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Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

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ISSN (imprimé / *print*) : 1631-0683/ ISSN (électronique / *electronic*) : 1777-571X

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Submitted on 27 March 2019 | accepted on 18 October 2019 | published on 12 October 2020

urn:lsid:zoobank.org:pub:E11C9380-B80E-414A-9EC0-6C44A8367982

Zaher H., Pol D., Navarro B. A., Delcourt R. & Carvalho A. B. 2020. — An Early Cretaceous theropod dinosaur from Brazil sheds light on the cranial evolution of the Abelisauridae. *Comptes Rendus Palevol* 19 (6): 101-115. <https://doi.org/10.5852/cr-palevol2020v19a6>

ABSTRACT

Abelisaurid theropods dominated the predator role across Gondwana during the Late Cretaceous. They are characterized by highly reduced forelimbs and one of the most specialized cranial morphologies among carnivorous dinosaurs, exemplified by a broad skull, short rostrum, high occipital region, and highly kinetic intramandibular joint, suggestive of a specialized feeding strategy. Late Cretaceous abelisaurids are known from some remarkably complete taxa with well-preserved skulls. However, little is known about the pattern of character transformation that led to their highly modified condi-

KEY WORDS
Abelisauridae,
Quiricó Formation,
Ceratosauria,
Aptian,
new genus,
new species.

tion because there are no well-preserved abelisaurids before the Late Cretaceous. Here we report a basal abelisaurid from the Early Cretaceous of Brazil that preserves a complete skull and reveals an early stage in the cranial evolution of the group. It lacks the specialized temporal and mandibular features characteristic of derived abelisaurids, including the kinetic intramandibular joint and knob-like dorsal projection of the parietals.

RÉSUMÉ

Un dinosaure théropode du Crétacé inférieur du Brésil met en lumière l'évolution crânienne des Abelisauridae. Les théropodes abélisauridés ont occupé la place de prédateur dans tout le Gondwana au cours du Crétacé supérieur. Ils sont caractérisés par des membres antérieurs très réduits et par l'une des morphologies crâniennes les plus spécialisées parmi les dinosaures carnivores, illustrée par un crâne large, un rostre court, une région occipitale haute et une articulation intramandibulaire très cinétique, ce qui suggère une stratégie d'alimentation spécialisée. Les abélisauridés du Crétacé supérieur sont connus grâce à certains taxons remarquablement complets dont le crâne est bien conservé. Cependant, on sait peu de choses sur le schéma de transformation des caractères qui a conduit à leur état très modifié, car il n'existe pas d'abélisauridés bien conservés avant le Crétacé supérieur. Nous présentons ici un abélisauridé basal du Crétacé inférieur du Brésil qui conserve un crâne complet et révèle un stade précoce de l'évolution crânienne du groupe. Il lui manque les caractéristiques temporelles et mandibulaires spécialisées caractéristiques des abélisauridés dérivés, notamment l'articulation cinétique intramandibulaire et la projection dorsale en forme de bouton des pariétaux.

MOTS CLÉS
Abelisauridae,
Formation Quiricó,
Ceratosauria,
Aptien,
genre nouveau,
espèce nouvelle.

INTRODUCTION

The Early Cretaceous is an interval of over 40 million years that is critical for understanding the latter phases in the evolutionary history of dinosaurs. In contrast with the well-known dinosaur diversity in continental ecosystems during the Late Cretaceous, current knowledge of Early Cretaceous dinosaurs is much more limited, especially for theropod dinosaurs (Barrett *et al.* 2009). The scarcity of Early Cretaceous theropods is particularly marked in Gondwanan landmasses, where a diverse assemblage is mainly known from the Late Cretaceous of South America (Novas 1997; Weishampel *et al.* 2004; Novas *et al.* 2013). Abelisauridae was a dominant clade of ceratosaurian theropods in Gondwana during this period, although they were also present in Europe (Accarie *et al.* 1995; Ősi & Buffetaut 2011; Tortosa *et al.* 2014).

Late Cretaceous abelisaurids include some remarkably complete taxa and are characterized by their highly reduced forelimbs and a bizarre skull anatomy, including a short, high and conspicuously fused cranium ornamented with a rugose external surface that evolved, in some cases, horns or domes on the parietal roof, and highly a kinetic intramandibular joint (Bonaparte 1991; Sampson *et al.* 1998; Sampson & Witmer 2007; Novas 2009; Novas *et al.* 2013).

The recent discovery of *Eoabelisaurus* in the Middle Jurassic of Argentina (Pol & Rauhut 2012) sheds some light on abelisaurid origins. However, some doubts exist about the phylogenetic affinities of this early species (Novas *et al.* 2013) and there is still a remarkable morphological gap between the plesiomorphic *Eoabelisaurus* (as well as other Jurassic abelisauroids) and well-known derived Late Cretaceous abelisaurids such as *Carnotaurus*, *Skorpiovenator* and *Majungasaurus* (Bonaparte

et al. 1990; Sampson *et al.* 1998; Sampson & Witmer 2007; Canale *et al.* 2009). The Early Cretaceous is in the midst of this obscure period of the history of abelisaurid evolution, given that known records from this time are limited to highly fragmentary remains (Rauhut *et al.* 2003; Sereno & Brusatte 2008; Smith *et al.* 2010), and many of which were reinterpreted as basal abelisauroids rather than true abelisaurids (Carrano & Sampson 2008; Farke & Sertich 2013; Novas *et al.* 2013).

Here we report a basal abelisaurid from the Early Cretaceous (Barremian-Aptian) of Brazil that represents the first definitive abelisaurid from this critical interval with a complete and well-preserved skull, mandible, and informative postcranial skeleton. This new taxon is placed as the sister-group of other Cretaceous abelisaurids and bears a unique combination of plesiomorphic and apomorphic features that reveal the pattern and timing of character acquisition toward the highly apomorphic skull anatomy of derived abelisaurids from the Late Cretaceous.

MATERIAL AND METHODS

SPECIMEN PREPARATION AND CT SCAN IMAGERY

The abelisaurid specimen described here was found underneath the holotype of *Tapuiasaurus macedoi*, a titanosaurian described by Zaher *et al.* (2011). The specimen is represented by an almost complete and articulated skeleton that was collected as a single block. Part of the skeleton was partly prepared in the field and the rest of the rock matrix was later removed at the Laboratório de Paleontologia of the Museu de Zoologia, Universidade de São Paulo. During preparation, the whole skull and some additional postcranial elements were isolated from the rest of the skeleton and scanned in the Museum's micro-CT

scan. The specimen and isolated bones were measured using a digital calliper (Appendix 1). The specimen was deposited in the Paleontological collection of the Museu de Zoologia under accession number MZSP-PV 833.

CT-scanning procedures with MZSP-PV 833 were conducted on a 300-kV μ -focus X-ray source micro-computed tomography GE Phoenix v|tome|x M 300 (General Electric Measurement & Control Solutions, Wunstorf, Germany) at the Laboratório de Microtomografia of the Museu de Zoologia, Universidade de São Paulo. Scan parameters such as exposure time (ms), number of projections, kilovoltage (kV), and current strength (μ A) were variously set for each individual bone element to obtain the maximized spatial resolution and better image contrast. X-ray projection images were recorded at 333 ms of time of exposure per image, with the images (varying from 1440 to 3500) in one slow stepwise rotation of the sample. The duration of the scanning procedure varied according to the configuration chosen for each element. For the skull, mandible and cervical series, we performed a Multiscan comprising 4 individual scans, to improve resolution, with projections varying from 1440 to 3500, voltage from 120 to 150 kV, current from 180 to 200 μ A, and voxel size resolution varying from 55 to 79 μ m. The other elements were scanned only in a single procedure, with projections varying from 1440 to 1700, voltage from 90 to 150 kV, current from 180 to 210 μ A, and voxel size from 51 to 131 μ m.

The acquired scan data were processed on a high-end computer HP Z820 workstation with eight-core Intel Xeon E5-2660, 2.20 GHz (2 processors), 128 GB of memory. A Microsoft Windows 7 Ultimate 64-bit operating system was used, with a graphics processing unit Cubix Elite Xpander (Cubix Corporation, Carson City, NV). Reconstruction of raw data was performed using the system-supplied software phoenix datos|x reconstruction v. 2.3.0 (General Electric Measurement & Control Solutions, Wunstorf, Germany). A beam hardening correction module was used to reduce beam artifacts, using a correction factor of five (values ranging from zero to 10). Three-dimensional visualization as well as the analysis of the reconstructed data were performed using VGStudio MAX 2.2.3 64 bit (Volume Graphics GmbH, Heidelberg, Germany).

PHYLOGENETIC ANALYSIS

The dataset used to test the phylogenetic relationships of MZSP-PV 833 is a recently published analysis (Rauhut & Carrano 2016), to which we have added recently described abelisauroids, as well as new information on the anatomy and characters from recent abelisaurid studies (Novas *et al.* 2010; Tortosa *et al.* 2014; Delcourt 2018). The complete dataset consisted of 37 terminals scored across 218 anatomical characters (Appendix 1). An equally weighted parsimony analysis was conducted in TNT v.1.5 (Goloboff *et al.* 2008) using a traditional heuristic search of 1000 replicates of Wagner trees followed by TBR branch swapping. A final round of TBR was applied to the best trees found during the replicates to find all MPTs. Unstable taxa in the MPTs were detected using the iterpcr method (Pol & Escapa 2009) in order to recover a reduced strict consensus that ignores the alternative positions of highly fragmentary and unstable taxa. Nodal support was assessed using Bremer support (Bremer

1994), Bootstrap (Felsenstein 1985), and Jackknife (Farris *et al.* 1996) in TNT software. Bremer support was calculated using the TNT script BREMER.RUN that combines heuristic tree searches of suboptimal trees as well as tree searches under negative constraints. Resampling techniques (for bootstrap and jackknife) consisted of 1000 pseudoreplicates with the same tree search strategy used for the parsimony analysis, and the resulting trees were summarized through absolute frequencies and GC frequencies (Goloboff *et al.* 2003; Appendix 1). Measures of support were calculated for the complete set of taxa but support values for the nodes exclusively present in the reduced consensus were evaluated *a posteriori* from the nodal support analysis (Appendix 1).

DATA AVAILABILITY

The holotype of *Spectrovenator ragei* n. gen., n. sp. (MZSP-PV 833) is housed at the Museu de Zoologia da Universidade de São Paulo, Brazil, and accessible to professionals for scientific study. Data regarding the taxonomic recommendations of this paper have been deposited in ZooBank under Life Science Identifier urn:lsid:zoobank.org:pub:E11C9380-B80E-414A-9EC0-6C44A8367982. The authors declare that all other data supporting this study are available within the paper and its Appendix 1. TNT software is available at <https://cladistics.org/tnt/>; R software is available at <https://www.r-project.org>.

SYSTEMATIC PALAEONTOLOGY

Superorder DINOSAURIA Owen, 1842
Suborder THEROPODA Marsh, 1881
Clade CERATOSAURIA Marsh, 1884
Superfamily ABELISAUROIDEA Bonaparte, 1991
Family ABELISAURIDAE Bonaparte & Novas, 1985

Genus *Spectrovenator* n. gen.

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TYPE SPECIES. — *Spectrovenator ragei* n. gen., n. sp.

DIAGNOSIS. — As for type and only species (type by monotypy).

ETYMOLOGY. — From the Latin *spectrum* (“ghost”) and *venator* (“hunter”). The generic name refers to the fact that the specimen was found unexpectedly underneath the holotype of *Tapuiasaurus macedoi* while the latter was being partially prepared in the field (Zaher *et al.* 2011).

Spectrovenator ragei n. sp.
(Figs 1-6)

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HOLOTYPE. — MZSP-PV 833, a partially articulated skeleton consisting of complete skull and mandibles, partially preserved cervicodorsal vertebrae and ribs, complete sacrum, partially preserved caudal series, complete pelvic girdle and hindlimbs.

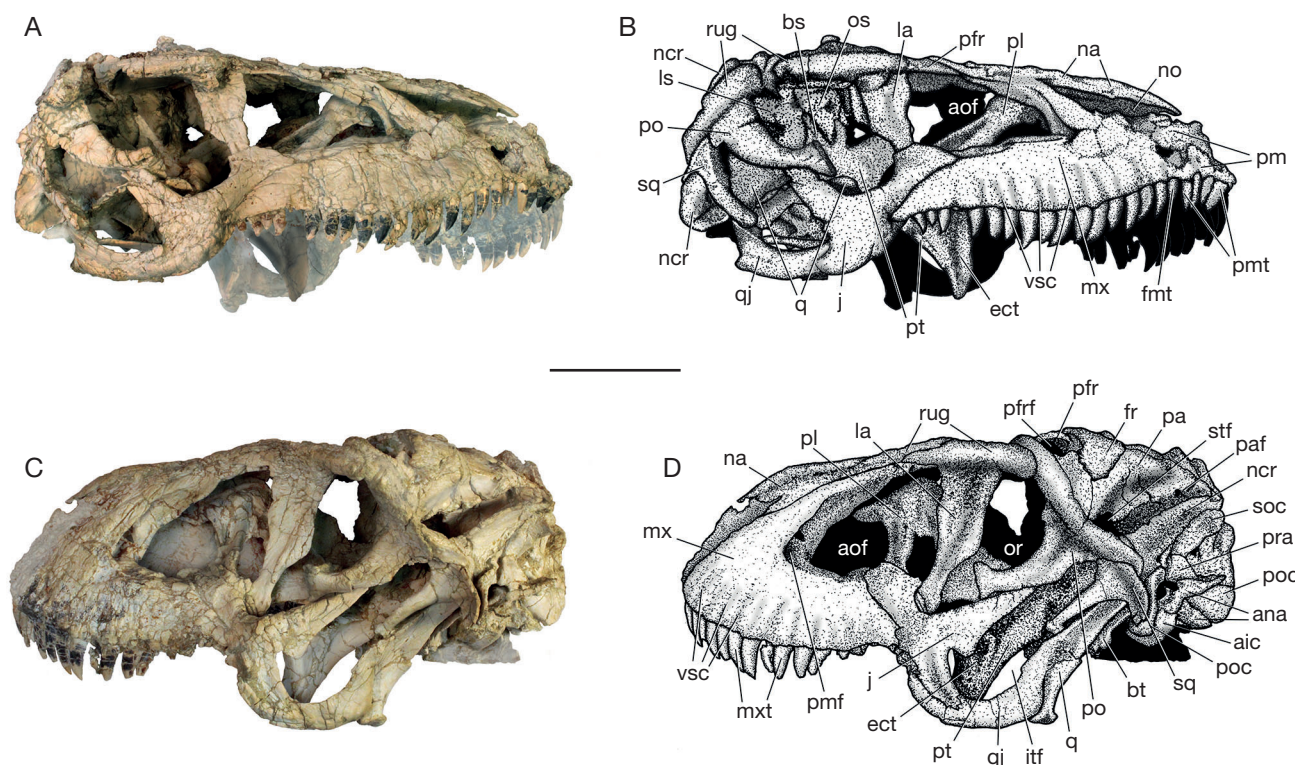


FIG. 1. — Skull of *Spectrovenator ragei* n. gen., n. sp. (MZSP-PV 833). Skull in right lateral view (A) and schematic drawing (B), left lateral view (C) and schematic drawing (D). Abbreviations: **aic**, atlantal intercentrum; **ana**, atlantal neural arch; **aof**, antorbital fenestra; **bs**, basisphenoid; **bt**, basal tubera; **ect**, ectopterygoid; **fnt**, first maxillary tooth; **fr**, frontal; **itf**, infratemporal fenestra; **j**, jugal; **la**, lacrimal; **ls**, laterosphenoid; **mx**, maxilla; **mxt**, maxillary teeth; **na**, nasal; **ncr**, nuchal crest; **no**, narial opening; **or**, orbit; **os**, orbitosphenoid; **pa**, parietal; **paf**, parietal foramen; **pfr**, prefrontal; **pfrf**, prefrontal fenestra; **pl**, palatine; **pm**, premaxilla; **pmt**, premaxillary teeth; **po**, postorbital; **poc**, paraoccipital process; **pra**, proatlas; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **rug**, rugosity; **soc**, supraoccipital; **sq**, squamosal; **stf**, supratemporal fenestra; **vsc**, vascular sulcus. Scale bar: 5 cm.

ETYMOLOGY. — The specific epithet ‘*ragei*’ is a patronym honouring Dr Jean-Claude Rage for his influential contribution to our knowledge on the Paleobiogeography of continental Mesozoic vertebrates.

DIAGNOSIS. — *Spectrovenator ragei* n. gen., n. sp. differs from all other abelisaurid theropods by the following unique autapomorphies: posterior ramus of maxilla ornamented with vertically oriented grooves except for the smooth region anterior to the maxilla-jugal suture; lacrimal lateral surface rugose except for smooth ventral region; ventrally bowed posterior process of jugal; nuchal crest with thin and smooth dorsal margin; straight ventral margin of dentaries with deep sulcus on lateral surface; dorsal margin of surangular slightly convex; longitudinal ridge along posteroventral end of mandibular ramus.

TYPE LOCALITY. — The only known individual of *Spectrovenator ragei* n. gen., n. sp. was recovered at the Embira Branca Range, a locality close to the Coração de Jesus Municipality (northern Minas Gerais State, Brazil). The deposits in which the remains were recovered are referred to the Quiricó Formation, Areado Group, Sanfranciscana Basin (Campos & Dardenne 1997; Zaher *et al.* 2011). The lacustrine sequence of the Quiricó Formation is constrained to the Barremian-Aptian boundary, based on stratigraphical relationships and biostratigraphical correlations, such as the presence of the goniorhynchiform teleostean *Dastilbe moraes* (Scorza & Santos 1955), the *Tucanopollis crisopollensis*, *Afropollis* sp. and *Sergipea naviformis* palynozones (Carvalho *et al.* 1994), as well as by the association of the ostracodans *Wolburgiopsis plastica*, *Wolburgiopsis chinamuertensis*, *Ilyocypris* sp., *Brasacypris* sp. 1, *Harbinia symmetrica* and *Darwinula martinsi* (Do Carmo *et al.* 2004).

DESCRIPTION AND COMPARISONS

Skull

The skull of *Spectrovenator ragei* n. gen., n. sp. is nearly complete, missing only portions of the left and right premaxillae and part of the right mandible (Figs 1–4). The skull is compressed anteroposteriorly in the left part of occipital region, lateromedially in the right of orbital region, and part of the left quadrate was broken and displaced anteriorly. Although the premaxillae are badly preserved, Micro-CT scan imaging revealed the presence of four premaxillary teeth and a strong premaxilla-maxilla contact (Appendix 1).

The rostrum (as preserved) corresponds to more than 50% of the total skull length (Fig. 1A–D; Appendix 1). The maxilla is ornamented, except below the antorbital fenestra where it bears a series of vertically oriented grooves. The anteriormost grooves, on the alveolar margin, are smaller than the posterior ones, as in *Majungasaurus*, *Kryptops*, and *Rugops* (Sampson & Witmer 2007; Sereno *et al.* 2004; Sereno & Brusatte 2008). The maxilla-jugal contact is smooth (Fig. 1A, B). The rostral ramus of the maxilla is relatively short, resembling the condition found in *Rugops* (Sereno *et al.* 2004). The ascending process of the maxilla is posteriorly slanted along its dorsal region and the antorbital fenestra is subtriangular and longer than high. The medial lamina of the maxilla is anteroposteriorly short, limiting the antorbital fossa to the anterior margin of the antorbital opening, as in most abelisaurids (Bonaparte

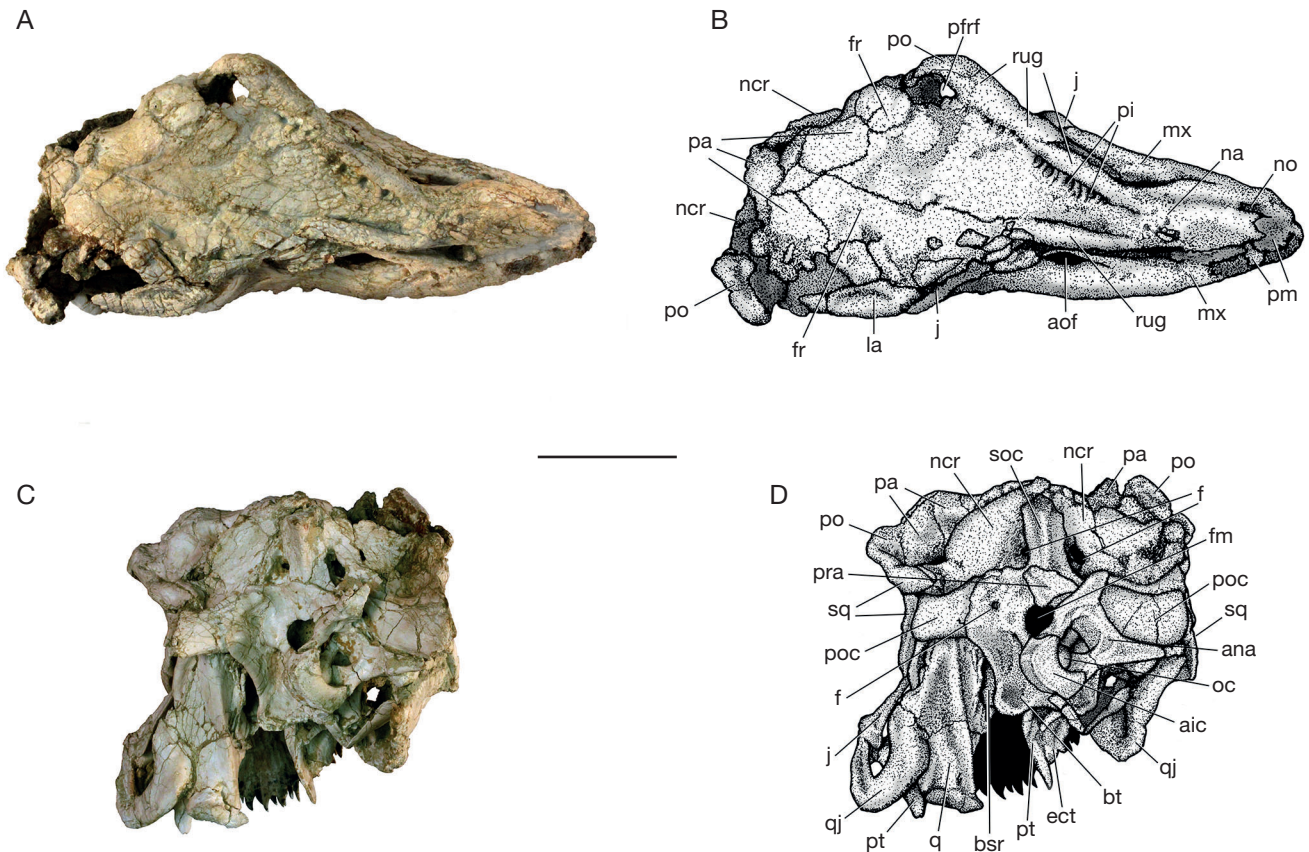


FIG. 2. — Skull of *Spectrovenator ragei* n. gen., n. sp. (MZSP-PV 833). Skull in dorsal (parietal) view (A) and schematic drawing (B), posterior (occipital) view (C) and schematic drawing (D). Abbreviations: **aic**, atlantal intercentrum; **ana**, atlantal neural arch; **aof**, antorbital fenestra; **bsr**, basisphenoid recess; **bt**, basal tubera; **ect**, ectopterygoid; **f**, foramen; **fm**, foramen magnum; **fr**, frontal; **j**, jugal; **la**, lacrimal; **mx**, maxilla; **na**, nasal; **ncr**, nuchal crest; **no**, narial opening; **oc**, occipital condyle; **pa**, parietal; **pfrf**, prefrontal fenestra; **pi**, pits; **pm**, premaxilla; **po**, postorbital; **poc**, paraoccipital process; **pra**, proatlas; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **rug**, rugosity; **soc**, supraoccipital; **sq**, squamosal. Scale bar: 5 cm.

et al. 1990; Carrano & Sampson 2008). A promaxillary recess is present, but hidden in lateral view, a feature found in other abelisaurids (Novas 2009). Posteriorly, the maxilla has a long anteroposteriorly directed contact with the jugal that precludes a maxilla-lacrimal contact. There are 18 maxillary teeth as in *Rugops* (Serenio *et al.* 2004). The medial surface of the maxilla above the alveolar margin bears fused paradental plates that are smooth (Fig. 3E), rather than rugose as in other abelisaurids.

The nasals are thick and at least partially fused anteriorly (Fig. 2A, B and Appendix 1). The nasals are anteriorly forked, with a long and acute maxillary process as in *Rugops* (Serenio *et al.* 2004). The flattened dorsal surface of the nasals is ornamented on its anterior third and smooth on its posteromedial region. The nasals bear a series of large pits and invaginations that are located medial to the ornamented ridge that form the lateral edge of the bone, a feature previously regarded as autapomorphic for *Rugops* (Serenio *et al.* 2004). Similar pits are also present in *Carnotaurus*, but this taxon lacks the invaginations and the lateral nasal ridge. The ornamentation of the dorsal surface of the nasals also resembles that of *Rugops* (Serenio *et al.* 2004), interpreted as indicative of overlying scales (Delcourt 2018). The nasal-premaxilla articulation is slightly ornamented, lacking the papillate texture present in *Rugops*, interpreted as indicative of armoured-like dermis (Delcourt 2018).

The lacrimal is massive, ornamented, and contacts the maxilla and nasal anteriorly, the prefrontal posterodorsally, and the postorbital and jugal ventrally (Figs 1C, D; 2A, B). The posterodorsal antorbital fossa on the lacrimal is exposed laterally whereas the pneumatic foramen is hidden in lateral view, as *Ceratosaurus* (Novas *et al.* 2013), *Euabelisaurus* (Pol & Rauhut 2012), and other abelisaurids (Carrano & Sampson 2008). The lacrimal bears a broad rugose ridge that divides its dorsal and lateral surfaces and extends posteriorly to contact the postorbital. Differently from other abelisaurids (Canale *et al.* 2009), the thin and ornamented rostral ramus of the lacrimal in *Spectrovenator* n. gen. forms part of the external posterodorsal border of the antorbital fossa (Figs 1C, D; 2A, B). The lacrimal has a short posterior process that projects posteriorly toward the suborbital process of the postorbital, as in most abelisaurids (Carrano & Sampson 2008). The prefrontals are fused to the lacrimal on the dorsal surface of the skull where the posterior process develops to contact the postorbital above the orbit. However, the lacrimal-prefrontal suture can be seen along the ventral descending process of these bones on the anteromedial region of the orbit.

The postorbital is not fused to the frontal but rather encloses, along with the lacrimal and the frontal, a small dorsally oriented fenestra located above each orbit (Figs 1A-D; 2A, B).

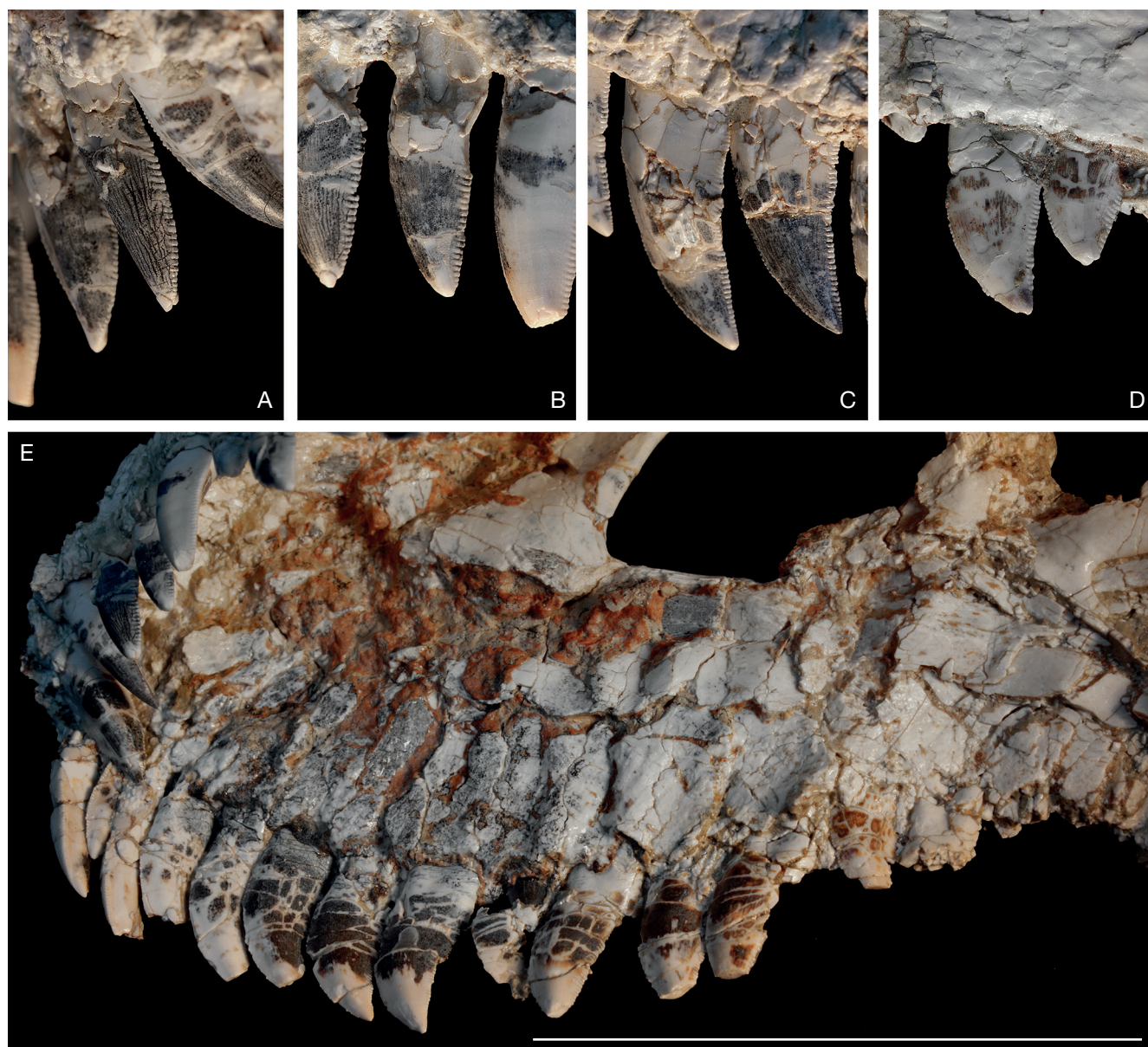


FIG. 3. — Teeth of *Spectrovenator ragei* n. gen., n. sp. (MZSP-PV 833). Mesial margin of left premaxillary tooth in oblique labial view (A); Right posterior premaxillary tooth in labial view (reversed, distal to the right) (B); Right mid maxillary tooth in labial view (reversed, distal to the right) (C); posterior maxillary teeth in labial view (reversed, distal to the right) (D); Left maxilla in labial view showing fused and smooth paradental plates (reversed, distal to the right). Scale bar: E, 5 cm.

The descending ramus of the postorbital is anteroventrally directed, instead of perpendicular to the dorsal ramus, and bears a moderately expanded suborbital process (Fig. 1C, D). The dorsal ramus retains a relatively well-developed squamosal process in comparison to those of other abelisaurids (Canale *et al.* 2009; Pol & Rauhut 2012).

The jugal is barely ornamented, dorsoventrally low below the orbit, and with a convex ventral margin (Fig. 1A-D). The anterior process separates the maxilla from the lacrimal whereas the posterior process is bifurcated and embraces the quadratojugal on its anterior third (Fig. 1A-D). The ascending process of the jugal is triangular and tapers distinctly on its dorsal tip. The dorsal process of the quadratojugal is anteroposteriorly broad and contacts the squamosal.

The suture between the prefrontal and lacrimal of *Spectrovenator* n. gen. is not visible on the dorsal skull surface and they may have been fused as in other abelisaurids (Canale *et al.* 2009; Sereno *et al.* 2004; Pol & Rauhut 2012). However, these elements are unfused along their descending processes on the anteromedial margin of the orbit. The frontals of *Spectrovenator* n. gen. are paired and their suture is visible dorsally as in *Rugops* (Sereno *et al.* 2004), but their dorsal surfaces are smooth and lack the rugosities present in other abelisaurids (Sereno *et al.* 2004; Paulina Carabajal 2011a; Fig. 2A, B). The frontals are proportionately wide and short, as in other abelisaurids (Canale *et al.* 2009; Paulina Carabajal 2011a), and have a median boss that extends longitudinally along the interfrontal suture. The lateral margins of the frontals are

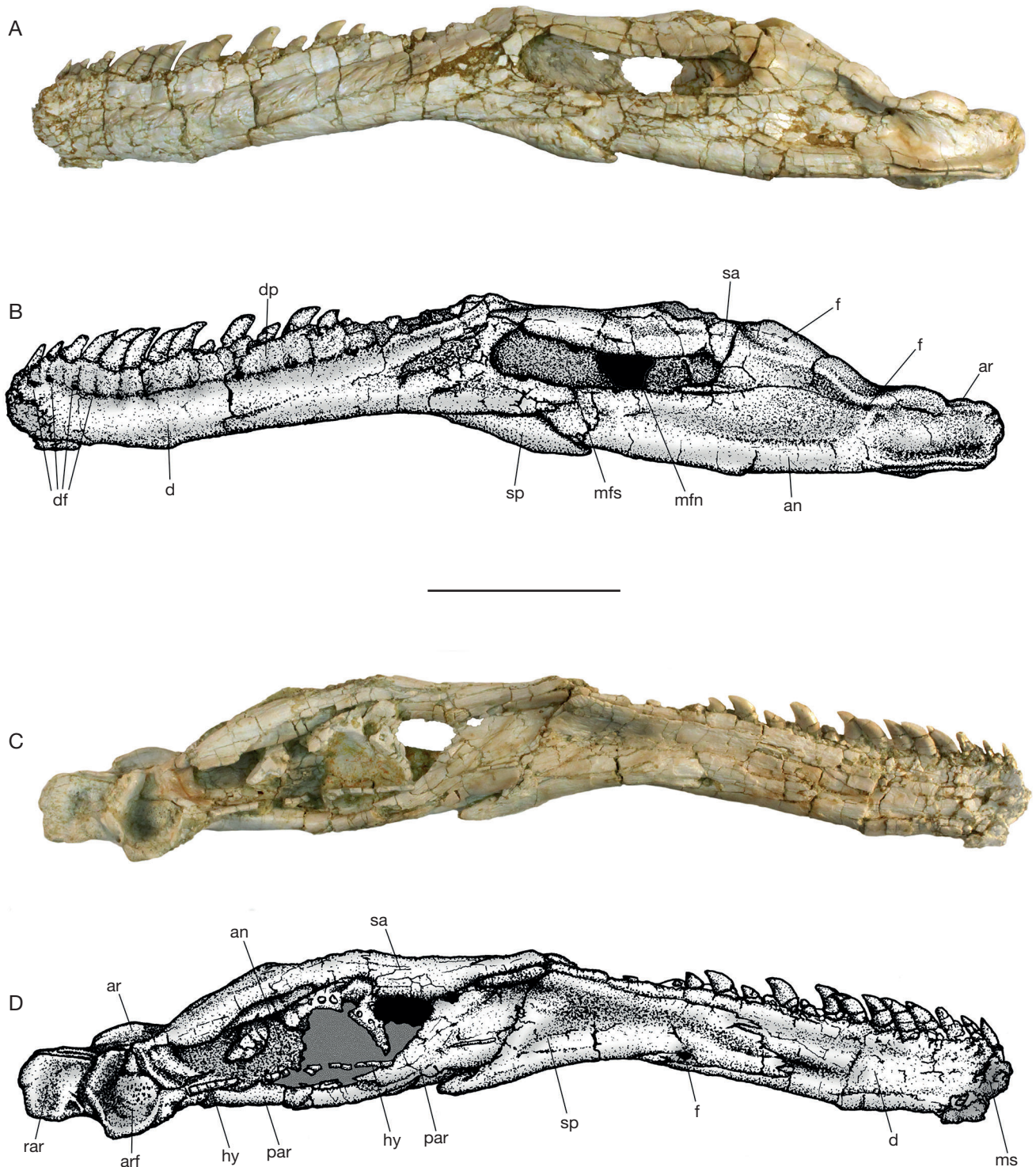


FIG. 4. — Mandible of *Spectrovenator ragei* n. gen., n. sp. (MZSP-PV 833). Left mandible in lateral (labial) view (A) and schematic drawing (B), in medial (lingual) view (C) and schematic drawing (D). Abbreviations: an, angular; ar, articular; arf, articular fossa; d, dentary; df, dental foramina; dp, dental plates; f, foramen; hy, hyoid apparatus; mfn, mandibular fenestra; mfs, mandibular fossa; ms, mandibular symphysis; par, prearticular; rar, retroarticular; sa, surangular. Scale bar: 5 cm.

dorsoventrally thin and have a short concave orbital margin. This margin is the medial edge of the fenestra that is laterally closed by the lacrimal-postorbital contact above the orbit, opening also present in *Rugops*, *Ekrixinatosaurus* and *Arcovenator* (Sereni *et al.* 2004; Novas *et al.* 2013; Tortosa *et al.* 2014). The frontal is not fused to the parietal, at least within

the supratemporal fossa where the suture is clearly present, in contrast to other abelisaurids (Paulina Carabajal 2011b). On this region, the dorsal surface formed by the frontals and parietal is flat, lacking the median fossa at the level of the anterior margin of the supratemporal fenestra and the narrow parietal crest separating the supratemporal fossae, both

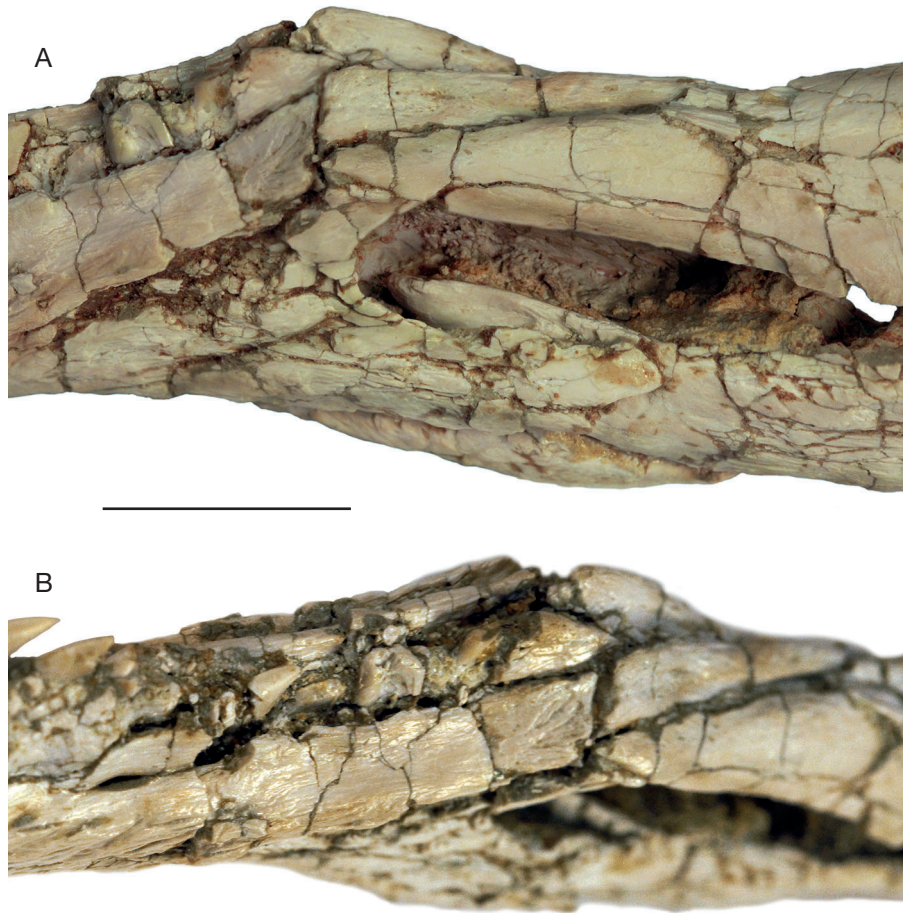


FIG. 5. — Detail of dentary-surangular suture on left mandibular ramus of *Spectrovenator ragei* n. gen., n. sp. (MZSP-PV 833), in lateral (A) and dorsal (B) views.

features that characterize the skull roof of most abelisaurids (Bonaparte & Novas 1985; Sereno *et al.* 2004; Canale *et al.* 2009; Tortosa *et al.* 2014). The flat parietal surface between the supratemporal fossae of *Spectrovenator* n. gen. is even broader than that of *Aucasaurus* (Paulina Carabajal 2011b).

The posterior end of the parietal is not significantly raised above the level of the skull roof but extends posteriorly, capping the supraoccipital crest (Fig. 2C, D). The parietal and squamosal form together a broad transversal nuchal crest, resembling but less developed than in other abelisaurids (Sampson *et al.* 1998; Carrano & Sampson 2008; Paulina Carabajal 2011b). The dorsal margin of this crest is thin and smooth rather than broad and rugose as in other abelisaurids. The squamosal has a smooth lateral surface with a marked concavity and a straight postquadratic process that extends posteriorly, as in other abelisaurids (Carrano & Sampson 2008). The descending process of the squamosal is thin and tapers gradually, forming the dorsal half of the posterior margin of the infratemporal fenestra down to its contact with the quadratojugal (Fig. 1A-D).

The supraoccipital has a thick and prominent median vertical crest, but this crest is not as sharp and does not project posteriorly to the level of the occipital condyle as it does in derived abelisaurids (Canale *et al.* 2009). The paroccipital processes are only slightly expanded at their distal ends rather

than flared as in *Carnotaurus* (Paulina Carabajal 2011a). The paracondylar recess of the otoccipital is well developed and bears two small foramina, one of which leads to a medially directed duct (hypoglossal canal) while the other extends to an anteromedially directed duct (vagal canal). The *crista tuberalis* is well developed and connects the posteroventral end of the paraoccipital process with the lateral margin of the basal tubera. The basioccipital is vertical, bears a slightly developed median ridge, and forms most of the basal tubera, which are wider than the basioccipital condyle, as in *Ceratosaurus* and abelisaurids (Carrano & Sampson 2008). The basisphenoid covers the anterior and ventral surfaces of the basal tubera and has basiptyergoid processes that are slightly recurved posteriorly, as in other ceratosaurians (Canale *et al.* 2009). The ventral surface of the basisphenoid bears a deep recess that is rounded in shape and laterally enclosed by the *crista ventrolateralis* (Paulina Carabajal & Currie 2017).

Mandible

The mandible has an anteroposteriorly elongated external mandibular fenestra that reaches anteriorly the level of the posteriormost dentary tooth, as in other abelisaurids (Carrano & Sampson 2008; Figs 4, 5; Appendix 1). The dentary is straight rather than ventrally convex as in *Carnotaurus* and *Ekrixinatosaurus* (Bonaparte *et al.* 1990; Calvo *et al.* 2004) and

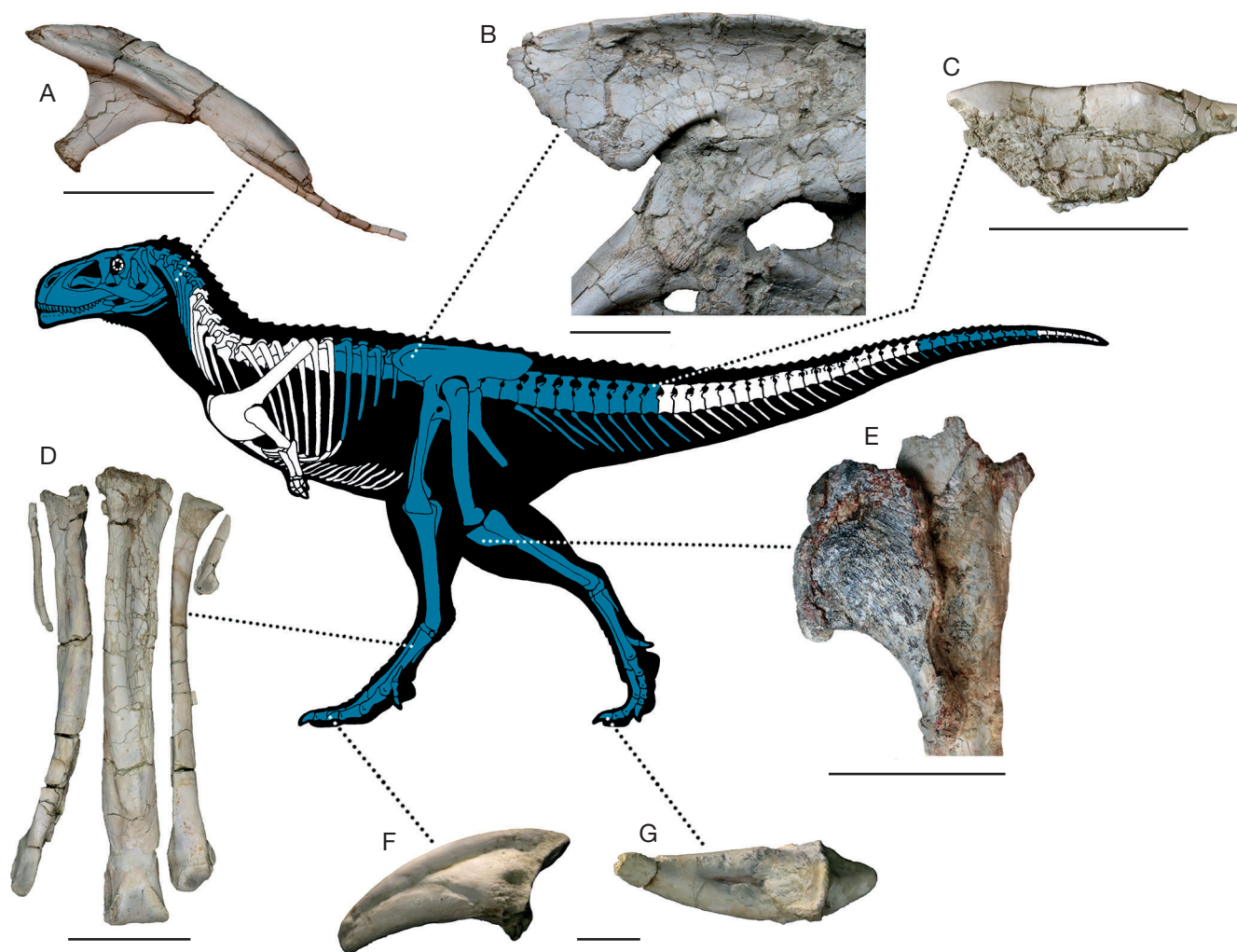


FIG. 6. — Phylogenetically informative characters in the postcranial skeleton of *Spectrovenator ragei* n. gen., n. sp. (MZSP-PV 833): Distally bifurcated left cervical rib, in ventral view (A); Preacetabular process of left ilium in lateral view, facing anteroventrally and showing anterior irregular margin (B); Anterior-middle caudal left transverse process, showing anteroposteriorly expanded end in ventrolateral view (C); Articulated right metatarsus in anterior view, showing the relative development of metatarsal II relative to III and IV (D); Detail of cnemial crest on left tibia, showing expanded asymmetrical distal end in lateral view (E); Pedal unguals in left lateral (F) and ventral views (G), showing bifurcated collateral grooves and ventral end with depression and lacking a flexor tubercle. Scale bars: A-E, 5 cm; F, G, 1 cm.

extends approximately along 50% of the mandibular length (Fig. 4A-D). There are 16 small and posteriorly recurved teeth. The lateral surface of the dentary bears a longitudinal sulcus that is located at its dorsoventral midpoint and contains aligned neurovascular foramina. Ventral to this sulcus the dentary is ornamented like the lateral surface of the skull. The posteroventral process of the dentary has a short overlapping contact with the angular (Fig. 5A), which is shorter than in *Carnotaurus* or *Majungasaurus* (Bonaparte *et al.* 1990; Sampson & Witmer 2007). The posterodorsal process of the dentary has a broad concave facet for the surangular (Fig. 5B), as in other abelisaurids (Pol & Rauhut 2012; Canale *et al.* 2009). The splenial bears an anteriorly placed ovoid foramen as in *Ceratosaurus* and abelisaurids (Sampson & Witmer 2007). The angular process of the splenial is broad, ornamented, and exposed on the lateral surface of the mandibular ramus. The posterior margin of the splenial is straight, angled, and sutured to the anterior margin of the prearticular.

The surangular has a slightly convex dorsal margin and a well-developed lateral shelf with a deep fossa underneath as in *Majungasaurus* (Sampson & Witmer 2007). The posteroventral margin of the surangular, along its suture with the prearticular, is laterally everted forming a well-developed anteroposterior crest on the ventrolateral margin of the mandibular ramus (Fig. 4A-D). The surangular bears an anterior foramen near its contact with the dentary, a posterior foramen ventral to the surangular crest, and an intermediately positioned foramen above the posterior margin of the mandibular fenestra as in *Carnotaurus* and *Majungasaurus* (Bonaparte *et al.* 1990; Sampson & Witmer 2007). The surangular forms the lateral part of the mandibular glenoid cavity along its contact with the articular. The glenoid fossa is deep and has elevated anterior and posterior buttresses (Fig. 4C, D). The retroarticular process is anteroposteriorly long, rounded, and has a dorsomedially concave surface, as in *Carnotaurus* and *Majungasaurus* (Bonaparte *et al.* 1990; Sampson & Witmer 2007).

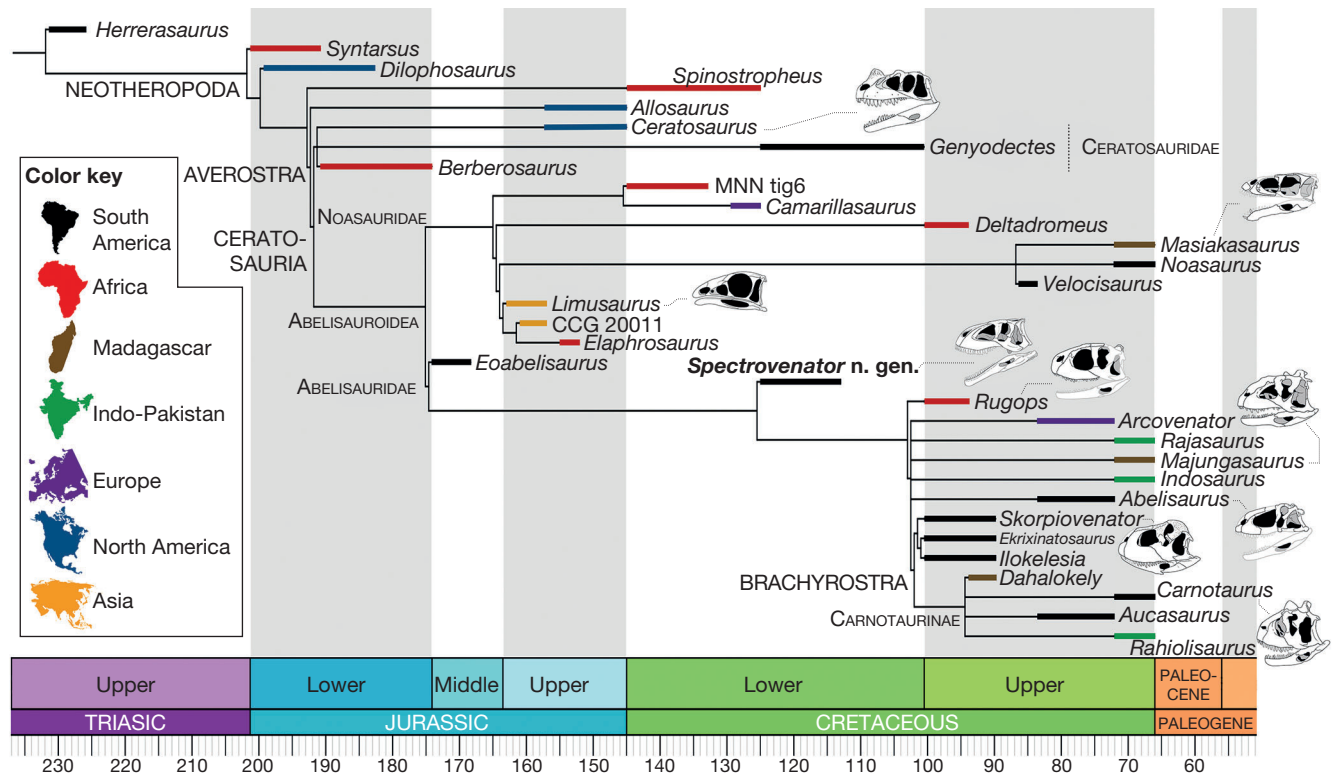


Fig. 7. — Phylogenetic relationships of *Spectrovenator ragei* n. gen., n. sp. (MZSP-PV 833) within Ceratosauria. Time-calibrated reduced strict consensus tree depicting the basal position of *Spectrovenator* n. gen. within Abelisauridae and the spatial distribution of taxon sampling.

Dentition

The upper dentition of *Spectrovenator* n. gen. includes 4 premaxillary and 18 maxillary teeth whereas the lower dentition includes 16 dentary teeth. The teeth vary in apicobasal height along the toothrow, reaching their maximal height at the level of the 6th to 8th maxillary teeth. The premaxillary teeth (Fig. 3A, B) are less distally recurved than the maxillary teeth and bear denticles that are similarly large on both their mesial (2.4 denticles per mm) and distal (2.4 denticles per mm) margins, taken at the midheight of the crown. The maxillary teeth become larger at the mid section of the toothrow (Fig. 3C) in comparison with the premaxillary teeth, although the size difference is not as large as in ceratosaurids (Rauhut, 2004). Similarly, the largest maxillary teeth are up to 70% of the height of the dentary, in contrast to proportionately higher teeth of ceratosaurids (Rauhut, 2004). The posterior maxillary teeth decrease in size and become more distally recurved posteriorly (Fig. 3D, E). The maxillary teeth have denticles on their distal margin that are similar in size to those of the premaxilla (2.8 denticles per mm) but those of their mesial margin are much smaller (3.4 denticles per mm). The dentary teeth also become larger at the midpoint of the toothrow and posterior elements are more distally recurved than anterior elements (Fig. 4).

Postcranium

The postcranial remains of *Spectrovenator* n. gen. reveal cervicodorsal vertebrae that are characterized by their elongated epiphyses and well-developed epiphyseal-prezygapophyseal laminae (EPRL), distally bifurcated cervical ribs, and transverse processes of caudal vertebrae distally anteroposteriorly expanded, as in most abelisaurids (Fig. 6A, C; Carrano & Sampson 2008). Other abelisaurid features present in the postcranium include the preacetabular process of the ilium directed anteroventrally and with an irregular anterior margin and the cnemial crest on the tibia with an expanded distal end (Fig. 6B, E). The astragalus is fused to the calcaneum, a feature present in other ceratosaurians (Carrano & Sampson 2008) that differs from that of basal tetanurans (Rauhut & Pol 2017) and non-averostrans (Ezcurra 2017). The astragalar ascending process is tall and laminar and lacks the fusion with the fibula present in *Masiakasaurus* (Carrano *et al.* 2011). The metatarsus of *Spectrovenator* n. gen. is gracile and proportionately more elongated than in other abelisaurids (Coria *et al.* 2002; Carrano 2007), lacking the reduced width of metatarsal II present in noasaurids (Fig. 6D; Carrano & Sampson 2008). The pedal unguals of *Spectrovenator* n. gen. have proximally bifurcated grooves (Y-shaped) and a flexor tubercle with an associated ventral depression, as in other abelisauroids (Fig. 6F, G; Novas *et al.* 2005; Carrano 2007; Novas *et al.* 2013).

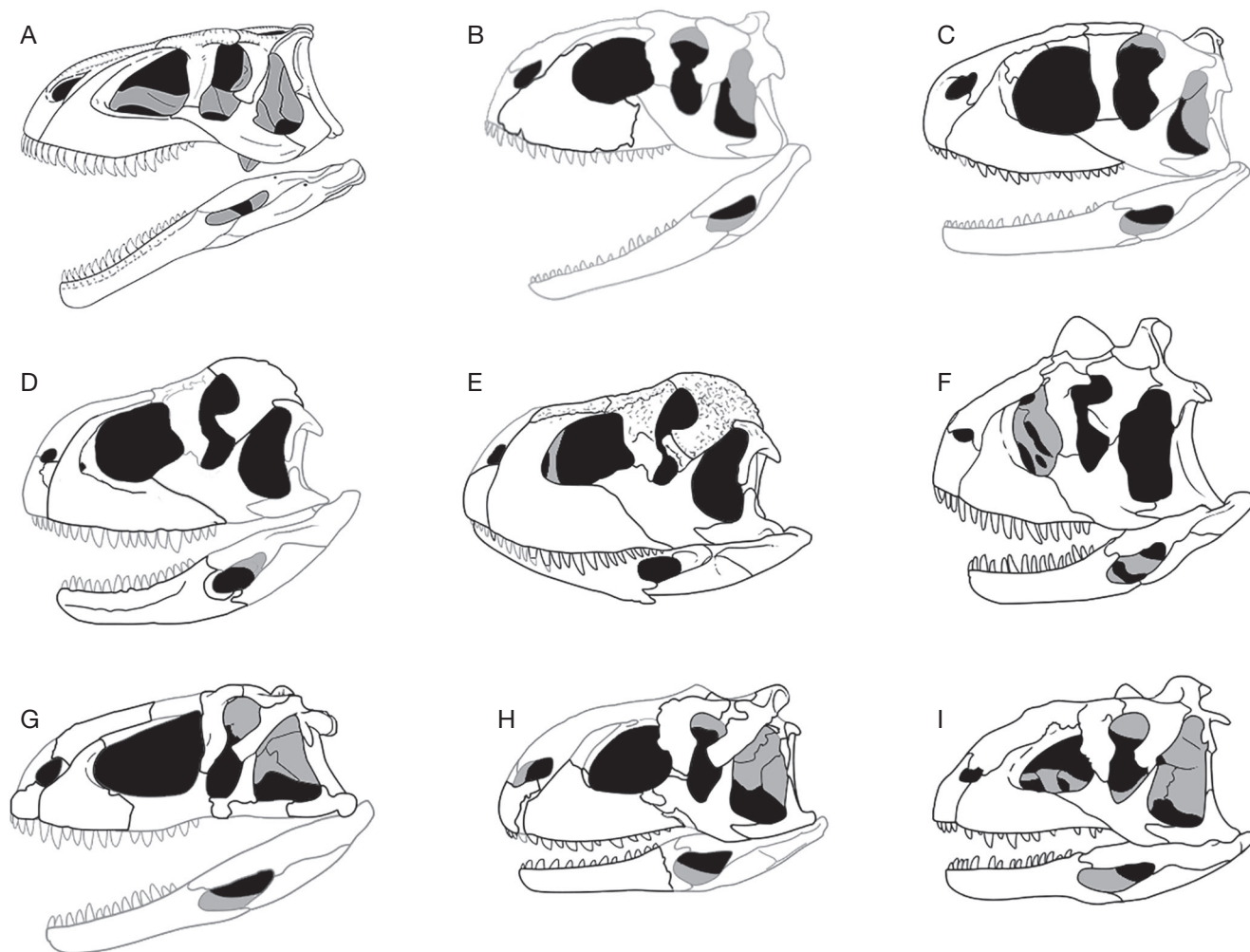


FIG. 8. — Reconstructions of the skull and mandible of abelisaurid theropods (missing parts in light grey): *Spectrovenator ragei* n. gen., n. sp. (MZSP-PV 833) (A) from the Barremian-Aptian, Quiricó Formation (Brazil); Partial left maxilla of *Kryptops palaios* (B) from the Aptian, Elrhaz Formation (Niger); Rostrum and skull roof of *Rugops primus* (C) from the Cenomanian, Echkar Formation (Niger); Partial skull and mandible of *Ekrixinatosaurus novasi* (D) from the Cenomanian, Candeleros Formation (Argentina); Complete skull and mandibles of *Skorpiovenator bustingorryi* (E) from the Cenomanian-Turonian, Huincul Formation (Argentina); Complete skull and mandibles of *Carnotaurus sastrei* (F) from the Campanian-Maastrichtian, La Colonia Formation (Argentina); Partial skull of *Abelisaurus comahuensis* (G) from the Campanian, Anacleto Formation (Argentina); Partial skull and mandible of *Rajasaurus narmadensis* (H) from the Maastrichtian, Lameta Formation (India); Complete skull and mandible of *Majungasaurus crenatissimus* (I) from the Maastrichtian, Maevarano Formation (Madagascar). Not in scale for comparative purposes.

PHYLOGENETIC ANALYSIS

The phylogenetic position of *Spectrovenator* n. gen. was tested using a dataset of ceratosaurian relationships that included the new taxon and integrates recently published information on abelisauroids (see Material and methods). All most parsimonious trees (MPTs) depict *Spectrovenator* n. gen. as a basal member of Abelisauridae, being the sister group of the clade formed by *Rugops* and more derived taxa (Fig. 7). Abelisaurid apomorphies supporting the inclusion of *Spectrovenator* n. gen. in this clade include a large list of features: external ornamentation in the maxilla, nasal, lacrimal, and postorbital, antorbital fossa failing to extend posteroventrally along the maxilla, partially fused nasals, prefrontal at least partly fused to the lacrimal, lacrimal-postorbital contact above the orbit, lacrimal with suborbital process, presence of suborbital flange of postorbital, postorbital anteroposteriorly longer than high and with descending process anteroventrally projected, max-

illary dentition with more than 12 teeth, anterior process in transverse processes in anterior caudal vertebrae, and straight dorsal margin of iliac blade. The long list of characters supporting the inclusion of *Spectrovenator* n. gen. in the Abelisauridae is reflected in high nodal support values for this node when the position of highly unstable and fragmentary taxa is ignored (bremer = 4; bootstrap = 94%; jackknife = 95%; Appendix 1). It should be noted that although this large list of synapomorphies does not diagnose Abelisauridae in our analysis given that *Eoabelisaurus* is retrieved as the most basal member of this clade. Other studies (e.g., Novas *et al.* 2013), however, have retrieved *Eoabelisaurus* as a basal abelisauroid and under these hypotheses the list of apomorphies diagnosing the clade formed *Spectrovenator* n. gen. and other abelisaurids would be synapomorphies of Abelisauridae.

The position of *Spectrovenator* n. gen. as the sister group to *Rugops* and more derived abelisaurids is supported by the absence in *Spectrovenator* n. gen. of the following derived characters:

maxillary-jugal contact larger than 40% of total maxilla length, knob-like dorsal projection of parietal, narrow sagittal crest between the supratemporal fenestrae, reduced anterior process of the lacrimal externally to the antorbital fossa, and rugose parietal plate on the maxilla. The monophyly of *Rugops* and more derived abelisaurids, excluding *Spectrovenator* n. gen. and *Euabelisaurus*, also reaches high support values when fragmentary taxa are ignored (Bremer = 4; bootstrap = 82%; jackknife = 89%; see Appendix 1).

DISCUSSION AND CONCLUSIONS

Spectrovenator n. gen. represents the first Early Cretaceous abelisaurid known with a complete skull (Fig. 8), demonstrating a key morphological intermediate between the basalmost Jurassic *Euabelisaurus* and the Late Cretaceous abelisaurids. Whereas the abelisaurid position of *Euabelisaurus* has been disputed (e.g., Novas *et al.* 2013), the long list of apomorphies shared by *Spectrovenator* n. gen. and other abelisaurids provide a strong support for the position of this taxon as a definitive basal abelisaurid. Its basal phylogenetic position provides critical additional information for understanding the stepwise acquisition of the highly specialized skull morphology that have characterized abelisaurids since their recognition as a clade, over 25 years ago (Bonaparte 1991). The overall plesiomorphic skull condition of primitive abelisaurids was known so far only for a fragmentary maxilla belonging to *Kryptops* from the Aptian-Albian Elrhaz Formation of Niger (Sereno & Brusatte 2008; Fig. 8B) and from a rostrum and skull roof preserved in *Rugops* from the Cenomanian Echkar Formation of Niger (Sereno *et al.* 2004; Fig. 8C). Although the position of the highly fragmentary *Kryptops* is still debated, including its validity (Delcourt 2018), there is a broad consensus in the placement of *Rugops* as one of the most basal abelisaurids (Sampson & Witmer 2007; Sereno & Brusatte 2008; Tortosa *et al.* 2014; Rauhut & Carrano 2016; Delcourt 2017). *Spectrovenator* n. gen. shares plesiomorphic features with *Rugops*, including a long and acute maxillary process, nasals with a smooth central dorsal surface flanked by an ornamented ridge on their lateral edges, a posterodorsal antorbital fossa exposed laterally on the lacrimal, unfused postorbitals, frontals and parietals (Canale *et al.* 2009), slightly elevated nuchal parietal alae, and the presence of a fenestra above the orbit between the lateral margin of the frontal and the lacrimal-postorbital suture. The remains of *Spectrovenator* n. gen. also include the temporal region and the mandible, which lack most of the apomorphic features that characterize the strongly modified anatomy of derived abelisaurids, illustrating a previously unknown intermediate stage between the more specialized Late Cretaceous abelisaurids and more generalized ceratosaurian theropods.

Spectrovenator n. gen. is the only abelisaurid with a plesiomorphic configuration of the temporal region, including a broad parietal surface between the supratemporal fossae and a narrow and elongated squamosal process of the postorbital. Alternatively, all known derived abelisaurids share a series of modifications that create a broader adductor chamber for the mandibular muscles, such as a broad infratemporal fenestra, a narrow parietal crest

dividing broad temporal fossae, and a robust, short and deep squamosal process of the postorbital. Previous studies (Rayfield 2011; Sereno 2017) suggested that similar modifications in the temporal region of different theropod groups were actually influenced by biomechanical constraints related to an evolutionary increase in body size and bite force, which is congruent with the skull of *Spectrovenator* n. gen. being approximately half the length of more derived abelisaurids (Foth & Rauhut 2013; Grillo & Delcourt 2017).

The mandible of *Spectrovenator* n. gen. also differs significantly from that of derived abelisaurids (Figs 4, 5). The mandibular fenestra is anteroposteriorly elongated, as in derived abelisaurids, but shows a reduced dorsoventral depth due to the retention of a high lateral lamina of the angular. Furthermore, *Spectrovenator* n. gen. has an extensive overlapping contact between the posteroventral process of the dentary and the anterior branch of the angular along the anteroventral margin of the external mandibular fenestra (Fig. 4A, B). Although crushed and somewhat distorted, the region of dorsal contact between the dentary and the surangular lacks the typical peg and socket condition present in derived abelisaurids (Fig. 5A, B). Previous authors underscored the presence of this joint as indicative of an unusual kinetic intramandibular joint in derived abelisaurids (Mazzetta *et al.* 1998; Canale *et al.* 2009). The absence of this feature in *Spectrovenator* n. gen. suggests that early abelisaurids may have retained a more generalized feeding strategy comparable to that of other theropods.

Both the temporal and mandibular regions of *Spectrovenator* n. gen. differ structurally and possibly functionally from that of more derived abelisaurids, which have been characterized as having a specialized feeding strategy that diverge from other theropods (Therrien *et al.* 2005; Canale *et al.* 2009). The Early Cretaceous age of *Spectrovenator* n. gen. (Barremian-Aptian) also indicates that the highly modified feeding strategy hypothesized for the group is restricted to derived abelisaurids and must have arisen during the Late Cretaceous, after the Cenomanian (100–93 My), and possibly influenced by an increase in body size in the late evolution of the group.

NOTE ADDED IN PROOF

Since this paper went to press, two other complete South American abelisaurid skulls have been redescribed: *Skorpiovenator bustingorryi* from the Upper Cretaceous (Cenomanian) Huincul Formation of Neuquén Province, northern Patagonia (Cerroni *et al.* 2020a), and *Carnotaurus sastrei* from the Upper Cretaceous (Campanian-Maastrichtian) La Colonia Formation of Chubut Province, central Patagonia, Argentina (Cerroni *et al.* 2020b). In these contributions, the authors identified two distinct morphologies in abelisaurid nasal bones: a) a strongly transversely convex nasal with heavily sculptured surfaces (*Carnotaurus*); and b) a transversely concave nasal with marked bilateral crests and poorly sculptured surfaces (*Rugops*, *Skorpiovenator*). In addition, the distinctive row of large foramina on the skull roof displayed by some abelisaurids (e.g., *Rugops*) was also described in detail for *Skorpiovenator* and *Carnotaurus*. Like *Rugops* and *Skorpiovenator*,

Spectrovenator ragei n. gen., n. sp. displays a transversely concave nasal and a similar row of large foramina on its skull roof. In all three taxa, the foramina are well-marked in dorsal view, due to their reduced nasal sculpturing, contrasting with the complex rugosity pattern observed in *Carnotaurus*. The reason for the occurrence of these foramina was previously associated with the presence of an integumentary coverage, such as scales or other cornified structures (Delcourt 2018). However, Cerroni *et al.* (2020a, b) hypothesized that the symmetry and disposition of the foramina in *Rugops*, *Skorpiovenator*, *Carnotaurus*, and now in *Spectrovenator* n. gen., may indicate a neurovascular path (i.e., blood vessels and nerves), probably related to the passage of the lateral nasal and supraorbital vessels and the trigeminal nerve.

Acknowledgements

We thank W. Arcoverde and E. Nico (Departamento Nacional de Produção Mineral – DNPM) for providing authorizations for excavation and transportation of the specimens, I. Ferreira for allowing access to the site, U. A. Macedo, M. V. Nobre, L. Lobo, M. G. Soler, M. A. Obeid, N. Brilhante, M. Padilha, B. Augusta, N. Mezzacappa, W. Pinto for support in the field, R. Rodrigues for specimen preparation, and F. A. Elias and S. Lages for help with illustrations. We also thank F. Agnolin and T. Tortosa for their help in improving a previous version of the manuscript. The phylogenetic analysis was performed with TNT v.1.5, a program made freely available through the Willi Hennig Society. BAN was supported by a fellowship from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq grant # 130.280/2018-6). This research was supported by grants from the Fundação de Amparo à Pesquisa do Estado de São Paulo (BIOTA/FAPESP grants # 02/13602-4 and 11/50206-9) to HZ. DP benefitted from a Visiting Researcher grant from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP grant # 2014/02805-9). HZ was supported by a Researcher grant from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq grant # 301298/94-7).

Author's contributions

HZ and DP conceived and designed the experiments. HZ, DP, ABC, RD, and BAN analyzed the data. HZ and ABC curated the fossil. ABC supervised fossil preparation, scanned and digitally segmented the specimen. HZ, DP, ABC, RD, and BAN contributed with reagents/materials/analysis tools. ABC and BAN photographed the fossil and prepared the figures. All authors discussed the results and provided input on the manuscript.

Supplementary material

Supplementary material associated with this article can be found in the Appendix 1, and includes micro-CT scan figures and reconstruction of the skull of *Spectrovenator ragei* n. gen., n. sp., annotated character list, data matrix in TNT format, strict and reduced consensus trees, support analyses, list of synapomorphies, and selected measurements from the skull of *Spectrovenator ragei* n. gen., n. sp.

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*Submitted on 27 March 2019;
accepted on 18 October 2019;
published on 12 October 2020.*

APPENDIX — Supplementary material.

APPENDIX 1. — An additional file is available at the address <http://sciencepress.mnhn.fr/sites/default/files/documents/fr/comptes-rendus-palevol2020v19a6-additional-material.pdf>. It contains the following supplementary material (page numbers correspond to the pages of this additional document):

1. Supplementary figures	S3
2. Phylogenetic analysis	S6
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