Isolated theropod teeth associated with a sauropod skeleton from the Late Cretaceous Allen Formation of Río Negro, Patagonia, Argentina

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The discovery of theropod shed teeth associated with sauropod remains is relatively common in Cretaceous deposits of Patagonia. However, only a handful of studies have thoroughly explored the phylogenetic affinities of the theropod dental material. Here, we describe and identify twelve theropod shed teeth associated with a partially complete skeleton of a titanosaur sauropod from the Allen Formation (middle Campanian–lower Maastrichtian; Upper Cretaceous) of Paso Córdoba, Río Negro, Argentina. Using three methods, namely a cladistic analysis performed on a dentition-based data matrix, and a discriminant and cluster analyses conducted on a large dataset of theropod teeth measurements, we identify three dental morphotypes which are confidently referred to abelisaurid theropods. Whether the morphotypes represent different abelisaurid subclades or different positional entities within the jaw of the same abelisaurid species, is unknown. Such an identification, nevertheless, provides additional evidence of abelisaurids feeding on sauropod carcasses. This study highlights the importance of using combined qualitative and quantitative methodologies to identify isolated theropod teeth, especially those that can provide direct information on feeding ecology.

Key words: Dinosauria, Abelisauridae, shed teeth, morphotypes, Cretaceous, Patagonia.

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Introduction

The Allen Formation (middle Campanian−lower Maastrichtian) of Northern Patagonia, Argentina, has yielded a large diversity of continental tetrapods dominated by theropod dinosaurs (Casamiquela 1964; Bonaparte et al. 1984; Albino 1986; Bonaparte 1987; Powell 1992; Salgado and Coria 1996; Salgado and Azpilicueta 2000; Coria 2001, 2007; Fuente et al. 2001; Martinelli and Forasiepi 2004; Coria and Salgado 2005; Novas et al. 2009; Salgado et al. 2009, 2007a, b; Agnolin et al. 2012). The latter are represented by at least four clades, i.e., Abelisauridae, Alvarezsauridae, Dromaeosauridae, and an indeterminate tetanuran (Coria 2001; Coria and Salgado 2005; Valieri et al. 2007; Novas et al. 2009; Salgado et al. 2009; Agnolin et al. 2012; Currie and Carabajal 2012). Abelisauridae from the Río Negro Province are currently known from two taxa namely, *Abelisaurus comahuensis* based on a partial skull from Cinco Saltos (Bonaparte and Novas 1985), and *Quilmesaurus curriei*, known from a partial hindlimb discovered in Salitral Ojo de Agua (Coria 2001; Valieri et al. 2007). In the latter locality, alvarezsaurid remains were reported by Salgado et al. (2009) and later referred to the new species *Bonapartenykus ultimus* (Agnolin et al. 2012). The unenlagiine *Austroraptor cabazai*, known from two specimens from the Bajo de Santa Rosa locality, Río Negro Province (Currie and Carabajal 2012; Novas et al. 2009), is the only dromaeosaurid from the Allen Formation. Fragmentary remains were additionally assigned to indeterminate small to medium-bodied tetanurans by (Coria and Salgado 2005), whereas (Martinelli and Forasiepi 2004) referred an isolated tooth to an indeterminate carcharodontosaurid from the Bajo Santa Rosa locality. This shed crown, however, likely belongs to a non-carcharodontosaurid theropod based on its morphology and stratigraphic distribution (JM personal observation).

Between 2014 and 2016, twelve isolated theropod teeth associated with the carcass of a titanosaur sauropod were discovered during a series of palaeontological fieldworks carried out in the middle Campanian–lower Maastrichtian Allen Formation of Paso Córdoba (Río Negro, Argentina). In this paper, we aim to: (i) provide a thorough description of the theropod dental material; (ii) identify each shed tooth using the latest phylogenetic and morphometric techniques; and (iii) discuss the palaeoecological implications of such an association.

Institutional abbreviations.—IIPG, Instituto de Investigación en Paleobiología y Geología, General Roca, Río Negro, Argentina; MCF-PVPH, Museo Carmen Funes, Paleontología de Vertebrados de Plaza Huincul, Neuquén, Argentina.

Other 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; CI, consistency index; 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; DFA, discriminant function analysis; DLAT, dentine thickness labially; DLIT, dentine thickness lingually; DMT, dentine thickness mesially; DSDI, denticle size density index; FABL, fore-aft basal length; L, 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; RI, retention index.

Geological and geographical setting

The twelve shed teeth here described (SOM 1: figs. A1, A2, Supplementary Online Material available at http://app.pan.pl/SOM/app66-Meso_etal_SOM.pdf) come from the Allen Formation, which outcrops in the locality of Paso Córdoba, 14 km southwest of the town of General Roca, Río Negro Province, Patagonia, Argentina (Fig. 1). The Allen Formation is currently dated to the middle Campanian–early Maastrichtian on the basis of its ostracods fauna (Ballent 1980). This lithostratigraphic unit at the base of the Malargüe Group is separated from the underlying Neuquén Group by a discordance (Andreis et al. 1974; Hugo and Leanza 2001). Isolated theropod teeth were found in association with a partially articulated and relatively complete skeleton referred to an titanosaur sauropod (Álvarez et al. 2015; Díaz Martínez et al. 2015; Meso 2017). The dinosaur material was found in 1 meter thick tabular layers of fine and coarse sandstone, representing a dune and dry interdune facies (Paz et al. 2014; Fig. 1). The sandstone shows roots marks as well as parallel and ondulitic laminations with inverse gradation (Paz et al. 2014). The presence of laminated sandstone with inverse gradation was interpreted by Paz et al. (2014) as indication of a migrating dune system.

Material and methods

Comparative methodology and terminology.—The theropod dental material comes from of a fossiliferous site denominated “Dino 1” site, and is deposited at the Instituto de Investigación en Paleobiología y Geología (CONICET-UNRN), General Roca, Argentina. Eleven measurement variables (i.e., CBL, CBW, CH, AL, MCL, MCW, CTU, MA, MC, DC, DA; Table 1) were taken on the best preserved crowns with a digital caliper of 150 mm, with an accuracy of 0.01 mm. We followed the dental nomenclature and protocol proposed by Hendrickx et al. (2015a) to describe the teeth exhaustively. The dental material was compared with the teeth belonging to 155 non-avian theropod species, with a particular attention to those from large-bodied ziphodont taxa. The majority of the dental material belonging to these theropods were personally examined (see Hendrickx et al. 2020a, b for the list of examined taxa) using a DinoLite microscope. The theropod shed teeth from the Allen Formation were examined using a binocular loupe Nikon SMZ/800 with different magnifications. A Scanning Electron Microscope (SEM) Zeiss brand model Evo MA15 variable pressure, housed at the IIPG, was additionally used to examine the smallest dental structures such as the denticles and the texture of the enamel.

The theropod teeth were oriented following the positional terminology of Smith and Dodson (2003) and Hendrickx et al. (2015a), whereas the dental terminol-

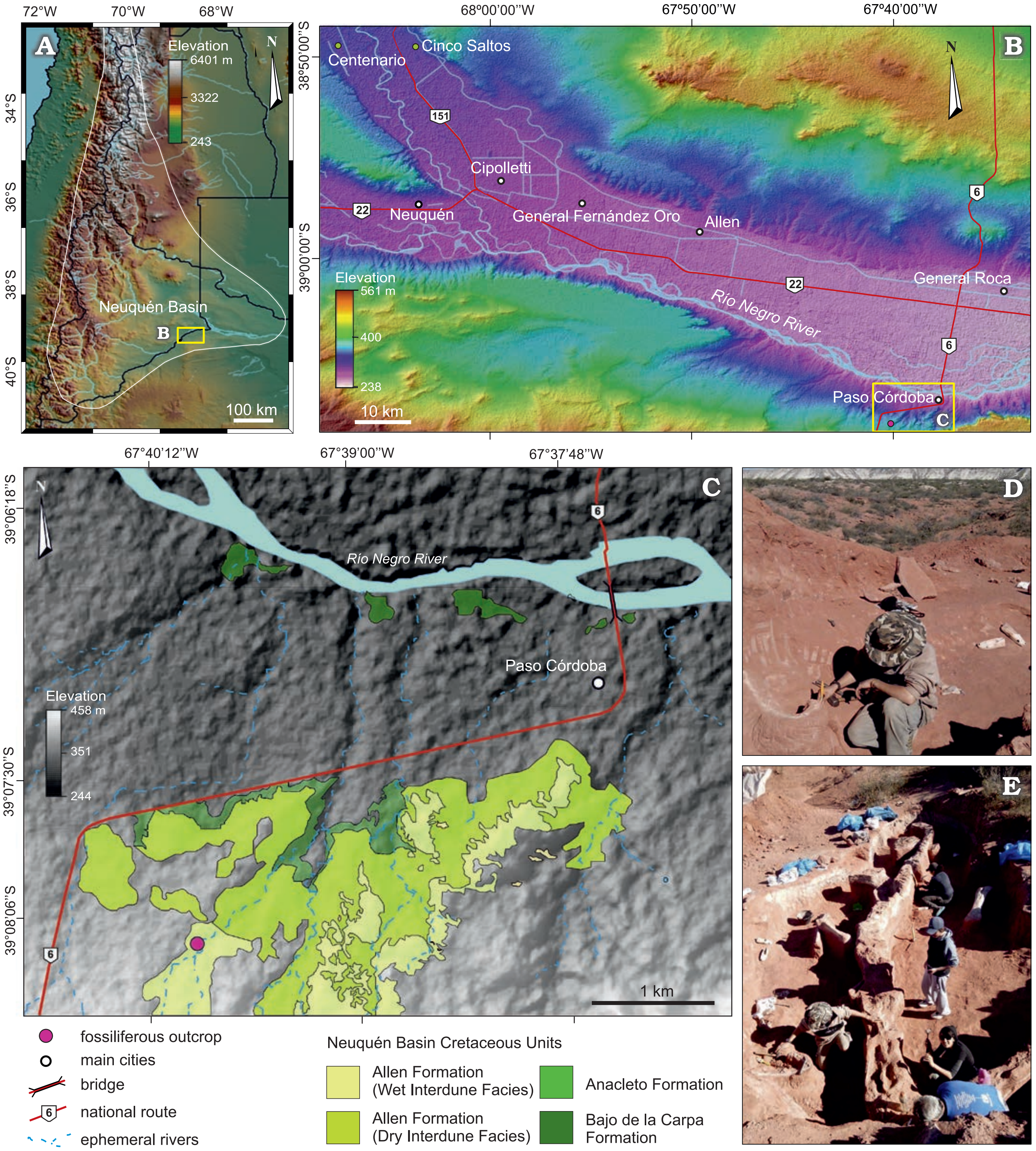

Fig. 1. Location maps of the study area within the Neuquén Basin (**A**, **B**). Geological map indicating the different units recognized in Paso Córdoba (Argentina), star marks collecting of specimens (**C**). Field photos of the excavation of specimens (**D**, **E**).

ogy proposed by Smith et al. (2005) and Hendrickx et al. (2015a) was used to describe and label each dental morphotype. The phylogenetic definitions of theropod clades finally follow those provided by Hendrickx et al. (2020b, 2015a).

Cladistic analysis.—The phylogenetic affinities of the dental material were first explored by performing a cladistic analysis on an updated version of the data matrix created by Hendrickx et al. (2015a), which focuses on the dentition of non-avian theropods. The most updated version of this

Table 1. Measurements (in mm) of the teeth crowns associated with a titanosaur skeleton. Number of denticles per five millimeters and crown angle in degrees. 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; DC, distocentral denticle density; DSDI, denticle size density index; MC, mesiocentral denticle density; MCL, mid crown length; MCR, mid-crown ratio; MCW, mid-crown width.

Specimen	Morphotype	CBL	CBW	CH	AL	CBR	CHR	CA	MC	DC	MCL	MCW	MCR	DSDI
IIPG-02	Morphotype I (mesial teeth)	10	7.78	22.46	24.58	0.77	2.24	65.99°	10	10	10.05	5.76	0.57	1
IIPG-03		12.9	11.6	26.18	29.18	0.89	2.02	63.76°	12	10	?	9.24	?	1.2
IIPG-07	Morphotype II (mesial teeth)	14.2	6.7	?	?	0.47	?	?	11	13	12.95	5.86	0.45	0.84
IIPG-08		?	4.72	16.8	?	?	?	?	15	15	7.3	2.6	0.35	?
IIPG-09		5.6	2.76	9.82	11.3	0.49	1.75	60.3°	13	14	5.2	2.5	0.48	0.92
IIPG-01	Morphotype III (lateral teeth)	21	8	35.5	41.24	0.38	1.69	59.39°	?	15	?	4.95	?	?
IIPG-04		15.1	9.5	24.3	28.6	0.62	1.6	58.14°	15	13	13.26	7.84	0.59	1.15
IIPG-05		13.8	5.6	20.4	24.62	0.4	1.47	55.92°	14	13	11.66	3.6	0.30	1.07
IIPG-06		8.46	3.9	16.98	18.97	0.46	2	63.51°	11	13	7.98	2.78	0.34	0.84
IIPG-10		?	?	?	?	?	?	?	10	11	?	4.32	?	0.90
IIPG-11		?	?	?	?	?	?	?	?	?	?	?	?	?
IIPG-12		?	?	?	?	?	?	?	11	11	9.05	3.94	0.43	?

data matrix was published by Hendrickx et al. (2020b) and includes 146 dental characters scored across 105 theropod genera (SOM 1.2, 1.3, 2). Instead of scoring each tooth, we recognized three dental morphotypes among the sample of theropod teeth (Table 1), that were treated as separated operational taxonomic units (OTUs).

We followed the methodology detailed by Young et al. (2019) and Hendrickx et al. (2020b) 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 (SOM 1.3). 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 neocoelurosaurs. 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, were used as the search strategy. The trees were subjected to a final round of TBR branch swapping (see Hendrickx et al. 2020b: 4). We also performed two additional cladistic analyses, one using the dentition-based dataset without constraints, and the second on a data matrix restricted to crown-based characters (see Young et al. 2019; Hendrickx et al. 2020b: 11).

Discriminant analysis.—To classify the twelve shed theropod teeth and predict their optimal classifications inside "family-level" groupings based on quantitative data, we included them in the largest published dataset of theropod teeth (i.e., Hendrickx et al. 2020a, b) and performed a discriminant function analysis (DFA) using Past3 version 3.19 (Hammer et al. 2001). 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 (SOM 3). Because many researchers measure dinosaur crowns differently (Hendrickx et al. 2020b), a second analysis was conducted on a dataset restricted to measurements taken by one of us (CH) using the same measuring method. Finally, because most of the isolated theropod teeth from "Dino 1" site belonged to ziphodont theropods with large-sized crowns (i.e., >2 cm), a third analysis was performed on a dataset restricted to theropod taxa whose teeth have a crown height of more than 20 mm. The last two datasets include 725 and 400 teeth belonging to 53 and 46 theropod taxa, respectively, both separated into 13 groups (SOM 3).

The discriminant function analysis was performed following the protocol detailed by Young et al. (2019), i.e., all variables were log-transformed to normalize the quantitative variables and the DFA was run in Past 3 version 3.19 (Hammer et al. 2001) using the discriminant analysis (LDA) function, treating each tooth from "Dino 1" site as a unknown taxon.

Cluster analysis.—In addition to the DFA, a cluster analysis was performed on the different datasets using the paired group algorithm and a neighbour joining clustering, choosing Euclidean distances for the similarity index, using Past3. This method, based on the measurements taken on the crown, finds hierarchical groupings in multivariate datasets, and allows visualizing the distribution of the twelve isolated theropod teeth on a drendrogram.

Systematic palaeontology

Dinosauria Owen, 1842
Saurischia Seeley, 1887
Theropoda Marsh, 1881

Ceratosauria Marsh, 1884

Abelisauroidea Bonaparte, 1991

Abelisauridae Bonaparte and Novas, 1985

Gen. and sp. indet.

Figs. 2–4.

Material.—The isolated teeth IIPG-01 to IIPG-12 from "Dino 1" site (S 39°08'; W 67°40'), Paso Córdoba locality, 14 km southwest of the town of General Roca, Río Negro Province; Allen Formation (middle Campanian–early Maastrichtian, Upper Cretaceous; Garrido 2011; Paz et al. 2014).

Description.—The isolated teeth, which are almost complete, are interpreted as shed crowns due to the absence of most of the root. The IIPG-02, -05, -06, -08, and -09 show the basal portion of the root and are the best-preserved of the sample. The apical two-thirds of the crown apex has been worn out along its mesial margin in IIPG-01, whereas a basal portion of the crown on the lingual surface, and ~2 mm of the apical portion of the distal carina are missing in IIPG-04. The IIPG-03, -07, -10, -11, and -12 are the most damaged teeth. They lack the basal portions of the crowns on both the labial and lingual surfaces. In addition, the distal carina is missing along the basal two-thirds of the crown, while denticles on the mesial carina are worn out and poorly preserved. IIPG-07 lacks its apical portion, whereas IIPG-10 lacks its apico-distal portion, the basal portion, and the two-thirds basal mesial margin. Respect to IIPG-11, it only consists of an apical portion of the crown, while IIPG-12 lacks its basalmost portion of the crown.

Morphotype I: IIPG-02 (Fig. 2) and IIPG-03. Crowns of Morphotype I are characterized by a weak labiolingual compression at the crown base (CBR > 0.7; Table 1), and by being moderately apico-basally elongated ($2 < \mathrm{CHR} \leq 2.5$). The mesial margin is strongly apicobasally and labiolingually convex. The distal margin of the crown IIPG-03 is straight to slightly concave in lateral view, with the apex almost at the same level of the distal carina. In IIPG-02, the distal margin is apico-basally convex, with the apex positioned almost on the middle of the crown (Fig. 2). Both labial and lingual surfaces are mesiodistally convex, and the lingual surface is strongly apicobasally concave (Fig. 2). The two crowns show well-developed mesial and distal carinae. In mesial view, the carina is straight and centrally positioned on the crown. However, the basalmost portion of the mesial carina is missing, so that it is unknown whether the denticles extended to the cervix or just above it. In distal view, the carina extends to the cervix and is either centrally positioned on the crown or slightly displaced labially. Teeth of Morphotype I have a salinon-shape (i.e., with labial margin convex and lingual margin biconcave) cross-sectional outline at the base crown (Fig. 2). Two concave surfaces adjacent to the mesial and distal carinae are seen and restricted to the lingual surface of the crown.

In IIPG-02, the mesial carina bears 10–11 denticles per 5 mm close to the apex, 10–12 denticles per 5 mm at mid-

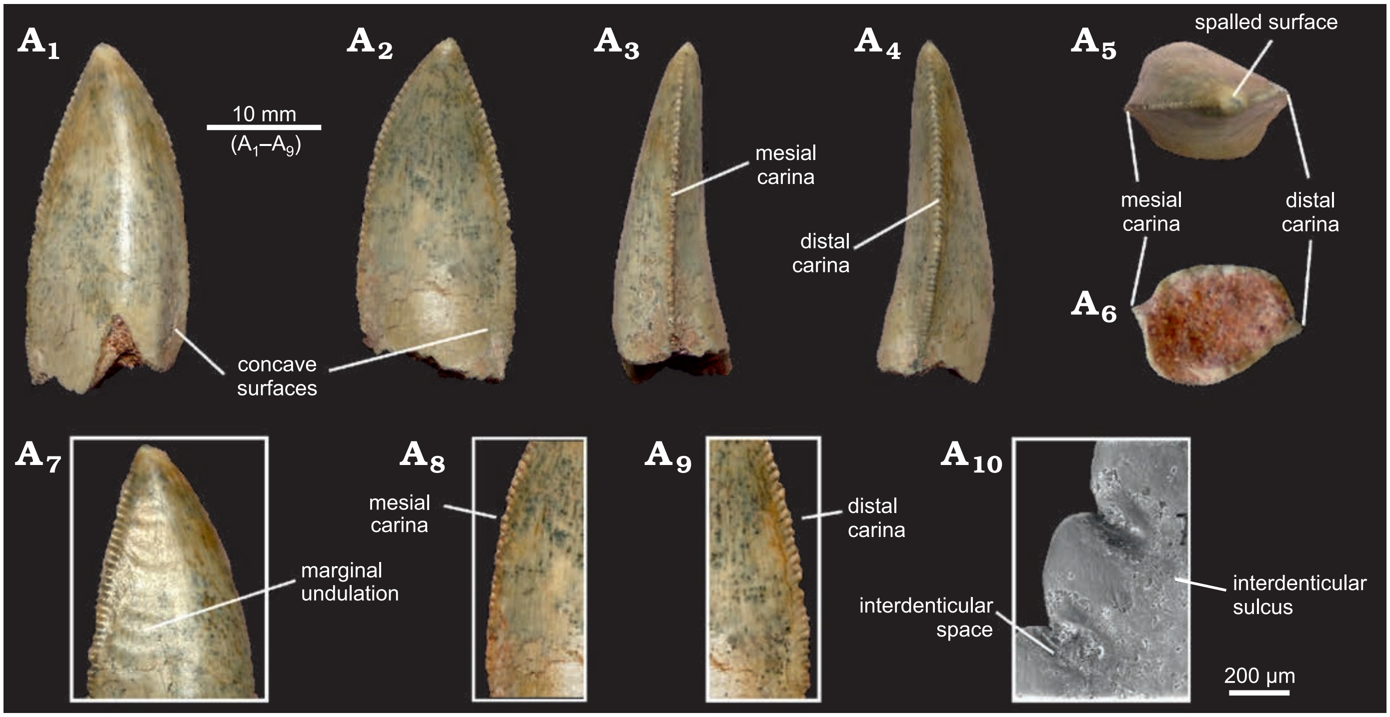

Fig. 2. Abelisaurid tooth of Morphotype I (IIPG-02) from "Dino 1" site (S 39°08'; W 67°40'), Paso Córdoba locality, 14 km southwest of the town of General Roca, Río Negro Province; Allen Formation (middle Campanian–early Maastrichtian, Upper Cretaceous); in labial (A_1), lingual (A_2), mesial (A_3), distal (A_4), apical (A_5), and basal (A_6) views; detail of marginal undulations (A_7); mesial (A_8) and distal (A_9) denticles at the apical three-fourths of the crown height; detail of the mesial denticles at the apical three-fourths of the crown height (A_{10}). Abbreviations: cs, concave surfaces; mca, mesial carina; dca, distal carina; sps, spalled surface; ids, interdenticular sulcus; idsp; interdenticular space.

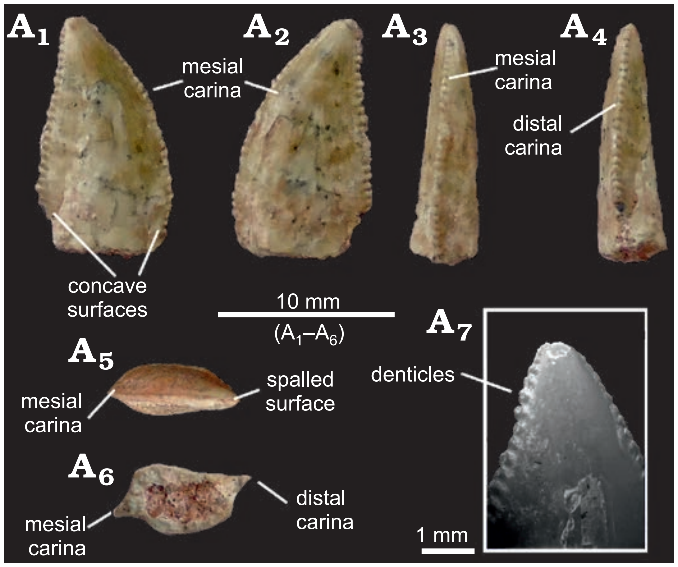

Fig. 3. Abelisaurid tooth of Morphotype II (IIPG-09) from "Dino 1" site (S 39°08'; W 67°40'), Paso Córdoba locality, 14 km southwest of the town of General Roca, Río Negro Province; Allen Formation (middle Campanian–early Maastrichtian, Upper Cretaceous); in labial (A_1), lingual (A_2), mesial (A_3), distal (A_4), apical (A_5), and basal (A_6) views; detail of the crown apex (A_7).

crown, and 12–16 denticles per 5 mm at the crown base. The distal denticle density ranges between 10–11 close to the apex, 10 at mid-crown, and 14 at the crown base. If the number of denticles is unknown at the base and mid-crown due to damage, IIPG-03 shows the same denticle density as IIPG-02. The denticle density increases gradually apically along both carinae. With a DSDI ranging from 1–1.2, there is no discrepancy between mesial and distal denticles. The latter are chisel-shaped, apically inclined, sub-quadrangular at the base, and their external margin is symmetrically convex. The denticles are also longer mesiodistally than baso-apically along all the carina. The mesiodistal main axis of the denticles is arranged at an acute angle to mesial and distal margins. IIPG-03 shows narrow interdenticular space and there are no interdenticular sulci between the denticles. Conversely, the interdenticular sulci are clearly visible in IIPG-02 where they are particularly well-developed at mid-crown.

The labial surface of IIPG-02 shows pronounced marginal undulations adjacent to the distal carina and covering the apical two-thirds of the crown surface. Teeth from Morphotype I, however, appear to lack transverse undulations, flutes, longitudinal grooves (which should not be confused with the concave surfaces adjacent to the carinae), and ridges. The texture is irregular and not oriented in any preferential direction in these two crowns.

Morphotype II: IIPG-07, -08, and -09 (Fig. 3). Similar to Morphotype I, the crowns possess a typical ziphodont morphology, with a distal curvature, important labiolingual compression of the crown (CBR $\geq$ 0.5; Table 1), and a weak apico-basal elongation (CHR $\leq$ 2). The mesial margin is strongly convex both apico-basally and labiolingually in lateral and basal views, respectively. The distal margin is straight so that the apex is located at the level of the distal carina (Fig. 3). Both labial and lingual surfaces are strongly mesiodistally convex, as seen in Morphotype I. The crown bears well-developed mesial and distal carinae. In IIPG-08, the mesial carina is almost straight and slightly lingually deflected; conversely, the mesial carina is strongly lingually deflected in IIPG-09 (Fig. 3). The denticles extend to the cervix in IIPG-09. It is, however, unknown whether the mesial carina extends to the root or just above it in IIPG-08. The distal carina is strongly displaced labially in IIPG-09, whereas it is centrally positioned to slightly displaced in IIPG-08. In each crown, the distal denticles all extend to the root or directly beneath the cervical line. A depression adjacent to the distal carina can be seen along the labial surface of the crown. The cross-section is lanceolate with acute and well-developed distal carina (Fig. 3).

As for Morphotype I, the mesial and distal carina show a gradual increase of the number of denticles per 5 mm towards the crown base. We counted 11–13 mesial denticles per 5 mm close to the apex, 13–15 at mid-crown, and 13–16 mesial denticles at the crown base. The distal carina shows a denticle density of 13–16 denticles per 5 mm close to the apex, 14 denticles at mid-crown, and 15–16 denticles at the crown base. The mesial denticles are therefore slightly larger than the distal denticles at mid-crown (DSDI = 0.92). Both mesial and distal denticles are chisel-shaped, sub-quadrangular at the base, and longer mesiodistally than wide baso-apically along the carina. Denticles from both the mesial and distal carinae are inclined apically and their external margin is symmetrically convex. The mesiodistal main axis of the denticles is orthogonal to both mesial and distal margins. The interdenticular space is narrow and interdenticular sulci are present between both mesial and distal denticles.

The enamel surface texture is irregular. IIPG-08 and IIPG-09 show transverse undulations and a single marginal undulation, respectively, at mid-crown, adjacent to the distal carina, on the labial surface.

Morphotype III: IIPG-01, -04, -05, -06, -10, -12 (Fig. 4), and possibly IIPG-11. The crowns are characterized by an important labiolingual compression (CBR < 0.5; Table 1) and a weak apico-basal elongation (CHR $\leq$ 2). The mesial margin is strongly convex apico-basally and labiolingually, whereas the distal margin is straight (IIPG-06, -10, and -12) to strongly concave (IIPG-01, -04, and -05) in lateral view. Both labial and lingual surfaces are slightly mesiodistally convex (Fig. 4). The crown bears well-developed carinae on the mesial and distal margins. The mesial carina is centrally positioned on the mesial margin of some teeth (IIPG-04, -05, -10, -12), and slightly curved lingually towards the base in other crowns (IIPG-01 and IIPG-06; Fig. 4). The denticulated carinae reach the base of the crown, and even extend well-beneath the cervix in some teeth (IIPG-05 and IIPG-06). The distal carina is either straight or strongly bowed labially. The cross-sectional outline of the crown at the cervix is lenticular to lanceolate (Fig. 4).

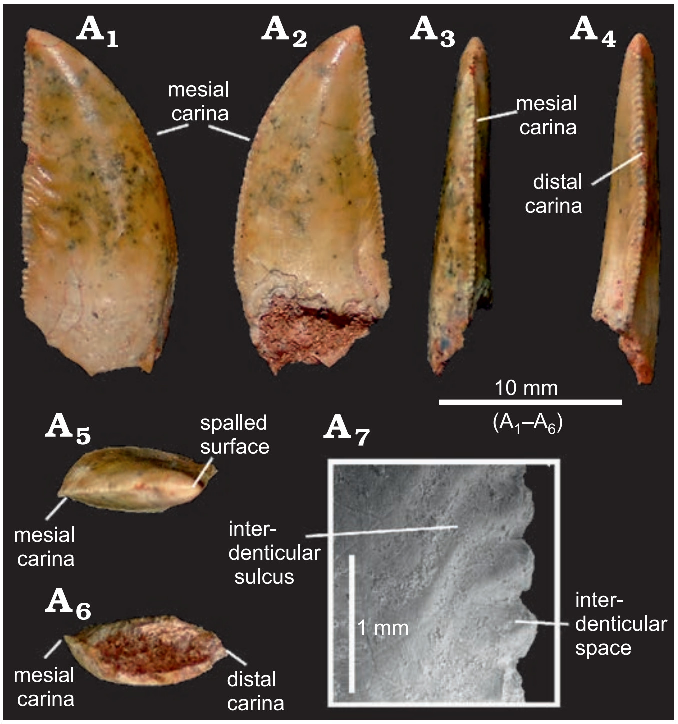

Fig. 4. Abelisaurid tooth of Morphotype III (IIPG-06) from "Dino 1" site (S 39°08'; W 67°40'), Paso Córdoba locality, 14 km southwest of the town of General Roca, Río Negro Province; Allen Formation (middle Campanian–early Maastrichtian, Upper Cretaceous); in labial (A_1), lingual (A_2), mesial (A_3), distal (A_4), apical (A_5), and basal (A_6) views; detail of the distal denticles at the apical three-fourths of the crown height (A_7).

The denticle density of the mesial carina ranges from 12–15 denticles per 5mm at the apex, 12–14 denticles at mid-crown, and 15–21 denticles at the crown base. The distal carina bears 11–14 denticles per 5 mm close to the apex, 11–15 denticles at mid-crown, and 15–17 denticles per 5 mm basally. As seen in the two previous morphotypes, the denticles densities increase gradually basally in both mesial and distal carinae. With a DSDI ranging from 0.84–1.15, the mesial denticles at mid-crown are slightly larger to similar in size than the distal denticles. Both mesial and distal denticles are chisel-shaped, apically inclined, and their external margin is symmetrically convex. They are sub-quadrangular at the base and longer mesiodistally than baso-apically along the carina. The interdenticular space is narrow and no interdenticular sulci appear to be present between the denticles.

As in the other two morphotypes, the enamel surface texture is irregular and no marginal undulations, transverse undulations, flutes, longitudinal grooves, or ridges can be seen on the crown.

Results

Cladistic analysis.—The cladistic analysis performed on the dentition-based data matrix using a fully constrained tree topology, recovered two most parsimonious trees (MPTs; CI = 0.1981; RI = 0.458; L = 1312 steps; SOM 1.3.4). All three morphotypes are found within Abelisauridae, Morphotype I being recovered as the sister taxon of *Chenanisaurus*, and Morphotype III as the sister taxon of a small subclade formed by *Majungasaurus* and *Indosuchus*. Morphotype II was either found as the sister taxon of *Skorpiovenator* or *Aucasaurus* (Fig. 5).

The cladistic analysis performed with no constraint found more than a hundred most parsimonious trees (CI = 0.2434; RI = 0.5837; L = 1068 steps). Morphotypes I and II are both classified within Abelisauridae in the resulting strict consensus tree (CI = 0.238; RI = 0.538; L = 1089 steps; SOM 1.3.4), with Morphotype I and Morphotype II recovered as the sister taxon of Carnotaurinae and within a polytomy formed by *Skorpiovenator*, *Chenanisaurus*, and Carnotaurinae, respectively. Only Morphotype III was found outside Abelisauridae in some MPTS, and consequently recovered in a polytomy within non-coelurosaurian Averostra in the strict consensus tree (Fig. 6A).

The cladistic analysis conducted on the crown-based data matrix with no constraint found a better-resolved strict consensus tree from a hundred MPTs (CI = 0.238, RI = 0.609, L = 669 steps; SOM 1.3.4). All morphotypes are recovered within a "crown-based" abelisaurid clade. In this analysis, Morphotype II is found in a subclade gathering *Skorpiovenator* and *Chenanisaurus* whereas Morphotype I + Morphotype III form the sister-clade of *Majungasaurus* + *Indosuchus* + *Aucasaurus* + *Abelisaurus* + *Rugops* + *Kryptops* (Fig. 6B).

Discriminant analysis.—The discriminant function analyses conducted on the whole dataset, classified the isolated teeth IIPG among abelisaurids, dromaeosaurids, neovenatorids, non-tyrannosaurid tyrannosauroid, metriacanthosaurid, and non-averostran neotheropod (clade-level analysis; PC1 and PC2 account for 38.08% and 30.78% of the total variance, respectively; Fig. 7A). At the taxon-level, the IIPG teeth are found closely related to members of Abelisauridae and Allosauridae (PC1 and PC2 account for 39.11% and 30.6% of the total variance, respectively; SOM 1.4.2). The reclassification rate (RR) is low, however, being only 58.84% at the clade-level and 57.73% at the taxon-level. The reclassification rate is slightly better in the DFA performed when the absence of denticles is considered as inapplicable, being 61.6% at the clade-level and 57.73% at the taxon-level. In this analysis, the isolated teeth IIPG are classified among abelisaurids, allosaurids, dromaeosaurids, neovenatorids, non-tyrannosaurid tyrannosauroids, and metriacanthosaurids (clade-level; PC1 and PC2 account for 47.39% and 27.61%). Conservely, the shed teeth are only classified among Abelisauridae and Allosauridae at the taxon-level (PC1 and PC2 account for 49.06% and 16.68%).

In the DFA performed on the datasets restricted to taxa with teeth larger than two centimetres (i.e., the whole dataset of Hendrickx et al.'s 2020b first-hand measurements), the shed teeth are classified as abelisaurids, megalosaurids,

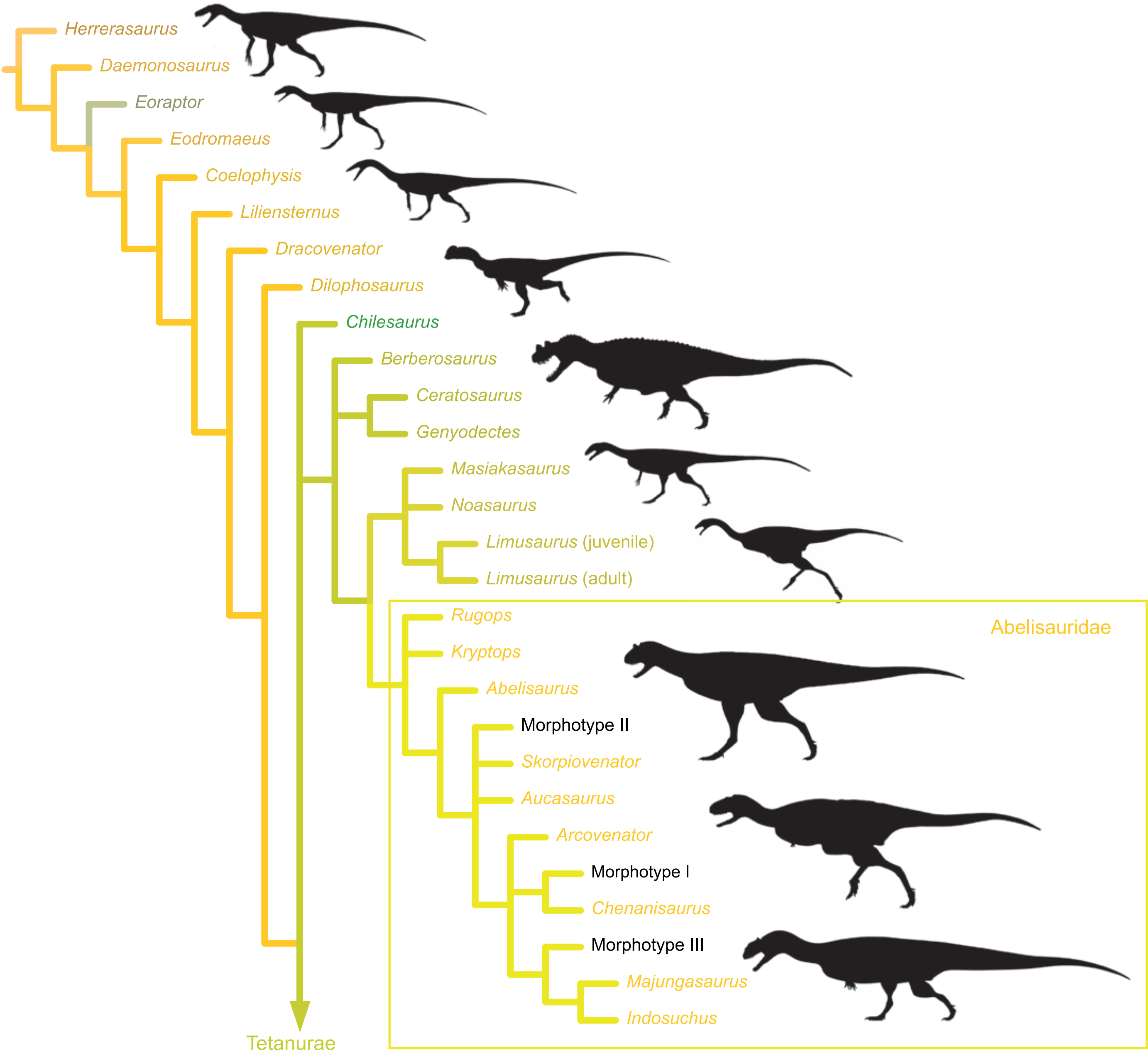

Fig. 5. Strict consensus tree of two most parsimonious trees (CI = 0.198; RI = 0.457; L = 1314) recovered in the cladistic analysis of the dentition-based data matrix with constrained search and setting the three morphotypes as floating terminals.

allosaurids, metriacanthosaurids, and non-tyrannosaurid tyrannosauroid (clade level; PC1 47.39% and PC2 27.61%; Fig. 7B). At the taxon-level (PC1 49.06% and PC2 16.68%), the isolated teeth IIPG were found closely related to members of Abelisauridae, and Tyrannosauridae. Reclassification rate is better at the taxon-level (61.81%) than at the clade-level (58.4%). The DFA made when the absence of denticles is considered as inapplicable resulted in that the teeth are grouped with the same clades. In turn, at taxon-level, these were found closely related to members of Abelisauridae, Allosauridae, Tyrannosauridae, and Megalosauridae (PC1 56.16% and PC2 23.96%). Reclassification rate is slightly higher both clade-level (60.9%) as taxon-level (61.09%).

Cluster analysis.—The cluster analysis using the hierarchical clustering option recovered the isolated teeth as belonging to Abelisauridae, Allosauridae, and Megaraptora. The cluster analysis performed on the dataset in which the absence of denticles is considered as inapplicable recovered a similar classification than the first analysis. Nevertheless, the cluster analysis based on the datasets restricted to taxa with teeth larger than two centimetres recovered the shed teeth IIPG as abelisaurids, allosaurids, and tyrannosaurids.

The cluster analysis using the neighbour joining option, recovered the crowns as members of abelisaurids, megaraptorids, and tyrannosaurids. When using the dataset when the absence of denticles is considered as inapplicable, the

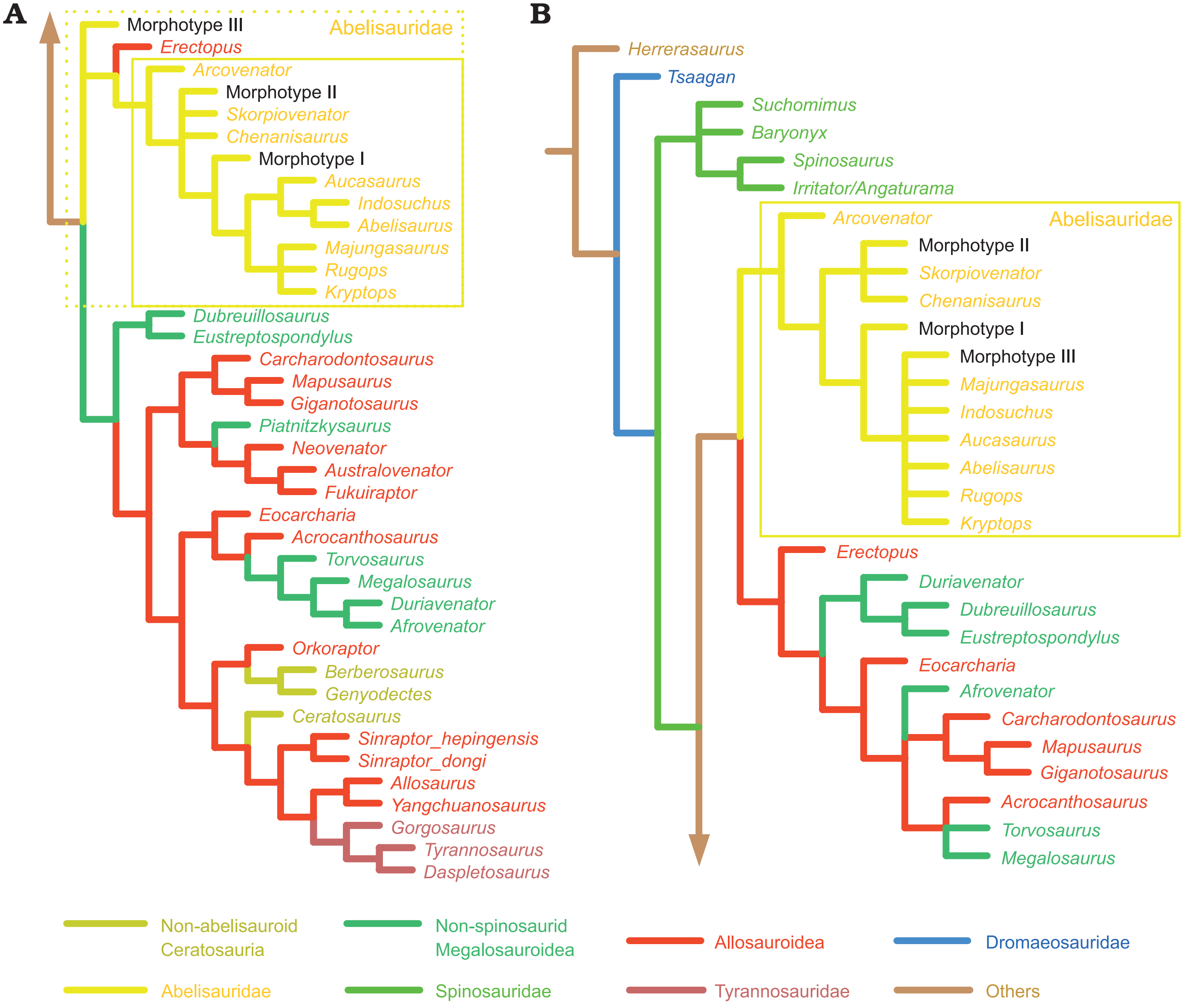

Fig. 6. **A**. Strict consensus tree of 100 most parsimonious trees (CI = 0.238; RI = 0.538; L = 1089) recovered in the cladistic analysis of the dentition-based data matrix with an unconstrained search. **B**. Strict consensus tree of 100 most parsimonious trees (CI = 0.238; RI = 0.609; L = 669) recovered in the cladistic analysis of the tooth-crown-based data matrix.

obtained results are similar to neighbour joining options. However, the cluster analysis based on the datasets restricted to taxa with teeth larger than two centimetres, when the absence of denticles is considered as inapplicable or not, threw as a result than the specimens were found closely related to members of abelisaurids, allosaurids, tyrannosaurids, and megaraptorids.

Discussion

Taxonomic identification.—Results of the cladistic, discriminant, and cluster analyses all support an abelisaurid affinity for the three morphotypes. If the DFAs and cluster analysis recovered mixed results, they both indicate that the three morphotypes show strong affinities with abelisaurid teeth in terms of qualitative data. The DFA performed on the datasets restricted to taxa with large-sized teeth shows that the teeth are found within the morphospace occupied by most large-bodied theropod groups. Only IIPG-02 and IIPG-05 are found within the a morphospace of Abelisauridae, whereas IIPG-06 and IIPG-09, where recovered outside all known theropod morphospaces.

Shed teeth from morphotypes I and II are here confidently referred to mesial teeth based on the weak labiolingual compression, their asymmetrical labial and lingual sides, and their cross-section outline (Hendrickx et al. 2015a). These morphotypes additionally show a combination of features only seen in the mesial dentition of Abelisauridae namely, a mesial carina reaching the cervix, a salinon to J-shaped cross-sectional outline at the crown

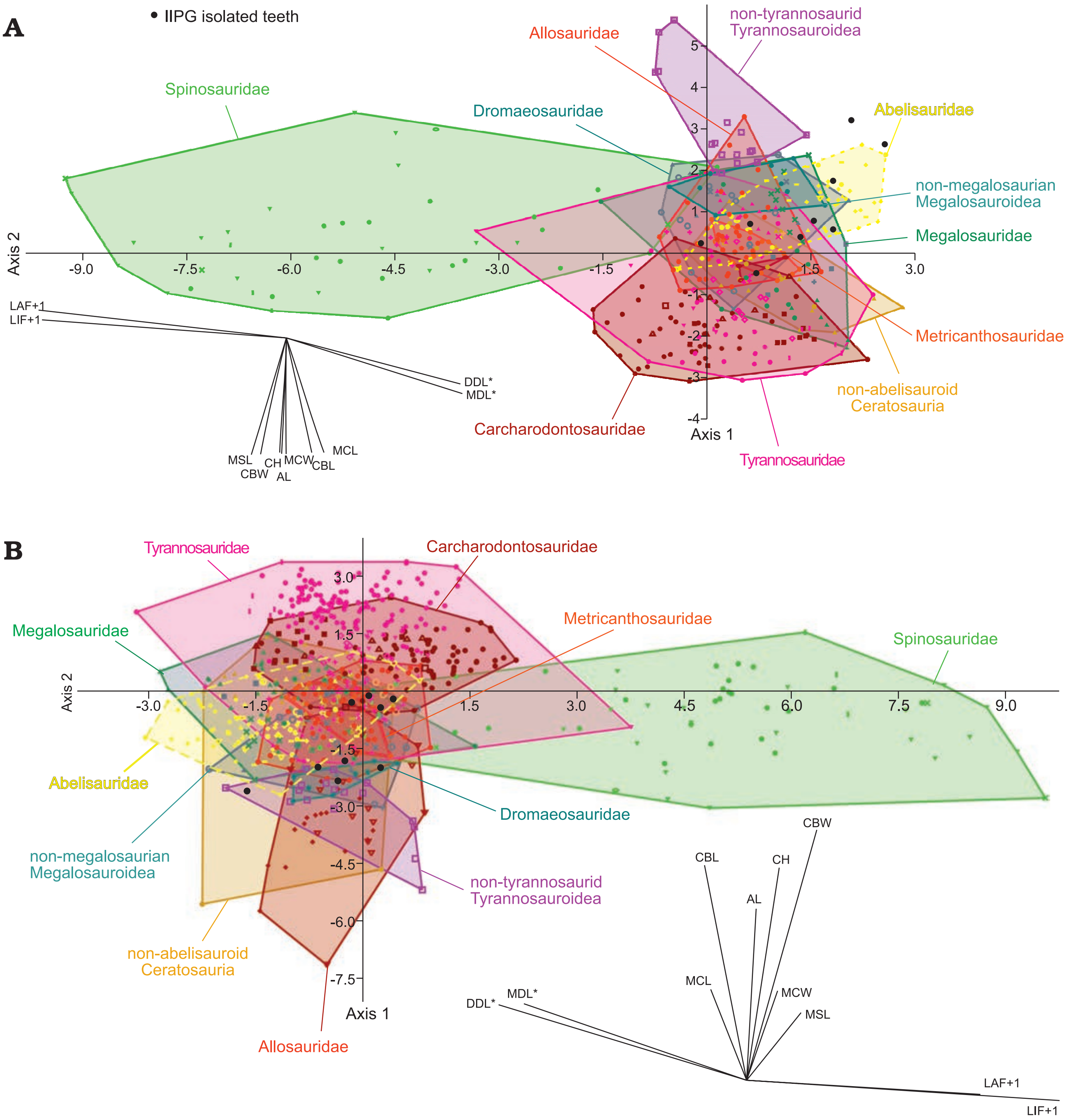

Fig. 7. Results of the discriminant analysis performed at the "group"-level on the whole dataset along the first two canonical axes of maximum discrimination in the dataset with personal measurements of CH (A) and teeth larger than two centimeters (B). **A**. For 400 teeth belonging to 46 theropod taxa and 12 groupings (PC1 and PC2 account for 38.08% and 30.78% of the total variance, respectively). **B**. For 725 teeth belonging to 53 theropod taxa and 13 groupings (PC1 and PC2 account for 47.39% and 27.61% of the total variance, respectively). Abbreviations: AL, apical length; CBL, crown base; CBW, crown base width; CH, crown height; MCL, mid crown length; MCW, mid-crown width; MSL, mesial serrated carina length.

base, a strongly convex labial margin and a gently biconcave to sigmoid lingual margin, apicobasally elongated concave surfaces adjacent to the distal and mesial carinae on the lingual surface, weakly elongated crowns (i.e., CHR not exceeding 2.5), apicobasally and proximodistally short denticles in the basalmost portion of the crown, a similar or lower number of denticles at the apex than at mid-crown, strongly developed interdenticular sulci, well-visible marginal undulations, and an irregular enamel surface texture (Hendrickx et al. 2020b).

Morphotype III is here considered as belonging to the lateral dentition based on its labiolingual compression and its symmetrical shape. Teeth belonging to this morphotype also presents a combination of dental features typically present in the lateral dentition of Abelisauridae namely, a straight or weakly convex distal margin, short (CHR < 2) and particularly compressed (CBR < 0.5) crowns, a mesial carina extending to the cervix, a distal carina centrally positioned on the distal margin of the crown, symmetrically convex lingual and labial surfaces, elongated interdenticular sulci, and an irregular enamel surface texture (Hendrickx et al. 2020b). With a relatively high CBR (0.62) and a slightly lingually twisted mesial carina, IIPG-04 is considered as a mesial tooth from the lateral dentition.

If the theropod fauna from the Allen Formation encompasses Abelisauridae, Unenlagiinae, Alvarezsauridae, and indeterminate Tetanurae (Martinelli and Forasiepi 2004; Coria and Salgado 2005; Novas et al. 2009; Agnolin et al. 2012), the theropod shed teeth associated with the sauropod carcass are all referred to abelisaurids. Unlike the IIPG crowns, the teeth of unenlagiine dromaeosaurids are unserrated, strongly distally recurved, and typically bear longitudinal ridges or flutes (Hendrickx et al. 2019). Some unenlagiines also bear conidont teeth (*Austroraptor*; Novas et al. 2009) or strongly compressed lateral teeth with an 8-shaped cross-section outline (*Buitreraptor*; Gianechini et al. 2011). Likewise, the alvarezsaurid dentition is made of tiny (<1 cm) folidont (i.e., basally constricted) unserrated crowns (Perle et al. 1993; Chiappe et al. 2002, 1998; Hendrickx et al. 2019), contrasting with the large blade-shape teeth with denticulated carinae seen in all large-bodied ziphodont theropods such as ceratosaurs, megalosauroids, allosauroids, and tyrannosauroids (Hendrickx et al. 2015b, 2019, 2020a, b). The IIPG theropod teeth can, however, be confidently referred to Abelisauridae due to a mesial carina reaching the cervix, a braided enamel surface texture, a J- to salinon-shaped cross section outline of the base crown in mesial teeth. Spinosaurid and most tyrannosaurid teeth are conidont and pachydont, respectively (Hendrickx and Mateus 2014; Hendrickx et al. 2019). The mesial carina of the large majority of megalosaurid teeth does not extend to the root and the enamel surface texture of the crown is braided in Megalosauridae (Hendrickx et al. 2015b). The dentition of noasaurids and piatnitzkysaurids show a strong discrepancy in size between mesial and distal denticles and their mesial dentition is either fluted or have a lenticular cross-section at the crown base (Hendrickx et al. 2019). The mesial carina of mesialmost teeth is strongly twisted lingually and/or does not extend to the root and the distal carina of mesial teeth is strongly displaced labially in Carcharodontosauridae (Hendrickx et al. 2019). Besides, most lateral teeth of carcharodontosaurids exceed 30 mm. Only metriacanthosaurid and allosaurid teeth share many dental features with abelisaurids, yet the mesial carina of the mesial teeth twists lingually in these two clades and the distal carina is slightly to strongly labially displaced in at least some lateral teeth (Hendrickx et al. 2020a; *Sinraptor*). Given the highly diagnostic dental morphology displayed by morphotypes I, II, and III, combined with their stratigraphic and palaeogeographic distribution in the Late Cretaceous of Argentina, all IIPG theropod teeth are confidently assigned to Abelisauridae.

Taphonomic and paleoecologic inferences.—The presence of some features in the IIPG dental material enables to explore taphonomic alteration mechanisms, i.e., processes that intervene in the transition from the biosphere to the lithosphere (Efremov 1940; Renzi 1975). Although the theropod shed teeth are particularly well-preserved (they are partially complete), some fractures of different origin are present in some teeth. Oblique fractures are for instance observed in the mesial carinae of IIPG-01, revealing that it was subjected to great tension on the apical part of the mesial carinae. These fractures have been interpreted as peri-mortem, since in previous studies they have been related to pathologies (dental deformations) caused by injuries (Becker et al. 2000), even more specifically with forces produced during the contact between the crown and the food. Oblique fractures of post-mortem type are also observed, attributed to the fall of the tooth and to processes that occurred afterwards (Shipman 1981).

Specimens IIPG-03, -10, and -12 are characterized by longitudinal fractures possibly related to the biostratinomic stage, indicating a brief period of subaerial exposure (Haynes 1980; Alcalá 1994). Finally, specimens IIPG-03, -04, -07, and -11 are characterized by fractures perpendicular to the major axis that would result to processes which occurred during the fossil diagenetic stage, that is, after the burial and during the processes of fossilization (Fernández-López and Fernández-Jalvo 2002).

Following Mazzetta et al.'s (2004) approach, the fracture observed in the middle third of the labiomesial surface of IIPG-01 (Morphotype III), may be attributed to a high tension by a compressive load in a vertical direction (immobile prey). In IIPG-03 and IIPG-12 (Morphotype I and Morphotype III), fractures are observed with a posterior displacement of the stress concentration region; in other words, fractures that are observed longitudinally on the posterior margins of these crowns, are caused when the compressive load is oriented on the longitudinal axis near the apex of the tooth with a certain angle (immobile prey). However, these fractures can also occur when a pulling force exerted by the control movements of the prey is applied anteriorly (prey exerting traction on the tooth). Canale et al. (2014) mention that the wear facets also indicate an interaction between the predator and its prey. Wear facets are present in the following teeth: IIPG-02, -03, -04, -06, -09, and -11, being located at the apex of the labial face, and characterized by developing diagonally in apico-basal sense. Finally, all teeth show a similar sedimentary filling, so it could be ruled out that these materials have undergone some type of taphonomic reworking. The IIPG-02, -03, -04, -07, and -08 present more carbonate matrices, but this can be attributed to changes in the fossil diagenetic stage.

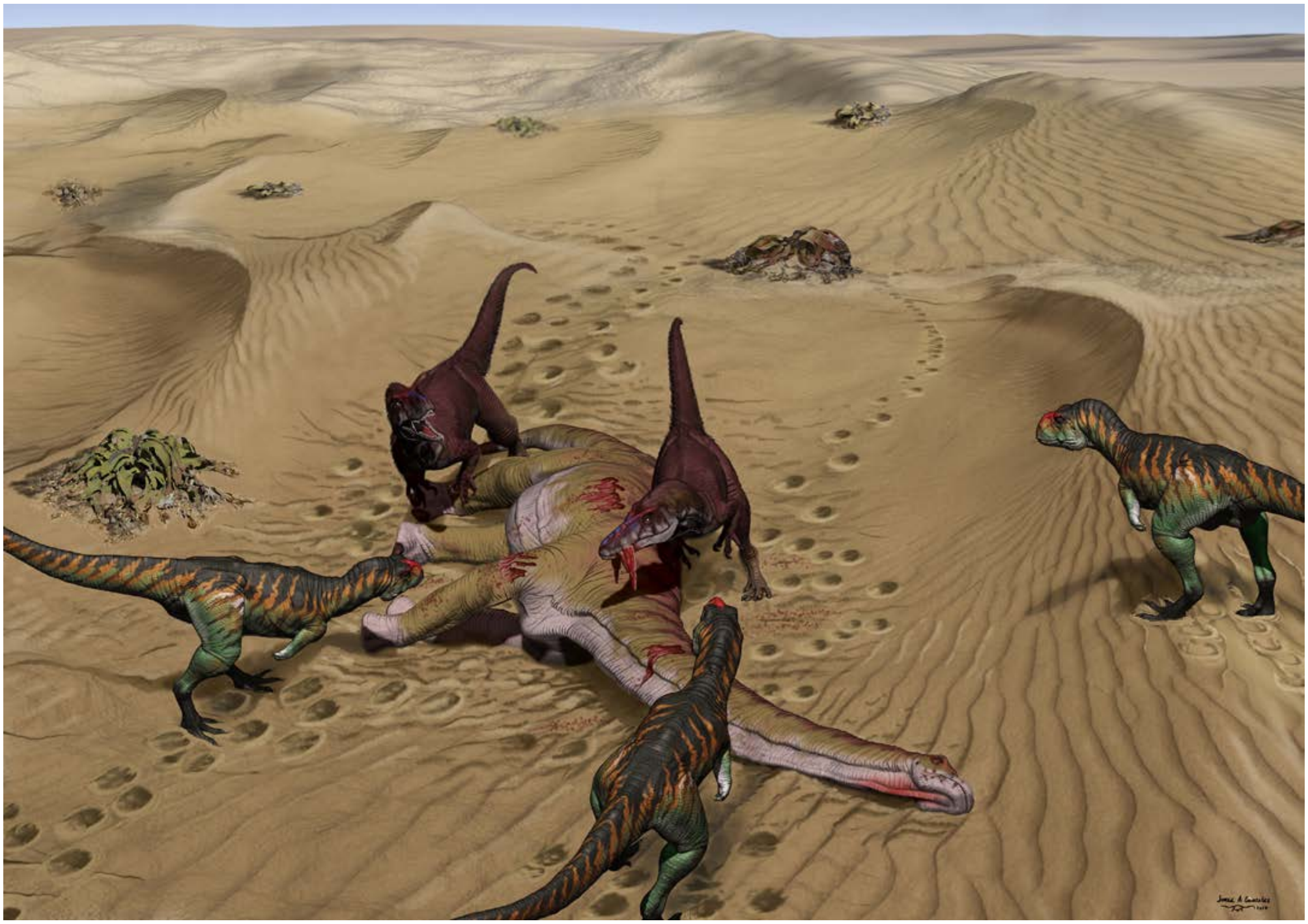

Fig. 8. One of the paleoecological interpretations of the Paso Córdoba site. Theropods scavenging the carcass of a sauropod. Artwork by Jorge González, San Salvador de Jujuy, Argentina.

In this regard, the isolated theropod teeth and sauropods remain conform to an oryctocoenosis (a set of fossils found together; see Fernández-López and Fernández-Jalvo 2002). Because the fossil bearing sediment has been interpreted as an aeolian system, it can be ruled out that the remains suffered transport (autochthonous elements). These materials had to be characterized by the naked eye because they do not have a root, so they are interpreted as isolated teeth, which means that these teeth were lost in life (peri-mortem process) by replacement of another one or by nibbling (Fig. 8). The presence of peri-mortem fractures, probably produced during chewing, allows us to postulate that the teeth along with the sauropod skeleton are a registered entity, i.e., remains of the activity/interaction of biological entities that managed to preserve themselves in the fossil record.

The association of a large number of abelisaurid shed teeth with the carcass of a single articulated titanosaurid sauropod suggests that South American abelisaurids fed on titanosaurs. A feeding behaviour seems indeed to be the most parsimonious explanation for the accumulation of theropod shed teeth around a dinosaur carcass (Alonso et al. 2017). This trophic interaction between abelisaurids and titanosaurids is not surprising given that tooth marks referred to the abelisaurid *Majungasaurus* were reported on the pubis of the titanosaurid *Rapetosaurus* from the Maastrichtian Maevarano Formation of Madagascar, already supporting the fact that Abelisauridae were feeding on titanosaurs (Rogers et al. 2003, 2007; Sampson and Witmer 2007). Some abelisaurids were also revealed to practice cannibalism as evidenced by the presence of tooth marks made by *Majungasaurus* on 12 postcranial elements belonging to the same taxon (Rogers et al. 2003, 2007). The presence of abelisaurid shed teeth with the carcass of a titanosaur does not permit to hypothesise whether abelisaurids killed the prey as active predators and fed on its carcass or only acted as scavengers after its natural death. The teeth, skull, neck, and fore- and hindlimb morphologies of Late Cretaceous abelisaurids such as *Majungasaurus* and *Carnotaurus*, nonetheless, indicate that these theropods were hypercarnivorous "head hunters" and ambush predators engaged in a bite-and-hold behaviour, i.e., they were capable to approach their prey with rapid acceleration and little engagement with the forelimbs, and use their powerful neck and jaws to inflict few, prolonged, penetrating bites, and powerful neck retraction to produce massive wounds (Therrien et al. 2005; Sampson and Witmer 2007; Snively and Russell 2007 Delcourt 2018). The dental, cranial, and postcranial adaptations displayed by derived Gondwanian abelisaurids would, consequently, lead to think that the titanosaur may have been killed by one or several abelisaurids before they fed on its carcass.

The discovery of isolated theropod teeth associated with sauropod carcasses is not rare in the fossil record, especially in Cretaceous deposits of Patagonia. Such an association was for instance reported in the Kimmeridgian–Tithonian Morrison Formation of Wyoming (Jennings and Hasiotis 2006), the Barremian Sao Khua Formation of Thailand (Buffetaut and Suteethorn 1989, 1999), and the Barremian–Aptian Castrillo de la Reina Formation of Spain (Alonso et al. 2017). In the Cretaceous fossil record of Southern Argentina, theropod shed teeth associated with the remains of sauropods were reported from the Berriasian–Valanginian Bajada Colorada Formation of Neuquén Province (Canale et al. 2017), the Albian Cerro Barcino Formation of Chubut Province (Canale et al. 2014), as well as the Turonian Portezuelo Formation (Veralli and Calvo 2004), the Coniacian–Santonian Plottier Formation (Canudo et al. 2009), and the Campanian Anacleto Formation of the Neuquén Province (Coria and Arcucci 2004). The theropod teeth are mainly referred to broad clades such as Theropoda indet. (Coria and Arcucci 2004; Canale et al. 2017) or Maniraptora indet. (Canudo et al. 2009) but a few authors identified the dental material to less inclusive clades such as Carcharodontosauridae and Dromaeosauridae (Canudo et al. 2009; Canale et al. 2014). Two teeth associated with at least six titanosaur carcasses from the Cerro Barcino Formation were ascribed to Abelisauridae by Canale et al. (2014), showing a trophic interaction between abelisaurids and titanosaurs already from the Early Cretaceous of South America.

Coria and Arcucci (2004) also noted a strong resemblance between indeterminate theropod teeth from the Anacleto Formation and those from the coeval abelisaurid *Aucasaurus*. At least one of these shed teeth (MCF-PVPH-421-4) illustrated in Coria and Arcucci (2004: fig. 2B), clearly belongs to an abelisaurid theropod, and most likely to *Aucasaurus*, whose dental anatomy has been examined in detail by two of us (CH and MAB). As seen in lateral teeth of *Aucasaurus* and many other abelisaurids, MCF-PVPH-421-4 includes a mesial carina extending to the cervix, a straight distal profile of the crown, strongly asymmetrical distal denticles whose apices of the external margin point apically, poorly developed interdenticular sulci between distal denticles, and weak transverse undulations (Hendrickx et al. 2020b). Although the mesial denticles have been described as significantly smaller than the distal ones by Coria and Arcucci (2004), a dental feature long thought to characterize dromaeosaurid teeth but widespread among theropods (Hendrickx et al. 2019), the illustration of MCF-PVPH-421-4 clearly shows that mesial and distal denticles share the same size at mid-crown. This tooth is, consequently, confidently referred to an abelisaurid. Interestingly, MCF-PVPH-421-4 and other theropod teeth were recovered in a layer that yielded titanosaur bones as well as several titanosaur eggs with embryos. If this association is taphonomical, it is possible that abelisaurid theropods also fed on titanosaur hatchlings, which may have been easier to capture than older and larger individuals.

Conclusions

Twelve isolated theropod teeth associated with a sauropod carcass from the Campanian–Maastrichtian Allen Formation of Patagonia are confidently referred to abelisaurid theropods on the basis of the results of the cladistic, discriminant, and cluster analyses. Three different morphotypes were identified and likely correspond to different positional entities along the tooth row possibly from a single abelisaurid taxon. The dental material is here interpreted as autochthonous elements, and together with sauropod remains, conforms to an oryctocoenosis. Such an association between a large number of abelisaurid shed teeth and a titanosaur carcass likely corresponds to a trophic interaction between abelisaurids and titanosaurids, which was already documented by tooth marks on long bones from Maastrichtian deposits of Madagascar. At least one theropod shed tooth associated with titanosaur bones and recovered in the same layer as titanosaur clutches with embryos from the Campanian Anacleto Formation is here confidently referred to abelisaurids. If taphonomic bias cannot be excluded, this association suggest that abelisaurid theropods may have also fed on hatchling titanosaurs.

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