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SHORT COMMUNICATION

CHANGES IN VERTEBRAL LAMINAE ACROSS THE CERVICODORSAL TRANSITION OF A WELL-PRESERVED REBBACHISAURID (DINOSAURIA, SAUROPODA) FROM THE CENOMANIAN OF PATAGONIA, ARGENTINA

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The fossil record of rebbachisaurid sauropods has greatly increased recently (Calvo and Salgado, 1995; Bonaparte, 1996; Dalla Vecchia, 1998; Sereno et al., 1999, 2007; Medeiros and Schultz, 2001; Pereda-Suberbiola et al., 2001, 2003; Salgado et al., 2004, 2006; Gallina and Apesteguía, 2005; Apesteguía, 2007; Mannion, 2009). The first fossil remains belonging to this group were described by Nopcsa (1902) but only recently recognized as a rebbachisaurid (Calvo and Salgado, 1995; Apesteguía, 2007). Lavocat (1954) erected *Rebbachisaurus garasbae*, which has a scapula with broad, 'racquet'-shaped blade, and a mid-dorsal vertebra with a very tall neural spine. This family is mostly known from rather fragmentary remains, and many specimens are unpublished or only partially described (Gallina and Apesteguía, 2005).

In this contribution, we present new materials assignable to Rebbachisauridae, recovered from the Huincul Formation, Neuquén Group, near Villa El Chocón, Neuquén Province (Fig. 1A, B). The lowermost section of this geological unit has yielded other dinosaur taxa, such as *Skorpiovenator bustingorryi* (Canale et al., 2009). The rebbachisaurid remains correspond to a single, partially articulated, and exceptionally preserved skeleton, which includes cervical and dorsal vertebrae, thoracic ribs, scapula, and a humerus (Fig 1C).

The importance of studying complete serial elements of the skeleton (e.g., vertebral series) lies on the ability to track specific elements (i.e., landmarks), which are useful to unambiguously recognize homologous structures (Wilson, 1999; Otero et al., In press; Wilson et al., 2011). In this regard, the preserved cervicodorsal series described herein gives remarkable anatomical and systematic information, allowing the recognition of the transitional morphology, topology, and extent of the vertebral laminae.

Institutional Abbreviations—MMCH-Pv, Museo Municipal "Ernesto Bachmann," Villa El Chocón, Neuquén Province, Argentina; **MPS-RV**, Museo de los dinosaurios de Salas de los Infantes, Salas de los Infantes, Burgos, Spain; **MUCPv**, Museo de Geología y Paleontología, Universidad Nacional de Comahue, Neuquén Province, Argentina.

Anatomical Abbreviations—ac, acromion; **acdl**, anterior centrodiapophyseal lamina; **cdf**, centrodiapophyseal fossa; **co**, coracoid; **cprf**, centroprezygapophyseal fossa; **cprl**, centroprezygapophyseal lamina; **d**, diapophysis; **dc**, deltopectoral crest; **eprl**, epipophyseal-prezygapophyseal lamina; **gl**, glenoid; **hh**, humeral head; **p**, parapophysis; **pcdl**, posterior centrodiapophyseal lamina; **po**, postzygapophysis; **pocdf**, postzygapophyseal-centrodiapophyseal fossa; **podl**, postzygodiapophyseal lamina; **pr**, prezygapophysis; **prcdf**, prezygapophyseal-centrodiapophyseal fossa; **prdl**, prezygodiapophyseal lamina; **sc**, scapular blade; **sdf**, spinodiapophyseal fossa; **spdl**, spinodiapophyseal lamina; **spof**, spinopostzygapophyseal fossa; **sprf**, spinoprezygapophyseal fossa; **sprl**, spinoprezygapophyseal lamina.

SYSTEMATIC PALEONTOLOGY

SAURISCHIA Seeley, 1887
SAUROPODOMORPHA von Huene, 1932
SAUROPODA Marsh, 1878
DIPLODOCOIDEA Upchurch, 1995
REBBACHISAURIDAE Sereno, Beck, Dutheil, Larsson, Lyon, Moussa, Sadleir, Sidor, Varricchio, Wilson, and Wilson, 1999 gen. et sp. indet.

Materials—MMCH-Pv-49 (Fig. 1C) consists of a partially articulated skeleton with an articulated series of seven cervical (MMCH-Pv-49/5–11) and four anterior dorsal (MMCH-Pv-49/1–4) vertebrae, seven disarticulated middle to posterior dorsal vertebrae (MMCH-Pv-49/12–18), fragmentary thoracic ribs (MMCH-Pv-49/21), a nearly complete right scapula and coracoid (MMCH-Pv-49/19), and a complete right humerus (MMCH-Pv-49/20).

Locality and Horizon—Las Campanas creek, 25 km southwest of Villa El Chocón, Neuquén Province, Argentina (Fig. 1A). The bones were preserved in the Huincul Formation (upper Cenomanian) of the Neuquén Group, which corresponds to fluvial deposits of quartzitic sandstones with high sinuosity and conglomeratic levels (Sánchez et al., 2008). The remains were found in sheet flood deposits associated with paleosols (Fig. 1B).

DESCRIPTION

The specimen MMCH-Pv 49 can be recognized as a rebbachisaurid based on the presence of six unambiguous derived characters of this family: accessory lateral lamina connecting podl and sprl in middle and posterior cervical vertebrae; 'petal'-shaped dorsal neural spines; 'racquet'-shaped scapular blade; presence of a hook-like acromion process; spdl webbing 'festooned' from spine; diapophyses on dorsal vertebrae inclined dorsally more than 30° from the horizontal; and spol divided near the postzygapophyses in posterior dorsal vertebrae (Wilson, 2002; Gallina and Apesteguía, 2005; Sereno et al., 2007; Whitlock, 2011).

The description of the cervical vertebrae is based mainly on the posterior-most cervical element preserved in the sequence (MMCH-Pv 49/5; Fig. 2C, D). The centrum is opisthocoelous and elongate (centrum length is 4 times the centrum height), with a well-developed ventral median ridge. Two pneumatic

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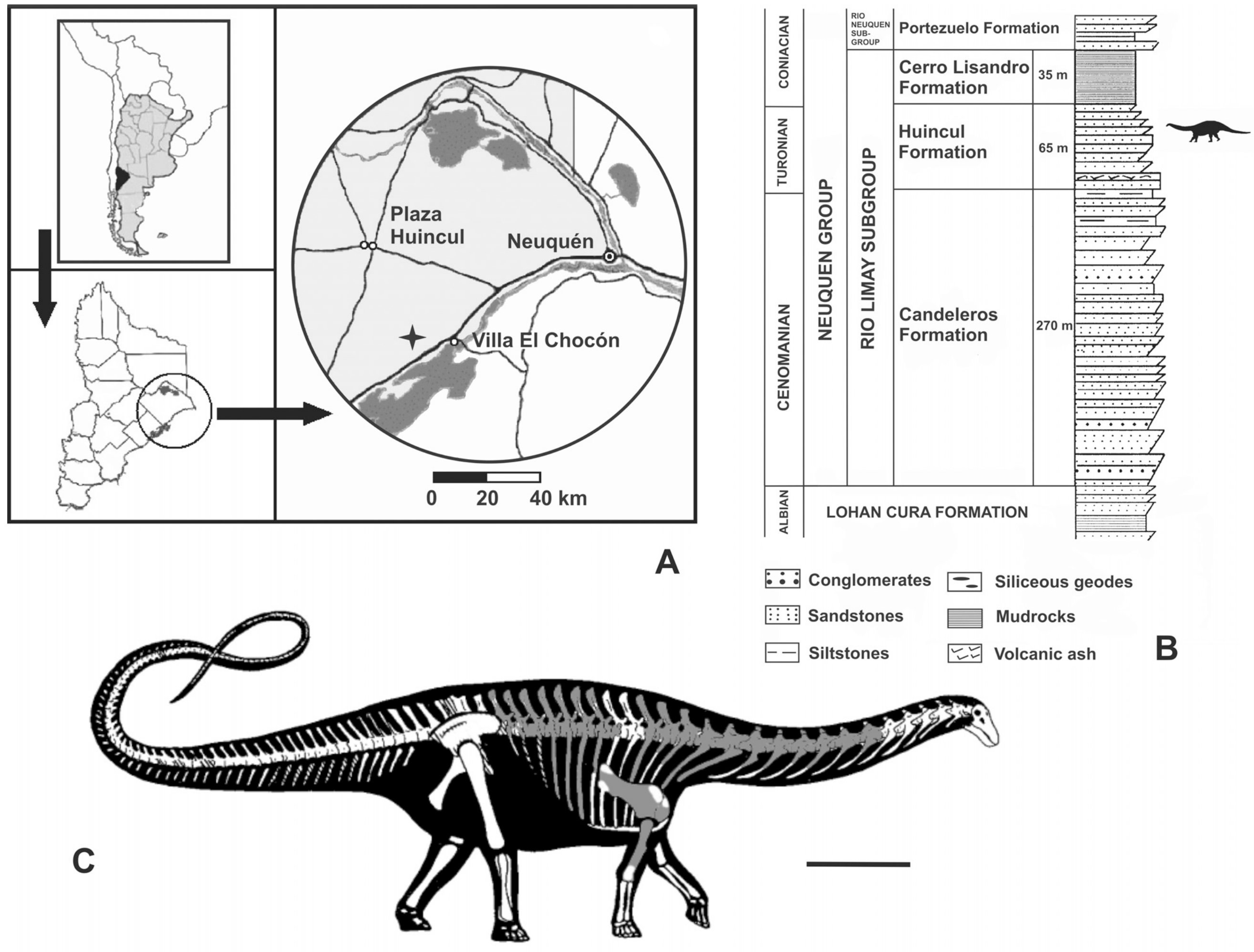

FIGURE 1. MMCH-Pv 49. **A**, locality map showing the Las Campanas creek locality (indicated by star), about 20 km SSE of El Chocón. **B**, stratigraphic position of the partial skeleton MMCH-Pv-49 (sauropod icon). **C**, reconstruction of a diplodocoid sauropod (adapted from Carvalho et al., 2003) showing preserved elements of MMCH-Pv-49 in grey. Scale bar equals 1 m.

cavities are present in the lateral centrum, which are separated by an oblique bony septum. However, the anterior-most vertebra preserved in the sequence (MMCHPv-49/11; Fig. 2A, B) has only one pneumatic cavity, which based on its position probably corresponds to the posterior pneumatic cavity of the posterior-most cervical. The prezygapophyses project past the anterior margin of the centrum and have subcircular articular facets. A deep spinopostzygapophyseal fossa (spof) is delimited posterodorsally by the neural spine, ventrally by the dorsal part of neural canal, and laterally by the spol and cpol. The postzygapophyses extend dorsolaterally from the junction of the spol and cpol. The diapophyses and parapophyses are slightly anteriorly placed, supporting ventrolaterally positioned cervical ribs that bear a short anterior process and a more elongated and sharp posterior process that does not exceed the length of the centrum. The neural spine of the anterior-most cervical vertebrae of the series (MMCH-Pv 49/11) is not as tall as the centrum is long and has a posteriorly inclined anterior margin. This proportion changes gradually along the cervical series, and the posterior-most neural spine (MMCH-Pv 49/5) is as tall as the centrum is long and has an anteriorly inclined anterior margin. A short and broad lamina divides the prezygapophyseal-centrodiapophyseal fossa (prcdf), which is delimited by cprl, prdl, and acdl. This lamina is comparable with the accessory lamina (AL2) described for *Cathartesaura anaerobica* (Gallina and Apesteguía, 2005). Another accessory lamina (most probably the eprl) connects the sprl and podl at their midlength (see Discussion). In posterior cervical vertebrae, the sprl acquires a ‘V’-shaped outline in lateral view (Fig. 3D). We refer to the posteriorly oriented vertex of the ‘V’ as the ‘flexion point,’ which separates a ‘spinal portion’ that extends parallel to the long axis of the neural spine and a ‘prezygapophyseal portion’ that extends parallel to the prezygapophyses. The dorsal vertebrae (Fig. 2E–G) are characterized by short centra (centrum length/centrum height is approximately 1) that are slightly opisthocoelous and have a single, suboval pneumatic foramen visible in lateral view, as in other rebbachisaurids (e.g., *Limaysaurus* MUCPv-205). Two diapophyseal laminae, the acdl and pcdl, delimit the cdf. The cprl arises from the centrum and is divided before it contacts the prezygapophyses, dividing the cprf. Both pairs of zygapophyses contact at the midline as a continuous ‘U-eaves and shelf complex’ that may have permitted wider movements between successive vertebrae (Apesteguía et al., 2010:fig. 5). The neural canal is low and subcircular in anterior view, with a straight dorsal edge. The ‘petal’-shaped

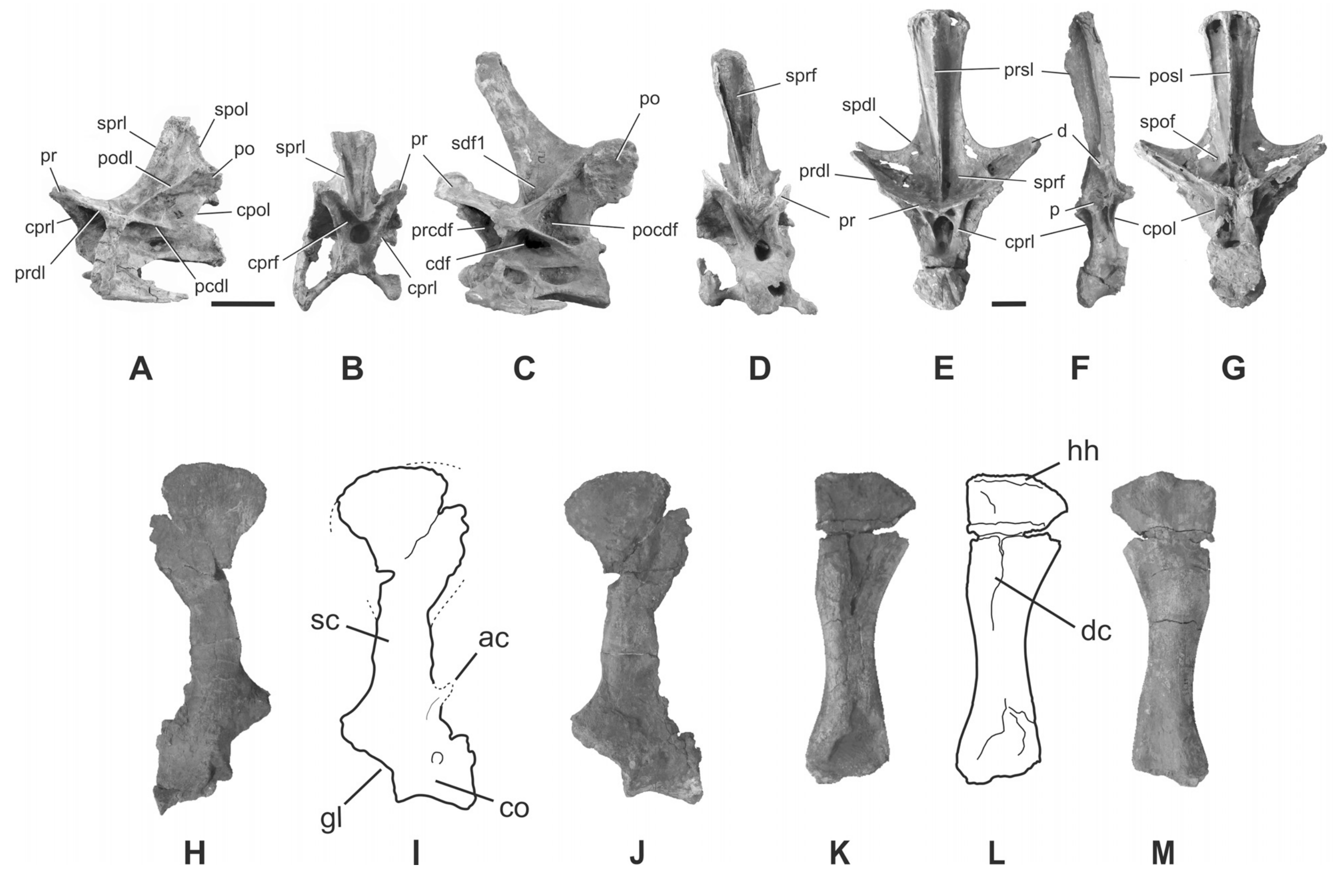

FIGURE 2. Axial and appendicular bones of MMCH-Pv 49. **A**, **B**, anterior cervical vertebra (MMCH-Pv 49/11) in right lateral (reversed) (**A**) and anterior (**B**) views. **C, D**, posterior cervical vertebra (MMCH-Pv 49/5) in right lateral (reversed) (**C**) and anterior (**D**) views. **E**–**G**, mid- to posterior dorsal vertebrae (MMCH-Pv 49/17) in anterior (**E**), right lateral (reversed) (**F**), and posterior (**G**) views. **H**–**J**, right scapula and coracoid (MMCH-Pv 49/19) in medial (**H**) and lateral (**I, J**) views (**I**, explanatory drawing of **J**). **K**–**M,** right humerus (MMCH-Pv 49/20) in anterior (**K**, **L**) and posterior (**M**) views (**L**, explanatory drawing of **K**). Scale bars equal 10 cm (**E**–**M** have the same scale).

neural spine is very tall (neural spine height/centrum length ratio is 3–4) and dorsally expanded. This complex structure is reinforced anteriorly by the prespinal lamina and both sprl, and posteriorly by the postspinal lamina plus both medial spol.

The right scapula is co-ossified to the coracoid and shows the characteristic morphology of Rebbachisauridae. It has a broad, 'racquet'-shaped blade (Fig. 2H–J) that forms a ca. 45° angle with the acromial process. Although not well preserved, its hook-like morphology was observable in the field, as is redrawn here. The glenoid is robust and broad, strongly medially bevelled, and mostly constituted by the scapula. The coracoid is only preserved in the area surrounding the glenoid fossa, with the coracoid foramen located near the scapulocoracoid suture.

The right humerus (Fig. 2K–M) is almost complete, lacking part of its proximal and distal ends. The humeral shaft cross-section is elliptical, with its long axis oriented transversely. The deltopectoral crest, which is damaged, spans one-third of the proximal shaft. A shallow olecranon fossa is present on the posterior surface of the distal end.

DISCUSSION

Comparisons with *Cathartesaura anaerobica*

The materials described herein (MMCH-Pv 49) and the rebbachisaurid *Cathartesaura anaerobica* come from exposures of the Huincul Formation near the border between Río Negro and Neuquén provinces, which raises the possibility that they are the same taxon. Unfortunately, however, the fragmentary nature of *C. anaerobica* limits comparisons between these specimens to a single posterior cervical vertebra. Despite the fact that the overall morphology of the posterior cervical vertebra of both specimens is similar, there are some notable differences in the centrum and neural arch.

The morphology of the two lateral pneumatic cavities of posterior cervical centra differs between these specimens. The anterior cavity of *C. anaerobica* has a kidney-shaped morphology, whereas in MMCH-Pv 49 it is oval. The posterior pneumatic fossa in the centrum of MMCH-Pv 49 has a thickened, straight dorsal margin that is anteroposteriorly oriented, whereas that of *C. anaerobica* has a posteroventrally oriented dorsal margin. In addition, the posterior pneumatic cavity of MMCH-Pv 49 does not excavate the interior of the centrum to its posterior end, as it does in *C. anaerobica* (Gallina and Apesteguía, 2005:155). The neural arch of the posterior cervical vertebra also differs between specimens. The specimen MMCH-Pv 49 differs from *C. anaerobica* in the presence of a posteriorly flexed sprl, giving a more anterior orientation to the neural spine. This flexion gives the sprl an anteriorly inclined 'V'-shaped outline in lateral view in MMCH-Pv 49, whereas in *C. anaerobica* the sprl present an anteriorly 'U'-shaped outline in lateral view, which generates a wide base of the neural spine in the latter taxon.

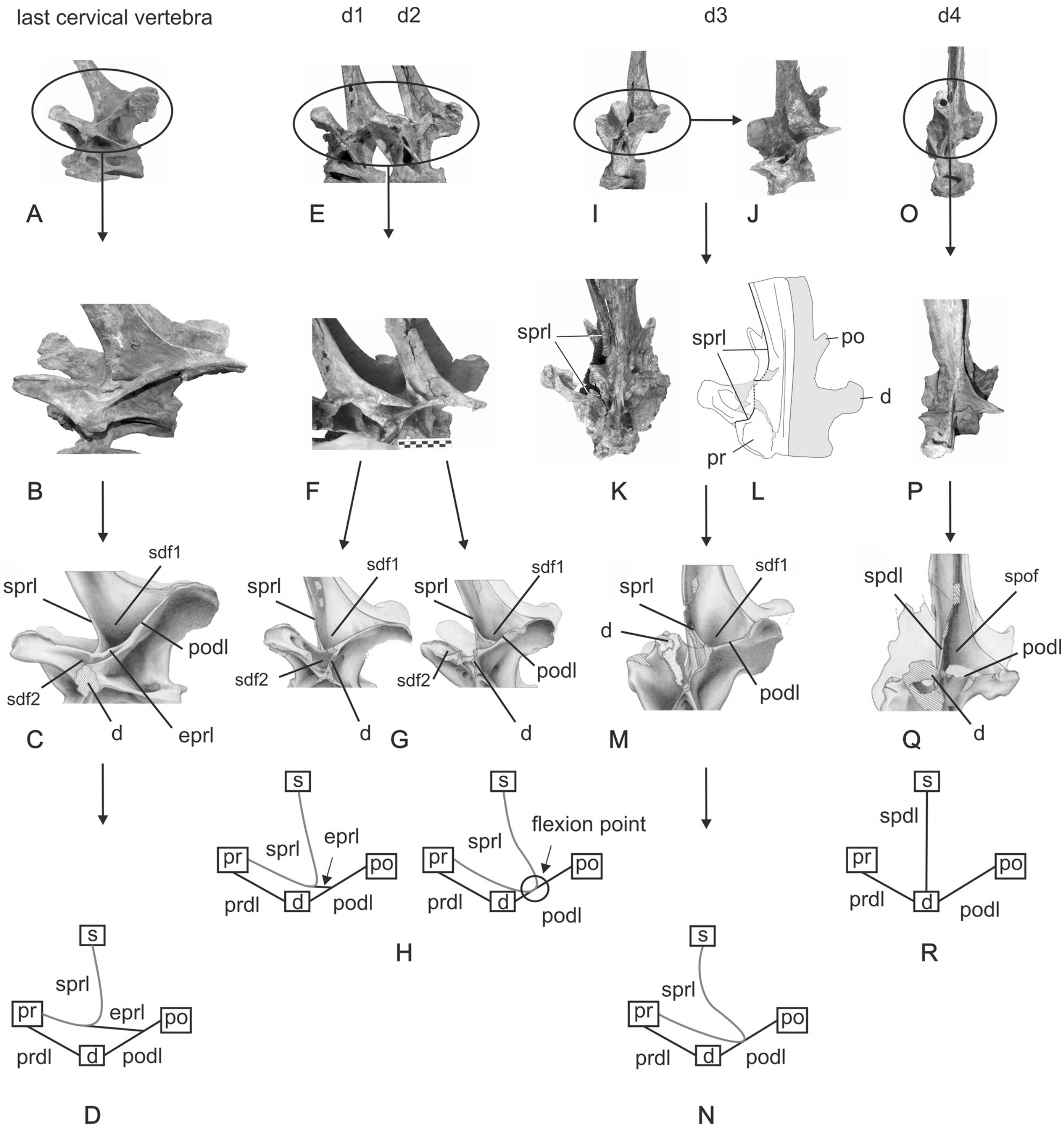

FIGURE 3. 'Pectoral vertebrae' of MMCH-Pv 49 showing the cervicodorsal transition above the zygodiapophyseal plane. **A**–**D**, last cervical vertebra (MMCH-Pv 49/5) in right lateral (reversed) (**A**) and dorsolateral (**B**–**D**) views. **C** and **D** are explanatory and schematic drawings of **B**, respectively. **E**–**H**, dorsal vertebrae 1 (MMCH-Pv 49/4) and 2 (MMCH-Pv 49/3) in right lateral (reversed) (**E**) and dorsolateral (**F**–**H**) views. **G** and **H** are explanatory and schematic drawings of **F**, respectively. **I**–**N**, dorsal vertebra 3 (MMCH-Pv 49/2) in right lateral (reversed) (**I**), dorsolateral (**J**, **M**, **N**) and anterior (**K**, **L**) views. **L** is an explanatory drawing of **K**; **M** and **N** are explanatory and schematic drawings of **J**, respectively. **O**–**R**, dorsal vertebra 4 (MMCH-Pv 49/1) in right lateral (reversed) (**O**) and dorsolateral (**P**–**R**) views. **Q** and **R** are explanatory and schematic drawings of **P**, respectively. Not to scale.

Emergence of the Spinodiapophyseal Lamina in Cervicodorsal Vertebrae

The neural arches of cervical vertebrae of rebbachisaurids have a horizontally oriented accessory lamina connecting the middle sections of sprl and podl. This short accessory lamina is visible on the lateral side of the neural arch of MMCH-Pv 49, dividing the sdf into two smaller fossae, an upper sdf1 and a lower sdf2 (Wilson et al., 2011; Fig. 3A–D). This lamina has been referred to as the "accessory lamina" (*Limaysaurus tessonei*; Calvo and

Salgado, 1995), the "accessory lamina 1" (*Cathartesaura anaerobica*; Gallina and Apesteguía, 2005), and most recently the "epipophyseal-prezygapophyseal lamina" (*Nigersaurus taqueti* [Wilson et al., 2011:fig. 6H]; *Euhelopus zdanskyi* [Wilson and Upchurch, 2009]). Gallina and Apesteguía (2005) recovered the eprl as a synapomorphy of Rebbachisauridae in their phylogenetic analysis, but it is also present in other sauropods and other saurischians (Wilson et al., 2011). Whereas this lamina is developed into a low ridge in *Cathartesaura anaerobica* and *Limaysaurus tessonei*, in MMCH-Pv 49 it is a well-developed crest with lateral and medial walls that clearly contact the sprl anteriorly and the podl posteriorly. A similar condition is present in *Nigersaurus* (Wilson et al., 2011:7) and *Euhelopus* (Wilson and Upchurch, 2009:fig. 10). *Erketu* also presents an eprl that divides the sdf, but with a slightly different arrangement in which it contacts the spol and podl (Wilson et al., 2011:fig. 6D).

The preservation of the nearly complete presacral vertebral series in the new materials presented herein, where this transition can be seen, provides improvement in the explanation of the anatomical changes in the lamination of the vertebral segment comprised between posterior cervical and anterior dorsal vertebrae and the fossae delimited ('pectoral series' sensu Wilson, 1999; Fig. 3). We will focus the description in the lamination above the zygodiapophyseal plane, defined by the zygapophyses and diapophyses, where major changes occur. The sprl experiences the most drastic changes in the cervicodorsal transition. These changes can be ordered in four stages, in an overlapping sequence from cervical to dorsal vertebrae: (1) posteroventral flexion of the sprl in the last cervical vertebra (Fig. 3A–D); (2) posterior displacement of the vertex of the sprl until it contacts the podl and shortening of the eprl in the first dorsal vertebra (Fig. 3E–H); (3) lateral migration of the vertex of the sprl, until it contacts the diapophysis, implying the lateral migration of the spinal portion of the sprl in the second dorsal vertebra (Fig. 3I–N); (4) the sprl and the eprl disappear, and the spdl appears in the third dorsal vertebra. This latter change is accompanied by a change in the arrangement of the spinodiapophyseal fossae, from dorsal (sdf1) and ventral (sdf2) fossae delimited by the eprl in cervical vertebrae, to anterior (sprf) and posterior (spof) fossae delimited by the spdl in dorsal vertebrae (Fig. 3O–R).

This scheme is similar to that seen in other sauropods with known cervicodorsal transition involving an eprl (e.g., *Euhelopus*: see Wilson and Upchurch, 2009). In this regard, the eprl disappears in dorsal 2 in MMCH-Pv 49 (Fig. 3H), whereas in *Euhelopus* it disappears in dorsal 3 (Wilson and Upchurch, 2009). As in the latter taxon, there is no vertebra in which the eprl and the spdl are both present. Nonetheless, the cervicodorsal transition present in MMCH-Pv 49 displays some interesting particularities not reported in any other sauropod. The sprl and the eprl vary together from the last cervical to dorsal 2. The eprl decreases its length as the sprl increases its length and gradually takes its place (Fig. 3D, H). In dorsal 3 the eprl is completely lost and the sprl contacts the podl (Fig. 3N). Finally, in dorsal 4 the sprl is not visible on the lateral side of the vertebra and, it might be fused to the prsl as a composite lamina (Fig. 3R), as seen in *Diplodocus.*

CONCLUSIONS

The well-preserved remains of Rebbachisauridae presented herein provided new information of the morphological changes in the cervicodorsal transition above the zygodiapophyseal plane, specifically those occurred in the sprl and the eprl. A close relationship between MMCH-Pv 49 and *Cathartesaura anaerobica* is possible, but comparisons are limited to a single vertebra at the moment. The affinities of MMCH-Pv 49 will be resolved with further discoveries.

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