duriavenator*; MUCPv 391 as *Abelisaurus*; UNPSJB-PV 969 as *Ceratosaurus*; Endemas-Pv 2 as *Carnotaurus*; Endemas-Pv 16 as *Marshosaurus*; and MACN-Pv-RN 1085 as *Carnotaurus* or *Dubreuillosaurus* (see supplementary information 2.1).

6. Discussion

6.1. Taxonomic inference of the Candeleros Formation tooth MDPA-Pv 005

From the obtained results, the three cladistic analyses allow to assign with confidence MDPA-Pv 005 as a tooth likely belonging to carcharodontosaurid. In all analyses it is recovered as a derived carcharodontosaurid within Carcharodontosauridae clade (*sensu* Novas *et al*., 2013). In fact, the DFAs and cluster analysis recovered the same results supporting the affinity of the shed tooth as carcharodontosaurid (see supplementary information). Regarding the plot generated from the DFA performed on the two datasets, it is observed that MDPA-Pv 005 is placed outside the occupied

morphospace by the different groups now, but close to the morphospace of Tyrannosauridae and Carcharodontosauridae, or, depending on the analysis, just near the edge of Tyrannosauridae; depending on the analysis (Figures 12 and 13).

Both Tyrannosauridae and Carcharodontosauridae possess lateral dentition with a CH, CBR, and CHR with slightly similar variation ranges, i.e., crowns with height higher to 6 cm, labiolingual compression of the crown that variates between ~0.4 to ~0.65 (in carcharodontosaurids) and ~0.4 to ~0.8 (in tyrannosaurids), and baso-apical elongation of the crown which varies between ~1.14 to ~2.3 (in carcharodontosaurids) and ~1.3 to ~2.75 (in tyrannosaurids). Nevertheless, the size differences between mesial and distal denticles differ lateral teeth of carcharodontosaurids and tyrannosaurids. Indeed, mesial and distal denticles are nearly the same size in tyrannosaurids, whereas the mesial denticles are larger than the distal in carcharodontosaurids as occurs in the Patagonian forms (i.e., *Mapusaurus* and *Giganotosaurus*, but unknown for *Lajasvenator*; see Coria *et al*., 2020). In tyrannosaurids, the mesial carina strongly twist onto the mesiolingual surface, whereas that in carcharodontosaurids the mesial carina is centrally positioned on mesial margin or is weakly curved lingually towards the base (Hendrickx *et al*., 2019). The distal carina in carcharodontosaurids is centrally positioned or slightly displaced, whereas in tyrannosaurids is strongly labially deflected (Hendrickx *et al*., 2019). Moreover, in lateral teeth of the carcharodontosaurids have a clearly observable braided enamel texture is clearly observed, whereas the tyrannosaurids possess irregular enamel texture (Hendrickx *et al.*, 2019).

6.2. Taxonomic inference of remaining teeth

The results of the three cladistic analyses support the affinity of the Cerro Lisandro, Bajo Barreal, Portezuelo (Morphotype I and II), Plottier, and Allen

Morphotypes with the typical dentition of Abelisauridae. Nevertheless, the DFAs and cluster analyses recovered poorly robust results, i.e., the crowns being assigned to Megalosauridae, Allosauridae, Abelisauridae, Carcharodontosauridae, and Tyrannosauridae. The most plausible explanation is that these mixed results are due to the small number of variables measured (see Table 1). On the other hand, the plot generated from the DFA on the two datasets is placed within the morphospace (convex hull) occupied by a high number of theropod groups, including Abelisauridae, Megalosauridae, Tyrannosauridae, Metricanthosauridae, non-abelisauroid Ceratosauria, and Allosauridae (Figures 12 and 13).

Unlike Veralli and Calvo (2004), we recognize the specimens MUCPv 381, MUCPv 384, MUCPv 386, and MUCPv 387 as lateral teeth, while MUCPv 391 is recognized as a mesial tooth. These authors argue that all these dental pieces possess enamel wrinkles while we observe that MUCPv 387 lacks both marginal undulations as well as transversal undulations. Furthermore, the only specimens that have marginal undulations in their crowns are MUCPv 381 and MUCPv 391. In the first specimen, these are arranged on both sides adjacent to the distal carina. In the second, they are only present on the lingual face and adjacent to both carinae, although those that are arranged in the mesial carina are more subtle than in the distal carina. Regarding MUCPv 384 and MUCPv 386 specimens are characterized to possess transversal undulations about in the labial face. Unlike Martinelli and Forasiepi (2004), Casal *et al*. (2009) and Salgado *et al*. (2009), we recognize the specimens UNPSJB-PV 969 and Endemas-Pv 16 as lateral teeth, whereas the specimens Endemas-Pv 2 and MACN-Pv-RN 1085 as mesial teeth based on their typical morphology (see Hendrickx *et al*., 2015).

The specimens studied here, and previously reported, are partially complete and well-preserved theropod teeth. However, previously reports on these teeth focused their

description and comparison on carcharodontosaurid taxa known at that time. Based on the presence of the arcuate marginal undulations visible on the crowns, the previous authors mention that this unique feature unites these teeth to Carcharodontosauridae and at the same time separates them from other clades of theropods.

In summarizing, the shed teeth of Cerro Lisandro, Bajo Barreal, Portezuelo, Plottier and Allen formations have an unique combination of features only observed in the dentition of abelisaurids. The lateral teeth are characterized by a weakly convex distal profile to almost straight, arcuate marginal undulations and transversal undulations; a mesial carina extending to the cervix or just above it; a centrally placed distal carina on the distal margin; symmetrically convex labial and lingual surfaces of the crown in the mesiodistal plane; apically inclined distal denticles and short interdenticular sulci between both mesial and distal denticles; and irregular, non-oriented texture of enamel (see Hendrickx *et al*., 2019, 2020). Specimens considered here as mesial teeth also possess a combination of features observed in abelisaurids. For example, they present a salinon-shaped cross-section outline, and apically hooked-shaped denticles (see Hendrickx *et al*., 2019, 2020).

An interesting fact that has been registered to date is the tendency to homogenization materials that come from the same stratigraphic unit. In this sense, the teeth from Allen Formation collected in Lago Pellegrini in northern, Río Negro Province, and deposited in the MPCA collections have been referred by Hendrix and Mateus (2014) to *Abelisaurus comahuensis*, because they come from the same area and stratigraphic unit. This assignment has been followed by subsequent works based on this dataset (i.e., Hendrix *et al*., 2015ab, Gerke and Wings, 2016; Hendrix *et al*., 2020). Here, we consider it as a composite OTU in accordance with previous authors, but the

referral of the Lago Pellegrini teeth to *Abelisaurus comahuensis* has to be revised in more detail.

6.3. Biostratigraphic implicances

The fossil record of middle to large bodied predators during the late Mesozoic has increased notably during the last decades, especially in Gondwanan landmasses, allowing to infer about the composition and evolution of their terrestrial faunas (i.e. Krause *et al*., 2007; Novas, 2013; Ibrahim *et al*., 2020). Patagonia, as the southern region of South America, has been considered to represent the consecutive changes of faunistic realms, following the successive paleobiogeographic scenarios relative to the fragmentation of Gondwana, intercontinental dispersal events, and still disputable regional isolation into the continent (i.e., Sereno *et al*., 2004; Coria and Salgado, 2005). The upper Mesozoic Patagonian theropod record includes elements from the Upper Jurassic of the Cañadón Calcareo and Toqui formations, consisting of basal tetanurans of uncertain or debated relationships (Novas *et al*., 2015; Rauhut and Pol, 2017). The lowermost Cretaceous (Berriasian to Barremian) theropod record is contained in the Bajada Colorada, Mulichinco and La Amarga formations, and consists of noasaurid and abelisaurid ceratosaurs, megalosauroids and a basal carcharodontosaurid, *Lajasvenator ascheriae* (Bonaparte, 1996; Apesteguía and Bonaparte, 2004; Canale *et al*., 2017; Coria *et al*., 2020). *Lajasvenator* represents the ancient proper Carcharodontosauridae (sensu Benson *et al.*, 2010). It appears to be included in a monophyletic group together with the african *Eocarcharia dinops* and the european *Concavenator corcovatus*, which in turns represent an early branch of the lineage of more derived taxa.

During the late Early Cretaceous and at the beginning of the Late Cretaceous (Aptian to middle Turonian), Patagonia contained a particular fauna with strong similarities with those of northern Africa (i.e., Leanza *et al*., 2004; Coria and Salgado, 2005; Krause *et al*., 2020). This fauna, called by Krause and colleagues the "Middle Cretaceous Faunal Assemblage of Gondwana" (MCFAG) (Krause *et al*., 2020), is represented by multiple lithostratigraphic units, including Cerro Barcino, Matasiete, Mata Amarilla, Lohan Cura, Rayoso, Candeleros, Huincul and Bajo Barreal formations. Their theropod faunas includes ceratosaurids, elaphrosaurine noasaurids and non-furileusaurian abelisaurids among ceratosaurians (Martínez *et al.*, 1986; Coria and Salgado, 1998; Rauhut, 2004; Canale *et al*., 2009; Juárez Valieri *et al*., 2011; Baiano *et al*., 2020; Cerroni *et al.*, 2020), the enigmatic bahariasaurids (Apesteguía *et al*., 2016; Motta *et al*., 2020), and multiple tetanuran lineages, as carcharodontosaurids (Coria and Salgado, 1995; Novas *et al*., 2005; Coria and Currie, 2006; Motta *et al.*, 2016), basal coelurosaurs (Martínez and Novas, 2006; Novas *et al*., 2012), megaraptorans (Casal *et al.*, 2016; Motta *et al.*, 2016), basal alvarezsaurians (Makovicky *et al*., 2012), and non-avian paravians including basal unenlagiids (Makovicky *et al*., 2005; Motta *et al*., 2020).

Within this assemblage, the carcharodontosaurids are represented by the highly derived Giganotosaurini clade, with the early record of the Albian *Tyrannotitan chubutensis*, *Giganotosaurus carolini* from early to middle Cenomanian and the slightly younger *Mapusaurus roseae* and their possible junior synonym *Taurovenator violantei* (Coria *et al*., 2020) from the late Cenomian to early Turonian. *Mapusaurus roseae* and *T. violantei* constitute the last convincing evidence of this lineage of large predators in Patagonia and South America. At this stage, theropods are represented by for particular sauropod lineages, including a high diversity of rebbachisaurid diplodocoids, basal

titanosaurs and giant non-lognkosaurid colossosaurians (Martínez *et al.*, 2016; Canudo *et al.*, 2018; Simón *et al.*, 2018). The crocodyliformes are represented primarily by uruguaysuchids (Fernández Dumont *et al.*, 2020).

A critical issue about the changes in the faunistic conformation of the Cretaceous faunas from Patagonia and even South America is the faunistic turnover from the "middle" to Late Cretaceous faunas from the Neuquén Basin that has been previously suggested (i.e., Coria and Salgado, 2005) which involve extinctions of some lineages and subsequent adaptive radiation of others. The persistence of lineages such as ceratosaurids, elaphrosaurine noasaurids and carcharodontosaurids, but also rebbachisaurid and basal titanosaurian among sauropods and uruguaysuchid mesoeucrocodylians, represents common components of the MCFAG that disappear from the fossil record of Patagonia, as well as from northern South America, Africa and Europe posterior to this stage. Several clades appear to generate a radiation of taxa just posterior to the end of the MCFAG in South America and particularly in Patagonia. An early stage of the fauna from South America posterior to the isolation of the continent with Africa, defined as the "Late Cretaceous Faunal Assemblage of South America" (LCFASA), is characterized by the presence of furileusaurian abelisaurids (Filippi *et al.*, 2016), as well as megaraptorids in the theropod component (Porfiri *et al.*, 2018), the radiation of patagonykine alvarezsaurians and derived unenlagiids (Novas *et al*., 2013) among the theropod dinosaurs, multiple lineages of small sized derived titanosaurs and long-spined lognkosaurids among sauropods (Carballido *et al*., 2017) large sized elasmarians (Cruzado Caballero, 2019; Ibiricu *et al*., 2020) and peirosaurids, advanced notosuchians and baurusuchids among the mesoeucrocodylians (Pol and Leardi, 2015).

In this context, the subsistence of the carcharodontosaurid lineage in Patagonia was proposed multiple times based on the assignation of the isolated teeth discussed in

the present study, which approach them methodologically for first time, by multivariate analysis. In fact, the recovery of the all previously purported carcharodontosaurid evidence posterior to the MCFAG from Patagonia results in the current study as belonging to abelisaurid theropods, in accordance with the hypothesis of the local extinction of the carcharodontosaurid theropods of Patagonia as part of a faunistic turnover apparently occurred between the late Turonian to early Coniacian.

Since the Neuquén Basin contains a succession of terrestrial vertebrate faunas during most of the Late Cretaceous, it is the best resource for biostratigraphic inferences. All the lineages representing the MCFAG previously discussed, including the carcharodontosaurids, are limited to the Huincul Formation. The overlying Cerro Lisandro Formation tetrapod fossil record, although less diverse than their underlying Huincul Formation and the overlying Portezuelo Formation, appears to have a fossiliferous record that is more closely related to the last one because of presence of peirosaurids, elasmarians and high-spined lognkosaurians. Therefore, the assignment of the Cerro Lisandro morphotype tooth to Abelisauridae instead of Carcharodontosauridae is concordant with this scenario. We consider the more diverse fauna recorded in the Portezuelo Formation, and its highly abundant fossiliferous record, as depicting a clearly differentiated fauna from those of the MCFAG, and representing the first clear stages of the denominated “Late Cretaceous Faunal Assemblage of South America” (LCFASA).

The assignation of the Portezuelo Formation morphotype teeth, as also those of the Plottier and Allen formations, to Abelisauridae leave without support the idea of survival of the carcharodontosaurids in Patagonia posterior to the MCFAG to LCFASA faunistic turnover. We consider that previous assumptions of the time of the events posterior to the deposition of the Portezuelo Formation in the Neuquén Basin (Coria and

Salgado, 2005) are incorrect. Instead, we propose that the faunistic turnover occurred previous to the deposition of the Portezuelo Formation, more precisely at the end of the deposition of the Huincul Formation and at the beginning or during the deposition of the Cerro Lisandro Formation, approximately in the late Turonian–earliest Coniacian.

On the other hand, the southern Golfo San Jorge Basin present in the Bajo Barreal a composition with mixed components, including rebbachisaurid and basal titanosaurians, that has typical components of the MCFAG and other more reminiscent to those of the LCFASA, with large clawed megaraptorans and elasmarians. In this context, the assignation of the Bajo Barreal morphotype tooth to abelisaurid is not unexpected, but it could be interpreted both as evidence of a slightly younger age of the Bajo Barreal Formation respect to the Huincul Formation or simply is part of the composition of a proper MCFAG, which already includes the abelisaurids. This is in accordance with previous faunistic comparisons between the Neuquén and Golfo San Jorge Basins (Canale *et al.*, 2011; Ibiricu *et al.*, 2020).

The geographical range can in fact not be restricted to Patagonia but cover even completely to South America, as indicated by the faunistic composition of the Salta, La Rioja and equivalent basins from northwestern Argentina (Novas and Agnolín, 2004; Agnolín and Chiarelli, 2010; D'Emic and Wilson, 2011; Fiorelli *et al.*, 2016; Hechenleitner *et al.*, 2018, 2020), the Norte Basin of western Uruguay (Perea *et al.*, 2011) or Bauru Basin faunas of Brazil (Martinelli and Teixeira, 2015; Brusatte *et al.*, 2017; Grillo and Delcourt, 2017; Geroto and Bertini, 2019; Langer *et al.*, 2019). However, the composition of some of these faunas during the Turonian-Santonian lapse is poorly or completely unknown. In the case of the Bauru Basin faunal assemblages, similar detailed analyses of dental and cranial material previously proposed as

belonging to carcharodontosaurids has been conclusive in discarding this assignment (Delcourt and Grillo, 2018; Delcourt *et al.*, 2020).

7. Conclusions

Our results, based on data obtained from cladistic analyses, DFAs, and cluster analyses, suggest that isolated shed tooth MDPA-Pv 005 of Candeleros Formation (lower Cenomanian) can be assigned to a carcharodontosaurid lateral tooth. However, remaining specimens previously considered as carcharodontosaurids actually belong to abelisaurids. In the case of Portezuelo teeth (upper Turonian to lower Coniacian) where two morphotypes have been found, they could even correspond to different positions within the tooth row of a single taxon. Even though the cladistic analysis was more precise and exact in comparison with the DFAs and cluster analyses, the latter should not be discarded. The lack of conclusive evidence could have been caused by a number of variables that could not be measured.

While this study supports not only the previous idea that, although morphologically distinct, carcharodontosaurids and abelisaurids share similar traits, it also supports the notion that carcharodontosaurids became extinct in South America during the late Turonian and were replaced by other large theropods such as megaraptorids and abelisaurids. The extinction of carcharodontosaurids in Patagonia, as well as in northern South America, are indicative of the faunal turnover event from the "Middle Cretaceous Faunal Assemblage of Gondwana" (MCFAG) to the early stages of the "Late Cretaceous Faunal Assemblage of South America" (LCFASA).

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FIGURE CAPTIONS

FIGURE 1. a) Schematic map of the Neuquén basin and extension of its Cenozoic sequences (*sensu* Andreis, 2001) and the Golfo San Jorge basin showing each specimen occurrence site. **b)** Stratigraphic column for the Upper Cretaceous of the Neuquén basin, highlighting the lithological units of occurrence for each one specimen (Modified from Garrido, 2010), and **c)** Stratigraphic column for the Upper Cretaceous of the Golfo San Jorge basin, highlighting the lithological unit of occurrence for the specimen, respectively.

FIGURE 2. Location maps of each specimen according to its occurrence *in situ* and the geological unit that is inserted, respectively. **a)** MDPA-Pv 005 (Aguada Pichana),

MUCPv 381, 384, 386, 387 (Morphotypes I) and MUCPv 391 (Morphotype II) (Futalognko Site); **b)** Endemas-Pv 2 (La Bajada Sector); Endemas-Pv 16 (Parrita Site); **c)** MACN-Pv-RN 1085 (Cerro Bonaparte); and **d)** UNPSJB-PV 969 (Estancia Ocho Hermanos).

FIGURE 3. MDPA-Pv 005 in **A**, labial; **B**, lingual; **C**, distal; **D**, mesial views; **E**, detail of marginal undulations; **F**, detail of enamel texture; **G**, distal denticles at the apical three-fourths of the crown height; **H**, basal; **I**, apical views. **Abbreviations**: **mca**, mesial carina; **dca**, distal carina; **mun**, marginal undulations; **ent**, enamel texture. Scale bar equal 1 cm.

FIGURE 4. Endemas-Pv 2 in **A**, lingual; **B**, labial; **C**, mesial; **D**, distal views; **E**, detail of marginal undulations; **F**, basal view. **Abbreviations**: **mca**, mesial carina; **dca**, distal carina; **mun**, marginal undulations. Scale bar equal 1 cm.

FIGURE 5. UNPSJB-PV 969 in **A**, labial; **B**, lingual; **C**, mesial; **D**, distal views. **Abbreviations**: **mca**, mesial carina; **dca**, distal carina. Scale bar equal 1 cm.

FIGURE 6. Morphotype I (**A-I**) and II (**J-N**). MUCPv 381 in **A**, labial; **B**, mesial views. MUCPv 384 in **C**, lingual; **D**, labial; **E**, distal; **F**, mesial views. MUCPv 386 in **G**, lingual; **H**, labial views. MUCPv 387 in **I**, labial view. MUCPv 391 in **J**, lingual; **K**, labial; **L**, mesial; **M**, distal; **N**, apical views. **Abbreviations**: **mca**, mesial carina; **dca**, distal carina; **mun**, marginal undulations. Scale bar equal 1 cm.

FIGURE 7. Endemas-Pv 16 in **A**, labial view; **B**, mesial denticles at the mid-crown; **C**, distal denticles at the mid-crown; **D**, distal denticles close to the base of crown. **Abbreviations**: **mca**, mesial carina; **dca**, distal carina. Scale bar equal 1 cm.

FIGURE 8. MACN-Pv-RN 1085 in **A**, lingual; **B**, labial; **C**, mesial; **D**, distal views; **E**, mesial and distal denticles at the mid-crown; **F**, basal view. **Abbreviations**: **mca**, mesial carina; **dca**, distal carina. Scale bar equal 1 cm.

FIGURE 9. Strict consensus tree of 100 most parsimonious trees (CI = 0.196; RI = 0.458; L = 1333) recovered in the cladistic analysis of the dentition-based data matrix with constrained search and setting the all morphotypes as floating terminals.

FIGURE 10. Strict consensus tree of 100 most parsimonious trees (CI = 0.178; RI = 0.346; L = 1458) recovered in the cladistic analysis of the dentition-based data matrix with an unconstrained search.

FIGURE 11. Strict consensus tree of 100 most parsimonious trees (CI = 0.112; RI = 0.05; L = 1433) recovered in the cladistic analysis of the tooth-crown-based data matrix.

FIGURE 12. Results of the discriminant analysis performed at the "group"-level on the whole dataset with personal measurements of C.H. on 400 teeth belonging to 46 theropod taxa and 12 groupings along the first two canonical axes of maximum discrimination in the dataset (PC1 and PC2 account for 38.19% and 30.88% of the total variance, respectively).

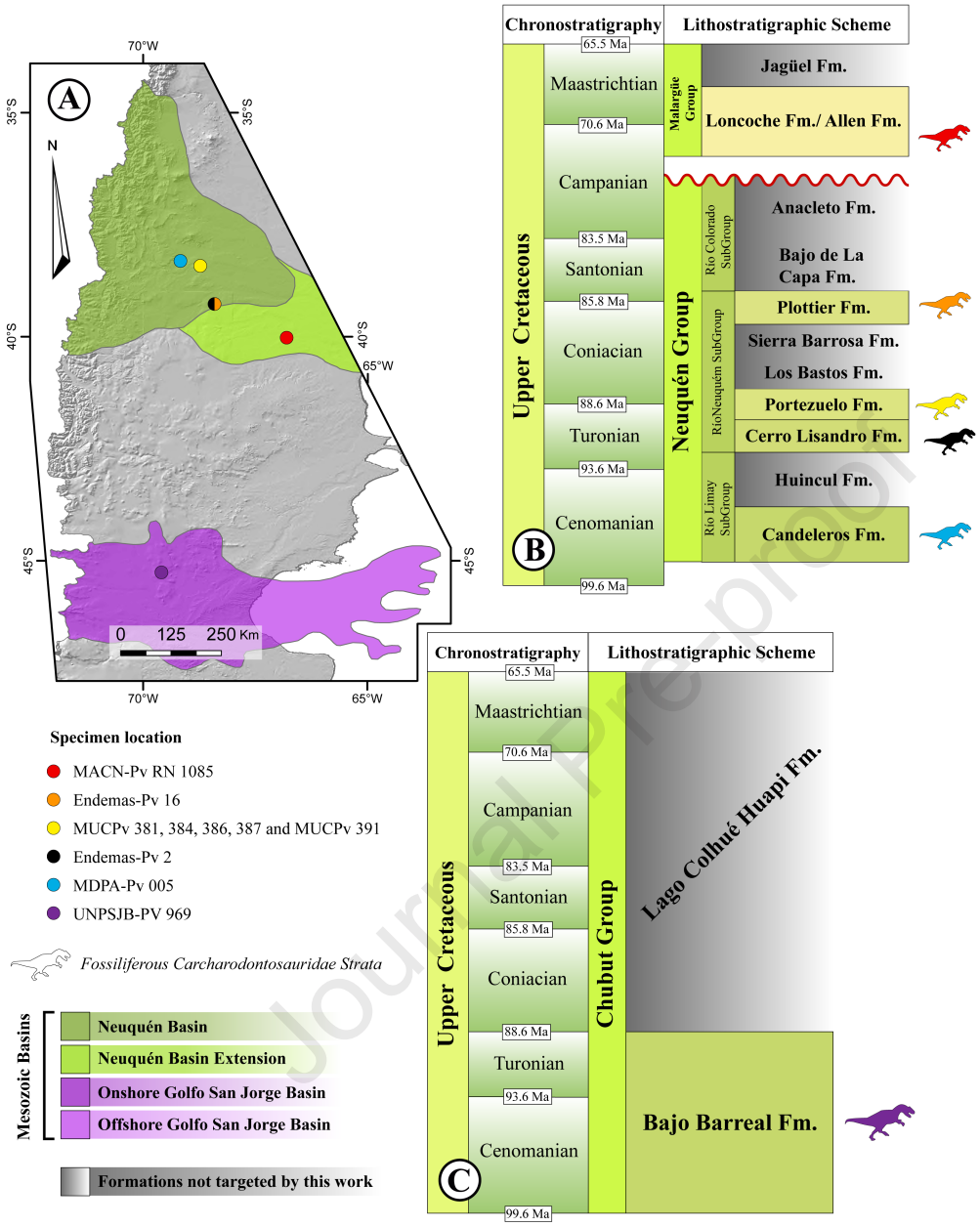
FIGURE 13. Results of the discriminant analysis performed at the "group"-level on the whole dataset with teeth larger than two centimeters, on 725 teeth belonging to 53 theropod taxa and 13 groupings along the first two canonical axes of maximum discrimination in the dataset (PC1 47.43% and PC2 27.57% of the total variance, respectively).

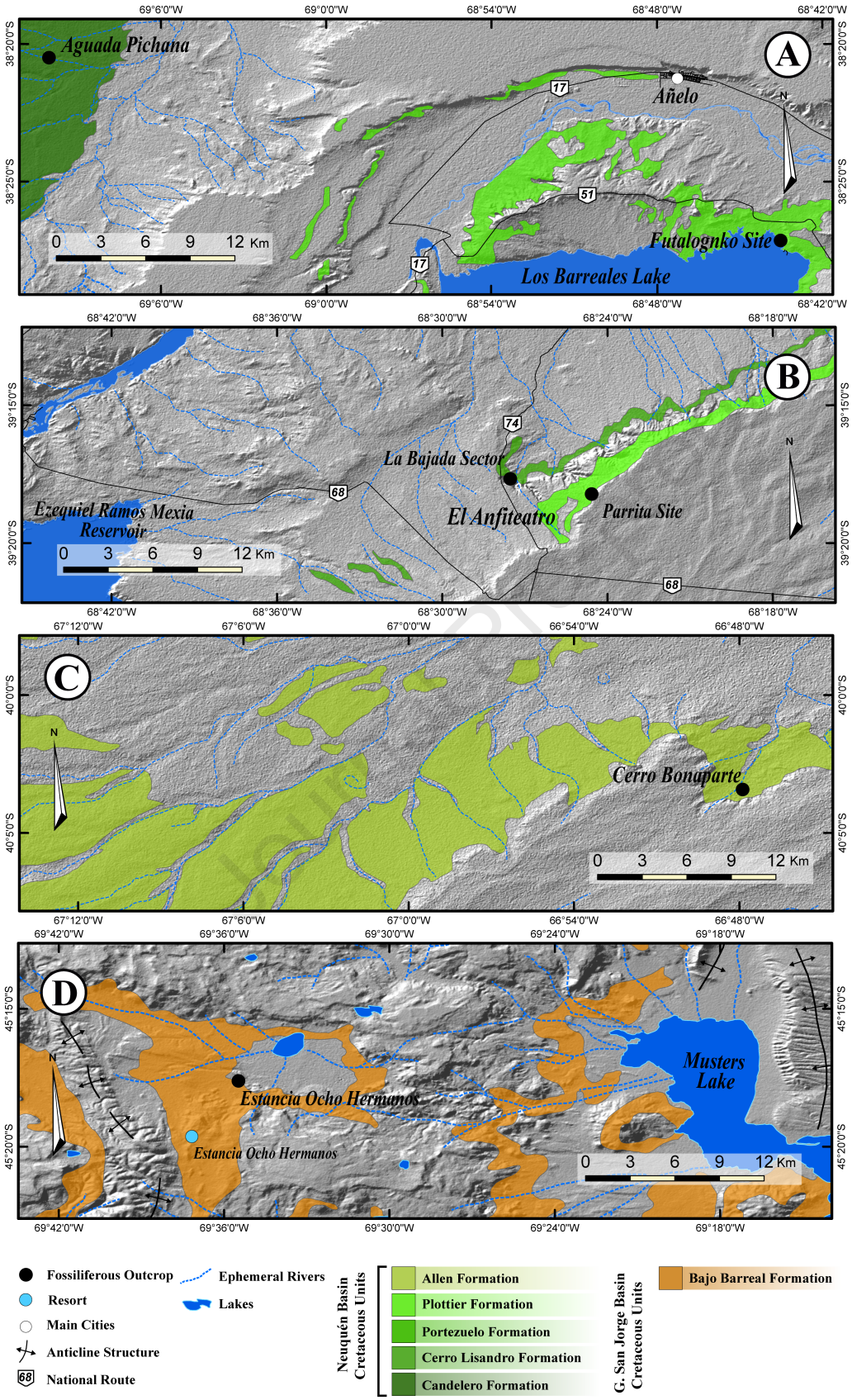
TABLES

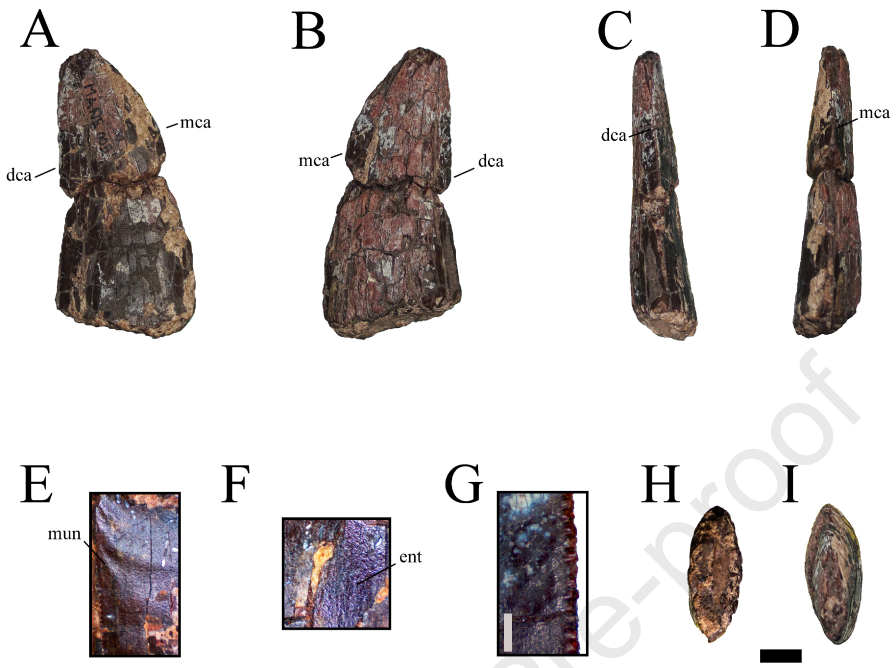
TABLE 1. Measurements of all teeth crowns. Measurements in millimeters, number of denticles per five mm and crown angle in degrees.

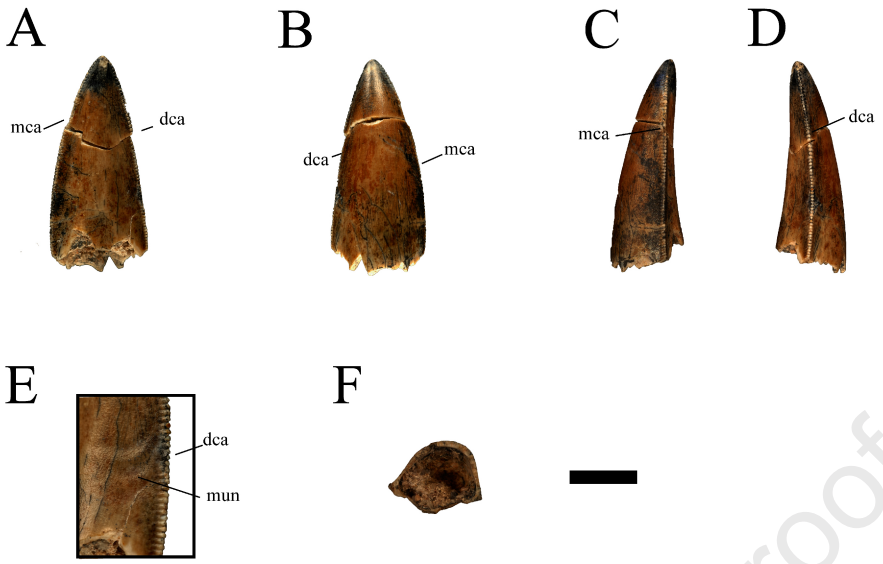
SUPPLEMENTARY DATA

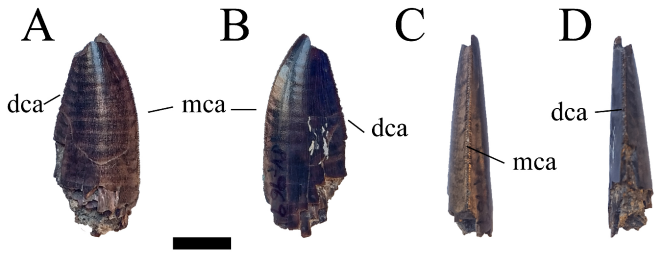
Specimen	Morphotype	Abbreviation	Anatomical placement	Fuente	CBL	CBW	CH	AL	CBR	CHR	CA	MC	DC	MCL	MCW	MCR	DSDI
MDPA-Pv 005	Candeleros Morphotype	CdM	Lateral	*Observ. Pers.*	36.35	16.1	?	?	0.44	?	?	10	15	28	10.6	0.37	1.5
ENDEMAS-Pv 2	Cerro Lisandro Morphotype	CLM	Mesial	*Observ. Pers.*	13.5	10.4	31.75	31	0.77	2.35	24.36	12	11	11.2	6.9	0.61	0.9
UNPSJB-PV 969	Bajo Barreal Morphotype	BBM	Lateral	*Observ. Pers.*	?	7.4	34.2	34.8	?	2.25	?	13	13	15.7	6.1	0.38	1
MUCPv386	Portezuelo Morphotype I	PoM1	Lateral	*Observ. Pers.*	17.2	9.6	?	?	0.55	?	?	11	10	13.2	7.2	0.54	0.9
MUCPv381				*Observ. Pers.*	?	?	?	?	?	?	?	11	10	10.4	5.6	0.53	0.9
MUCPv384				*Observ. Pers.*	19.6	9.4	?	?	0.48	?	?	11	12	14.5	7.3	0.50	1.09
MUCPv387				*Observ. Pers.*	16.4	9	?	?	0.54	?	?	11	11	12.8	6.5	0.50	1
MUCPv391	Portezuelo Morphotype II	PoM2	Mesial	*Observ. Pers.*	?	?	?	?	?	?	?	12	11	14.8	8.7	0.58	0.9
ENDEMAS-Pv 16	Plottier Morphotype	PlM	Lateral	*Observ. Pers.*	9.5	5	22.8	24.5	0.52	2.4	23.85	15	14	8.1	3.7	0.45	0.9
MACN-PV RN 1085	Allen Morphotype	AlM	Mesial	*Observ. Pers.*	?	?	?	?	?	?	?	10	9	10.1	4.9	0.48	0.9

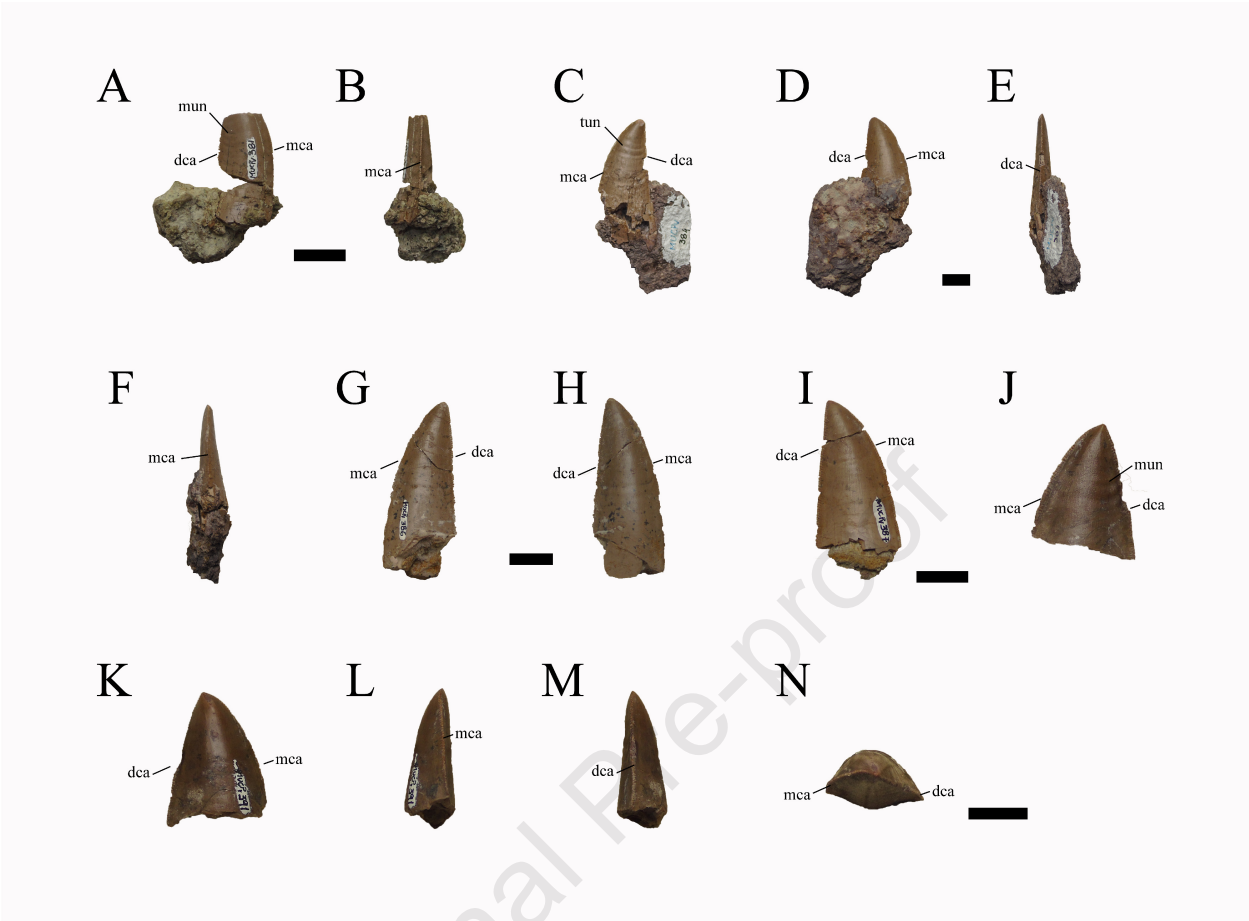


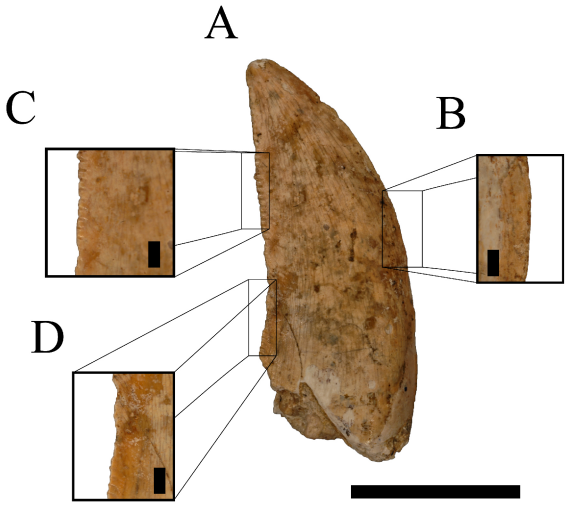

A
Aguada Pichana
Añelo
Futalognko Site
Los Barreales Lake
17
51
0 3 6 9 12 Km
B
La Bajada Sector
El Anfiteatro
Parrita Site
Ezequiel Ramos Mexia Reservoir
74
68
C
Cerro Bonaparte
D
Estancia Ocho Hermanos
Musters Lake
Fossiliferous Outcrop
Resort
Main Cities
Anticline Structure
National Route
Ephemeral Rivers
Lakes
Neuquén Basin Cretaceous Units
Allen Formation
Plottier Formation
Portezuelo Formation
Cerro Lisandro Formation
Candelero Formation
G. San Jorge Basin Cretaceous Units
Bajo Barreal Formation

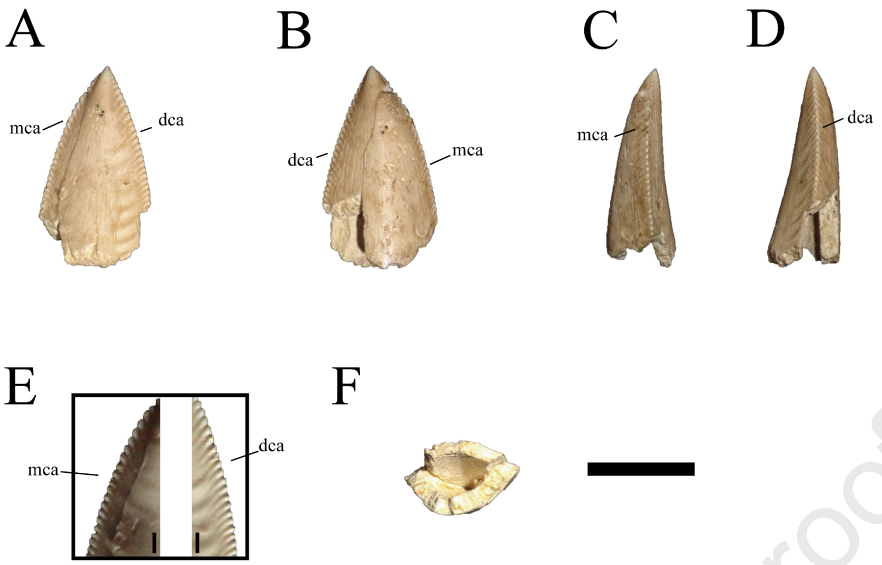


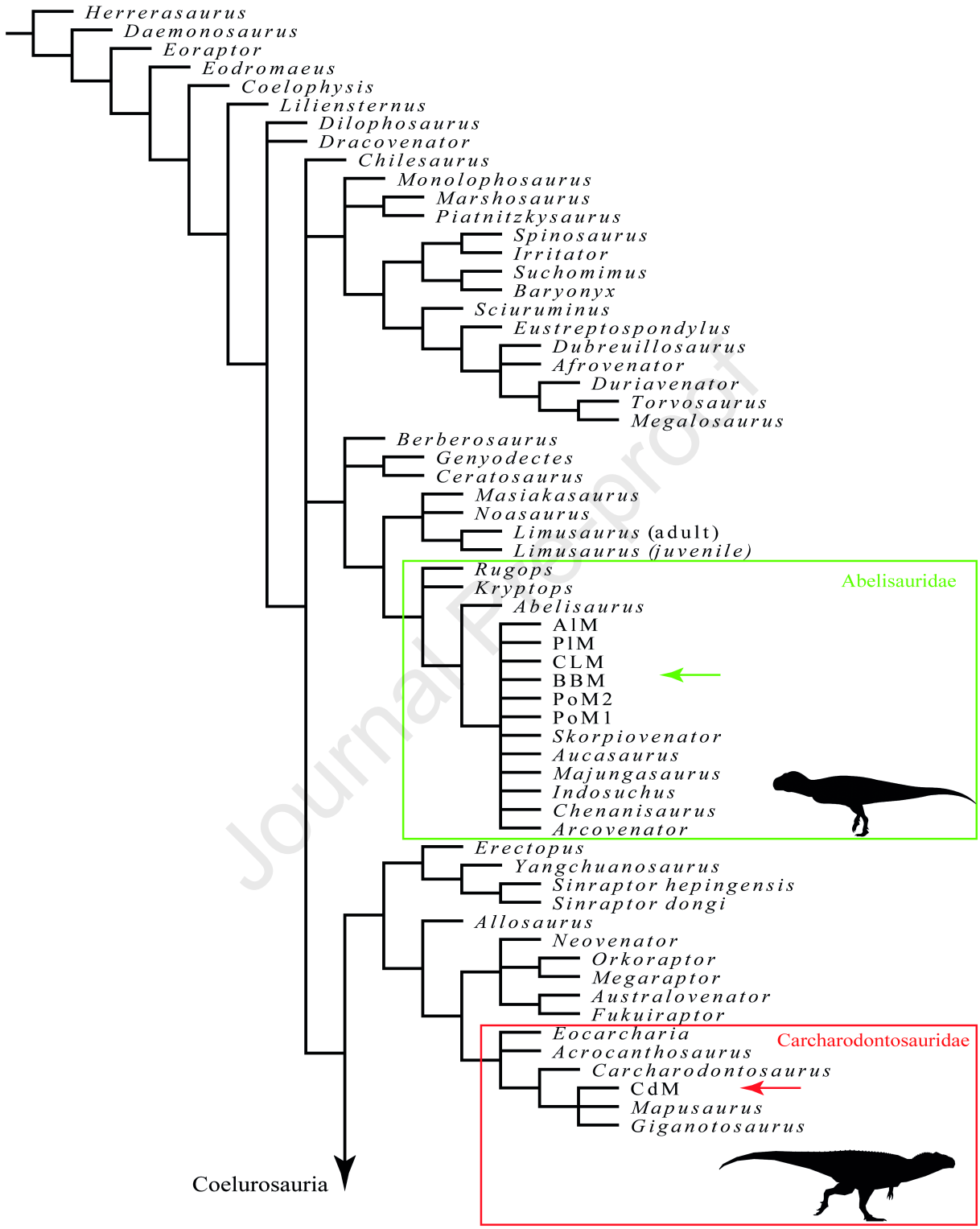


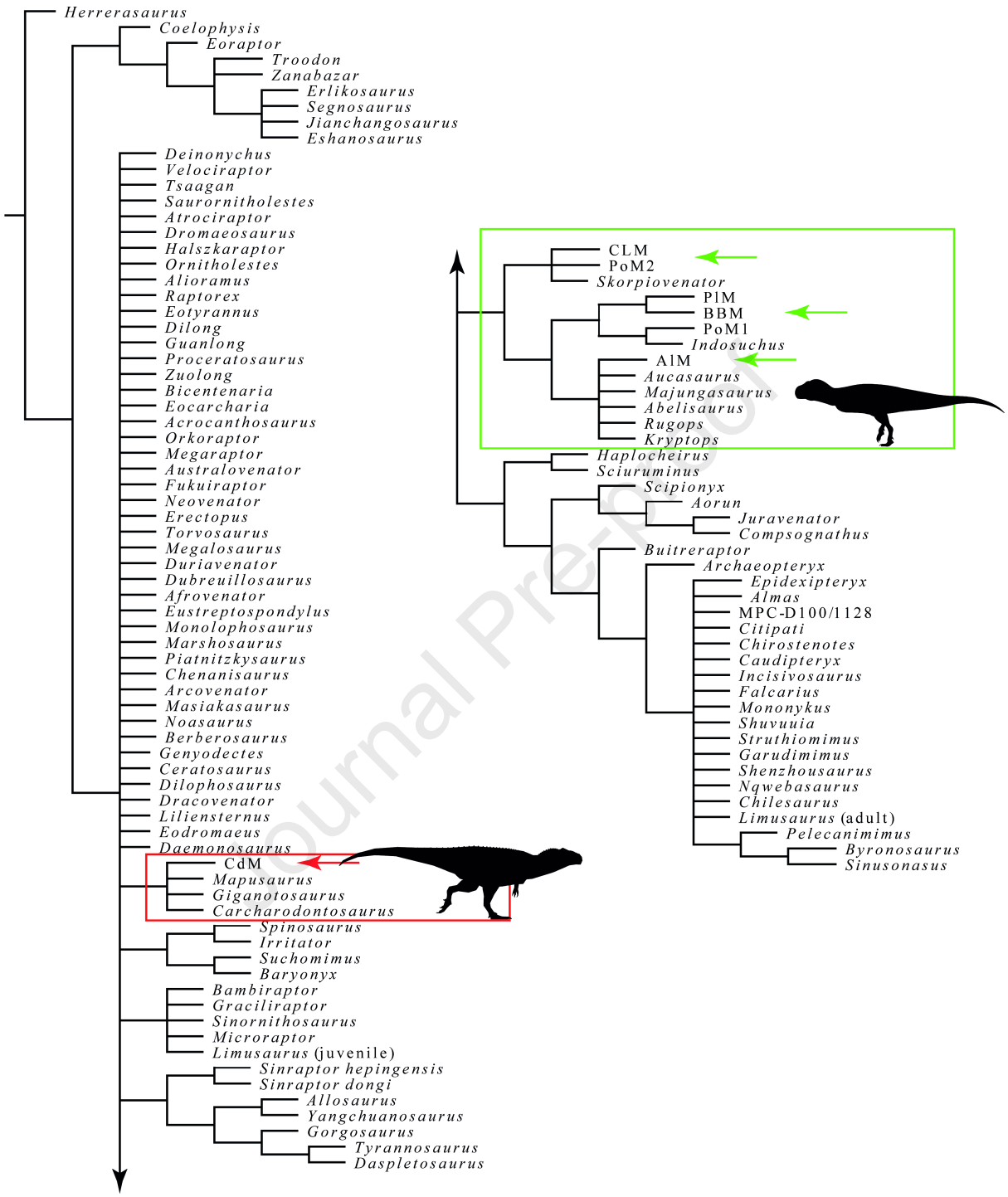


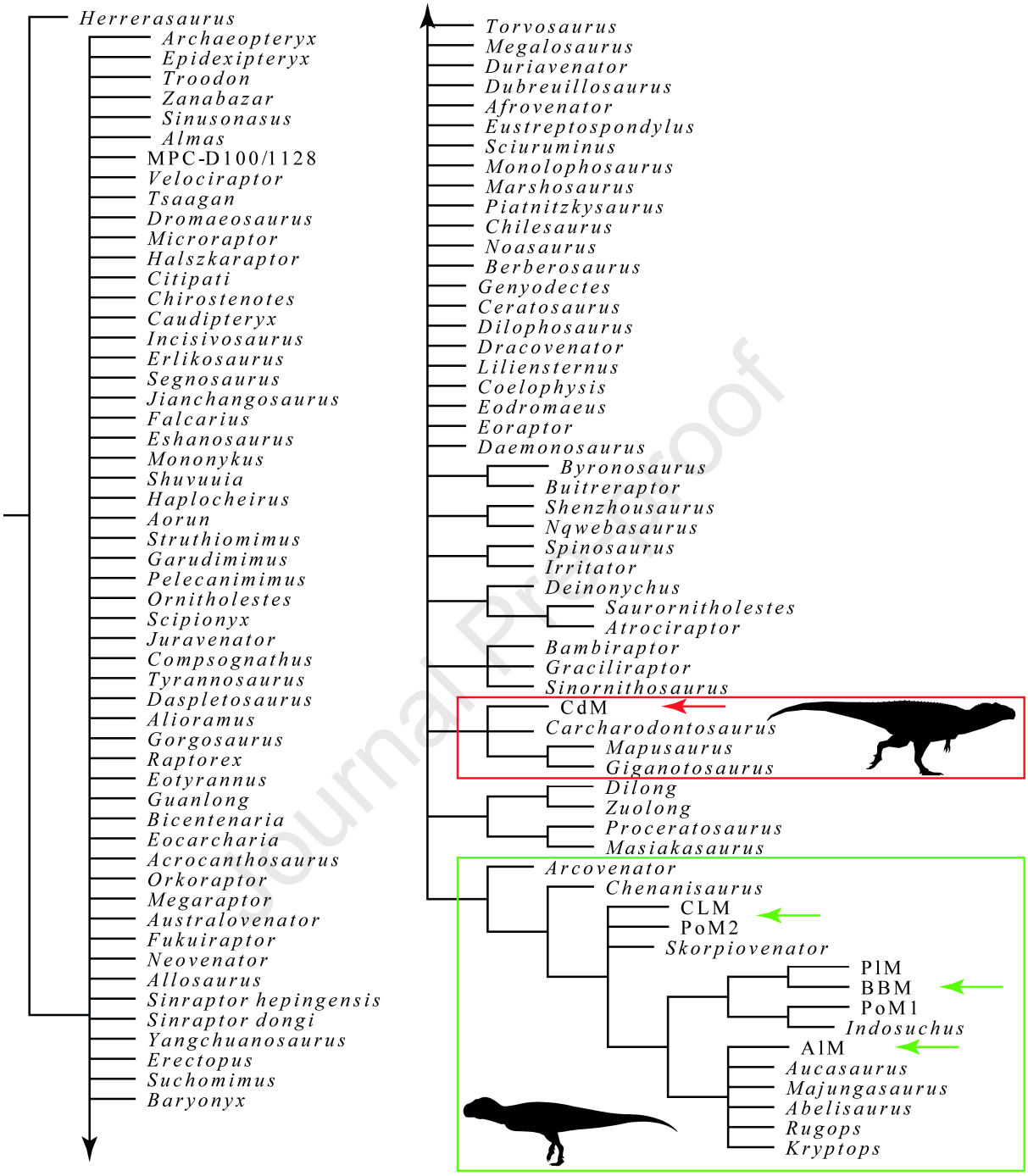


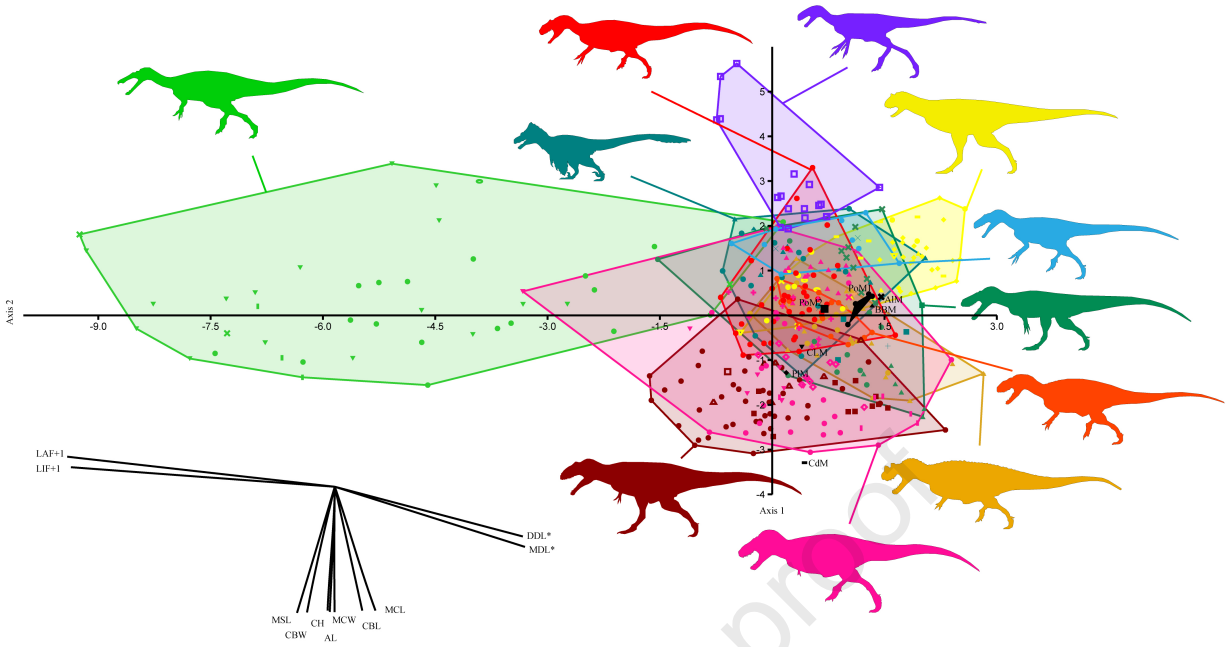












Spinosauridae

Abelisauridae

Non-abelisauroid Ceratosauria

Non-tyrannosaurid Tyrannosauroidea

Non-megalosaurian Megalosauroidea

Metricanthosauridae

Allosauridae

Tyrannosauridae

Carcharodontosauridae

Dromaeosauridae

Megalosauridae

Candeleros Morphotype

Cerro Lisandro Morphotype

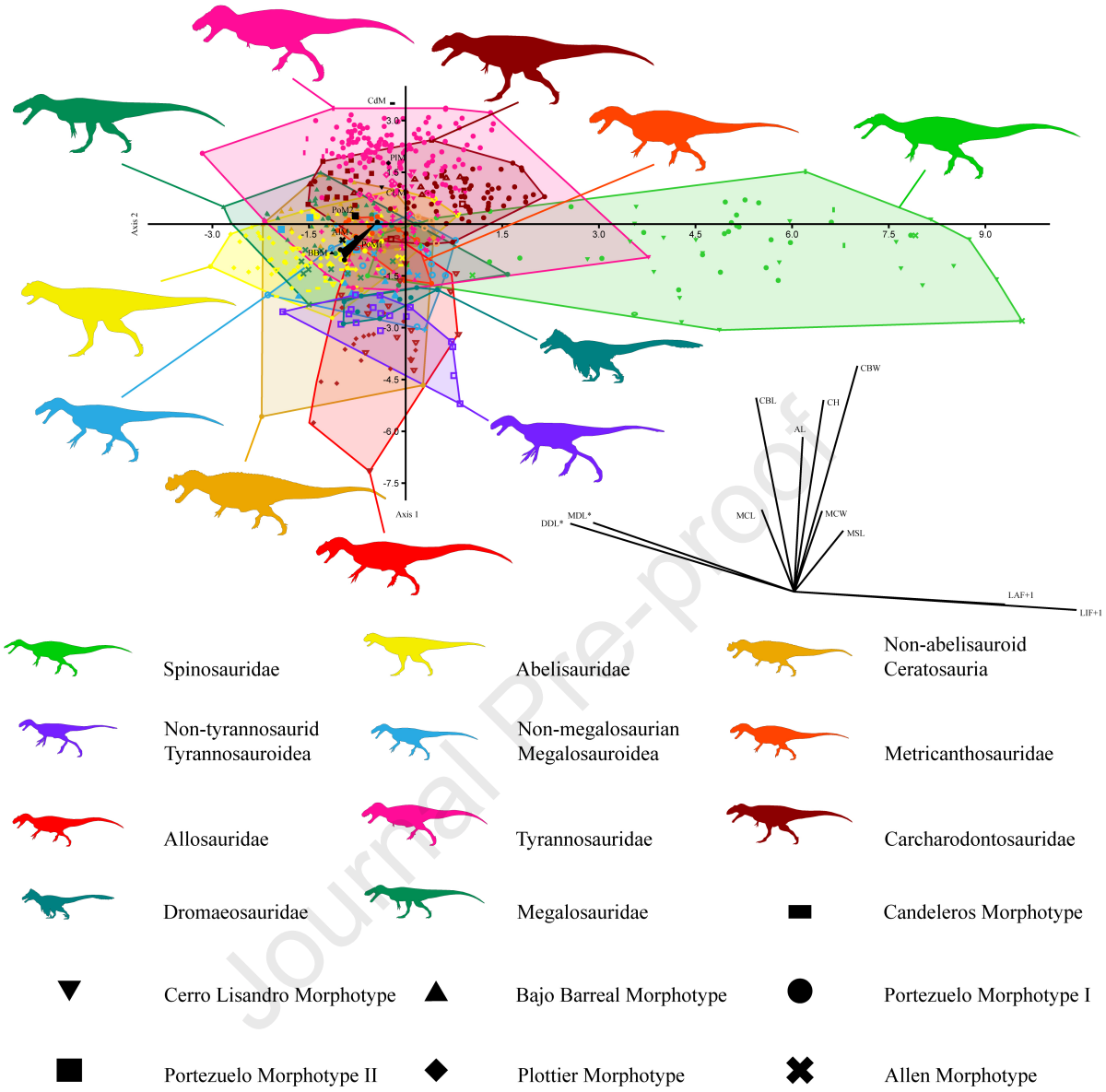
Bajo Barreal Morphotype

Portezuelo Morphotype I

Portezuelo Morphotype II

Plottier Morphotype

Allen Morphotype



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Megalosauridae

Candeleros Morphotype

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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: