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ARTÍCULO

NEW REBBACHISAURID REMAINS FROM THE HUINCUL FORMATION (MIDDLE CENOMANIAN–EARLY TURONIAN) OF THE CENTRAL NEUQUÉN BASIN, PATAGONIA, ARGENTINA

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Abstract. In the central Neuquén Basin, the Huincul Formation comprises thick successions of Upper Cretaceous fluvial deposits widely exposed at the south and north-west of Huincul High. The vertebrate fossil record from the Huincul Formation is very abundant, especially considering the saurischian dinosaurs, including several theropod (*Mapusaurus*, *Taurovenator*, *Aoniraptor*, *Skorpiovenator*, *Ilokelesia*, *Gualicho*, *Overoraptor*, *Tralkasaurus*, and *Huinculsaurus*) and sauropod specimens (*Choconsaurus*, *Argentinosaurus*, *Cathartesaura*, *Limaysaurus*, and the indeterminate rebbachisaurid MMCH-Pv-49). In this contribution, we describe new rebbachisaurid sauropod findings from the El Orejano locality (Neuquén Province, Argentina), where coarse sandstones outcrop referred to the lower section of the Huincul Formation. The new material includes three axial elements that we refer to Rebbachisauridae: a partial dorsal neural arch (MAU-Pv-EO-633), an incomplete dorsal vertebra (MAU-Pv-EO-634), and an almost complete caudal vertebra (MAU-Pv-EO-666). These new findings share different features with other members of that family, although show some morphological differences with other rebbachisaurid taxa, which suggest a more diversified fauna in the central Neuquén Basin than previously known, at least during the Cenomanian/Turonian interval. This record from the new fossiliferous locality of El Orejano allows us to improve our knowledge about the morphological diversity of the Rebbachisauridae during the early Late Cretaceous. Furthermore, it represents one of the most modern records of the family, adding new information on the last stages of the evolutionary history of rebbachisaurids.

Key words. Rebbachisauridae. Faunal change. Upper Cretaceous. Osteology. Neural laminae.

Resumen. NUEVOS RESTOS DE REBAQUISÁURIDOS DESDE LA FORMACIÓN HUINCUL (CENOMANIANO MEDIO–TURONIANO TEMPRANO) DEL CENTRO DE LA CUENCA NEUQUINA, PATAGONIA, ARGENTINA. En el centro de la Cuenca Neuquina, la Formación Huincul está caracterizada por potentes depósitos fluviales del Cretácico Superior que afloran ampliamente al sur y al noroeste de la Dorsal de Huincul. El registro fósil de vertebrados de la Formación Huincul es particularmente abundante, sobre todo considerando la fauna de dinosaurios saurisquios, la cual incluye diferentes formas de terópodos (*Mapusaurus*, *Taurovenator*, *Aoniraptor*, *Skorpiovenator*, *Ilokelesia*, *Gualicho*, *Overoraptor*, *Tralkasaurus* y *Huinculsaurus*) y saurópodos (*Choconsaurus*, *Argentinosaurus*, *Cathartesaura*, *Limaysaurus* y el rebaquisáurido indeterminado MMCH-Pv-49). En este trabajo presentamos nuevas evidencias de saurópodos rebaquisáuridos procedentes de la localidad de El Orejano (provincia del Neuquén, Argentina), donde afloran areniscas gruesas referidas a la sección inferior de la Formación Huincul. Estos nuevos materiales corresponden a tres elementos axiales que atribuimos a la familia Rebbachisauridae: un arco neural dorsal incompleto (MAU-Pv-EO-633), una vértebra dorsal incompleta (MAU-Pv-EO-634), y una vértebra caudal casi completa (MAU-Pv-EO-666). Estos especímenes comparten distintos caracteres con los miembros de dicha familia, sin embargo presentan algunas diferencias morfológicas con otras formas de rebaquisáuridos que indican una fauna más diversificada en el centro de la Cuenca Neuquina de lo que se conocía, por lo menos durante la transición Cenomaniano/Turoniano. Este registro de la nueva localidad fosilífera de El Orejano no solo permite ampliar nuestro conocimiento sobre la diversidad morfológica de la familia Rebbachisauridae durante el Cretácico Tardío temprano, sino que también aporta nueva información sobre los últimos estadios de la historia evolutiva del clado, representando uno de los registros más modernos de la familia.

Palabras clave. Rebbachisauridae. Cambio faunístico. Cretácico Superior. Osteología. Láminas neurales.

In Gondwana, the Cenomanian/Turonian boundary represents a crucial time-lapse for the evolutionary history of several terrestrial tetrapod lineages, representing one of the latest faunistic replacement of Mesozoic (see Apesteguía, 2002; Leanza *et al.*, 2004). Indeed, it precedes the final establishment of typical Late Cretaceous reptile lineages, before the extinction of non-avian dinosaurs at the Cretaceous/Paleogene boundary (Coria & Salgado, 2005; Novas *et al.*, 2005, 2013; Krause *et al.*, 2020). The Cenomanian/Turonian turnover seems to be closely related to paleoclimatic, paleogeographic, and paleoecological variations linked with the opening of the South Atlantic Ocean, which occurred during the mid-Cretaceous (Aptian–Turonian; *e.g.*, Schlanger & Jenkyns, 1976; Arthur *et al.*, 1987; Elder, 1987; Hut *et al.*, 1987; Jenkyns, 2010; Pol & Leardi, 2015; Petrizzo *et al.*, 2021). In particular, analyzing the saurischian fossil record, a post-Turonian faunistic turnover can be recognized when mid-Cretaceous (Aptian–Turonian) faunas are compared with the post-Turonian ones (see Leanza *et al.*, 2004; Candeiro *et al.*, 2011; Novas *et al.*, 2013; Candeiro, 2015; Krause *et al.*, 2020; Ibiricu *et al.*, 2020). Indeed, within Sauropoda, there is fossil evidence of Rebbachisauridae and both broad-toothed and narrow-toothed Titanosauriformes until the Cenomanian–Turonian interval (*e.g.*, Canudo *et al.*, 2018; Bellardini *et al.*, 2022), whereas after the Turonian only the narrow-toothed titanosauriformes (all members of Titanosauria) represent the mega-herbivores saurischian fauna worldwide (*e.g.*, Carballido *et al.*, 2017). On the other hand, carcharodontosaurid and spinosaurid theropods were abundant until the early Late Cretaceous but disappeared after the Turonian. These theropod lineages have been supplanted by abelisaurids and megaraptorids, which were particularly abundant in Gondwana, where they became the dominant carnivores until the end of the Cretaceous (Coria & Salgado, 2005; Novas *et al.*, 2013). However, knowing the exact moment of such marked faunistic turnover is difficult given the paucity of the fossil record with robust stratigraphic control.

Recent fieldwork in the new fossiliferous locality El Orejano (Fig. 1; Neuquén Province, Argentina), in which the base of the Huincul Formation is widely exposed resulted in several new rebbachisaurid remains. This new material includes three axial elements: a partial anterior-to-middle dorsal vertebra (MAU-PV-EO-633), a well-preserved posterior dorsal vertebra (MAU-PV-EO-634), and an almost complete anterior caudal vertebra (MAU-PV-EO-666).

Rebbachisauridae represents a basal family of Diplodocoidea sauropods, whose biochrone extends from the Early Cretaceous of Europe (Dalla Vecchia, 1998, 2005; Pereda Suberbiola, 2003) to the early Late Cretaceous of Patagonia (Calvo & Salgado, 1995; Gallina & Apesteguía, 2005; Ibiricu *et al.*, 2013, 2015). Considering the paleobiogeographic evolution of Rebbachisauridae, South America in general and Patagonia in particular have an important role in the diversification and distribution of the clade, yielding most of the rebbachisaurid fossil record worldwide. Whereas the Patagonian Early Cretaceous record of this clade is entirely dominated by basal forms, all of them from the Neuquén Basin (*e.g.*, *Zapalasaurus*, *Comahuesaurus*, *Lavocatisaurus*; Salgado *et al.*, 2006; Carballido *et al.*, 2012; Canudo *et al.*, 2018), the early Late Cretaceous record includes more nested taxa, all members of Khebbashia (Limaysaurinae+Rebbachisaurinae (=Nigersaurinae)), such as *Katepensaurus, Cathartesaura*, and *Limaysaurus* (Calvo & Salgado, 1995; Gallina & Apesteguía, 2005; Ibiricu *et al.*, 2013). Indeed, four of the five taxa closely related to the early evolution of Rebbachisauridae come from the Early Cretaceous of Neuquén Basin (Canudo *et al.*, 2018), whereas the remaining basal form (*i.e.*, *Amazonsaurus*; Carvalho *et al.*, 2003) comes from Parnaíba Basin (Aptian–Albian) of northern Brazil. On the other hand, the most modern rebbachisaurid specimens were found in the early Late Cretaceous outcrops of Patagonia closely related to the Cenomanian/Turonian transition, such as *Katepensaurus*, *Cathartesaura*, and *Limaysaurus* (Calvo & Salgado, 1995; Gallina & Apesteguía, 2005; Ibiricu *et al.*, 2013). However, Rebbachisaurinae, the most nested rebbachisaurid clade, encompasses taxa from the Early Cretaceous of Africa, South America, and Europe (Sereno *et al.*, 1999; Pereda Suberbiola, 2003; Lindoso *et al.*, 2019).

The new material here described shows morphological differences with already known rebbachisaurids, indicating the presence of an additional taxon in the Huincul Formation. Although the material presented here is too fragmentary to be recognized as a new taxon, it suggests that Rebbachisauridae was more diversified in different parts of southern Gondwana than previously known, at least during the late Cenomanian.

Additionally, this material represents one of the most modern rebbachisaurid records from the Neuquén Basin and the northernmost evidence of the lineage during the Cenomanian/Turonian transition. Thus, it adds not only new information on the sauropod faunal composition of the central Neuquén Basin but also contributes to reconstructing part of the last stage of the evolutionary history of Rebbachisauridae, a lineage that became completely extinct after the Turonian.

GEOGRAPHIC AND STRATIGRAPHIC PROVENANCE OF THE REMAINS

In north Patagonia, the Cenomanian/Turonian transition is lithostratigraphycally represented by the Río Limay Subgroup, the basal unit of the Neuquén Group, which is composed of a sequence of 1,200 m of fluvial red beds and worldwide known for its great wealth of oil and fossiliferous sites (Garrido, 2010). The Río Limay Subgroup includes two formations: the Candeleros Formation (lower Cenomanian) and the Huincul Formation (middle Cenomanian–lower Turonian). The Candeleros Formation outcrops are well-exposed in the southern region of Neuquén Basin and marginally, in terms of thickness and extension, in the core and northwestern sector of the basin (Garrido, 2010). Lithologically, the Candeleros Formation is characterized by a dominance of fine to coarse grained sands with an abundant muddy matrix, reddish to purple in color.

On the other hand, the upper-layer stratigraphic unit, the Huincul Formation, is particularly extensive and well-exposed in the central Neuquén Basin, as well as at the south and north-west to the Huincul High (*e.g.*, Ploszkiewics *et al.*, 1984; Cevallos, 2005; Mosquera *et al.*, 2011). Regarding the lithological composition, two sedimentological sections are consensually regarded for the Huincul Formation (Garrido, 2010): a lower section dominated by fine sands and muds, and an upper section, known as typical-Huincul

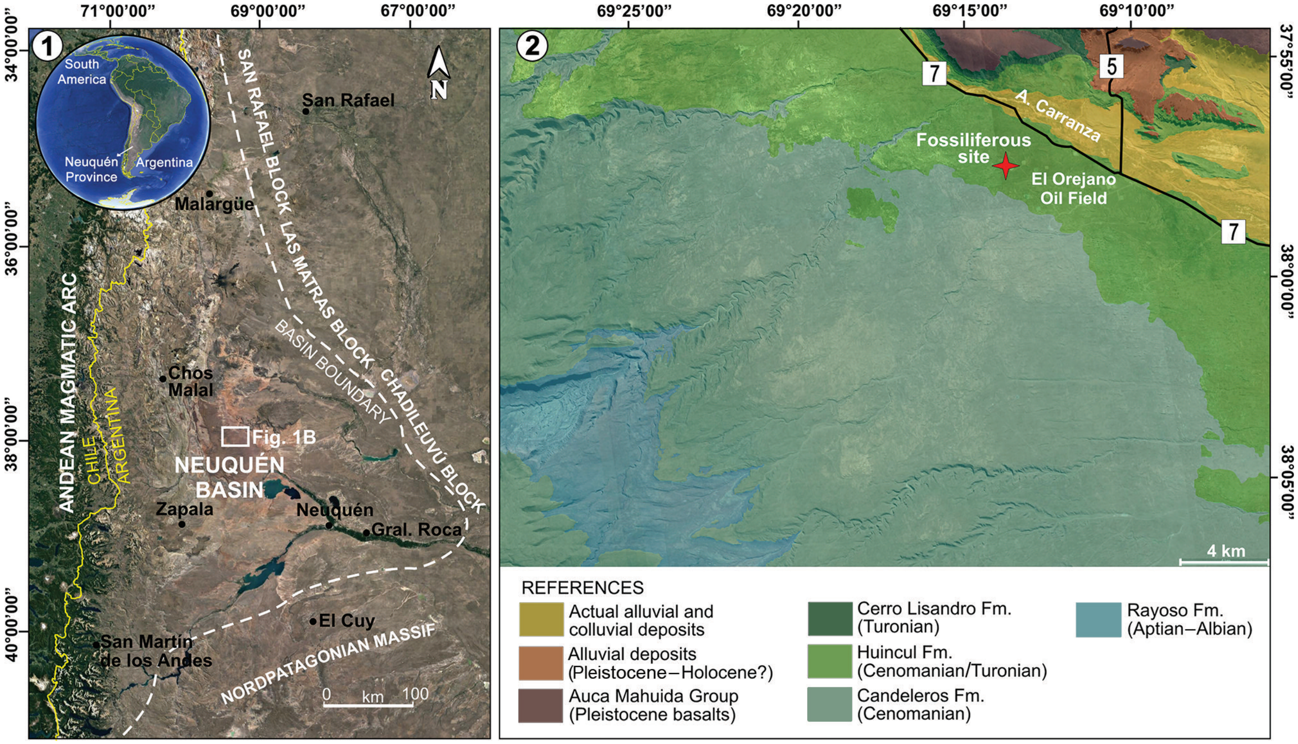

Figure 1. 1–2, Geographic location and stratigraphic maps; **1,** Satelital map of the Neuquén Basin (northern Patagonia, Argentina) showing the approximate boundary and more relevant structures. The new fossiliferous locality of El Orejano is highlighted by a white rectangle; **2,** Stratigraphic map of the study area showing the relative extensions of the lithostratigraphic outcropping units in the El Orejano locality. The new rebbachisaurid remains here described come from the lower section of the Huincul Formation (Cenomanian/Turonian; in light green). Geological mapping carried out on the basis of satellite image, acquired from earth.google.com (Date 11/5/2020).

(Garrido, 2010), characterized by medium to coarse grained sands with thin fine sandy and muddy intercalations at the base, and muddy levels gradually more abundant toward the top of the sequence.

In particular, El Orejano Oil Field is located close to the eastern border of the Dorso de los Chihuidos, a structural unit characterized by the presence of a set of anticline folds of low wave amplitude and large radius, which expose a thick succession of continental red bed deposits of Cretaceous age (Herrero Ducloux, 1946; Ramos, 1978, 2011). This area shows extensive outcrops of the upper section of the Bajada del Agrio Group (Rayoso Formation, Aptian–Albian in age), and of the lower section of the Neuquén Group (Candeleros, Huincul and Cerro Lisandro formations, Cenomanian–Turonian in age) (Ardolino & Franchi, 1996) (Fig. 1.2).

The Candeleros and Huincul formations are the ones that offer the greatest areal distribution of their outcrops in this sector, forming extensive and wide slightly stepped erosional plains, with a structural dip of about 5° to 10° E-NE. To a large extent, this relief is controlled both by the structure of the area (large anticline flank) and by the presence of extensive and erosional resistant sandy sheet bodies of fluvial origin (amalgamated channel deposits) that frequently characterize outcrops of the aforementioned lithostratigraphic units (Garrido, 2010).

A stratigraphic profile was made along a transect of approximately 5 km in length, which joins the exposed base of the Huincul Formation with the outcrops of the fossiliferous site, obtaining a 23.7 m thick stratigraphic column (Fig. 2.2). Although it is a partial section, being limited in its top by the current erosion level, it allows us to locate the new fossil remains within the basal levels of the Huincul Formation. Although there is no precise data on the total thickness of the Huincul Formation in this area, Ramos (1981) estimated a thickness of 195 m for this unit in the central Neuquén Basin.

The new bones here presented were found isolated (Fig. 2.1), contained in fluvial sandstone beds that are lithofacially interpreted as bottom channel-fill and downstream accretion bar deposits. The low degree of abrasion and breakage presented by the bones suggests that they have suffered a relatively short transport, implying a parautochthonous origin for the specimens.

The age of the Huincul Formation has been attributed, based on their stratigraphic relationships, to the upper Cenomanian–lower Turonian (Legarreta & Gulisano, 1989; Garrido, 2010). Radiometric data obtained by Corbella *et al.* (2004) from a weathered ash level located close to the base of the Huincul Formation, gave a zircon fission track age of 88 ± 3,9 Ma (upper Turonian); however, this value is taken with caution and it is considered necessary to carry out new dates in this regard. On other hand, Vallati (2001) determined, on the basis of palynological studies, an age of the paleofloristic association of the Huincul Formation not younger than Cenomanian.

In summary, and based on the data available to date, a late Cenomanian age is inferred for the fossil-bearing rocks of the El Orejano locality.

MATERIALS AND METHODS

All fossil bones here described were mechanically prepared in the paleontological laboratory of the MAU where they are actually housed under the MAU-PV-EO acronym. The complete list of specimens from the El Orejano locality is detailed in Table S1 (see Online Supplementary Information). For the osteological description, we followed the terminology used in Romer (1956), Wilson & Sereno (1998), Harris (2004), Upchurch *et al.* (2004), and Wilson (2006), and the terminology and abbreviations proposed by Wilson (1999, 2012) and Wilson *et al.* (2011) for vertebral laminae and fossae. To assess the phylogenetic position of the specimens reported here, we carried out a cladistic analysis using a modified version of the data matrix of Bellardini *et al.* (2022) (see NEXUS and TNT files in Online Supplementary Information). The data matrix was edited using Mesquite v. 2.74 (Maddison & Maddison, 2011) to include specimens from the El Orejano locality, which were codified as independent OTUs and analyzed separately as they cannot be confidently assigned to the same species. The resulting data matrix, composed of 418 characters and 95 taxa, was exported to TNT format (see NEXUS and TNT files in Online Supplementary Information). A heuristic tree search was performed using TNT v.1.5 software (Goloboff & Catalano, 2016), starting with 3,000 replicates of Wagner trees followed by TBR branch swapping and saving 10 trees per replicate. The resulting trees were subjected to an additional

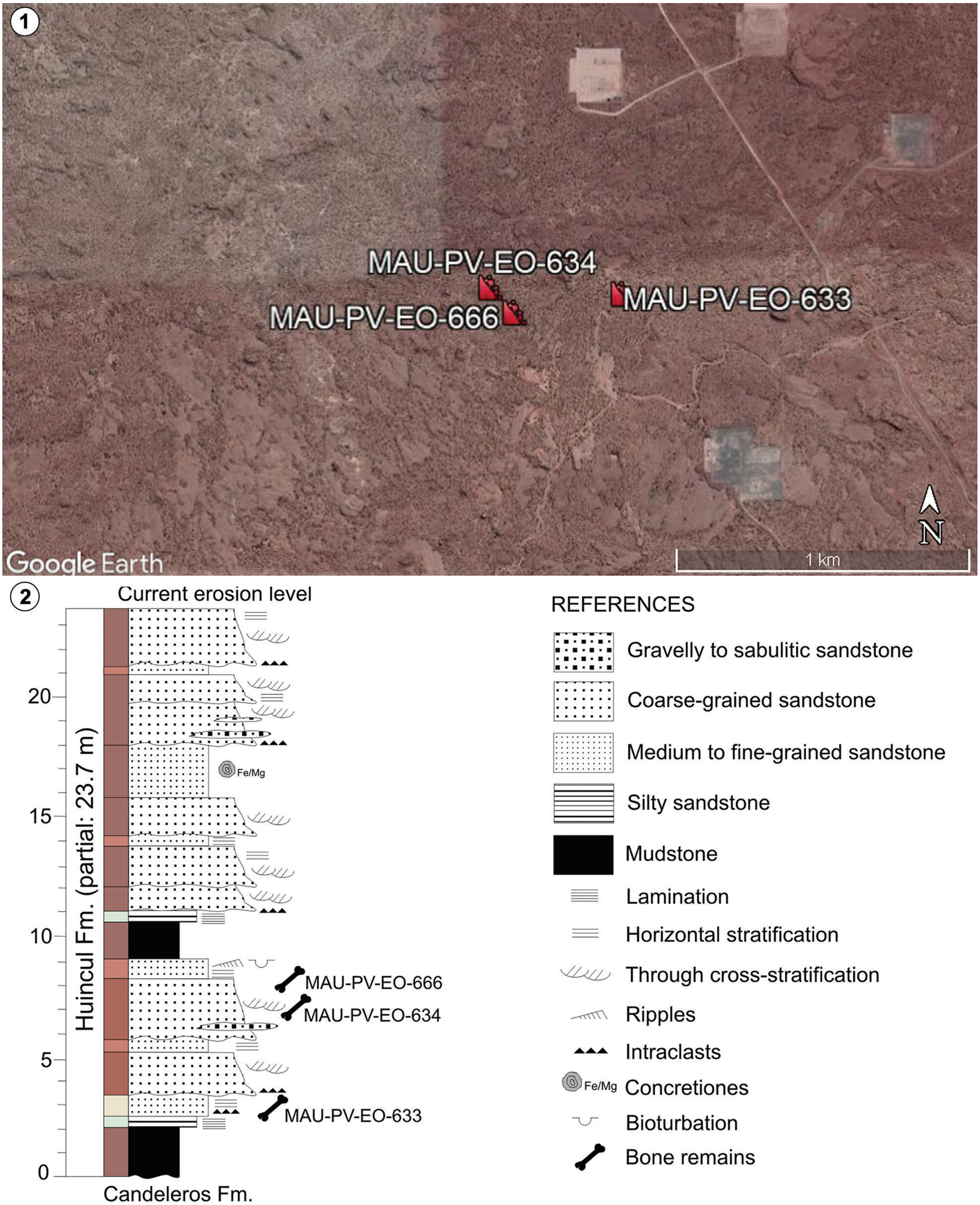

Figure 2. **1–2,** Fossiliferous sites location and lithologic profile; **1,** The new rebbachisaurid specimens come from three sites in the western sector of El Orejano YPF SA oil field (red symbols); **2,** Schematic log of the Huincul Formation outcrops on the El Orejano oil field, Neuquén Province, Patagonia, Argentina. The new rebbachisaurid axial elements come from the lower section of the sequence (black bone silhouettes). Satellite image modified from earth.google.com website (date 11/05/2020).

round of branch swapping (TBR) to find remaining most parsimonious trees (MPTs).

Institutional acronyms. AMNH, American Museum of Natural History, New York, USA; **MACN,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciudad de Buenos Aires, Argentina; **MAU,** Museo Municipal "Argentino Urquiza", Rincón de los Sauces, Argentina; **MDS,** Museo de Dinosaurios de Salas de los Infantes, Salas de los Infantes, Spain; **MIWG,** Museum of Isle of Wight Geology (now Dinosaur Isle Visitor Centre), Sandown, Isle of Wight, United Kingdom; **MMCH,** Museo Municipal "Ernesto Bachmann", Villa El Chocón, Argentina; **MNHN,** Museum National d'Histoire Naturelle, Paris, France; **MOZ,** Museo Provincial de Ciencias Naturales "Prof. Dr. Juan A. Olsacher", Zapala, Argentina; **MPCA,** Museo Provincial "Carlos Ameghino", Río Negro, Argentina; **MPEF,** Museo "Egidio Feruglio", Trelew, Argentina; **MUCPv,** Museo Universidad Nacional del Comahue, Neuquén, Argentina; **NHMUK,** Natural History Museum, London, United Kingdom; **UNPSJB,** Universidad Nacional de la Patagonia San Juan Bosco, Comodoro Rivadavia, Argentina.

Anatomical abreviations. aas, anterior articular surface; **acc. spdl,** accessory spinodiapophyseal lamina; **acdl,** anterior centrodiapophyseal lamina; **acpl,** anterior centroparapophyseal lamina; **amedl,** anterior medial lamina; **cpaf,** centroparapophyseal fossa; **cpof,** centropostzygapophyseal fossa; **cpol,** centropostzygapophyseal lamina; **cprf,** centroprezygapophyseal fossa; **cprl,** centroprezygaphophyseal lamina; **di,** diapophysis; **f,** foramen; **fo,** fossa; **lat. cprl,** lateral centroprezygapophyseal lamina; **lat. spdl,** lateral spinodiapophyseal lamina; **lat. spol,** spinopostzygapophyseal lamina; **lat. sprl,** lateral spinoprezygapophyseal lamina; **ll,** lateral lamina; **med. cprl,** medial centroprezygapophyseal lamina; **med. spdl,** medial spinodiapophyseal lamina; **med. sprl,** medial spinoprezygapophyseal lamina; **mp,** medial pillar; **ms,** medial septum; **nc,** neural canal; **pa,** parapophysis; **pacprf,** parapophyseal centroprezygapophyseal fossa; **pas,** posterior articular surface; **pas*,** cast of the posterior articular surface; **pc,** pneumatic chamber; **pcdl,** posterior centrodiapophyseal lamina; **pcpl,** posterior centroparapophyseal lamina; **pf,** pneumatic fossa; **pl,** lateral pneumatic foramen ('pleurocel'); **posl,** postspinal lamina; **posr,** postspinal ridge; **poz,** postzygapophysis; **prz,** prezygapophysis; **prdl,** prezygodiapophyseal lamina; **prl,** intraprezygapophyseal lamina; **prpl,** prezygoparapophyseal lamina; **prsl,** prespinal lamina; **prsr,** prespinal ridge; **spdl,** spinodiapophyseal lamina; **spof,** spinopostzygapophyseal fossa; **spol,** spinopostzygapophyseal lamina; **sprf,** spinoprezygapophyseal fossa; **sprl,** spinoprezygapophyseal lamina; **tlp,** triangular lateral process; **tp,** transverse process; **vc,** ventral concavity; **vf,** vascular foramina.

SYSTEMATIC PALEONTOLOGY

SAURISCHIA Seeley, 1888
SAUROPODOMORPHA von Huene, 1932
SAUROPODA Marsh, 1878
NEOSAUROPODA Bonaparte, 1986
DIPLODOCOIDEA Marsh, 1884 (*sensu* Upchurch, 1995)
REBBACHISAURIDAE Bonaparte, 1997

Gen. et ***sp.*** indet.
Figure 3

Referred specimen*.* MAU-PV-EO-633, partial anterior-to-middle dorsal vertebra.

Description and comparisons. This axial element is composed of the dorsal part of the centrum and the ventral portion of the neural arch, including the right prezygapophysis with part of the right diapophysis, the proximal portion of the left prezygapophysis, and the base of the neural spine (Fig. 3.1–2). Considering the posteroventral position of the parapophysis with respect to the high diapophysis, the relative low neural arch, and the wide dorsal pneumatic lateral cavities, we tentatively refer MAU-PV-EO-633 to a dorsal vertebra; furthermore, the morphological comparisons with *Katepensaurus*, *Comahuesaurus*, and the diplodocid indet. MPEF-PV-1324-2 (Carballido *et al.*, 2012; Ibiricu *et al.*, 2013; Rauhut *et al.*, 2015), suggest to consider the El Orejano specimen as an anterior-to-middle dorsal vertebra. The centrum lacks most of the articular surfaces; however, the anterior articular surface seems to be slightly convex, whereas the posterior one is slightly concave in lateral view. MAU-PV-EO-633 shares this condition with the dorsal vertebrae of *Rebbachisaurus*, *Demandasaurus* (Torcida *et al.*, 2011; Wilson & Allain, 2015), and other diplodocoids, where the centra are not typically opisthocoelous but with the dorsal portion of the articular surfaces slightly convex (or concave) and ventral portion rather straight (Canudo *et al.*, 2018). Ventrally, two wide and deep lateral chambers open on both sides of a thin medial bone septum (Fig. 3.1), as seen in several rebbachisaurids (Fig. 3.3–5), such as *Rebbachisaurus*, *Lavocatisaurus*,

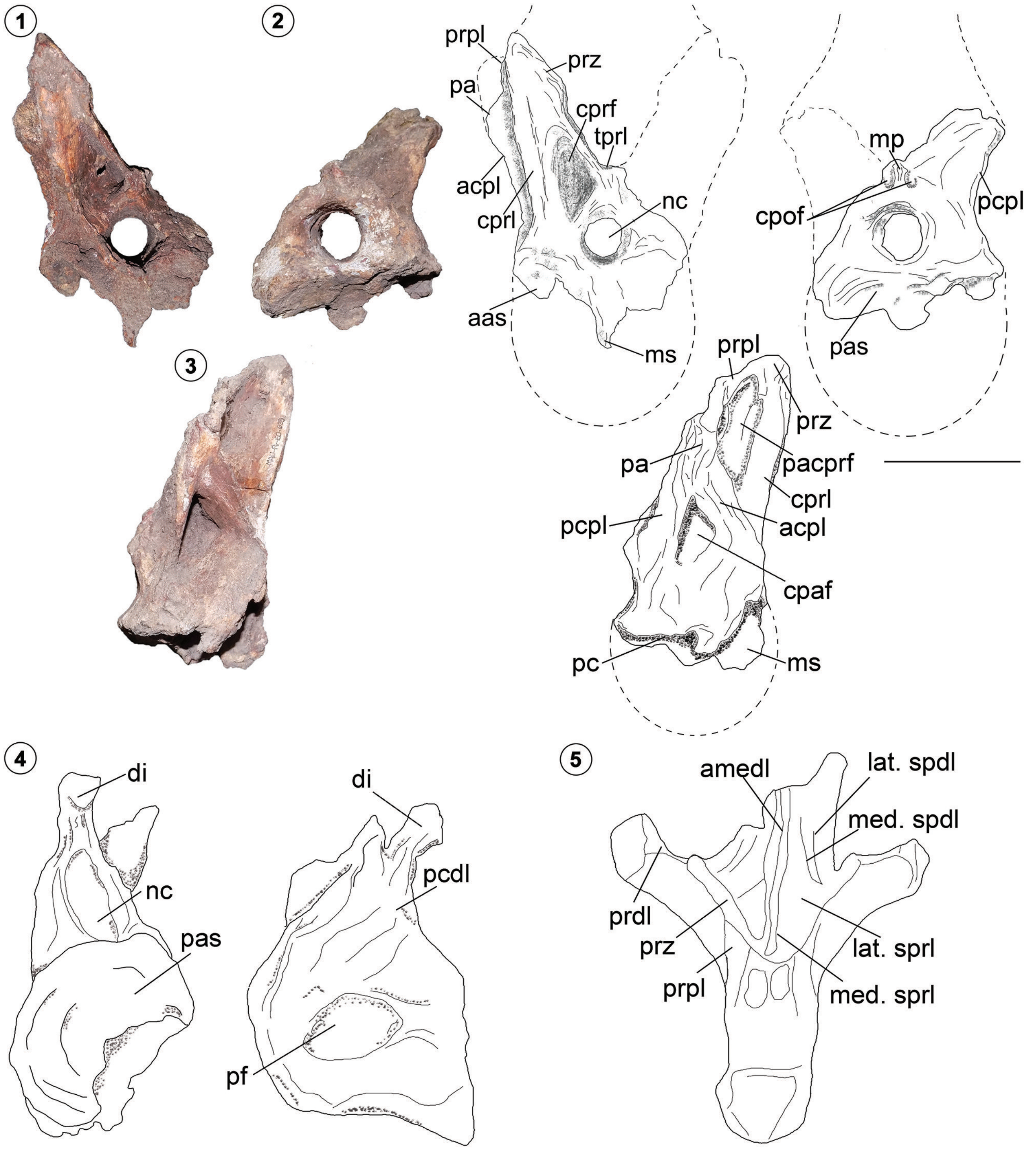

Figure 3. 1–3, Photos and line drawings of the anterior-to-middle dorsal vertebra **MAU-PV-EO-633**; **1,** anterior; **2,** posterior; and **3,** right lateral views; **4,** line drawings of the anterior-to-mid dorsal vertebra of ***Katepensaurus*** **UNPSJB-PV 1007/13** in anterior and left lateral views (modified from Ibiricu *et al.*, 2015); **5,** line drawings of the anterior dorsal vertebra of ***Comahuesaurus*** **MOZ-PV 6750** in anterior view (modified from Carballido *et al.*, 2012). Scale bar= 100 mm.

Amazonsaurus, and *Demandasaurus* (Carvalho *et al*., 2003; Torcida *et al*., 2011; Wilson & Allain, 2015; Canudo *et al*., 2018). On the dorsal surface of the chambers, remains of internal secondary septa are present.

In MAU-PV-EO-633, the anterior opening of the neural canal is circular and laterodorsally framed by wide and triangular cprf (Fig. 3.1). The prezygapophyses are laterodorsally directed in anterior view and slightly anteriorly inclined in lateral view. The articular surface is preserved only in the right prezygapophysis and is oval in dorsal view, whereas results straight and medially inclined with an angle of almost 45° in anterior view (Fig. 3.1). Anteroventrally, the prezygapophysis links with the dorsal portion of the centrum by a robust and proximally wider cprl, whereas a fragmented and strongly inclined tprl runs medially from the prezygapophysis to the dorsal margin of the neural canal (Fig. 3.1). In the right lateral surface, the parapophysis is incomplete and joins dorsally the prezygapophysis through a short prpl, whereas ventrally, the acpl and pcpl frame a deep and triangular cpaf. On the other hand, a wider and oval pacprf opens between the prpl, the acpl and a prominent cprl (Fig. 3.1). In posterior view, dorsally to the neural canal there are two cpof at the sides of an incomplete mp (Fig. 3.2).

REBBACHISAURIDAE Bonaparte, 1997

Gen. et ***sp.*** indet.
Figure 4

Referred specimen. MAU-PV-EO-634, partial anterior-to-mid dorsal vertebra.

Description and comparisons. A very fragmented dorsal vertebra composed of both prezygapophyses and a large part of the neural spine is described (Fig. 4.1). Most of the centrum is lost, however, the cast of its posterior articular surface indicates that MAU-PV-EO-634 has an oval centrum, slightly taller than wide. The centrum seems to be relatively low, being almost one-fifth of the total vertebra height. Considering the preserved cast, the posterior articular surface is slightly concave, as in *Rebbachisaurus*, *Demandasaurus*, and other rebbachisaurid dorsal vertebrae (Torcida *et al*., 2011; Carballido *et al*., 2012; Haluza *et al*., 2012; Wilson & Allain, 2015). Considering the lateral inclination of the transverse process, the high angle of the articular surfaces of the prezygapophyses (>45°), and the height of the neural arch, we tentatively consider MAU-PV-EO-634 as an anterior-to-mid dorsal element, but more posterior than MAU-PV-EO-633.

Both prezygapophyses are almost complete in MAU-PV-EO-634, preserving straight and dorsomedially directed articular surfaces in anterior view (Fig. 4.1). Ventrally, part of a robust cprl runs distally towards the anterodorsal margin of the centrum, whereas medially, a ventrally inclined thin bone is tentatively considered as part of the tprl. Furthermore, from the ventrolateral margin of the prezygapophysis a lateromedially concave prdl is directed towards the dorsolateral margin of the transverse process, whereas only few fragments of the spdl are present more laterodorsally respect to the prdl.

In MAU-PV-EO-634, the neural spine is almost complete and well preserved, lacking only part of the proximal third. The neural spine is tall, more than three times the centrum height, and petal-shaped in anterior view (Fig. 4.1), being the distal portion transversely expanded. In the anterior face of the neural spine there is a complex system of prominent neural laminae and deep fossae, as seen in *Rebbachisaurus* (Fig. 4.4), the indeterminate rebbachisaurids MACN-PV-N-35 (Fig. 4.3), and MMCH-PV-49/2-4 (Apesteguía, 2007; Haluza *et al*., 2012; Wilson & Allain, 2015). Indeed, a rough and prominent amedl runs dorsally up to half of the neural spine (Fig. 4.1–2), forming a laminar complex tentatively composed of a pair of med. sprl? and a single prsl?. The med. sprl? are thin and smooth, and diverge on the distal third of the spine where contact with robust and prominent lat. sprl. Between the med. sprl? and the prsl? there are smooth and triangular small fossae, whereas the lat. sprl and the amedl frame two dorsoventrally extended and deep fossae (Fig. 4.1). The morphology of the distal third of the neural spine of MAU-PV-EO-634 resembles MACN-PV-N-35; however, in the isolated neural arch from the La Amarga Formation, the apical fossae are oval and separated from the longer proximal fossae by a pair of ventromedially directed acc. spdl and not by dorsally divergent med. sprl (Fig. 4.3). The dorsal surface of the neural spine is convex in anterior view,

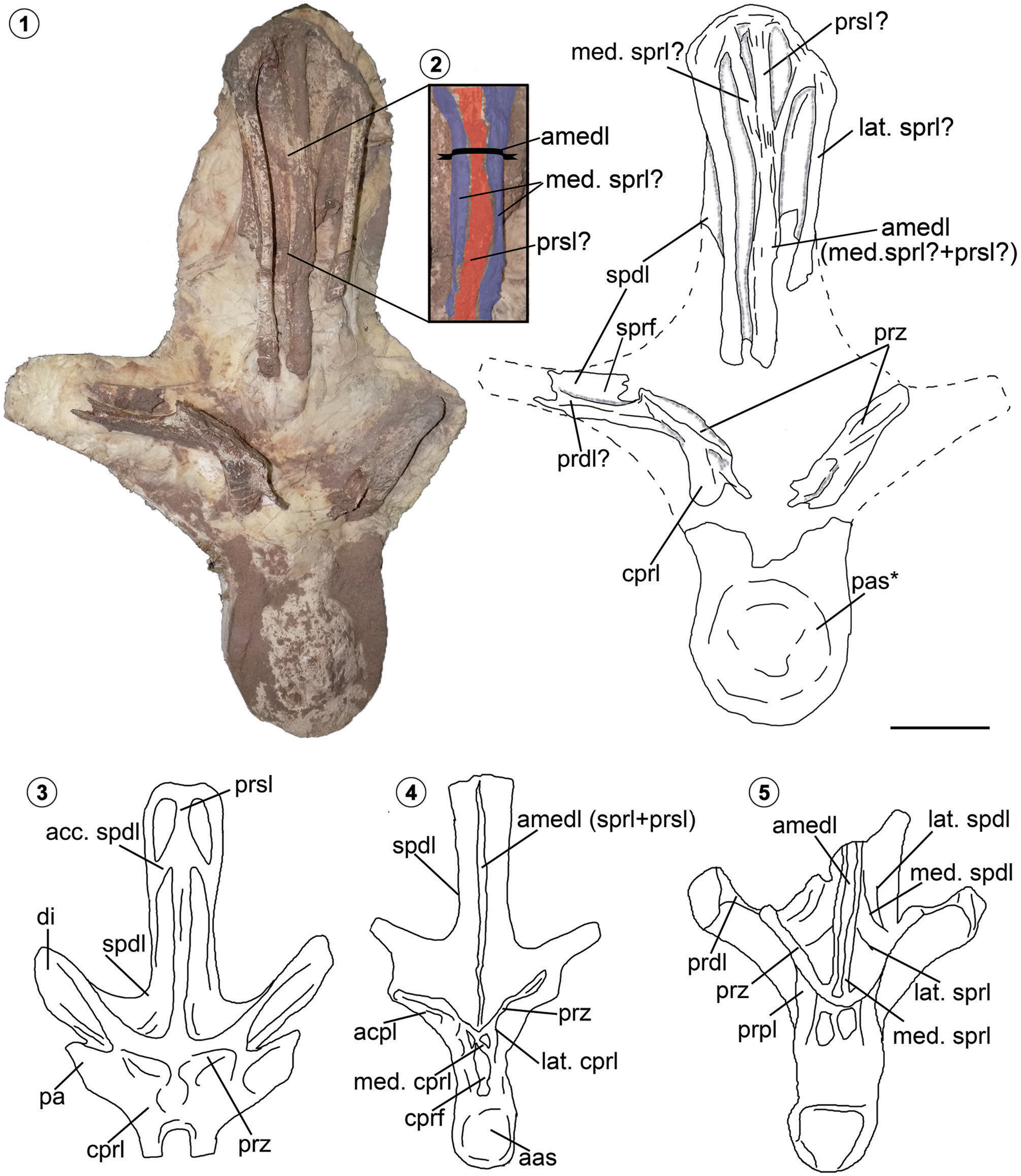

Figure 4. 1, Photo and line drawings of the anterior-to-middle dorsal vertebra **MAU-PV-EO-634** in anterior view; and **2,** detail of the amedl on the basal portion of the neural spine; **3,** line drawings in anterior view of the mid-to-posterior dorsal neural arch of indeterminate rebbachisaurid **MACN PV N35** (modified from Apesteguía, 2007; Carballido *et al.*, 2012; Wilson & Allain, 2015); **4,** line drawings in anterior view of the dorsal vertebra of ***Rebbachisaurus* MNHN-MRS 1958** (modified from Apesteguía, 2007; Carballido *et al.*, 2012; Wilson **&** Allain, 2015); **5,** line drawings in anterior view of the anterior dorsal vertebra of ***Comahuesaurus* MOZ-PV 6656** (modified from Apesteguía, 2007; Carballido *et al.*, 2012; Wilson & Allain, 2015). Scale bar= 100 mm.

as in the *Rebbachisaurus* MNHN-MRS 2000 and the MMCH-PV-49 (Fig. 7.1) (Haluza *et al.*, 2012; Wilson & Allain, 2015).

REBBACHISAURIDAE Bonaparte, 1997

Gen. et ***sp.*** indet.
Figure 5

Referred specimen. MAU-PV-EO-666, anterior caudal vertebra.

Description and comparisons. We describe an almost complete and well-preserved anterior caudal vertebra, lacking most of the anterior portion of the centrum and neural arch (Fig. 5.1–5). The centrum is short, higher than long in lateral view and hexagonal in posterior view (Fig. 5.2–3, 5). The posterior articular surface is slightly concave, whereas the anterior one is eroded. However, considering that the opisthocoelic caudal vertebrae are only recorded in *Opisthocoelicaudia* within Sauropoda (Borsuk-Bialynicka, 1977), and that Rebbachisauridae usually show an amphicoelous articulation with the posterior articular surface more concave than the anterior one (Carballido *et al.*, 2012), MAU-PV-EO-666 is here tentatively considered as amphicoelous. The ventral surface is anteroposteriorly and transversally concave (vc, Fig. 5.4), without medial grooves, ventrolateral crests, or ventral keels. The lateral surfaces are dorsoventrally convex and slightly concave anteroposteriorly, bearing some small and oval vascular foramina close to the anterior rim (Fig. 5.3, 5). A wide and elliptical lateral pneumatic opening ('pleurocel') is present close to the anterodorsal margin of the lateral surfaces, as in some diplodocoids (*e.g.*, *Diplodocus* and the indeterminate rebbachisaurids NHMUK-R36636 and UNPSJB-PV 580; Ibiricu *et al.*, 2012; Mannion & Barrett, 2013; Tschopp *et al.*, 2015), with the anterior half slightly dorsoventrally taller in lateral view (Fig. 5.3, 5). The pleurocel deeps medially within the centrum one third than centrum width, as well as seen throughout the broken anterior bone surface (Fig. 5.1).

The neural arch is located on the anterior half of the dorsal surface of the centrum, being slightly anterodorsally inclined (Fig. 5.3, 5). The transverse processes are dorsoventrally expanded, more than half of the centrum height, anteroposteriorly short and slightly anteriorly inclined in lateral view, and dorsolaterally directed in anterior view (Fig. 5.1), with an angle of 48°. The lateral surface of the transverse process is oval in shape and slightly convex in anterior view; furthermore, the ventral surface of the transverse process is transversely concave (Fig. 5.1–2), whereas the dorsal one is straight, as in *Nigersaurus* (Sereno *et al.*, 1999) and the indeterminate rebbachisaurid MIWG 5384 (Mannion *et al.*, 2011) (Fig. 5.8). The posterior surface of the transverse process is slightly concave (Fig. 5.2), as in *Demandasaurus*, *Itapeuasaurus*, and MIWG 5384 (Mannion *et al.*, 2011; Torcida *et al.*, 2011; Lindoso *et al.*, 2019), whereas the anterior one is strongly eroded and apparently there is not the pneumatic excavation seen in most Rebbachisauridae (*e.g.*, *Demandasaurus*, *Limaysaurus*, *Itapeuasaurus*, MIWG 5384, and NHMUK R36636; Calvo & Salgado, 1995; Mannion *et al.*, 2011; Torcida *et al.*, 2011; Mannion & Barrett, 2013; Lindoso *et al.*, 2019).

The posterior opening of the neural canal is tall, more than one third of the posterior centrum height, and semicircular in outline (Fig. 5.2). The postzygapophyses are distally incomplete but form a prominent V-shaped structure at the base of the neural spine in posterior view. The spof is transversely narrow and oval in shape, being particularly deep only between the postzygapophysis processes.

The neural spine is tall, almost two times than the posterior centrum height and petal-shaped in anterior view, as in *Nigersaurus*, *Demandasaurus* (Fig. 5.9), *Limaysaurus*, and MIWG 5384 (Calvo & Salgado, 1995; Sereno *et al.*, 1999; Mannion *et al.*, 2011; Torcida *et al.*, 2011) (Fig. 5.8). In MAU-EO-PV-666, the neural spine is dorsally directed in lateral view (Fig. 5.3, 5), differing from the posteriorly inclined neural spines of most Rebbachisauridae (*Amazonsaurus*, *Tataouinea*, *Itapeuasaurus*, *Demandasaurus*, *Cathartesaura*, *Limaysaurus*, MIWG 5384, UNPSJB-PV 580; Calvo & Salgado, 1995; Carvalho *et al.*, 2003; Gallina & Apesteguía, 2005; Mannion *et al.*, 2011; Torcida *et al.*, 2011; Ibiricu *et al.*, 2012; Fanti *et al.*, 2013, 2015; Lindoso *et al.*, 2019). The ll, the prsr, and the posr are prominent with a tetraradiate arrangement in cross-section, as in most Rebbachisauridae (*e.g.*, Calvo & Salgado, 1995; Pereda Suberbiola, 2003; Fanti *et al.*, 2013, 2015; Wilson & Allain, 2015). Furthermore, there is a prominent lateral triangular process on the distal third of the neural spine (Fig. 5.1–2), where the ll are particularly robust in

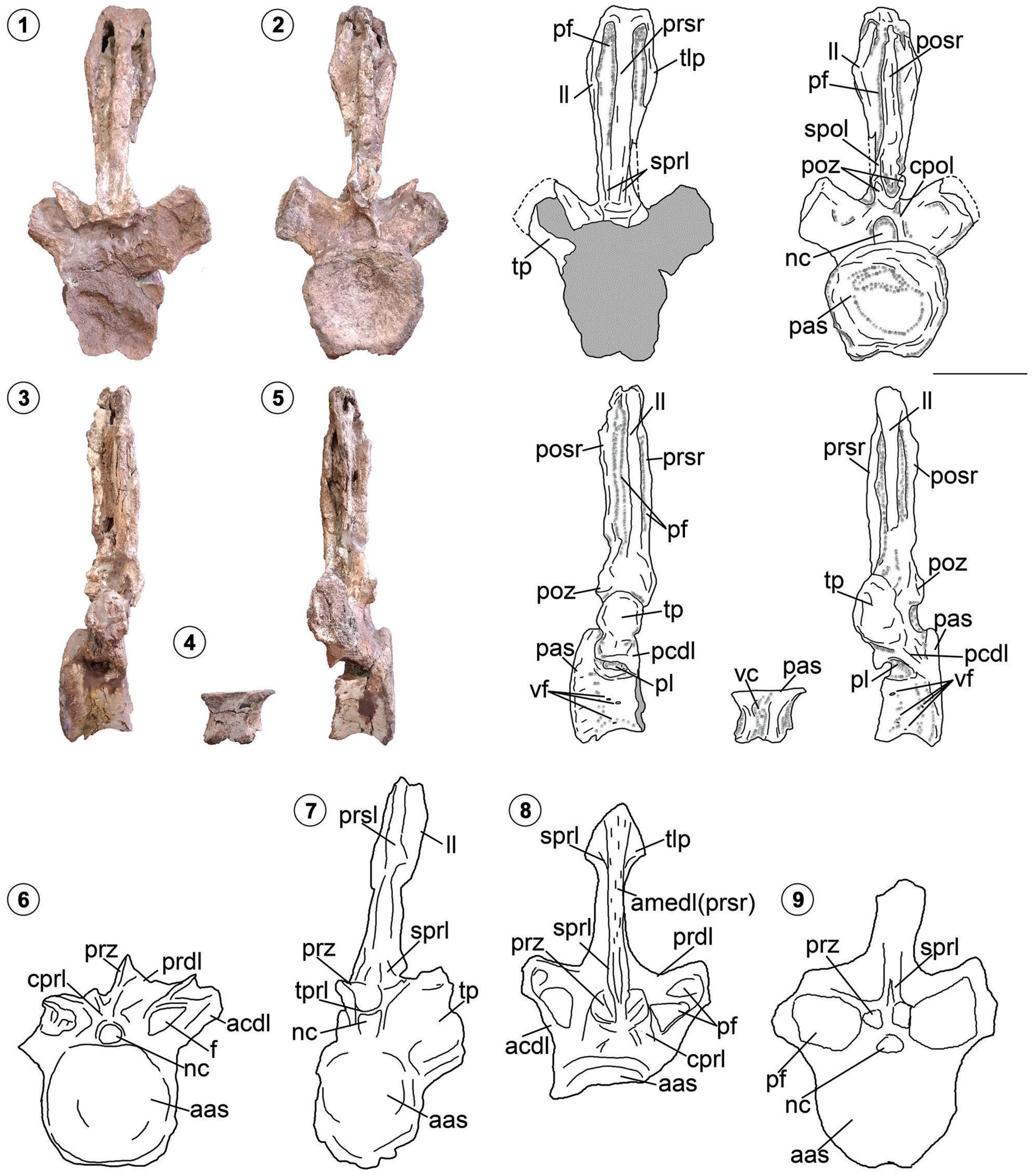

Figure 5. **1–5,** Photo and line drawings of the anterior caudal vertebra **MAU-PV-EO-666; 1,** anterior; **2,** posterior; **3,** right lateral; **4,** ventral; **5,** and left lateral views. **6.** Line drawings in anterior view of the anterior caudal vertebrae of indeterminate rebbachisaurids **NHMUK R36636** (modified from Mannion *et al*., 2011; Torcida *et al*., 2011; Ibiricu *et al*., 2012; Mannion & Barrett, 2013). **7,** Line drawings in anterior view of the **UNPSJB-PV 580** (modified from Mannion *et al*., 2011; Torcida *et al*., 2011; Ibiricu *et al*., 2012; Mannion & Barrett, 2013). **8,** Line drawings in anterior view of the **MIWG 5384** (modified from Mannion *et al*., 2011; Torcida *et al*., 2011; Ibiricu *et al*., 2012; Mannion & Barrett, 2013). **9,** Line drawings in anterior view of the *Demandasaurus* **MDS–RVII,610** (modified from Mannion *et al*., 2011; Torcida *et al*., 2011; Ibiricu *et al*., 2012; Mannion & Barrett, 2013). Scale bar= 100 mm.

lateral view, as in *Rebbachisaurus*, *Nigersaurus*, *Demandasaurus*, and MIWG 5384 (Fig. 5.8–9) (Sereno *et al.*, 1999; Mannion *et al.*, 2011; Torcida *et al.*, 2011; Wilson & Allain, 2015). In MAU-PV-EO-666, the ll seems to be a laminar complex composed of the merging of two neural laminae: the spdl and the lateral branch of the lat. spol, as in *Limaysaurus* sp., Pv-6722-MOZ, and *Apatosaurus* (Marsh, 1877; Upchurch *et al.*, 2004; Gallina & Apesteguía, 2005). However, the proximal portion of the neural spine is incomplete, and the origin of the lat. spol is unknown; thus, we prefer to consider the lat. spol as a single neural lamina and the lateral lamina as a laminar complex of uncertain composition. The sprl are short and reduced to the most proximal part of the neural spine, as in *Itapeuasaurus* (Lindoso *et al.*, 2019), being the distal portion of the anterior surface of the spine occupied by a wide and rough prsr. Two deep and dorsoventrally elongated fossae open between the ll and the prsr, as in *Amazonsaurus*, *Rebbachisaurus*, *Tataouinea*, the indeterminate rebbachisaurids MIWG 5384 (Fig. 5.8), and MMCH-Pv-45 (Carvalho *et al.*, 2003; Mannion *et al.*, 2011; Fanti *et al.*, 2013, 2015; Wilson & Allain, 2015). In anterior view, the dorsal surface of the neural spine is transversely concave (Fig. 5.1), as in *Zapalasaurus* (Salgado *et al.*, 2006), and not convex as in most of Rebbachisauridae (Fig. 5.6–9) (*e.g.*, *Amazonsaurus*, *Nigersaurus*, *Demandasaurus*, *Rebbachisaurus*, MIGW 5384; Sereno *et al.*, 1999; Carvalho *et al.*, 2003; Mannion *et al.*, 2011; Torcida *et al.*, 2011; Wilson & Allain, 2015). In posterior view, the spol are poorly preserved and limited to the basal portion of the spine, whereas the posr is prominent, rough, and slightly wider proximally than distally (Fig. 5.2). Between the posr and the ll, the dorsoventrally extended fossae are slightly shallower than in the anterior surface of the spine, where the ll are more anteromedially prominent.

DISCUSSION

Taxonomic attribution

The new axial remains from the lower section of the Huincul Formation of the central Neuquén Basin share a set of morphological features with Diplodocoidea sauropod dinosaurs, such as dorsal and anterior caudal vertebrae with tall neural arches (more than two and one-half times the dorsoventral centrum height), and a wide and deep lateral excavation in the dorsal edge of the dorsal centrum (Wilson & Sereno, 1998). Furthermore, the presence of dorsolaterally directed transverse processes and petal-shaped neural spine with tetraradiate neural laminar arrangement allows referring the dorsal vertebrae (MAU-PV-EO-633 and MAU-PV-EO-634) and the anterior caudal vertebra (MCF-PV-EO-666) from El Orejano to Rebbachisauridae (Canudo *et al.*, 2018). Indeed, the dorsal vertebra MAU-PV-EO-633 shows a slightly opisthocoelic condition and bears wide and deep lateral chambers in the centrum, whereas in the dorsal MAU-PV-EO-634 the neural spine is almost five times taller than the centrum height and petal-shaped in anterior view, with robust and prominent neural laminae (*e.g.*, amedl, sprl). The anterior caudal vertebra MAU-PV-EO-666 is considered amphicoelic, with laterodorsally directed transverse processes and high neural pedicels and neural spine; moreover, the spdl is well-developed and the hyposphenal ridge is absent, two conditions considered as synapomorphic of Rebbachisauridae (Canudo *et al.*, 2018). Furthermore, in the new anterior caudal vertebra from El Orejano there is a prominent triangular lateral process in the distal third of the neural spine, a condition that MAU-PV-EO-666 shares with most derived rebbachisaurids, Rebbachisaurinae (Canudo *et al.*, 2018).

Phylogenetic analysis

With the aim of exploring the phylogenetic relationships of the new specimens from El Orejano with other sauropods, equally weighted parsimony analyses were carried out. The preliminary round of traditional search results in 2,160 MPTs with a tree length of 1,469 steps (216 hits, CI =0.28, RI =0.61). The additional round of branch swapping (TBR) recovers 200,000 trees, collapsing the available trees set in the memory. In the resulting strict consensus, three major poly-tomies emerge, including Rebbachisauridae, Lithostrotia, and Colossosauria (Fig. S1). In this context, the three OTUs from El Orejano (MAU-PV-EO-633, MAU-PV-EO-634, MAU-PV-EO-666) are recovered as rebbachisaurid members of an unresolved clade within Diplodocoidea. To attempt to resolve the phylogenetic relationship within Rebbachisauridae, we run the IterPCR methodology set on TNT v.1.5, which detected the 24 following wild-cards: *Isanosaurus*,

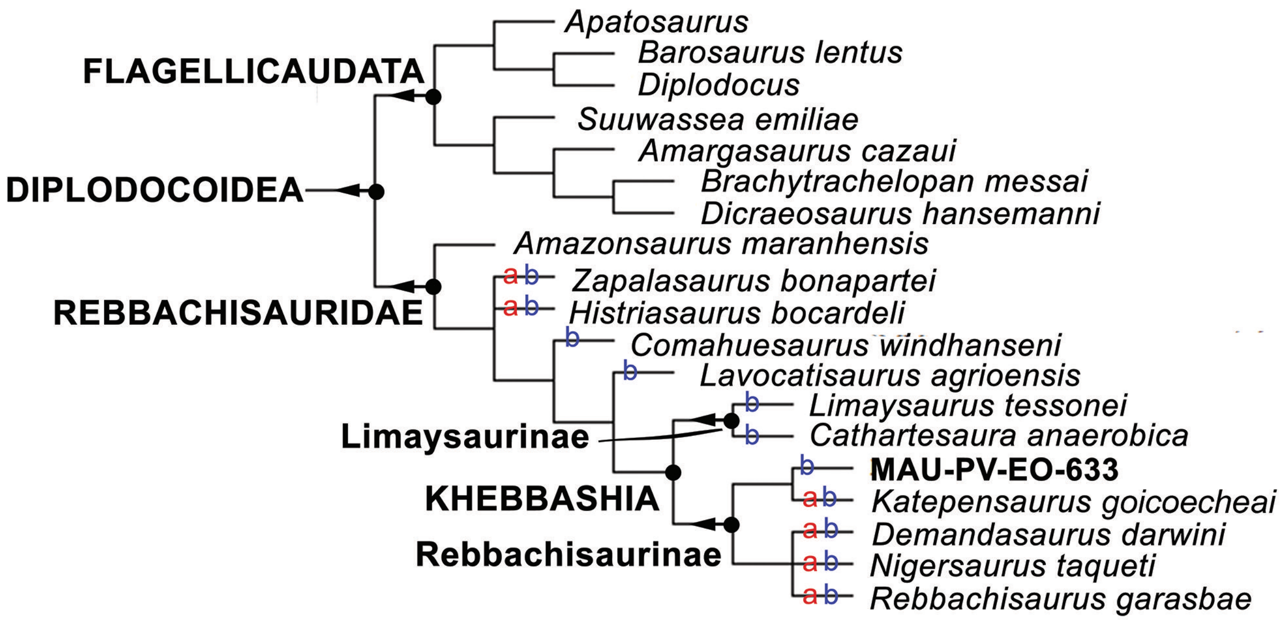

Figure 6. Detail of the reduced strict consensus tree derived from the Bellardini *et al.* (2022) matrix, recovering the new fossil remains from El Orejano locality as Rebbachisauridae members. The axial elements **MAU-PV-EO-634** (a) and **MAU-PV-EO-666** (b) were recovered as unstable taxa within Rebbachisauridae. The complete reduced strict consensus tree is available in the Online Supplementary Information (see Fig. S2).

Haplocanthosaurus, *Malarguesaurus*, *Tehuelchesaurus*, *Tastavinsaurus*, *Chubutisaurus*, *Padillasaurus*, *Venenosaurus*, *Abydosaurus*, *Brachiosaurus*, *Andesaurus*, *Nemegtosaurus*, *Tapuiasaurus*, *Rapetosaurus*, *Trigonosaurus*, *Isisaurus*, *Bonitasaura*, *Puertasaurus*, *Ninjatitan*, *Quetecsaurus*, *Rayososaurus*, *Tataouinea,* and the new axial elements from El Orejano MAU-PV-EO-634 and MAU-EO-PV-666. Despite the number of unstable taxa recovered in this analysis, we solely pruned *a posteriori* the conflictive rebbachisaurid OTUs (*i.e.*, *Rayososaurus* and *Tataouinea*) and analyzed the position of each new specimen within Rebbachisauridae alternatively (Figs. 6, S2).

The incomplete dorsal vertebra MAU-EO-PV-633 is herein recovered as a derived rebbachisaurid and the sister-taxon of *Katepensaurus*, a position supported by the presence of a dorsal centrum slightly opisthocoelic (char. N° 207, 1). *Katepensaurus* and MAU-PV-EO-633, in turn, represent the sister group of the more inclusive group of euroafrican rebbachisaurines (Fig. 6), which includes *Rebbachisaurus*, *Demandasaurus*, and *Nigersaurus*, based on three synapomorphies: the presence of an intrapostzygapophyseal lamina (tpol) on the middle-posterior dorsal vertebrae (char. N° 182, 1), the presence of a tlp on the anterior caudal neural spine (char. N° 235, 1), and the presence of cprf on dorsal neural arch (char. N° 409, 1). On the other hand, both MAU-PV-EO-634 and MAU-PV-EO-666 were recovered as unstable taxa in different positions within Rebbachisauridae. Indeed, the dorsal vertebra MAU-PV-EO-634 occupies all the alternative positions more derived than *Amazonsaurus* (Fig. 6), which is herein considered as the basalmost Rebbachisauridae, a condition that suggests the presence of a set of plesiomorphic and apomorphic features on the poorly preserved axial element from El Orejano, at least amongst Rebbachisauridae. The position of MAU-PV-EO-634 within the clade that includes *Zapalasaurus* and every other rebbachisaurid more derived than *Amazonsaurus* is supported by two synapomorphic features: the presence of a “festooned” spdl on the dorsal neural spines (char. N° 199, 1), and the dorsally directed transverse process on the anterior caudal vertebrae (char. N° 230, 1). Similarly, the almost complete anterior caudal vertebra MAU-PV-EO-666 is unstable within Rebbachisauridae; however, it is herein recovered as a basal rebbachisaurid, being alternatively sister taxon of *Zapalasaurus*, *Histriasaurus*, and the most derived rebbachisaurid *Katepensaurus*, *Demandasaurus*, *Rebbachisaurus*, and *Nigersaurus*.

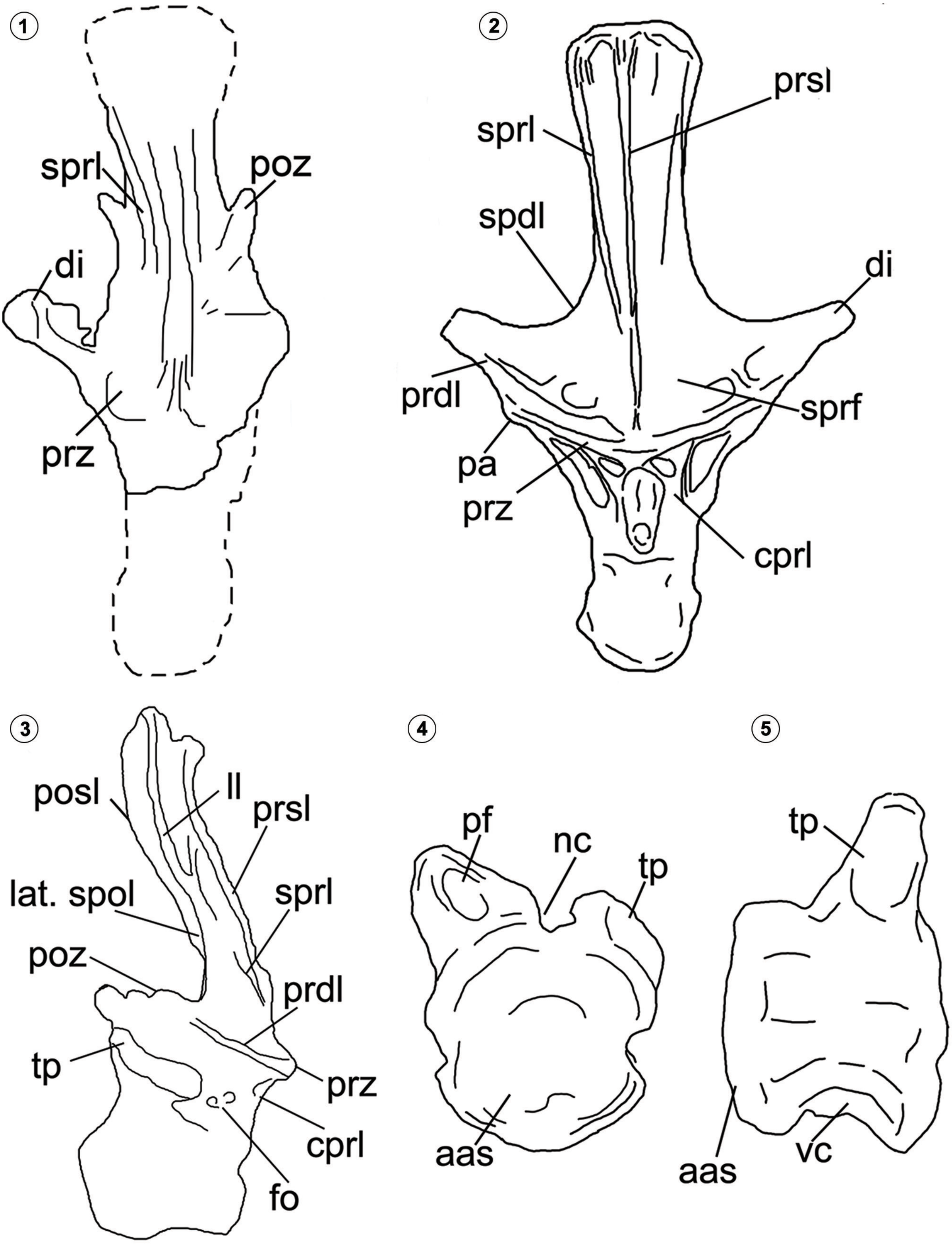

Figure 7. 1–5, Line drawings of the rebbachisaurid specimens from the Huincul Formation, considered for the morphological comparisons with the new findings from El Orejano locality (modified from Gallina & Apesteguía, 2005 and Haluza *et al*., 2012); **1,** anterior dorsal vertebra **MMCH-PV-49/2** in anterior view; **2,** posterior dorsal vertebra **MMCH-PV-49/17** in anterior view; **3,** anterior caudal vertebra of ***Cathartesaura*** **MPCA-232** in right lateral view; **4,** anterior caudal vertebra of ***Limaysaurus*** **MUCPv-153** in anterior view; **5,** anterior caudal vertebra of ***Limaysaurus*** **MUCPv-153** in left lateral view. Not in scale.

Comparisons with other rebbachisaurids from Huincul Formation

The osteological and phylogenetic analyses strongly indicates that the new axial elements from the El Orejano are related to rebbachisaurid sauropod dinosaurs, being the element MAU-PV-EO-633 recovered as a Rebbachisaurinae and MAU-PV-EO-634 and MAU-PV-EO-666 occupying multiple positions amongst rebbachisaurids (Fig. 6). In order to analyze the morphological diversity of Rebbachisauridae from the Neuquén Basin, we compared the rebbachisaurids known for the Huincul Formation with the new specimens described here (Fig. 7). As noted above, the rebbachisaurids described for this formation are all coming from the lower section of the southern Neuquén Basin: *Cathartesaura anaerobica* Gallina & Apesteguía, 2005, the paratype of *Limaysaurus tessonei* Calvo & Salgado, 1995, and the indeterminate rebbachisaurid specimen from "Cañadón de las Campanas" MMCH-PV-49 (Haluza *et al.*, 2012).

Cathartesaura was formalized on the basis of few postcranial bones coming from the lower section of the Huincul Formation of "La Buitrera" locality, in the northewestern of Río Negro Province, Patagonia, Argentina. The holotype (MPCA-232) includes poorly preserved axial and appendicular elements, among which only the anterior caudal vertebra can be compared with MAU-PV-EO-666 (Fig. 7.5). In *Cathartesaura* the caudal centrum is amphiplatyan, subcircular in anterior view and lacks pneumatic cavities, unlike MAU-PV-EO-666 where the centrum is amphicoelous, ventrally concave in anterior view and with two deep and oval pneumatic fossae that open anterodorsally in lateral view (Fig. 5.3, 5). In MPCA-232 the neural arch is at least twice the centrum height and located toward the anterior half of the centrum (Fig. 7.5), as in the anterior caudal vertebra from El Orejano; moreover, as in other rebbachisaurids, in both caudal vertebrae the transverse processes are wing-like and laterodorsally directed. However, in MPCA-232 the transverse process falls posteriorly to the neural spine in lateral view and not below them as in MAU-PV-EO-666 (Fig. 5.3, 5). The caudal vertebrae of both rebbachisaurids from the Huincul Formation also differ with respect to the morphology of the neural spine, being straight and dorsally directed in MAU-PV-EO-666 and sinusoidal and posteriorly inclined in *Cathartesaura* (Fig. 7.5). Moreover, in the latter rebbachisaurid both prsl y posl are robust and prominent, especially distally, reaching the base of the neural arch, whereas in MAU-PV-EO-666 there are prsr and posr instead of single prsl and posl. Indeed, the prsr and posr are roughly laminar complexes that proximally comprise short and thin sprl and spol, respectively. Finally, the lateral lamina of *Cathartesaura* represents a laminar complex resulting from the joint of the lat. spol, the spdl, and the sprl on the middle of the neural spine in lateral view (Fig. 7.5). Conversely, in MAU-PV-EO-666 the preserved lateral lamina is a simple structure whose laminar components (*i.e.*, lat. spol?+spdl) probably merge more proximally than in *Cathartesaura*; however, the base of the spine is poorly preserved and it is difficult to discern which neural laminae form part of the lateral lamina.

The type material of *Limaysaurus* includes several cranial and postcranial elements belonging to different individuals and coming from the top of the Candeleros Formation (the holotype MUCPv-205, and the referred specimen MUCPv-206) and the base of the Huincul Formation (the referred specimen MUCPv-153), which outcrop to the southwest of the Villa El Chocón locality, in the southern of Neuquén Basin. Despite the poorly preserved conditions of the axial elements of *Limaysaurus*, different morphological features of caudal vertebrae can be compared with the new rebbachisaurid specimens from the El Orejano (Fig. 7.4–5). In the anterior caudal vertebrae of *Limaysaurus* MUCPv-153 the centra are anteroposteriorly short and subcircular in anterior and posterior views, with a slightly concave posterior articular surface, as in MAU-PV-EO-666 (Fig. 5.2). However, *Limaysaurus* lacks a lateral pleurocoel and the ventral surface of the caudal centrum is convex in anterior view (Fig. 7.4), whereas the El Orejano specimen shows a ventral surface anteroposteriorly and transversely concave. Furthermore, *Limaysaurus* has a longitudinal groove on the ventral surface, absent in MAU-PV-EO-666. The transverse processes are dorsolaterally directed and slightly forward inclined in both rebbachisaurids; however, in MUCPv-153 they are composed of dorsal and ventral bars (Fig. 7.4), a condition that is considered as an autapomorphic feature by Calvo & Salgado (1995). Considering the neural spine, *Limaysaurus* shares with MAU-PV-EO-666 a tall and petal-shaped spine with a tetraradiate arrangement of the neural laminae, but differs from the El Orejano caudal vertebra for showing a convex dorsal surface and lacking a triangular lateral process (Fig. 5.1–5.2; Calvo & Salgado, 1995, fig. 10). Furthermore, *Limaysaurus* and MAU-PV-EO-666 differ for the inclination of the neural spine, being slightly backward inclined in the former and dorsally directed in the latter (Fig. 5.3, 5; Calvo & Salgado, 1995, fig. 10).

Further rebbachisaurid record is represented by MMCH-PV-49, a well-preserved specimen composed of several axial and appendicular elements from the southern Neuquén Basin, only briefly described by Haluza *et al.* (2012). The dorsal vertebrae of MMCH-PV-49 (Fig. 7.1–2) show low subcircular centra and tall neural arches with petal-shaped neural spines, as in MAU-PV-EO-634 (Fig. 4.2). On the other hand, in MMCH-PV-49 a simple prsl runs throughout the anterior surface of the spines, lacking the divergent med. sprl and the laminar complex with prsl seen in the El Orejano specimen (Fig. 4.2).

Considerations on the Rebbachisauridae fossil record

Rebbachisauridae represents a diplodocoid neosauropod clade less nested than Flagellicaudata (Dicraeosauridae+ Diplodocidae), known from the Hauterivian of Europe (Dalla Vecchia, 1998, 2005) to the Cenomanian–Turonian of Patagonia (Calvo & Salgado, 1995; Gallina & Apesteguía, 2005; Ibiricu *et al.*, 2013, 2015). Despite the fossil record, some authors argued an earlier origin of Rebbachisauridae, placing the divergence from Flagellicaudata in the Middle Jurassic on the basis of two proofs: the new dicraeosaurid *Lingwulong* from the Middle Jurassic of Asia, and the reassessment of "*Amphicoelias fragillimus*" (Tschopp *et al.*, 2015; Carpenter, 2018; Xu *et al.*, 2018). Indeed, the recent description of *Lingwulong* from the Yanan Formation (upper Toarcian–Bajocian; late Lower–early Middle Jurassic) represents not only the earliest dicraeosaurid but also the oldest flagellicaudatan record, suggesting the presence of a ghost-lineage at least from the late Toarcian. Therefore, the putative Rebbachisauridae-Flagellicaudata divergence time-lapse would have happened during the Hauterivian, when the first rebbachisaurid occurrence was recorded (*i.e.*, *Histriasaurus*; Dalla Vecchia, 1998, 2005), or even earlier if we consider the recent reassessment of *Xenoposeidon* from the Berriasian of England as a rebbachisaurid sauropod (Taylor, 2018). On the other hand, the incomplete dorsal neural arch AMNH-FR-5777 from the Morrison Formation (late Kimmeridgian–early Tithonian) that Cope (1878) described as the holotype of "*Amphicoelias fragillimus*", was recently considered as a basal rebbachisaurid by Carpenter (2018). Only on the basis of the original pictures, the author recognizes a new set of diagnostic features and formalizes the new genus *Maraapunisaurus* on the missed axial element AMNH-FR-5777, identifying a robust and "festooned" spdl as an unambiguous synapomorphic feature of Rebbachisauridae. Despite the enigmatic *Maraapunisaurus* would represent the earliest rebbachisaurid evidence, playing a crucial role to reconstruct part of the ghost-lineage linked with Rebbachisauridae origin and evolution, the validity of the taxon is still debated (Whitlock & Wilson Mantilla, 2020), especially considering the impossibility to access and review the holotype. Therefore, pending on more consistent data, we prefer to take with care the hypothesis that *Maraapunisaurus* represents the earliest Rebbachisauridae member, not including it between the rebbachisaurid fossil record (Fig. 8; Tab. 1).

Although the origin of Rebbachisauridae is still debated and uncertain, probably due to a low taxonomic diversification and a poorly geographical dispersion of the clade during the Late Jurassic, most recent analyses show two major dispersion events: the Early Cretaceous spot during the Hauterivian–Barremian (Fig. 8.1) (Dalla Vecchia, 1998; Pereda Superbiola, 2003; Salgado *et al.*, 2006; Apesteguía, 2007; Mannion, 2009; Mannion *et al.*, 2011) and the last dispersion event (Fig. 8.3) during the early Late Cretaceous (Cenomanian) in Patagonia (*e.g.*, Whitlock, 2011; Carballido *et al.*, 2012; Wilson & Allain, 2015; Canudo *et al.*, 2018). In this context, the evidence of different taxa in the Hauterivian–Barremian of Laurasia (*i.e.*, *Histriasaurus, Demandasaurus*) and Gondwana (*Zapalasaurus*; Salgado *et al.*, 2006) suggests a wide geographical dispersion since the Early Cretaceous, a condition that would support the early origin of the clade. On the other hand, during the Cenomanian–Turonian the Rebbachisauridae fossil record was limited to Gondwana (Fig. 8.3) (Calvo & Salgado, 1995; Gallina & Apesteguía, 2005; Ibiricu *et al.*, 2012, 2013, 2015, 2020; Lindoso *et al.*, 2019) and particularly diversified in Patagonia, where, together with basal titanosaurians, rebbachisaurids represent the most important paleoecological modelers of the early

Upper Cretaceous terrestrial ecosystems (Otero & Salgado, 2015). Despite the high faunal diversification during the Cenomanian–Turonian, there is no evidence of Rebbachisauridae in the fossil record from the Coniacian, revealing a post-Turonian sauropod faunal change, with Titanosauria as the only worldwide dominant mega-herbivores of the Late Cretaceous (*e.g.*, Carballido *et al.*, 2017; Gallina *et al.*, 2021).

Rebbachisauridae was considered for many years a low-diversified sauropod clade due to the presence of few taxa and very fragmented and poorly preserved specimens (Lavocat, 1954; Calvo & Salgado, 1995; Bonaparte, 1997; Carvalho *et al.*, 2003; Pereda Superbiola, 2003). However, recent works have improved the rebbachisaurid fossil

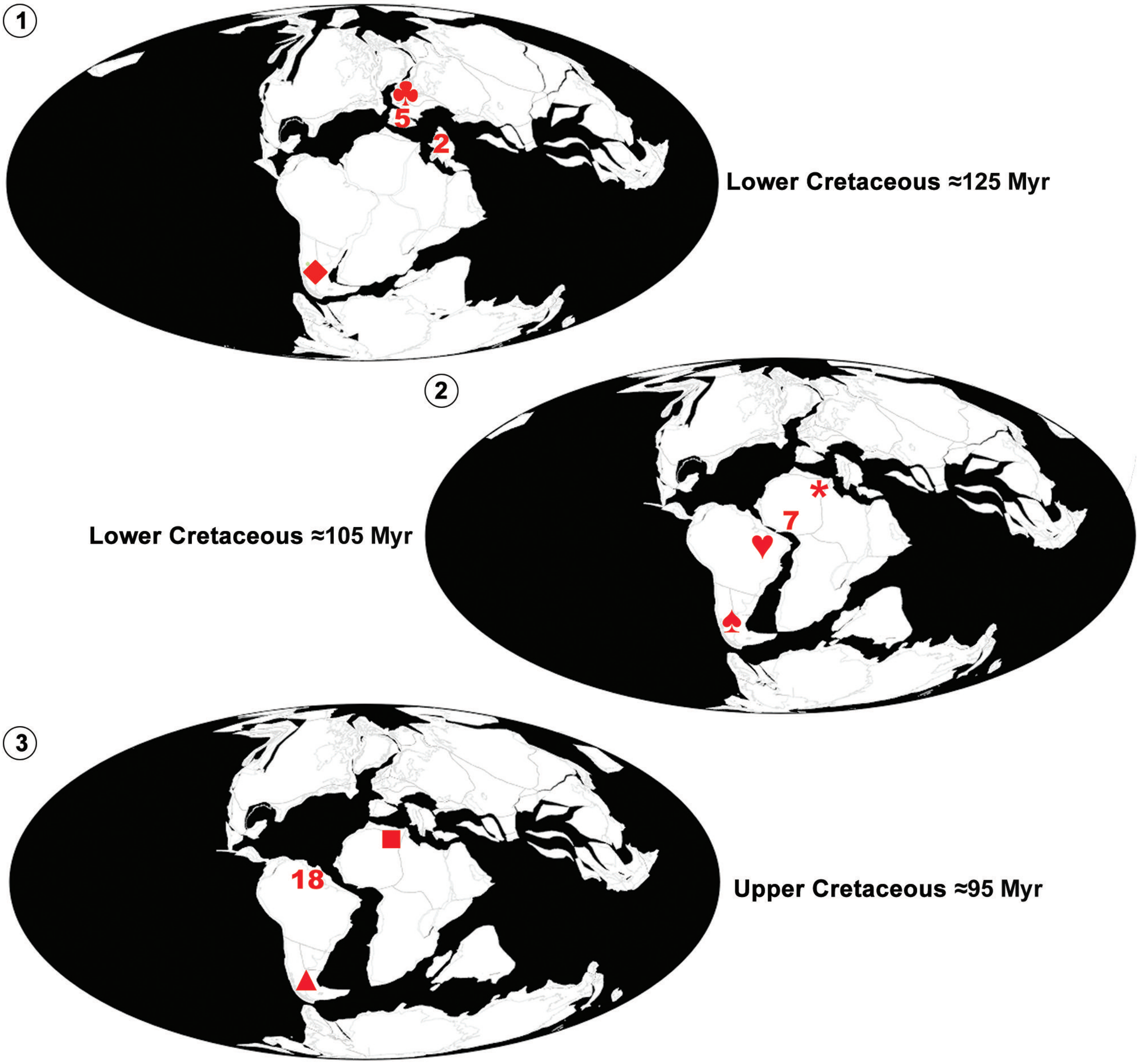

Figure 8. Paleogeographycal locations of the Rebbachisauridae fossil record during the **1,** Hauterivian–Barremian; **2,** Aptian–Albian; and **3,** Cenomanian–Turonian lapse-time. Red numbers and symbols refer to the rebbachisaurid occurrences listed in Table 1. The maps were modified from www.paleobiodb.org.

TABLE 1 - Rebbachisauridae fossil record

N°	Specimen/Taxon	Collection number	Geographical provenance	Stratigraphic provenance	Stage	Bibliographic reference
				LATE CRETACEOUS		
28 (▲)	Rebbachisauridae indet.	MAU-PV-EO-633; MAU-PV-EO-634; MAU-PV-EO-666	El Orejano, Neuquén Province, Argentina	Lower section of the Huincul Formation	Cenomanian–Turonian	This contribution
27 (▲)	Rebbachisauridae indet.	UNPSJB-PV 580; UNPSJB-PV 1004; UNPSJB-PV 1005; UNPSJB-PV 1098	Estancias Laguna Palacios and Ocho Hermanos, Musters Lake, Chubut Province, Argentina	Lower member (UNPSJB-PV 580; UNPSJB-PV 1005; UNPSJB-PV 1098) and upper member (UNPSJB-PV 1004) of the Bajo Barreal Formation	Cenomanian–Turonian	Ibiricu *et al.* (2012, 2020)
26 (▲)	*Katepensaurus*	UNPSJB-PV 1007	Estancia Laguna Palacios, Chubut Province, Argentina	Lower Member of the Bajo Barreal Formation	Cenomanian–Turonian	Ibiricu *et al.* (2013, 2015)
25 (▲)	Rebbachisauridae indet.	MMCH-PV-49	Las Campanas Creek, Villa El Chocón, Neuquén Province, Argentina	Huincul Formation	Cenomanian–Turonian	Apesteguía *et al.* (2010); Haluza *et al.* (2012)
24 (▲)	Rebbachisauridae indet.	MCF-PVPH-633	Aguada Grande, Neuquén Province, Argentina	Huincul Formation	Cenomanian–Turonian	Gallina & Apesteguía (2005)
23 (▲)	*Limaysaurus* (paratype)	MUCPv-153	Villa El Chocón, Neuquén Province, Argentina	Lower section of the Huincul Formation	Cenomanian–Turonian	Calvo & Salgado (1995)
22 (▲)	*Cathartesaura*	MPCA- 232	La Buitrera, Río Negro Province, Argentina	Lower section of the Huincul Formation	Cenomanian–Turonian	Gallina & Apesteguía (2005)
21 (▲)	*Rayososaurus*	MACN-N 41	Agrio del Medio, Neuquén Province, Argentina	Upper section of the Candeleros Formation	Cenomanian	Bonaparte (1996, 1997); Carballido *et al.* (2010)
20 (▲)	Rebbachisauridae indet.	MMCH-PV-41; MMCH-PV-71	Villa El Chocón, Neuquén Province, Argentina	Upper section of the Candeleros Formation	Cenomanian	Haluza & Canale (2011); Paulina Carabajal *et al.* (2016)
19 (▲)	*Limaysaurus* (holotype)	MUCPv-205	Villa El Chocón, Neuquén Province, Argentina	Upper section of the Candeleros Formation	Cenomanian	Calvo & Salgado (1995)
18	*Itapeuasaurus*	UFMA. 1.10.1960	Cajapio,Maranhão State, Brazil	Alcântara Formation	Cenomanian	Lindoso *et al.* (2019)
17 (■)	*Rebbachisaurus*	MNHN-MRS 1958, 1979, 1980, etc.	Gara Sbaa, Morocco	Lower section of Kem Kem beds	Cenomanian	Lavocat (1954); Russell (1996); Sereno *et al.* (1996); Wilson & Allain (2015)
16 (■)	Rebbachisauridae indet.	NHMUK R36636	Tafilalt, Morocco	Lower section of Kem Kem beds	Cenomanian	Mannion & Barrett (2013)
15 (▲)	*Nopcaspondylus*	lost	Picún Leufú, Neuquén Province, Argentina	Candeleros Formation?	Cenomanian?	Nopcsa (1902); Apesteguía (2007)

TABLE 1 - Continuation

N°	Specimen/Taxon	Collection number	Geographical provenance	Stratigraphic provenance	Stage	Bibliographic reference
				EARLY CRETACEOUS		
14 (♥)	Rebbachisauridae indet.	UFRJ-DG 535 R; UFRJ-DG 700 R; UFRJ-DG 578 R; UFRJ-DG 646 R; UFRJ-DG 701 R	Chapada do Apodi, Ceará State, Brazil	Açu Formation	Albian (Albian–Cenomanian?)	Da Costa Pereira *et al.* (2020)
13 (*)	*Tataouinea*	ONM DT 1–36	Jebel El Mra, Tunisia	Oum ed Diab Member, Ain el Guettar Formation	Albian	Fanti *et al.* (2013, 2015)
12 (*)	Rebbachisauridae indet.	MT 210	Tataouine, Tunisia	Oum ed Diab Member, Ain el Guettar Formation	Albian	Fanti *et al.* (2014)
11 (♥)	Rebbachisauridae indet.	CCC-17; CCC-30; CCC-60	Coroatá, Maranhão State, Brazil	"Undifferentiate Unit"	Albian?	Castro *et al.* (2007)
10 (♥)	*Amazonsaurus*	MN 4555, etc.; UFRJ-DG 58-R/1; etc.	Mata, Maranhão State, Brazil	Itapecuru Formation	Aptian–Albian	Carvalho *et al.* (2003)
9 (♠)	*Comahueasaurus*	MOZ-PV 6722	Cerro Aguada del León, Neuquén Province, Argentina	Puesto Quiroga Member, Lohan Cura Formation	Aptian–Albian	Salgado *et al.* (2004); Carballido *et al.* (2012)
8 (♠)	*Lavocatisaurus*	MOZ-Pv 1232	Agrio del Medio, Neuquén Province, Argentina	Pichi Neuquén Member, Rayoso Formation	Aptian–Albian	Salgado *et al.* (2012); Canudo *et al.* (2018)
7	*Nigersaurus*	MNN GAD512	Gadoufaoua, Niger	El Rhaz Formation	Aptian–Albian	Sereno *et al.* (1999)
6 (♦)	*Zapalasaurus*	Pv-6127-MOZ	La Picaza, Neuquén Province, Argentina	Piedra Parada Member, La Amarga Formation	Barremian–Aptian	Salgado *et al.* (2006)
5	*Demandasaurus*	MPS-RV II-2, 3, 4; etc.	Salas de los Infantes, Burgos Province, Spain	Upper section of the Castrillo de la Reina Formation	Barremian–Aptian	Pereda Superbiola *et al.* (2003); Torcida *et al.* (2011, 2012)
4 (♦)	Rebbachisauridae indet.	MACN PV N35	La Amarga, Neuquén Province, Argentina	Puesto Antigual Member, La Amarga Formation	Barremian	Apesteguía (2007)
3 (♣)	Rebbachisauridae indet.	MIWG 6544; MIWG 5384	Isle of Wight, England	Wessex Formation	Barremian	Mannion (2009); Mannion *et al.* (2011)
2	*Histriasaurus*	WN-V6 (lost)	Kolone, Istria Peninsula, Croatia	Adriatic Dinaric Platform	Hauterivian–Barremian	Dalla Vecchia (1998, 1999, 2005)
1 (♣)	*Xenoposeidon*	NHMUK PV R2095	Hastings, East Sussex, England	Ashdown Formation?	Berriasian?	Lyddeker (1893); Taylor & Naish (2007); Taylor (2018)

The specimens are listed following their chronostratigraphic provenances, from most modern to earliest. The numbers and symbols refer to the landmarks of Figure 8.

record with new and more complete evidence (Mannion *et al.*, 2011; Torcida *et al.*, 2011; Carballido *et al.*, 2012; Canudo *et al.*, 2018; Lindoso *et al.*, 2019), allowing to shed light on the taxonomic and morphological diversification of the family. To date, 14 taxa are consensually recognized as Rebbachisauridae members (*e.g.*, Canudo *et al.*, 2018; Lindoso *et al.*, 2019; Lerzo *et al.*, 2021), in addition to further specimens that are referred to the clade but are generally excluded from the phylogenetic analyses due to the high-fragmentary conditions, such as *Xenoposeidon*, *Nopcsaspondylus*, and other indeterminate rebbachisaurids (Tab. 1). Considering the phylogenetic relationships within Rebbachisauridae, *Histriasaurus*, *Amazonsaurus*, *Lavocatisaurus*, *Zapalasaurus*, and *Comahuesaurus* are consensually recovered as the basalmost taxa (Mannion *et al.*, 2011; Torcida *et al.*, 2011; Carballido *et al.*, 2012; Canudo *et al.*, 2018), whereas the clade recently formalized as Kebbashia by Fanti *et al.* (2015), comprises the more nested rebbachisaurids, which are included in the Limaysaurinae and Rebbachisaurinae sub-families. In particular, Limaysaurinae includes the South American rebbachisaurids *Cathartesaura* and *Limaysaurus*, and probably *Rayososaurus* (Carballido *et al.*, 2010; Canudo *et al.*, 2018), whereas *Katepensaurus* is recovered in different analyses, although with low support, as the only Gondwanan member of Rebbachisaurinae, the clade composed of African and European taxa (*e.g.*, Ibiricu *et al.*, 2013, 2015; Canudo *et al.*, 2018). Indeed, considering the Gondwanan less nested forms and the more nested European and African members, some authors proposed a Gondwanan origin of Rebbachisauridae and a subsequent dispersion to Eurasia (Mannion *et al.*, 2011; Torcida *et al.*, 2011; Carballido *et al.*, 2012). In this context, four specimens from the Cenomanian–Turonian of Patagonia, MMCh-PV-49, *Cathartesaura,* and *Limaysaurus* from the Neuquén Basin, and *Katepensaurus* from Golfo San Jorge Basin, would represent the most modern record of Rebbachisauridae. However, lacking radiometric dating, no direct chronostratigraphic correlationships are available between the different lithostratigraphic units of both basins, which make it difficult to discern the most modern evidence of Rebbachisauridae. Indeed, *Katepensaurus* comes from the upper part of the Lower Member of the Bajo Barreal Formation (Upper Cretaceous, Chubut Group), which is considered by Ibiricu *et al.* (2020) as Cenomanian in age. However, recent chronostratigraphic analyses on Chubut Group (Ibiricu *et al.*, 2020; Krause *et al.*, 2020) suggest a Cenomanian–Turonian age for Bajo Barreal Formation, indicating a possible correlation with the Huincul Formation of the Neuquén Basin. On the other hand, *Cathartesaura* and *Limaysaurus* (paratype) come from the lower section of the Huincul Formation, which is considered upper Cenomanian in age. In this context, the new rebbachisaurid evidence from the lower section of the Huincul Formation of El Orejano also represents one of the most modern records of Rebbachisauridae. Moreover, the new rebbachisaurid specimens from the central Neuquén Basin suggest that different populations of derived Rebbachisauridae inhabited also to the north of Huincul High before of the Turonian faunal turnover. Finally, in spite of these considerations about the most modern rebbachisaurid evidence, which lack of further geological supports, we consider that the new findings from El Orejano are significant to attest a more diversified rebbachisaurid fauna close to the Cenomanian–Turonian transition than previously known.

CONCLUSIONS

We present new rebbachisaurid evidence from the Huincul Formation, which is here considered as one of the most modern records of Rebbachisauridae for the Neuquén Basin. The new axial elements were found isolated and in poorly preserved conditions; however, they show a set of morphological features that allow us to refer them to Rebbachisauridae, such as pneumatized dorsal and caudal neural arches with tall and petal-shaped neural spines, an amphicoelic caudal articulation, and a tetraradiate arrangement of the dorsal and caudal neural laminae. The osteological and morphological comparisons between the new material and the Rebbachisauridae members from the Huincul Formation suggest that there is at least a new form, different to the other known taxa. However, due to the incomplete preserved conditions of the bones and lacking different diagnostic features, we consider more parsimoniously to refer the new specimens from El Orejano to Rebbachisauridae indet. Regardless, the almost complete dorsal element MAU-PV-EO-634 shows a lateral inclination of the med. sprl in the distal portion of the neural spine never seen in other sauropods, adding new information about the morphological diversification of Rebbachisauridae. Furthermore, despite the ambiguous phylogenetic results of the new remains, which were expected considering the poorly preserved conditions of the specimens, our analysis suggest that different derived forms of Rebbachisauridae inhabited the central Neuquén Basin during the Cenomanian/Turonian transition. Finally, the new rebbachisaurid record from El Orejano proves that every kind of new findings, however fragmentary, can contribute to improve our knowledge about the morphological and taxonomic diversity of the last Rebbachisauridae, shedding light on the faunal composition of Late Cretaceous ecosystems.

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