A new rebbachisaurid sauropod from the Aptian–Albian, Lower Cretaceous Rayoso Formation, Neuquén, Argentina

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Rebbachisaurids are a group of basal diplodocimorph sauropods that diversified in Gondwana at the end of the Early Cretaceous and the beginning of the Late Cretaceous. It is a group of great palaeobiogeographical interest, for it clearly illustrates various processes of dispersal throughout Gondwana and to Laurasia prior to the breakup of Africa and South America. However, the relationships within the group are still under discussion owing to the scarcity of cranial material that would help clarify them. In the present paper we describe the new rebbachisaurid *Lavocatisaurus agrioensis* gen. et sp. nov. from the Aptian–Albian (Lower Cretaceous) of Neuquén (Argentina). Remains have been recovered belonging to an adult specimen (holotype) and two immature specimens (paratypes). Taken together, almost all the bones of the taxon are represented, including most of the cranium. *Lavocatisaurus agrioensis* gen. et sp. nov. is the first rebbachisaurid from Argentina with an almost complete cranium, making it possible to recognize differences with respect to other rebbachisaurids, such as the highly derived *Nigersaurus*. Among its most notable characters are the presences of a large preantorbital fenestra and maxillary teeth that are significantly larger than those of the dentary. Our phylogenetic study places *Lavocatisaurus* amongst basal rebbachisaurids, as the sister lineage to Khebbashia (the clade formed by Limaysaurinae + Rebbachisaurinae). This position, which is somewhat more derived than that previously suggested for *Comahuesaurus* and *Zapalasaurus* (the Argentinean rebbachisaurids closest in geographical and geological terms), reaffirms the presence of different basal rebbachisaurid lineages in the Early Cretaceous of Patagonia.

Key words: Dinosauria, Rebbachisauridae, phylogeny, Cretaceous, Rayoso Formation, Argentina.

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Introduction

Rebbachisaurids are a group of diplodocimorph sauropods that are thought to have diversified around the middle of the Early Cretaceous (Salgado et al. 2006; Sereno et al. 2007; Carballido et al. 2012; Fanti et al. 2013; Wilson and Allain 2015). They are the last diplodocimorphs to go extinct and the only ones to reach the Upper Cretaceous of Gondwana (Ibiricu et al. 2013; Wilson and Allain 2015). Phylogenetic studies place their appearance in the Middle Jurassic as the sister group to the diplodocids and dicraeosaurids (Wilson

and Allain 2015; Tschopp et al. 2015), yet they are maintained as a ghost lineage through the Jurassic and part of the Lower Cretaceous, since rebbachisaurids are unrecorded in this period. The oldest rebbachisaurid is *Histriasaurus*, described from fragmentary remains from the upper Hauterivian–lower Barremian of Croatia (Dalla Vechia 1998). The most modern rebbachisaurids are several taxa recovered from the Cenomanian–Turonian of Argentina (Calvo and Salgado 1995; Garrido 2010; Haluza et al. 2012; Ibiricu et al. 2012).

The identification of the rebbachisaurid lineage is relatively recent. Bonaparte (1997) first proposed its differentiation from other sauropods on the basis of fragmentary

postcranial material from the Upper Cretaceous of Neuquén (Patagonia, Argentina), currently identified as *Rayososaurus agrioensis* (Carballido et al. 2010). Bonaparte (1997) noted the singular morphology of the scapula of *R. agrioensis*, which was similar to that of *Rebbachisaurus garasbae*, from the Cenomanian of Morocco (Lavocat 1954; Wilson and Allain 2015). *Rebbachisaurus* was described on the basis of a scapula and a dorsal vertebra (Lavocat 1954); moreover, there are some bones stored in the Museum National d'Histoire Naturelle of Paris (France) that were not part of the original description (Wilson and Allain 2015). One of the consequences of the presence of rebbachisaurids in Africa and South America is their special palaeobiogeographical interest for the Early–Late Cretaceous transition. This was pointed out initially by Calvo and Salgado (1995) and subsequently used to identify dispersal and vicariance events of terrestrial tetrapods between different parts of Gondwana and between Gondwana and Laurasia (Canudo et al. 2009; Mannion 2009; Torcida-Baldor et al. 2011; Carballido et al. 2012; Fanti et al. 2015).

Recent years have seen major advances in what is known of the anatomy and palaeogeographical distribution of the rebbachisaurids, both in South America (Carvalho et al. 2003; Gallina and Apesteguía 2005; Carballido et al. 2012; Ibiricu et al. 2013) and Africa (Sereno et al. 1999; Fanti et al. 2013), as well as their unexpected presence in Europe (Pereda Suberbiola et al. 2003; Mannion 2009; Torcida-Baldor et al. 2011). These discoveries have allowed the rebbachisaurids to be placed beyond question at the base of the radiation of the diplodocimorph diplodocoids, and in all the phylogenies they are grouped in a clade that is clearly differentiated from the rest of the diplodocimorphs (e.g., Calvo and Salgado 1995; Wilson and Allain 2015; Tschopp et al. 2015). Recently, a consensus has been reached on the existence of two main lineages of rebbachisaurids (Limaysaurinae and Rebbachisaurinae), currently grouped in Khebbashia. Most species are described using only fragmentary material and, except for *Nigersaurus*, with little cranial material. This has resulted in a degree of instability in certain taxa, as well as major gaps in what is known about the early evolutionary stages of the group, in particular with respect to its cranial morphology.

In 2009, the Spanish-Argentinean research group that has authored the present paper began to look for the exact site where the bones of the rebbachisaurid *Rayososaurus agrioensis* had been recovered, our aim being to reopen the excavation in search of more elements from the holotype. In the course of our revision of the Rayoso Formation in the area where *R. agrioensis* had been collected, we found the remains of another rebbachisaurid, which was excavated between 2010 and 2011. These remains correspond to a partially articulated adult specimen and two juvenile individuals, ascribed provisionally to cf. *Zapalasaurus* (Salgado et al. 2012). These fieldwork campaigns resulted in the recovery of elements that afford a good idea of the anatomy of this new dinosaur, including cranial remains. Over the last few years, the material has been prepared by mechanical means

in the Olsacher Museum (MOZ) and the Trelew Museum (MEF). The aim of the present article is to provide a brief description of this rebbachisaurid, which represents the first dinosaur from the Rayoso Formation, and to discuss its systematics and its phylogenetic importance.

Institutional abbreviations.—MEF, Museo paleontológico Egidio Feruglio, Trelew, Chubut, Argentina; MNN GDF, Musée National Boubou Hama, Niamey, Niger; MOZ, Museo Provincial de Ciencias Naturales "Dr. Prof. Juan A. Olsacher", Zapala, Argentina.

Other abbreviations.—ITR, isolated tooth rows; MDR, more derived rebbachisaurids.

Geographical and geological setting

The rebbachisaurid bones studied in this paper were recovered near the locality of Agrio del Medio, a small town in the central part of the province of Neuquén (Patagonia, Argentina; Fig. 1). In geological terms, Salgado et al. (2012) situated the fossils in the Rayoso Formation, one of the Lower Cretaceous units that outcrop in the Neuquén Basin (Leanza 2003). The four members of this formation can be clearly identified in the area around Agrio del Medio; from the oldest to youngest these are the Rincón, Quili Malal, Pichi Neuquén, and Cañadón de la Zorra members. Two narrow-gauge sauropod trackways attributed to rebbachisaurids have been found in two distinct outcrops of the Rincón Member (Canudo et al. 2017; Fig. 1). The rebbachisaurid bones studied in this paper were found in the middle part of the Pichi Neuquén Member, approximately 44 metres from its base (Fig. 1). Lithologically, this member is made up of a stratified sequence of detritic levels of quartz-bearing sandstone and reddish clay deposited in coastal environments (Leanza 2003). There is no consensus regarding the age of this member, for no direct datings have been taken. Some authors place it in the Aptian (Musacchio and Vallati 2000), whereas Leanza (2003) considers it to be rather more modern (lower Albian). In this paper, we ascribe an age range from Aptian to lower Albian to the new rebbachisaurid.

The fossils of the new sauropod were found in a thin stratum of sandstone of reddish-brown colour. This sandstone displayed slight lamination, with levels of current ripples and mudcracks. However, the fossil bones did not coincide with a surface of current ripples. Furthermore, the sandstone was slightly bioturbated, with full-relief burrows both vertical (*Skolithos*-type) and random in distribution and unbranching (*Planolites*-type). The geometry of the sandstone and the structures they present suggest that it was deposited in non-confined deposits formed by decantation in areas with high sedimentation and low energy (Salgado et al. 2012).

The nomenclature for the vertebral laminae follows Wilson (1999), with modifications (accessory posterior centrodia-
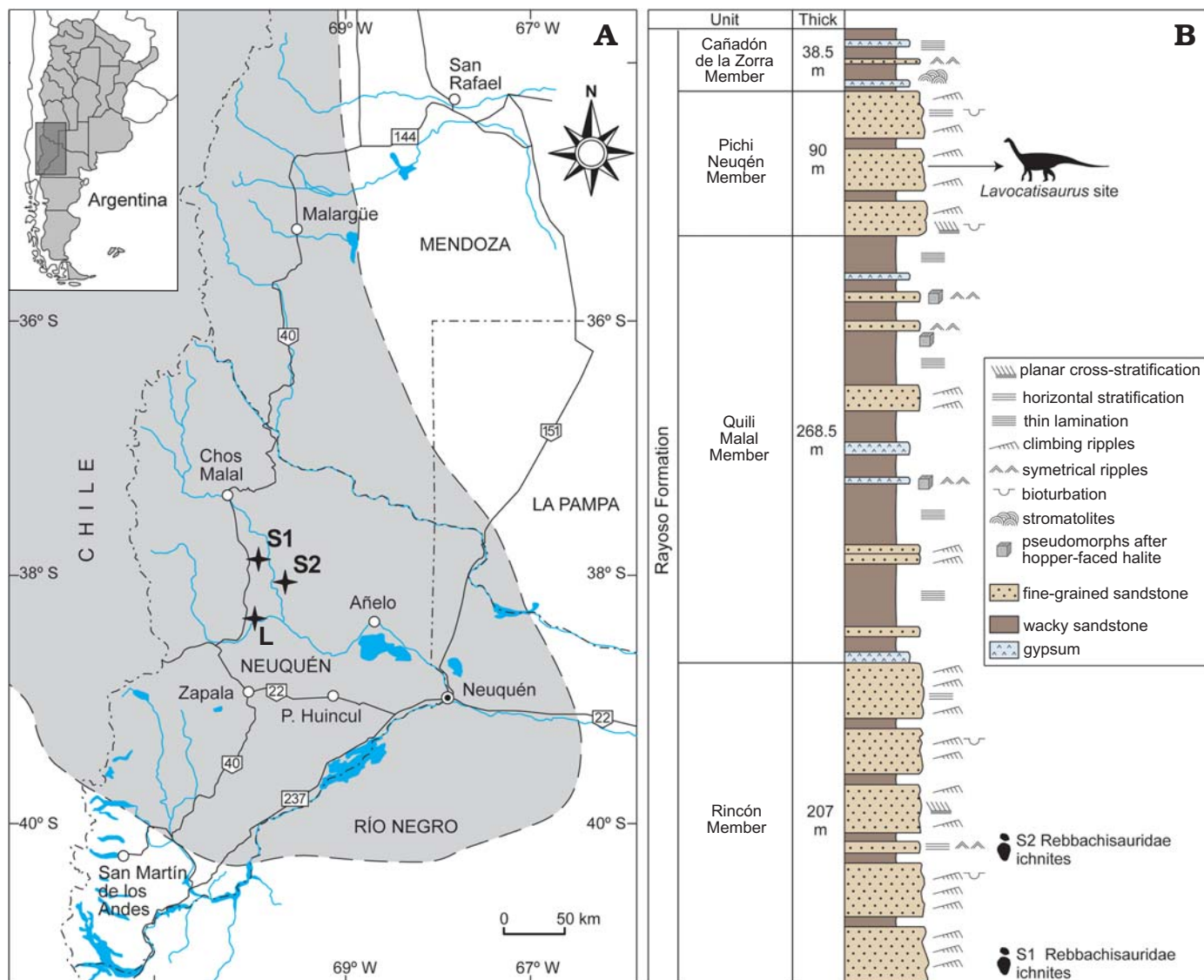
Fig. 1. **A**. Map of location and geological outcrops of the region of Agrio del Medio (Neuquén, Argentina), where the material was collected; gray area represents the Neuquén Basin. **B**. Lithostratigraphic column of the Rayoso Formation in the study area. L, *Lavocatisaurus* site; S1 and S2, sites of the Rebbachisauridae ichnites (Canudo et al. 2017). {Fig will be grayscale in printed version}

pophyseal lamina) from Salgado et al. (2005) and Wilson et al. (2011). The nomenclature for the vertebral pneumatic structures follows Wedel (2003) and Wilson et al. (2011).

Systematic palaeontology

Saurischia Seeley, 1887

Sauropoda Marsh, 1878

Diplodocoidea Marsh, 1878 sensu Upchurch, 1995

Diplodocimorpha Calvo and Salgado, 1995

Rebbachisauridae Bonaparte, 1997

Genus *Lavocatisaurus* nov.

Type species: *Lavocatisaurus agrioensis* sp. nov., see below.
Etymology: In honour of the French researcher René Lavocat (1909–

2007), who described *Rebbachisaurus*, the first known representative of Rebbachisauridae.

Diagnosis.—As for the type and only known species.

Lavocatisaurus agrioensis sp. nov.

Figs. 2, 3.

Etymology: In reference to the locality of Agrio del Medio, from which the new species was found.

Type material: Holotype: MOZ-Pv1232, partially articulated specimen: dentaries, left surangular, premaxillae and maxillae, left jugal, right squamosal, quadrates, 23 isolated teeth and two series of 8 and 9 maxillary teeth, hyoid bone, 11 cervical vertebrae (including atlas and axis), 28 caudal vertebrae, cervical ribs, 2 dorsal ribs, humerus, fragment of ?radius. Paratypes, all from type locality: the juvenile specimens (Salgado et al. 2012): MOZ-Pv 1248, posterior cervical centrum; MOZ-Pv 1249, cervical neural arch; MOZ-Pv 1251, dorsal neural arch; MOZ-Pv 1252, 1253, 1254, anterior caudal centra; MOZ-Pv 1255,
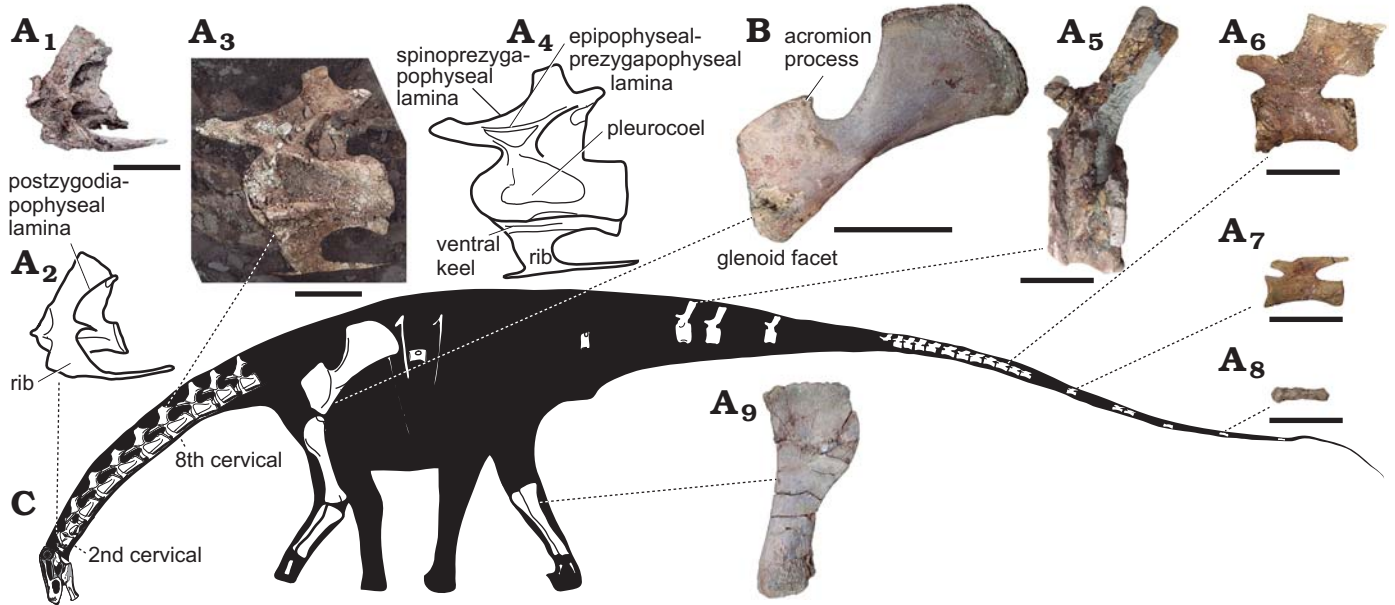
Fig. 2. Rebbachisaurid sauropod *Lavocatisaurus agrioensis* gen. et sp. nov. from Agrio del Medio (Argentina), Aptian–lower Albian. **A**. MOZ-Pv1232, axis in lateral view (A_1, photograph; A_2, drawing); eight cervical vertebrae in lateral view view (A_3, photograph; A_4, drawing,); anterior caudal vertebra in lateral view (A_5); middle caudal vertebra in lateral view (A_6); posterior caudal vertebra in lateral view (A_7); posteriormost caudal vertebra in lateral view (A_8); left tibia in lateral view (A_9). **B**. MOZ-Pv 1255, left scapula from a juvenile specimen, in lateral view. **C**. Skeletal reconstruction based on the holotype and paratype specimens. Scale bars 10 cm.{Fig will be grayscale in printed version}

scapula; MOZ-Pv 1267, left radius; MOZ-Pv 1256, left ulna; MOZ-Pv 1257, right metatarsal I; MOZ-Pv 1258, ?metatarsal V. An association of MOZ-Pv 1233, 1250, cervical centra; MOZ-Pv 1236, 1237, incomplete cervical neural arches; MOZ-Pv 1238, 1239, fragmentary neural arches; MOZ-Pv 1240, dorsal centrum; MOZ-Pv 1241, rib fragments; MOZ-Pv 1242, haemal arch; MOZ-Pv 1243, right ulna; MOZ-Pv 1244, left tibia; MOZ-Pv 1245, left fibula; MOZ-Pv 1246, end of metatarsal; MOZ-Pv 1247, indeterminate flat fragment.

Type locality: Agrio del Medio site, Neuquén Province, Argentina.

Type horizon: Aptian–lower Albian, Lower Cretaceous.

Diagnosis.—A middle-sized rebbachisaurid sauropod diagnosed by the following combination of characters (unique characters are marked with an *): extremely well-developed preorbital fenestra (shared with *Nigersaurus*); marked laterodorsal fossa in the dentary (shared with *Demandasaurus* and *Nigersaurus*); ventrally expanded squamosal (shared with *Limaysaurus*); dentary with pronounced ventral projection in the mesio-ventral corner; jugal long and contacting the squamosal (shared with *Nigersaurus*) but without foramina as present in *Nigersaurus*; *maxillary teeth significantly larger than the mandibular teeth; middle caudal vertebrae with anteriorly (nearly horizontally) projecting prezygapophysis

Remarks.—*Lavocatisaurus agrioensis* gen. et sp. nov. is represented by almost all the anatomical elements, with the exception of the neural arches of the dorsal vertebrae (there is only one dorsal centrum, corresponding to one of the paratypes). Salgado et al. (2012) described in detail the bones of the juvenile specimens such as the radius, fibula, ulna, metacarpals, etc.; that description will not be repeated in the present work. Rather, we shall briefly describe the bones of the holotype, and any bones of the paratypes not

described in the work cited above. Most of the adult material here presented is still under preparation, therefore a detailed description of it is out of the scope of the present work and will be presented once all the materials have been prepared. At the moment, and given the low number of elements in common between the juvenile specimens and the adult specimen, we couldn't find any reliable ontogenetic difference.

Rebbachisaurids skull anatomy is mainly based on the reconstructions of *Nigersaurus*, the single taxon of this clade that preserved enough bones for allowing such reconstruction (Sereno et al. 2007). The new taxon here described allowed us to present an almost complete skull reconstruction, which was through comparisons with *Nigersaurus* (Sereno et al. 2007) and diplodocids (e.g., *Diplodocus*; Whitlock et al. 2010). As reconstructed (Fig. 3), the cranium of *Lavocatisaurus* was elongated, as in diplodocids. Indeed, the general shape of the skull resembles that of *Diplodocus* more than that of *Nigersaurus* (although sharing some new characters with the latter). The premaxilla is elongated, with space for 4 teeth, as in other sauropods. The maxilla is anteroposteriorly elongated, with a long ascending process, and pierced by a very large oval preorbital fenestra (Fig. 3A, B). A completely opened preorbital fenestra is present in derived titanosaurs such as *Tapuiasaurus* and diplodocids such as *Diplodocus* (Marsh 1884; Zaher et al. 2011). A similar opening was initially labelled in *Nigersaurus* as the antorbital fenestra (Sereno et al. 1999: fig. 2D). Based on our personal observation on the skull elements of *Nigersaurus* we reinterpret this opening as the preorbital fenestra, which is not reconstructed in following reconstructions published for this taxon (Sereno and Wilson 2006; Sereno et al. 2007).
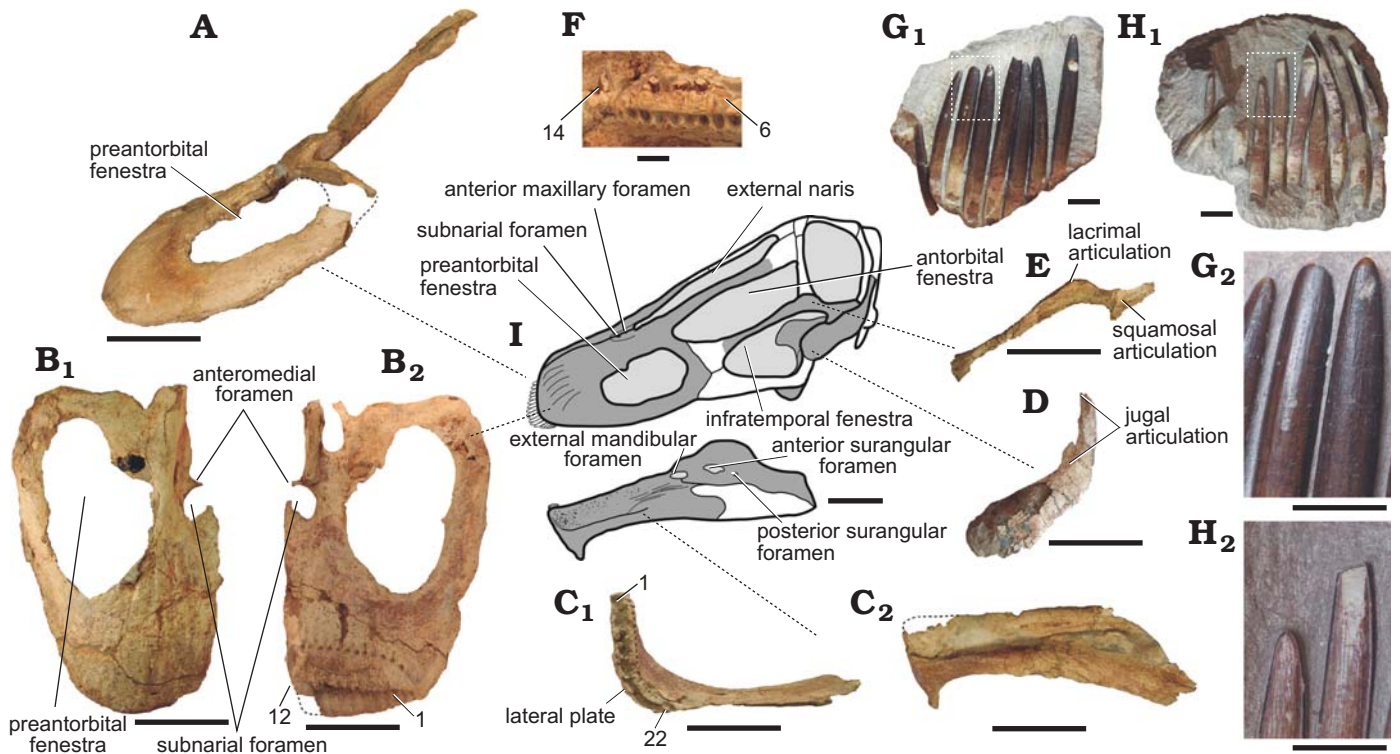
Fig. 3. Rebbachisaurid sauropod *Lavocatisaurus agrioensis* gen. et sp. nov. from Agrio del Medio (Argentina), Aptian–lower Albian. **A**. Left maxilla in lateral view. **B**. Right maxilla in anterodorsal (B_1) and posteroventral (B_2) views, numbers indicate the tooth positions. **C**. Left dentary in dorsal (C_1) and lateral (C_2) views, numbers indicate the tooth positions. **D**. Right squamosal (inverted) in lateral view. **E**. Right jugal (inverted) in lateral view. **F**. Dentary teeth, numbers indicate the tooth positions. **G**. Eight associated teeth in labial view (G_1), close up of two teeth in labial view (G_2), showing the absence of wear facets. **H**. Nine associated teeth in lingual view (H_1), close up of the teeth in labial view (H_2), showing the wear facets. **I**. Skeletal reconstruction, based on the holotype MOZ-Pv1232. Scale bars: A–E, 10 cm; F–H, 1 cm. {Fig will be grayscale in printed version}

There are only 12 dental positions in the preserved maxillae, differing from the 25 dental positions of *Nigersaurus* (Sereno et al. 2007) but having a similar number of maxillary teeth presents in diplodocids (Whitlock et al. 2010; Tschopp and Mateus 2017). The maxillary teeth are large, decreasing in size laterally, as evidenced by the shape of the lateral plate of the maxillae (Fig. 3B_2) and the two series of isolated functional teeth (see below). The nutritional foramina of the premaxilla and maxilla are small and circular as in most sauropods and differing from the extremely elongated nutritional foramina of *Nigersaurus* (Sereno et al. 1999: fig. 2D). The jugal is elongated and fragile bone, lacking the foramina present in *Nigersaurus*. A novel articulation of the jugal with the squamosal excludes the postorbital from the infratemporal fenestra, resulting in an uncommon morphology not described for other sauropods. Nevertheless, a similar articulation and the resulting exclusion of the postorbital from the infratemporal fenestra can be detected in *Limaysaurus* (Calvo and Salgado 1995: fig. 4) and *Nigersaurus* (Sereno et al. 2007: fig. 1), indicating that this is a relatively widespread morphology amongst rebbachisaurids. The squamosal is ventrally expanded as in *Limaysaurus*, although in the latter the broad ventral expansion of the squamosal was interpreted as the quadratojugal by Calvo and Salgado (1995: fig. 4). The mandible has the typical rectangular outline, as in other diplodocids and derived titanosaurs, and presents

22 dental positions. The elevated number of dentary teeth in *L. agrioensis* gen. et sp. nov. is an uncommon character amongst Neosauropoda, differing from the 9 tooth positions of *Demandasaurus* (Torcida Fernández-Baldor et al. 2011) but also from the 34 dentary teeth of *Nigersaurus* (Sereno et al. 2007). Although no functional teeth are preserved in any of the dentaries, several replacement teeth are observed, which seem to correspond to the first line of replacement teeth. These are much smaller and more fragile than those of the maxillae, an unusual discrepancy in size interpreted as an autapomorphy of the new taxon. A laterodorsal fossa is present in the dentary, as is a pronounced ventral projection in the mesio-ventral corner. The presence of an anteroventrally directed triangular process is a widespread morphology amongst Diplodocimorpha, with a reversion in more derived rebbachisaurids (*Demandasaurus* and *Nigersaurus*). Teeth are located exclusively in the anteriormost part of the maxilla and the mandibles (Fig. 3). The teeth are elongated, with an slenderness index (sensu Upchurch 1998) of around 7–8, fine and pencil-like, as in all other diplodocimorphs known up to date (e.g., *Nigersaurus*, *Diplodocus*, *Galeamopus*; Sereno et al. 2007; Whitlock et al. 2010; Tschoopp and Mateus 2017). The compression index (sensu Díez Díaz et al. 2013) cannot be evaluated at the moment as most of the teeth are still embedded in the matrix (Fig. 3G_1, H_1). The enamel is asymmetrical, being around 5 times thicker on the labial

surface than on the lingual one. Three series of functional teeth were recovered in what seems to be their natural position. One is composed by 9 teeth from the left maxilla (Fig. 3G$_1$), the second has 10 teeth from the right maxilla (Fig. 3H$_1$), and the third is composed by 4 teeth from the premaxilla. Given their size and in comparison with the alveoli of the upper and lower jaws and preserved dentary teeth, they are interpreted as upper teeth. As noted by Wiersma and Sander (2016), isolated tooth rows (ITRs) are not uncommon and have been reported for other sauropods such as *Shunosaurus*, *Apatosaurus*, *Europasaurus*, *Giraffatitan*, and *Phuwiangosaurus* (see Wiersma and Sander 2016, and references therein). As mentioned above, the dentary teeth are much smaller than the maxillary teeth and lack wear facets (at least those preserved), whereas the maxillary teeth have a single, low-angle lingual wear facet (Fig. 3H$_1$).

The spongy tissue of the bone is normal in all the bones of the skeleton. The cervical vertebrae are still embedded in the plaster with the right lateral side exposed. The cervical vertebrae are opisthocoelous and short (Fig. 2). The eighth cervical is the longest (26 cm), and otherwise the fourth to the tenth vary between 20–22 cm in length. The cervical centra have pleurocoels, which are apparently undivided as in *Nigersaurus*, and are teardrop-shaped, with the more excavated side in the anterior part. From the third cervical vertebra on, there is a keel in the ventral part of the centrum. The neural spine of the axis is anteriorly elongated and V-shaped as in *Demandasaurus*. The neural spine of the rest of the cervical vertebrae is simple and slightly displaced anteriorly. The cervical neural spines of *Lavocatisaurus* are relatively higher than in *Nigersaurus* and *Demandasaurus* (Sereno et al. 2007; Torcida Fernández-Baldor et al. 2011). The parapophysis is situated outside the centrum. The cervical vertebrae possess a well-developed system of laminae, as is characteristic of Eusauropoda (Wilson 2002). These include the anterior centrodiapophyseal, posterior centrodiapophyseal, spinoprezygapophyseal, spinopostzygapophyseal, prezygodiapophyseal and postzygodiapophyseal laminae (Fig. 2). The epipophyseal-prezygapophyseal lamina is well marked, although none of the cervical present a well-developed epipophysis, resembling the cervical vertebrae of other rebbachisaurids (e.g., *Zapalsaurus*, *Limaysaurus*; Salgado et al. 2006: fig. 4; Calvo and Salgado 1995: fig. 8B) and differing from *Nigersaurus* (Sereno et al. 2007: fig. 3B). In the axis, the centropostzygapophyseal laminae are united halfway along by a horizontal lamina, as in the third cervical of *Zapalasaurus*. The third cervical has postzygodiapophyseal and epipophyseal-prezygapophyseal laminae, as in *Zapalasaurus* (Salgado et al. 2006). In all the cervical vertebrae, the prezygapophyseal fossa is located between the prezygodiapophyseal and the centroprezygapophyseal laminae. The third cervical of *Lavocatisaurus* is similar in size to that of *Zapalasaurus*, but its laminae are more delicate, being in this character more similar to *Nigersaurus* than to *Limaysaurus*. The cervical rib has a well-marked anterior projection. The third and fourth cervical preserved their cervical ribs, which are as long as the centrum (Fig. 2), as in other diplodocoids (Wilson and Sereno 1998).

The centra of the caudal vertebrae are generally amphicoelous, although there are variations within the series. The anteriormost preserved vertebrae have centra with plano-convex anterior faces. The posterior face in these vertebrae is more concave than the anterior face. Both articular faces of the middle and posterior caudal vertebrae are concave. The distal caudal vertebrae have centra with convex articular faces. The caudal centra lack pleurocoels, with the exception of the most anterior one preserved, which has a small one. The anterior caudal vertebral centra have a ventral surface that is transversely concave, whereas in the middle caudal centra it is flat.

The neural spine in the caudal vertebrae is well developed, expanded anteroposteriorly, and slightly projecting posteriorly throughout the series. In the anterior ones, it is located in the middle part of the centrum, whereas in the middle and posterior ones it is located in the anterior part of the centrum as in other rebbachisaurids (e.g., *Limaysaurus*) but not as anteriorly as is in titanosaurs (Salgado et al. 1997; Wilson and Sereno 1998). The neural spine is rectangular in lateral view (Fig. 2). The posteriormost part of the neural spine in the middle caudal vertebrae is in the same plane as the posterior articular face. The transverse processes are dorsally directed in the anteriormost caudal vertebrae, becoming perpendicular to the centrum in the more posterior of the anterior caudals. The pedicles are low beneath the prezygapophyses. In the middle caudal vertebrae, the prezygapophyses are oriented nearly horizontally, projecting anteriorly in such a way that they protrude beyond the anterior articular face of the vertebra. The prespinal lamina is present in the anterior caudal vertebrae, which lack a hyposphene ridge and a triangular process. The distal vertebral centra are distinctively elongated.

The scapula is racket-shaped (Fig. 2). The scapular blade is perpendicular with respect to the orientation of the coracoid and shows a distal expansion. The scapular acromion is broad and well developed, and the dorsal face has a V-shaped concavity. The highest point of the dorsal margin of the scapular blade is higher than the dorsal margin of the proximal end. The ventral edge of the scapula does not show any sign of the ventral process observed in some diplodocids and titanosauriforms (Tschopp et al. 2015; Mannion et al. 2017). The cross section of the scapular blade at its base is D-shaped.

The humerus is crushed and badly preserved, but some anatomical traits can be observed. Compared to other sauropods, the humerus of *Lavocatisaurus* is relatively gracile (medium sensu Wilson and Upchurch 2003). The lateral margin of the proximal half of the bone is almost straight. Its proximolateral corner is pronounced, with the dorsal surface almost flat. The midshaft cross-section is elliptical. The deltopectoral attachment is relatively narrow and has a low crest throughout its length. The articular surface of the condyles is restricted to the distal portion of the humerus.

Remarks.—The scapula of *Lavocatisaurus agrioensis* gen. et sp. nov. shows the typical racket shape, which is one of the

diagnostic characters of Rebbachisauridae (Bonaparte 1997; Carballido et al. 2010; Wilson and Allain 2015). The bones of the new species are comparable to most of the rebbachisaurid specimens from Neuquén Basin. Among the taxa that are closest in geographical terms, it is notable that the scapula is reasonably similar to that of *Rayososaurus* (Bonaparte 1997; Carballido et al. 2010), although it is distinguished by the development and orientation of the acromial process.

The deltopectoral crest of the humerus of *Lavocatisaurus* differs from *Comahuesaurus* in its position and lesser development. Particularly, the humeral articular head of the new species is more developed than in *Comahuesaurus* (Carballido et al. 2012).

Lavocatisaurus preserves the third cervical, as does *Zapalasaurus*. They are similar in size, but the one from *Zapalasaurus* is significantly more robust. The middle and posterior caudal vertebrae of *Zapalasaurus* have a neural spine that is anteroposteriorly elongated as in *Lavocatisaurus*. Nevertheless, the dorso-anterior corner of the neural spines of *Zapalasaurus* is located on a higher level than the posterior end, unlike in *Lavocatisaurus*, where the two corners are on the same level. The inclination of the prezygapophysis in the caudals of the new species is different from that of *Zapalasaurus* and is more similar to the more derived rebbachisaurids.

The holotype presented the cervical vertebrae and the first twenty vertebrae of the caudal series, articulated and arched, all of these together with the rest of the material scattered over an area of some 8 m² (map of site in Salgado et al. 2012). The paratypic material was differentiated on the basis of its size, as well as by the fact that the neural arch of the only dorsal vertebra preserved was unfused, unlike in the adult specimen. The state of preservation of the bones is good, without signs of abrasion or breakages prior to burial; nor do they show signs of scavenging. Accordingly, the presence of a disarticulated cranium, articulated vertebral series, the low dispersion of the bones, and a low-energy sedimentary environment suggest that the preserved specimens were conserved in an autochthonous mode of concentration (Salgado et al. 2012).

Stratigraphic and geographic range.—Type locality and horizon only.

Phylogenetic analysis

The phylogenetic position of *Lavocatisaurus agrioensis* gen. et sp. nov. was examined through a cladistic analysis including the new taxon in a modified version of the data matrix recently used by Carballido et al. (2017). In addition to *Lavocatisaurus*, two recently described rebbachisaurids were included in the data matrix, *Katepensaurus* (Ibiricu et al. 2013, 2015) and *Tataouinea*, thus including all valid rebbachisaurid genera described to date, except for the fragmentary taxa *Nopcsaspondylus* (Apesteguía 2007) and

Xenoposeidon (Taylor 2018). The resulting data matrix of 413 characters and 90 taxa was constructed using Mesquite V. 2.74 (Maddison and Maddison 2011) and exported into TNT format (see Supplementary Online Material available at http://app.pan.pl/SOM/app63-Canudo_etal_SOM.pdf). An equally weighted parsimony analysis was carried out using TNT v.1.5 (Goloboff and Catalano 2016). A heuristic tree search was performed starting from 1000 replicates of Wagner trees followed by TBR branch swapping and saving 10 trees per replicate. Under this procedure, we retrieved 180 most parsimonious trees (MPTs) found in 18 of the replicates and with a tree length of 1365 steps. The resulting trees were subjected to an additional round of branch swapping (TBR), obtaining 75 000 trees and collapsing the possible trees in memory. The resulting complete strict consensus tree recovered the rebbachisaurid lineage as completely collapsed (Fig. 4A; SOM), due to the multiple positions that *Rayososaurus* could take inside this clade (Fig. 4B). The same analysis was repeated excluding *Rayososaurus* and *Lusotitan* (which caused a large polytomy at the base of titanosauriforms) from the analysis, obtaining 9900 MPTs of 1363 steps. The strict consensus tree recovered is identical to the reduced consensus tree obtained once *Rayososaurus* is pruned from the analysis. The general topology recovered is fairly similar to that obtained in previous analyses (Carballido et al. 2012; Wilson and Allain 2015; Fanti et al. 2015). *Lavocatisaurus* was recovered as a relatively basal rebbachisaurid, being the sister lineage to Khebbashia (Figs. 4B, C, 5). Below we provide a short discussion of the principal nodes obtained in the analysis and the characters supporting them.

Rebbachisauridae.—As in most previous analyses, *Amazonsaurus* was recovered at the base of Rebbachisauridae (e.g., Mannion et al. 2012; Carballido et al. 2012; Torcida-Baldor et al. 2011), a position slightly different from that suggested by some previous works (e.g., Carvalho et al. 2003; Salgado et al. 2006; Carballido et al. 2010). Rebbachisauridae are here supported by the same three synapomorphies recently obtained by Wilson and Allain (2015): character 241, absence of the hyposphenal ridge on anterior caudal vertebrae (reversed in *Demandasaurus* and *Tataouinea*); character 244, presence of spinodiapophyseal lamina (convergently present in Lognkosauria; Carballido et al. 2017); character 250, middle caudal vertebrae with a flat ventral surface; and character 413, middle caudal vertebrae with anterodorsally oriented prezygapophyses (reverted in *Lavocatisaurus* and more derived rebbachisaurids (MDR).

***Histriasaurus–Zapalasaurus–*MDR**.—*Histriasaurus*, *Zapalasaurus*, and MDR were recovered with unresolved relationships at the base of the rebbachisaurids more derived than *Amazonsaurus*. This polytomy was caused by the three different positions that *Zapalasaurus* can take (Fig. 4C): as the sister taxon to *Histriasaurus* and MDR, as the sister taxon to *Histriasaurus*, or as a more derived rebbachisaurid (with *Histriasaurus* as the sister taxon of *Zapalasaurus* and MDR). A similarly unresolved relationship for these two taxa has
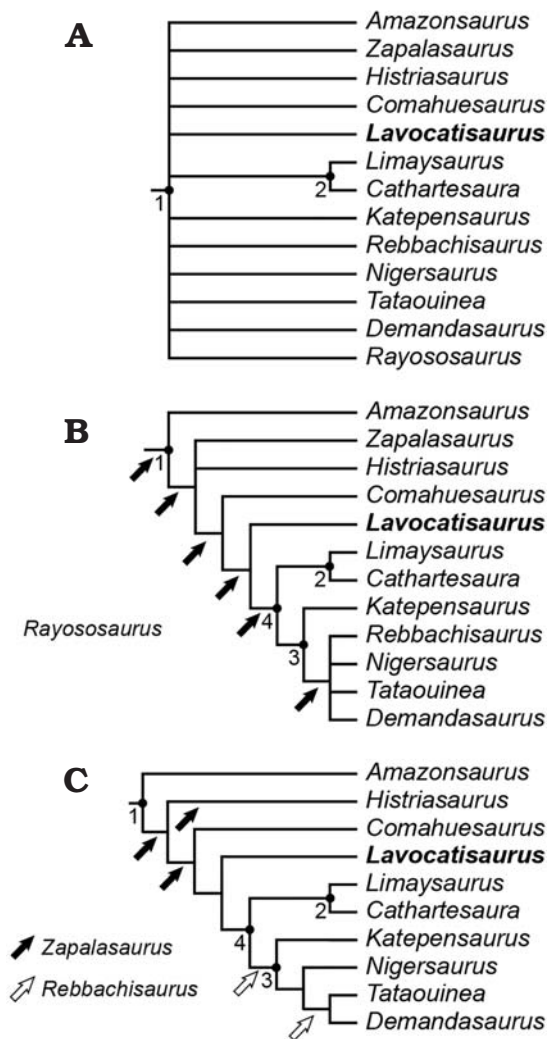
Fig. 4. Results of the phylogenetic analysis. A. Strict consensus tree of the 49 500 most parsimonious trees found, showing a complete polytomy amongst Rebbachisauridae with the sole exception of Limaysaurinae. **B**. Reduced consensus tree after pruning *Rayososaurus*, showing all possible positions of this taxon. **C**. Reduced consensus tree after pruning *Rayososaurus*, *Zapalasaurus*, and *Rebbachisaurus* (whose possible positions are indicated by the arrows). Resolved clades are indicated with numbers: 1, Rebbachisauridae; 2, Limaysaurinae; 3, Rebbachisaurinae; 4, Khebbashia.

been recovered in other recent analyses (Ibiricu et al. 2015; Fanti et al. 2015; Wilson and Allain 2015). Rebbachisauridae except for *Amazonsaurus* are supported by two derived characters, obtained as ambiguous synapomorphies due to the absence of information in *Zapalasaurus* or *Histriasaurus*: 198, festooned spinodiapophyseal laminae (unknown in *Zapalasaurus*); and character 23, dorsally directed transverse process (unknown in *Histriasaurus*).

Comahuesaurus + **MDR**.—As in Carballido et al. (2012), *Comahuesaurus* was recovered as a basal rebbachisaurid more derived than *Histriasaurus* and *Zapalasaurus*. Three characters (180, 231, 338) diagnose this clade, but these characters are unknown in *Histriasaurus* and/or *Zapalasaurus*, so they were recovered as ambiguous synapomorphies of the

clade. The characters are: the reduced hyposphene in dorsal vertebrae (character 180); the posterior articular surface of anterior caudal vertebrae markedly more concave than the anterior one (character 231); and the ischium acetabular articulation narrower in its central part (character 338).

Lavocatisaurus + **MDR**.—Two synapomorphic characters support the clade formed by *Lavocatisaurus* and more derived rebbachisaurids: asymmetrical enamel with the lingual layer thinner than the labial one (character 117); and middle caudal vertebrae with anteriorly (nearly horizontally) projecting prezygapophysis (character 413).

Khebbashia.—This is a clade recently proposed by Fanti et al. (2015), which is formed by Limaysaurinae+Rebbachisaurinae. It is supported by three derived characters: 113, teeth with one high-angle and one low-angle wear facet; 118, teeth with lingual grooves; and 304, gracile humerus with robustness index (sensu Wilson and Upchurch 2003) lower than 0.27.

Limaysaurinae.—The clade Limaysaurinae is composed of two taxa, *Limaysaurus* and *Cathartesaura*, and supported by a broad scapular acromion (character 284).

Rebbachisaurinae.—*Katepensaurus*, the basalmost taxon of this clade, and *Demandasaurus*, *Nigersaurus*, *Rebbachisaurus*, and *Tataouinea* here constitute Rebbachisaurinae. This clade is supported by the presence of a deep centroprezygapophyseal fossa on middle and posterior dorsal vertebrae (character 409). The position of *Katepensaurus* within Rebbachisaurinae was recently recovered by Fanti et al. (2015) and contrasted with that originally proposed by Ibiricu et al. (2013) and subsequently recovered by Ibiricu et al. (2015). Indeed, some characters widespread in Rebbachisaurinae are also present in *Katepensaurus*, as previously noted by Ibiricu et al. (2013). Three further characters present in *Katepensaurus* are ambiguously optimized in this clade due to the absence of information. These are: the presence of a posterior centroparapophyseal lamina in dorsal vertebrae (character 194, unknown for *Tataouinea*); anterior caudal vertebrae with a triangular lateral process on the neural spine (character 235, absent in *Rebbachisaurus*; Wilson and Allain 2015); and the presence of a divided centroprezygapophyseal lamina in middle and posterior dorsal vertebrae (character 411, absent in *Rebbachisaurus*). The polytomy recovered for Rebbachisaurinae is caused by the two different positions that *Rebbachisaurus* can take within this group.

Cranial evolution in Rebbachisauridae

The amount of information recovered from the skull of *Lavocatisaurus* and its position amongst the basal rebbachisaurids provides the first opportunity to investigate the
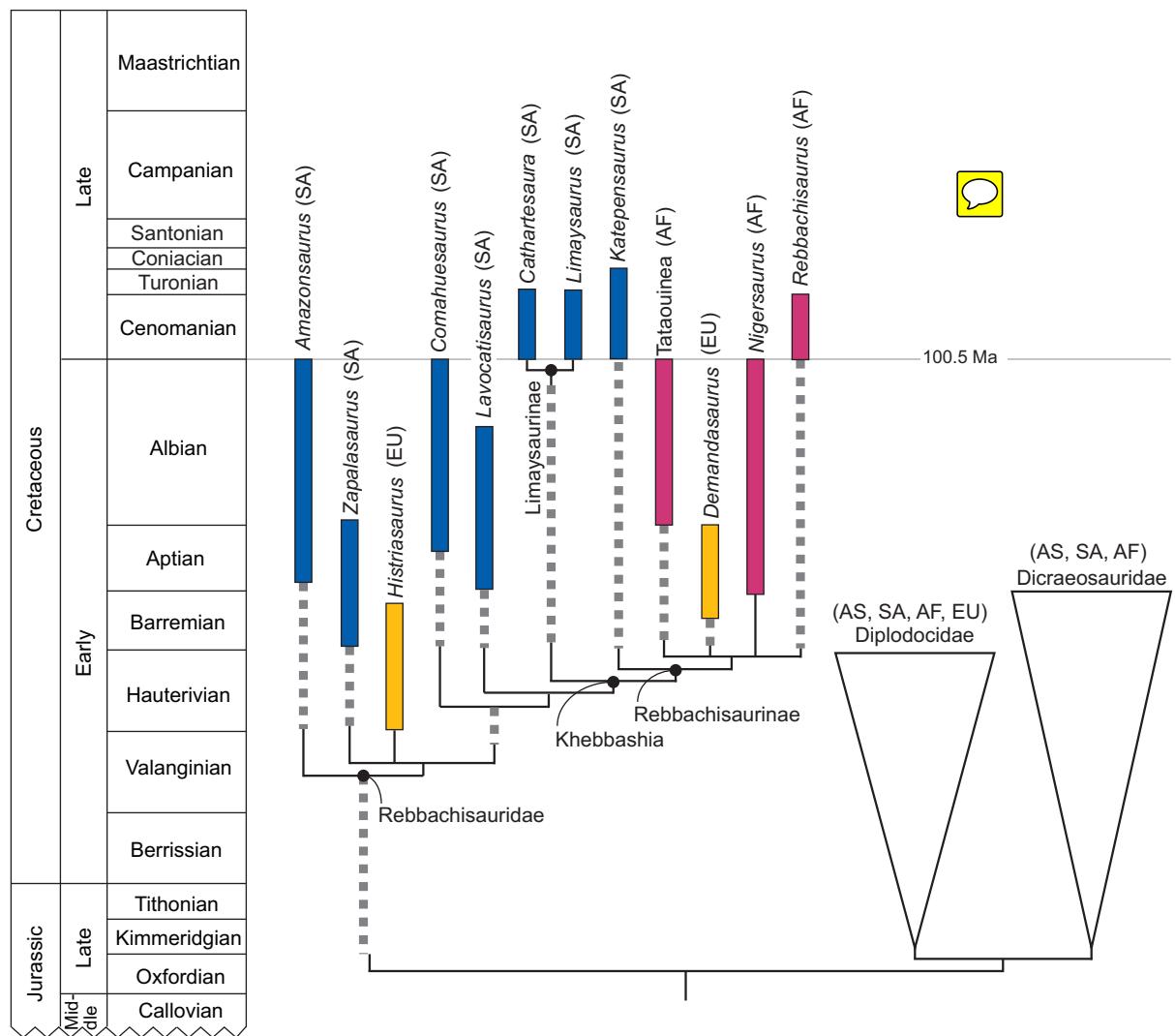
Fig. 5. Stratigraphically calibrated strict tree after pruning *Lavocatisaurus*, showing the geographical provenance of the taxa (silhouettes of continents) and ghost lineages (dashed lines). Abbreviations: AF, Africa, AS, Asia; EU, Europe; SA, South America. {Fig will be grayscale in printed version}

evolution of certain characters in one of the least-known lineages of Neosauropoda. Below, we list and briefly discuss the evolution of certain characters upon which the new taxon described here sheds further light.

Preantorbital fenestra.—The presence of a preantorbital fenestra was recognized as a derived character of *Jobaria* and more derived sauropods (Wilson and Sereno 1998; Wilson 2002). Amongst Neosauropoda it is a widespread character but with varying degrees of development. This fenestra is poorly developed in basal macronarians (e.g., *Camarasaurus*, *Giraffatitan*; Madsen et al. 1995; Janensch 1935), being similar in shape and size to the posterior maxillary foramen of basal sauropodomorphs (e.g., *Plateosaurus*; Sereno 2007). It differs from the posterior maxillary foramen in its anteroventral direction and in its connection to the antorbital fenestra (Wilson and Sereno 1998). Its presence in derived titanosaurs and diplodocids is much clearer, as the preantorbital fenestra is usually a well-developed opening in the maxilla (e.g., *Diplodocus*, *Tapuiasaurus*; Marsh 1884;

Zaher et al. 2011). The maxillae here described possess a large opening that can be identified as the preantorbital fenestra. Although it resembles that of diplodocids and derived titanosaurs, in *Lavocatisaurus* the preantorbital fenestra is extremely developed, occupying a great area of the maxilla. As noted above, a similarly placed and apparently equally large fenestra was first identified as the antorbital fenestra in *Nigersaurus* (Sereno et al. 1999: fig. 2D; Sereno and Wilson 2005: fig. 5.5). To judge by the published images (Sereno et al. 1999; Sereno and Wilson 2005) and personal observation of the preserved *Nigersaurus* maxilla (MNN GDF512), the latter fenestra corresponds more probably to the preantorbital fenestra. Indeed, the anterior margin of the preantorbital fenestra is at the height of the subnarial foramen in *Nigersaurus* (Sereno et al. 1999: fig. 2D), whereas the antorbital fenestra, as reconstructed (Sereno and Wilson 2005; Sereno et al. 2007), is well above the foramen. Therefore, *Lavocatisaurus* and *Nigersaurus* share the presence of a large preantorbital fenestra, which occupies around half of the maxillary body. The preantorbital

fenestra of both rebbachisaurids is not inset in any kind of fossa, differing from most flagellicaudatans known (e.g., *Dicraeosaurus*, *Apatosaurus*; see Tschopp et al. 2015).

Infratemporal fenestra. In basal sauropodomorphs, the infratemporal fenestra is posteriorly placed with respect to the orbit, being anteriorly delimited by the postorbital (anterodorsally) and jugal (anteroventrally), and posteriorly by the squamosal (posterodorsally) and the quadratojugal (posteroventrally) (e.g., *Plateosaurus*). A similar position and configuration of the infratemporal fenestra is observed in *Camarasaurus* and *Europasaurus* (Madsen et al. 1995; Marpmann et al. 2015), although in these taxa the fenestra is placed posteroventrally to the orbit, with the anterior margin close to the anterior margin of the orbit. In contrast, in most sauropods the squamosal–quadratojugal contact is missing, with the quadrate forming a small posterior edge of the infratemporal fenestra (see Wilson and Sereno 1998). This is observed in most basal sauropods and neosauropods (e.g., *Giraffatitan*, *Diplodocus*). In diplodocimorphs, the infratemporal fenestra projects anteriorly, its anterior margin going beyond that of the orbit (e.g., *Diplodocus*, *Apatosaurus*; Berman and McIntosh 1978). This anterior displacement of the infratemporal fenestra seems to be greater in rebbachisaurids, with that of *Nigersaurus* placed completely anteriorly to the orbit (Sereno et al. 2007). The anterior displacement of the infratemporal fenestra in rebbachisaurids seems to have had its origin early in their evolution, as most of the infratemporal fenestra is positioned anteriorly to the orbit in *Lavocatisaurus*, with its posterior margin slightly posterior to the anterior margin of the orbit (Fig. 3). Amongst rebbachisaurids, this is not the only morphological change in the configuration of the infratemporal fenestra. In *Lavocatisaurus* the jugal articulates with the squamosal, a novel articulation not previously described for any sauropodomorph, but that can also be detected in *Limaysaurus* and *Nigersaurus* (see description). Therefore, the infratemporal fenestra of rebbachisaurids is not delimited by the postorbital. In *Lavocatisaurus* this fenestra is certainly bounded by the jugal (anteriorly and posterodorsally) and the squamosal (posteriorly). The wide ventral end of the squamosal shows no signs of articulation with the quadratojugal, making it possible that the squamosal fails to contact the quadratojugal, as in Flagellicaudata (Tschopp et al. 2015). Nevertheless, a badly preserved articulation for the quadratojugal (ventrally) and the jugal (dorsally) can be detected in the preserved quadrate, making it impossible to discern whether the squamosal–quadratojugal contact was present or not. Based on the restoration of *Nigersaurus*, the ventral margin of the infratemporal fenestra should be bounded by the quadratojugal (not preserved either in *Lavocatisaurus* or in *Nigersaurus*).

Teeth and keratinized sheaths.—The well-preserved premaxillae, maxillae, dentaries and teeth of *Lavocatisaurus* yield an improved understanding of many aspects of the feeding adaptations in Rebbachisauridae. A great number

of teeth were described for *Nigersaurus*, which has 58 upper teeth (4 premaxillary and 25 maxillary per side) and 68 lower teeth (34 in each dentary). In contrast, only 7 alveoli are present in the single dentary recovered for *Demandasaurus* (Torcida-Baldor et al. 2011). In *Lavocatisaurus* we found 32 teeth in the upper series (4 in the premaxilla and 12 in the maxilla per side), and 44 teeth are present in the lower series (22 per dentary). The number of teeth in *Lavocatisaurus* is similar to that of non-neosauropod sauropods (e.g., 20 dentary teeth are present in *Jobaria*; Sereno et al. 1999), but differs from the number of lower tooth positions in other, non-rebbachisaurid diplodocimorphs and camarasauromorphs (Wilson and Sereno 1998). Basal rebbachisaurids thus seem to keep the plesiomorphic state (20 teeth or more per dentary), with a marked increment in tooth positions in *Nigersaurus* and a decrease in *Demandasaurus*.

All the preserved teeth in *Lavocatisaurus* (both upper and lower) have highly asymmetrical enamel, as in derived rebbachisaurids (*Nigersaurus*, *Limaysaurus*, *Demandasaurus*) and differing from the symmetrical enamel of the more basal rebbachisaurid *Comahuesaurus* (Salgado et al. 2004). This indicates that, whereas symmetrical enamel was present in basal forms, asymmetrical enamel evolved prior to the diversification of the clade into its two major lineages (Rebbachisaurinae and Limaysaurinae). As noted above, the upper teeth of *Lavocatisaurus* are much larger (both longer and wider) than those of the lower series. Although a similar pattern was mentioned for *Nigersaurus* (Sereno et al. 2007), in the case of *Lavocatisaurus* this difference is of an order such that the largest maxillary teeth are almost three times bigger than the dentary teeth (Fig. 3). The upper teeth present a low-angle wear facet on their lingual surface, but none of them has the second, labial, wear facet as described for *Nigersaurus*, although slightly polished surfaces are recognized on its tips. The lingual low-angle wear facet in *Nigersaurus* has been interpreted as being a result of tooth-tooth occlusion. The enormous differences in tooth size in *Lavocatisaurus*, especially close to the mid-point of the tooth series, make it less likely that the smooth and planar low-angle wear facets were the product of tooth-to-tooth occlusion. This is due to the fact that a single lower tooth cannot produce a single wear facet wider than its root. Therefore, the tooth-to-tooth abrasion producing this low-angle wear facet should be revised, at least in *Lavocatisaurus*, pending further studies on its micro-wear (see below). The second, labial high-angle facet present in *Nigersaurus* is also present in diplodocids and dicraeosaurids, and has been regarded as being a result of tooth-to-plant abrasion during ground-level browsing (Sereno et al. 2007). The absence of a labial, high-angle wear facet in *Lavocatisaurus* could indicate a different browsing height in basal rebbachisaurids or different movements when cutting plants, although another possibility is that it results from different types of food in diplodocoids. Whether or not the dentary teeth present similar facets to those of the upper teeth remains an open question calling for further and more complete discoveries.

It is widely accepted that sauropods lacked any masticatory adaptation, such as cheeks (Upchurch et al. 2007) or beaks (Sereno 2007). Nevertheless, the presence of a beak was suggested for *Bonitasaura* and other related taxa, based on the horizontal edge posterior to the tooth-bearing region (Apesteguía 2004; but see Wilson 2005). The presence of a keratinized sheath was suggested in *Nigersaurus* (Sereno et al. 2007) on the basis of the presence of numerous neurovascular grooves in the maxilla and dentary. The presence of a keratinous beak was recently proposed by Wiersma and Sander (2016) in *Camarasaurus* and other sauropods, based on the presence of exposed roots and extensive vascular foramina. For these authors, the presence of such a structure would explain the numerous ITRs reported for several sauropods; it would have served as extra protection from abrasive plants and provided a continuous cutting surface. The presence of ITRs and dentigerous bones in *Lavocatisaurus* is evidence against the consumption of bones by insects (Britt et al. 2008), reinforcing the taphonomic separation of the teeth as suggested by Wiersma and Sander (2016). As in *Nigersaurus*, the premaxilla and maxilla of *Lavocatisaurus* are laterally covered with numerous irregular grooves that are more numerous in the lower part of these bones. A similar pattern, though much more developed, can be observed in the dentaries. The dorsal margin of the dentaries has a depressed area that runs posteriorly from the whole lateral margin of the dentary ramus and ascends dorsally at the anterolateral margin. A similar, but less developed, morphology was described in *Demandasaurus* and suggested to be equivalent to the vascular canal shown in *Nigersaurus* by Sereno et al. (2007; see also Torcida-Baldor et al. 2011). In *Lavocatisaurus* the laterodorsal surface of the dentary, above this marked step, is full of irregular, middle-to-large-sized pores and neurovascular foramina. Such morphology is frequently cited as evidence of keratin sheaths (see Sereno 2007). This region of the dentary coincides with the horizontally placed, anterior lateral edge of the maxilla (Fig. 3), which is sharp and covered with irregular grooves, both medially and laterally. Given this morphology, we do not rule out the presence of keratinous sheaths in the anteriormost edentulous region of the maxillae and dentaries. The presence of a keratinous sheath covering the anteriormost region of the snout could explain the ITRs of *Lavocatisaurus* (see Wiersma and Sander 2016), as well as the polished, single, low-angle wear facet of the upper teeth (see above). If this is the case, the lingual surface of the teeth, with thinner enamel, will have been subject to wear against a keratinous beak. Nevertheless, further analyses are needed in order to test this hypothesis further.

Paleobiogeographical remarks

Some interesting information of a palaeobiogeographical nature can be inferred from the calibrated phylogeny (Fig. 5). African forms such as *Nigersaurus*, *Rebbachisaurus*, and *Tataouinea* and the European *Demandasaurus* are grouped together in the clade Rebbachisaurinae. The presence in South America of *Katepensaurus* as a sister taxon to this clade could indicate an early evolution in South America and a subsequent dispersal of Rebbachisaurinae in Africa and Europe. However, the initial establishment of the clade in Africa and its dispersion in South America cannot be ruled out either, with subsequent vicariant evolution in both continents fostered by the opening of the South Atlantic and the definitive separation of Gondwana.

The taxa placed outside Khebbashia, such as *Comahuesaurus*, *Zapalasaurus*, and *Lavocatisaurus* (Fig. 5), could either be among the primitive rebbachisaurids prior to the dispersal to Africa or the first representatives that migrated to South America. This possibility cannot be ruled out since *Histriasaurus* from the Hauterivian of Croatia the oldest rebbachisaurid in the fossil record, is Gondwanan in palaeobiogeographical terms and could indicate an African origin of the rebbachisaurid lineage. However, the fragmentary nature of the *Histriasaurus* record could be distorting its real phylogenetic position. Another possible scenario, given the presence of phylogenetically more primitive taxa in South America, could be that *Histriasaurus* is a representative of a dispersion of primitive rebbachisaurids from South America to Africa and beyond at the beginning of the Cretaceous period, a dispersion for which we have no further information.

Conclusions

Lavocatisaurus agrioensis is the first of the South American rebbachisaurids that preserves the rostral region of the cranium, which has allowed us to undertake a reliable enough reconstruction of the skull. The skull has a combination of morphological characters that justifies its definition as a new taxon within Rebbachisauridae along with the less derived rebbachisaurids from the Early Cretaceous of Argentina such as *Zapalasaurus* and *Comahuesaurus*. Our phylogenetic study situates *Lavocatisaurus* as the sister lineage of Khebbashia (Fig. 5). *Lavocatisaurus* is the most derived basal rebbachisaurid known to date, providing reliable information on the evolutionary steps that occurred just prior to the diversification of Rebbachisaurinae.

Acknowledgements

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