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BONAPARTESAURUS RIONEGRENSIS, A NEW HADROSAURINE DINOSAUR FROM SOUTH AMERICA: IMPLICATIONS FOR PHYLOGENETIC AND BIOGEOGRAPHIC RELATIONS WITH NORTH AMERICA

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ABSTRACT—The Gondwanan hadrosaurid dinosaur record is relatively poorly known and very complicated. A new hadrosaurid, *Bonapartesaurus rionegrensis*, gen. et sp. nov., from the late Campanian–early Maastrichtian of the Salitral Moreno site, Argentina, is characterized by the following combination of characters: the ratio between the height of the neural spines and that of the centrum of the sacral vertebrae greater than 3.5; neural spines of the anterior section of the caudal vertebrae extremely long and evenly expanding distally; a preacetabular process of the ilium slightly deflected ventrally, with the angle greater than 150°; the ratio between the maximum dorsoventral depth of the posterior end of the preacetabular process and the dorsoventral distance from the pubic peduncle to the dorsal margin of the ilium less than 0.50; the ratio between the dorsoventral height and anteroposterior length of the iliac blade 0.8 or greater; asymmetrical lateral profile of the supraacetabular process; the posterior portion of the postacetabular process markedly thicker mediolaterally as a result of the dorsomedial twist of the postacetabular process; an anteriorly expanded cnemial crest restricted to the proximal end of the tibia; and articular surface of the astragalus for the internal malleolus of the tibia moderately expanded medially, articulating with only part of the ventral surface of the tibial internal malleolus. Our phylogenetic analysis indicates that *Bonapartesaurus* is located within the Tribe Saurolophini. Paleobiogeographically, its presence suggests at least two saurolophine dispersal events from North America, one toward South America and another toward Asia, no later than the late Campanian.

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SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

In the Upper Cretaceous, the most abundant and diverse clade of ornithomimid dinosaurs was the Hadrosauridae. This clade recorded its maximum diversity during the Campanian, decreasing in diversity in the Maastrichtian (Horner et al., 2004). Its distribution was nearly worldwide; the Laurasian record is the best known (Lund and Gates, 2006; Cruzado-Caballero et al., 2010a, 2010b, 2013, 2014; Prieto-Márquez et al., 2013). The lesser-known Gondwanan record is principally from Patagonian Argentina (Coria, 2013, 2014). Accordingly, the remains found in this region are very important for understanding the phylogeny and paleobiogeography of this clade in Gondwana.

The Argentinean record includes four taxa thus far: one basal hadrosaurid (*Lapampasaurus cholinoi* Coria, Gonzalez Riga, and Casadio, 2012) and three hadrosaurines (*Secernosaurus koerner* Brett-Surman, 1979; *Kritosaurus australis* Bonaparte, Franchi, Powell, and Sepúlveda, 1984; and *Willinakaqe salitralensis* Juárez Valieri, Haro, Fiorelli, and Calvo, 2010). Currently, the

systematic and phylogenetic positions of some of the taxa are not stable, and other taxa have recently been synonymized or invalidated.

Prieto-Márquez and Salinas (2010) proposed that ‘*K.*’ *australis* was a junior synonym of *S. koerner*, inferring it to be a member of the *Kritosaurus*–*Gryposaurus* clade as the sister taxon of *W. salitralensis* within Hadrosaurinae. However, the results of a phylogenetic analysis of *S. koerner* did not support the inclusion of this species within the genus *Kritosaurus*. Subsequently, Coria (2014) noted the presence of morphological differences between these two taxa that provide sufficient evidence to necessitate a reevaluation of their remains. He proposed that this is likely to result in the recognition of at least two closely related but distinct taxa of hadrosaurids. Given all these considerations and the results of a new revision of the remains of ‘*K.*’ *australis* deposited in the Museo Argentino de Ciencias Naturales (MACN), we agree with Coria. For the purpose of comparison in the present paper, we will thus distinguish between *S. koerner* and ‘*K.*’ *australis*.

Juárez Valieri et al. (2010) described the taxon *W. salitralensis* on the basis of bones from the Salitral Moreno site (southeastern Río Negro, Argentina) and the locality of Islas Malvinas (southwestern La Pampa Province, Argentina). Coria et al. (2012) assigned the remains of *W. salitralensis* from Islas Malvinas to

*Corresponding author. [†]Deceased, February 2016. During the final stages of preparation of the manuscript, co-author Jaime Powell passed away. This paper is dedicated to his memory.

the species *L. cholinoi*. Later, Coria (2014) cast some doubt on the taxonomic validity of most of the material referred to *W. salitralensis*, considering the holotype specimen, an incomplete premaxilla, to be the only material representing that taxon. In a revision of the cranial and postcranial remains of *W. salitralensis* deposited in the Museo Provincial Carlos Ameghino (Cipolletti, Río Negro), Cruzado-Caballero and Coria (2016) have recently noted several differences in the cranial and postcranial bones. These authors described two different morphotypes and proposed *W. salitralensis* to be a *nomen vanum*.

Here we present systematic and phylogenetic studies of a partial skeleton (MPCA-Pv SM2) from the Salitral Moreno site, without taking into account the remains studied in the paper by Cruzado-Caballero and Coria (2016) due to the problems exposed by these authors. The problems I (P. C.-C.) address are the presence of two different morphotypes among the remains from Salitral Moreno, which indicate differences of taxonomic significance among the specimens assigned to *W. salitralensis*, and the invalidity of all the characters of the original diagnosis. The remains were excavated by Jaime Powell and collaborators in 1984 and described in 1987 by Powell, who assigned them to an indeterminate lambeosaurine. Later, Juárez Valieri et al. (2010) included it as a paratype of *W. salitralensis*. At present, MPCA-Pv SM2 is provisionally deposited in the Vertebrate Paleontology Collection at the National University of Tucumán and the Fundación Miguel Lillo (Tucumán, Argentina).

Institutional Abbreviations—FMNH, the Field Museum, Chicago, Illinois, U.S.A.; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; MPCA-Pv, Museo Provincial Carlos Ameghino, Cipolletti, Río Negro, Argentina.

GEOLOGY

The hadrosaurid material is from an area located in the cliffs situated 8 km east of Salitral Moreno, in the north-central part of Río Negro Province, Argentina (Fig. 1). The fossiliferous level is constituted by poorly sorted, medium to coarse, yellowish, sometimes gray-greenish sandstones. It might be correlative to the Lower Member of the Allen Formation (Hugo et al., 2001). The Allen Formation is the basal part of the Malargüe Group and is principally exposed in Neuquén and Río Negro provinces of Argentina. Its estimated age is late Campanian–early Maastrichtian according to Hugo et al. (2001). The Lower Member of this unit was deposited in a moderate-energy fluvial environment, interrupted by the presence of important tributary channels (Hugo et al., 2001).

The levels bearing the fossils described here have provided an abundant collection of isolated remains dominated by hadrosaurids of different ontogenetic stages, titanosaurian sauropods (*Rocasaurus muniozi* Salgado and Azpilicueta, 2000, *Aeolosaurus* sp., Saltasaurinae indet.), ankylosaurs, non-avian and avian theropods, turtles, gastropods, and plants (Powell, 1987; García and Salgado, 2013).

SYSTEMATIC PALEONTOLOGY

Superorder DINOSAURIA Owen, 1842

Order ORNITHISCHIA Seeley, 1887

Infraorder ORNITHOPODA Marsh, 1881

Family HADROSAURIDAE Cope, 1869

Subfamily HADROSAURINAE Cope, 1869, non Lambe, 1918

BONAPARTESAURUS, gen. nov.

Etymology—In honor of the paleontologist José Fernando Bonaparte, for his contribution to paleontology in Argentina.

Diagnosis—As for the type and only known species.

Type Species—*Bonapartesaurus rionegrensis*.

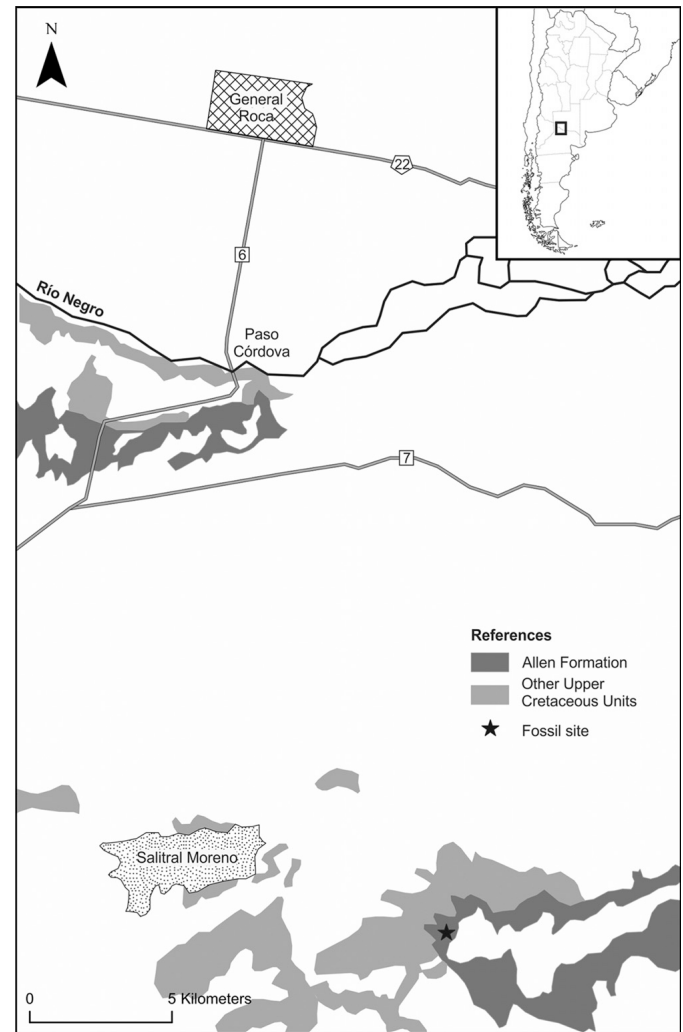


FIGURE 1. Map showing the location of the Salitral Moreno site, General Roca, Río Negro, Argentina.

BONAPARTESAURUS RIONEGRENSIS, sp. nov.

Holotype—MPCA-Pv SM2, a partial, articulated skeleton.

Etymology—From Río Negro Province, Argentina, the area where the fossils were found.

Type Locality and Horizon—The Salitral Moreno site in General Roca city, Río Negro, Argentina; Allen Formation, Late Cretaceous, late Campanian–early Maastrichtian.

Diagnosis—Hadrosaurine hadrosaurid characterized by the following unique combination of characters: ratio between the height of the sacral neural spines and that of the centrum greater than 3.5; neural spines of the anterior section of the caudal vertebrae extremely long (between three and a half and four times the height of the centrum) and evenly expanding distally; a preacetabular process slightly deflected ventrally, with the angle greater than 150°; the ratio between the maximum dorsoventral depth of the posterior end of the preacetabular process and the dorsoventral distance from the pubic peduncle to the dorsal margin of the ilium less than 0.50; the ratio between the dorsoventral height and anteroposterior length of the iliac blade 0.8 or greater; asymmetrical lateral profile of the supraacetabular process; the posterior portion of the postacetabular process markedly thicker mediolaterally as a result of the dorsomedial twist of the postacetabular process; an anteriorly expanded

cnemial crest restricted to the proximal end of the tibia; and articular surface of the astragalus for the internal malleolus of the tibia moderately expanded medially, articulating with only part of the ventral surface of the tibial internal malleolus.

Holotype—MPCA-Pv SM2/1–71, a partial skeleton that includes four dorsal vertebrae (SM2/1–4), a complete sacrum (SM2/5), eight anterior caudal vertebrae (SM2/6–13), nine medial caudal vertebrae (SM2/14–22), two blocks with five medial caudal vertebrae each (SM2/23–24), 18 hemal arches (SM2/25–42), three dorsal ribs (SM2/43–45), a distal fragment of the right scapular blade (SM2/46), a distal fragment of the left humerus (SM2/47), a left ulna (SM2/48), a right ilium (SM2/49), an almost complete left pubis (SM2/50), distal fragments of two ischia (SM2/51), both femora (SM2/52–53, left and right, respectively), both tibiae (SM2/54–55, left and right, respectively), both fibulae (SM2/56–57, left and right, respectively), a left astragalus (SM2/58), a right calcaneum (SM2/59), an almost complete, articulated left pes (SM2/60–69), and two blocks with tendons (SM2/70–71).

DESCRIPTION

Dorsal Vertebrae—The last four dorsal vertebrae have been found (MPCA-Pv SM2/1–4; Fig. 2A, B). Every vertebra has its left side eroded and has lost part of or the whole of the neural spine. The vertebral elements are very similar to those of other hadrosaurids (Horner et al., 2004). Only the dorsal vertebra SM2/3 conserves a fragment of the neural spine, which is anteroposteriorly extended and transversally flat. Because the apex is not preserved, we cannot know if this was expanded as in the anterior caudal vertebrae (see Caudal Vertebrae). Expansion of the apex of the postcervical neural spines can be observed in other iguanodontoids and hadrosaurids, as exemplified by the

dorsal vertebrae of *Shantungosaurus giganteus* Hu, 1973, the dorsal vertebrae of *Tanais sinensis* Wiman, 1929, the dorsal and caudal vertebrae of *Barsboldia sicinskii* Maryańska and Osmólska, 1981, and the dorsal vertebrae of *Pararhabdodon isonensis* Casanovas-Cladellas, Santafé-Llopis, and Isidro-Llorens, 1993 (Wiman, 1929; Maryańska and Osmólska, 1981; Prieto-Márquez, 2011). Because the apex is broken, it is not possible to ascertain whether the pattern of expansion is as in *B. sicinskii*.

The vertebral centra are slightly opisthocelous. The articular surfaces are typically heart-shaped and dorsoventrally taller than mediolaterally wide. A strong ridge runs along the ventral side of the centrum. Above the ridge, the lateral sides of the centrum are anteroposteriorly concave and pierced by several linearly distributed nutritive foramina. The transverse processes are broken in all the vertebrae. The conserved fragments of these processes have a triangular cross-section with a deep ridge on the ventral side. The prezygapophyses are located anteriorly to the base of the neural spine, have oval-shaped, flat articular surfaces, and are lateromedially wider than the postzygapophyses. The postzygapophyses are ellipsoidal and have a flat surface that faces downwards and outwards.

Three dorsal ribs (MPCA-Pv SM2/43–45) are represented by two fragmentary shafts without capitula and tubercula. These were found associated with the skeleton and have the typical hadrosaurid morphology (Horner et al., 2004). The shafts of the dorsal ribs are anterolaterally to posteromedially compressed.

Sacrum—Specimen MPCA-Pv SM2/5 is a complete sacrum formed by eight fused centra, with six complete neural spines (Fig. 3A–C). In this case, unlike the dorsal vertebrae, the sacral vertebrae have their right side eroded. The articular surfaces of the first and last vertebrae are elliptical in outline, wider than high, and concave. The rest of the vertebrae do not preserve their centrum. In ventral view, the first vertebra has a slight keel that has disappeared in the last vertebra, as in *Bactrosaurus johnsoni* Godefroit, Dong, Bultynck, Li, and Feng, 1998 (Godefroit et al., 1998). In this case, due to the erosion of part of the centra of the whole sacrum, it is not possible to ascertain whether the keel continues or there is a sulcus, as in *Ba. johnsoni*.

All the neural spines are complete, except for the first two, which are broken. The ratio between the height of the neural spines and that of the centrum of the tallest sacral vertebra is greater than 3.5, as in lambeosaurines (Xing et al., 2014). These spines are characterized by their great anteroposterior and lateromedial widths at their distal end, but they do not become evenly expanding distally like the caudal vertebrae (the transverse section is rectangular). The anteroposterior width of the neural spines decreases posteriorly. The lateromedial width does not form a characteristic expansion like that recorded in other iguanodontoids or hadrosaurids (see Dorsal Vertebrae).

Caudal Vertebrae—About half of the caudal series is preserved, with eight caudal vertebrae from the anterior section (MPCA-Pv SM2/6–13; Fig. 4A, B) and 19 caudal vertebrae from the middle section (MPCA-Pv SM2/14–22; MPCA-Pv SM2/23, a block with five vertebrae; and MPCA-Pv SM2/24, a block with five vertebrae; Fig. 5A). The caudal vertebral centra are indistinguishable from those of other hadrosaurids. The most anterior centra are typically amphiplatyan, anteroposteriorly narrow, with subhexagonal articular surfaces and transverse processes. The hemapophyseal facets on the ventral side appear in the fourth vertebra. The lateral sides of the centra are slightly anteroposteriorly concave and pierced by linearly distributed nutritive foramina. The medullary canal is small. The transverse processes up to the third vertebra are higher dorsoventrally than wide anteroposteriorly. The prezygapophyses are inclined medially, and the postzygapophyses are inclined laterally. The articular facets in the pre- and postzygapophyses are elliptical, and their size progressively decreases towards the end of the series.

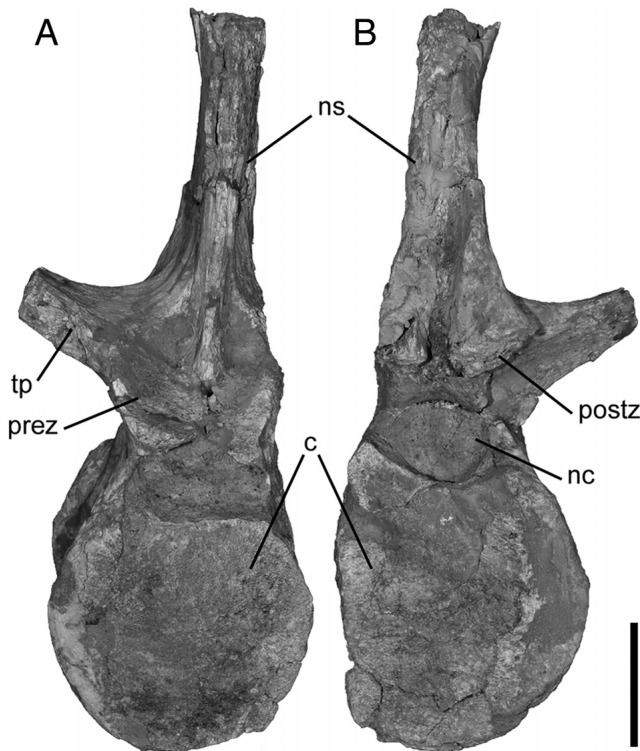


FIGURE 2. *Bonapartesaurus rionegrensis*, MPCA-Pv SM2/3, posterior dorsal vertebra in A, anterior and B, posterior views. **Abbreviations:** c, centrum; nc, neural canal; ns, neural spine; postz, postzygapophysis; prez, prezygapophysis; tp, transverse process. Scale bar equals 5 cm.

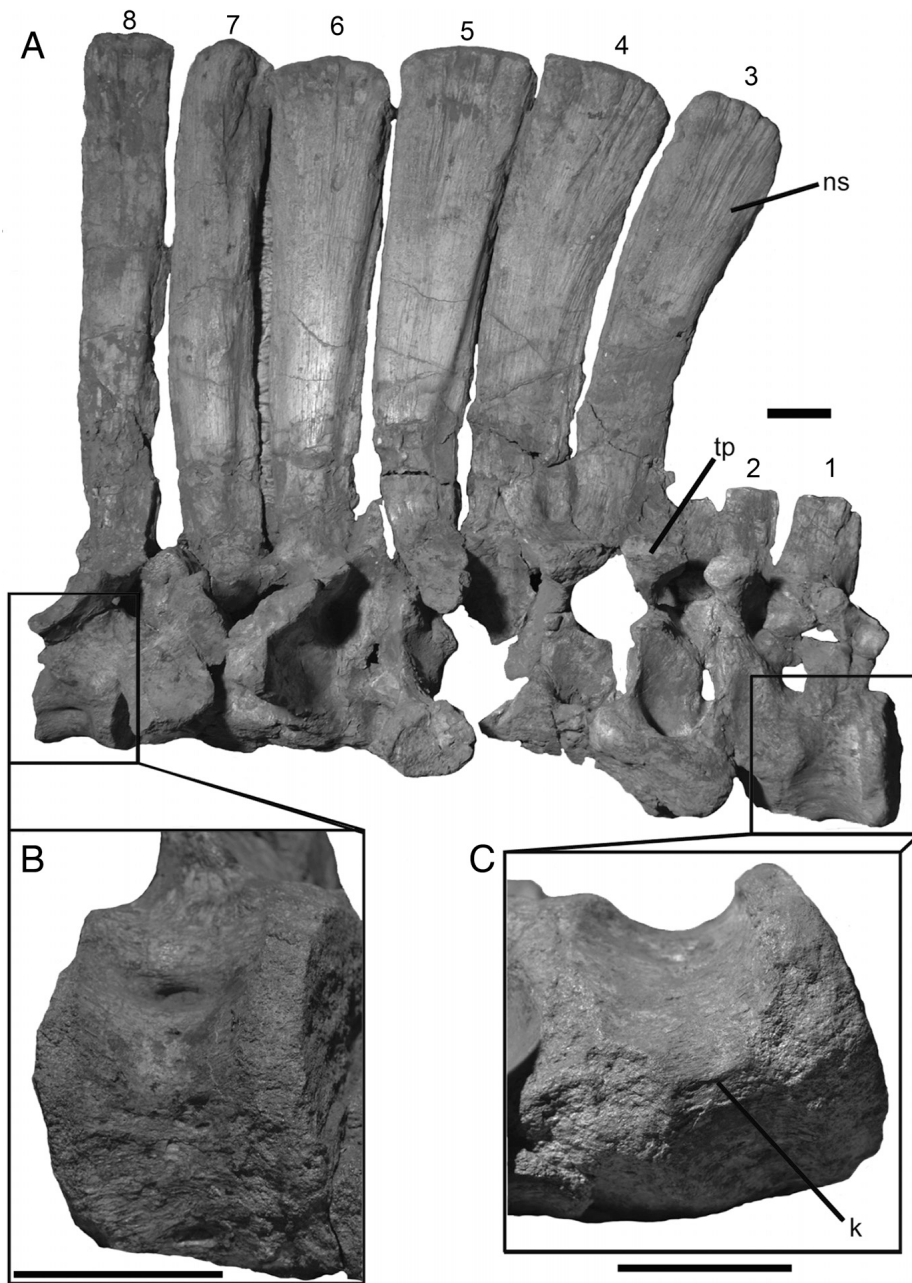


FIGURE 3. *Bonapartesaurus rionegrensis*, MPCA-Pv SM2/3, sacrum in **A**, right lateral view. **B**, last and **C**, first centra in ventral view. **Abbreviations:** k, keel; ns, neural spine; tp, transverse process. Scale bar equals 5 cm.

The vertebral centra present a sequence of dorsoventral reduction and anteroposterior enlargement towards the end of the tail.

The neural spines of the anterior section are very long (between three and a half and four times the height of the centrum), approximately vertical, robust, and with a characteristic evenly distal expansion. The great elongation of the neural spines is shared with *B. sicinskii*; *Hypacrosaurus altispinus* Brown, 1913; *Hypacrosaurus stebingeri* Horner and Currie, 1994; *Magnapaulia laticaudus* Prieto-Márquez, Chiappe, and Joshi, 2012; and *T. sinensis* (Prieto-Márquez, 2011). According to Prieto-Márquez (2011), *Bonapartesaurus rionegrensis* would be the second case, after *B. sicinskii*, of a large elongation of the neural spines in the hadrosaurine clade. On the other hand, the neural spines of the anterior caudal vertebrae have a great mediolateral expansion of the apex, with a mediolateral/anteroposterior width ratio greater than 1. This expansion gives a

baseball-bat-like appearance to the anterior caudal vertebrae. When we compare the evenly expanding distal pattern of expansion of the anterior caudal vertebrae, the only similar taxa are the Asian taxa *T. sinensis* and *B. sicinskii*. The pattern of *Bo. rionegrensis* differs in having an expansion that is more uniform than in *T. sinensis* and *B. sicinskii*, which have a more globular apex (Wiman, 1929; Maryńska and Osmólska, 1981). From the middle to the top of the neural spines, there are strong longitudinal ridges due to muscular or tendinous insertions. These marks are less strong in the vertebrae of the middle section, where the spines are robust and steeply inclined backwards. The apexes of these spines are slightly thickened lateromedially and anteroposteriorly, giving a rectangular cross-section.

In the middle section, two vertebrae (MPCA-Pv SM2/17, 19; Fig. 5B–D) show pathological marks in the neural spine that are probably due to callus tissue growth around a fracture. The neural

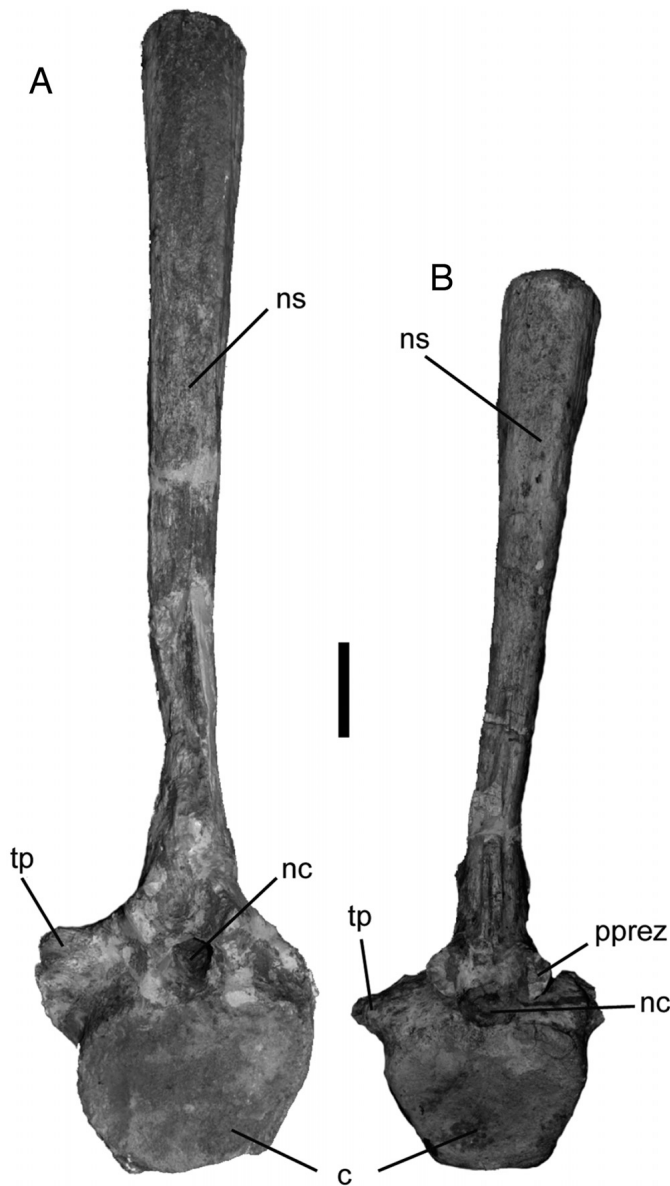


FIGURE 4. *Bonapartesaurus rionegrensis*, anterior caudal vertebrae. **A**, MPCA-Pv SM2/6 and **B**, MPCA-Pv SM2/13 in anterior view. **Abbreviations:** **c**, centrum; **nc**, neural canal; **ns**, neural spine; **pprez**, prezygapophysis; **tp**, transverse process. Scale bar equals 5 cm.

spine MPCA-Pv SM2/17 presents a deviation near the midpoint that produces a distinctive convexity on the left side and concavity on the right side. The neural spine MPCA-Pv SM2/19 presents a major growth of callus tissue near its tip. This type of pathology with growth of callus tissues has previously been described in other hadrosaurid material (e.g., Canudo et al., 2005).

Hemal Arches—Eighteen hemal arches (MPCA-Pv SM25–42) have the typical hadrosaurid ‘Y’ shape, are long and mediolaterally flat, and have the articular facets separated by an open hemal canal (Horner et al., 2004). The angle between the hemal arches and the centra cannot be measured because the hemal arches were discovered disarticulated from the caudal series.

Scapula—Specimen MPCA-Pv SM2/46 is a distal fragment of a right scapular blade with an approximate length of 335 mm (Fig. 6A). The dorsal and ventral borders are divergent towards the distal end. The scapular blade is narrow and conserves a

wide scapular neck, such that the blade is slightly less than 50% the width of the proximal neck. The ventral margin along the caudal half of the scapular blade is almost straight or slightly convex ventrally. These latter two characters are shared by more basal hadrosaurids and hadrosaurines, in contrast to almost all lambeosaurines except *Parasaurolophus cyrtocristatus* Ostrom, 1961, and *Tsintaosaurus spinorhinus* Young, 1958 (Xing et al., 2014).

Humerus—A distal fragment of a left humerus has been collected (MPCA-Pv SM2/47; Fig. 6B). The fragment only preserves the ulnar condyle and a small portion of the diaphysis. This has a rectangular cross-section.

Ulna—Specimen MPCA-Pv SM2/48 is a complete left ulna (Fig. 7A, B). It is relatively robust, with a very well-developed olecranon process and gently curves in an ‘S’ shape, as occurs in several hadrosaurines and lambeosaurines (*Brachylophosaurus canadensis* Sternberg, 1953, *Kundurosaurus nagorny* Godefroit, Bolotsky, and Lauters, 2012, *Amurosaurus riabinini* Bolotsky and Kurzanov, 1991, and *Latirhinus uitstani* Prieto-Márquez and Serrano Brañas, 2012; Godefroit et al., 2004, 2012; Cuthbertson and Holmes, 2010; Prieto-Márquez and Serrano Brañas, 2012). The anterior process is particularly high and robust, whereas the lateral process is distinctly lower and thinner. The two processes form an angle of approximately 130°. The articular facet for the proximal part of the radius, located between the anterior and lateral processes, is particularly enlarged; longitudinal striations indicate strong ligamentous attachment with the radius. Under this area, the body of the ulna is particularly high anteroposteriorly. The ulna progressively tapers distally. Its distal end is rounded, laterally compressed, and triangular in cross-section. The large triangular articular surface for the distal end of the radius faces craniomedially; it also bears strong longitudinal striations. The proximodistal length/anteroposterior depth ratio of MPCA-Pv SM2/48 at midlength is 7.96. Within Hadrosauridae, a similarly low ratio is found in *Saurolophus angustirostris* Rozhdestvensky, 1952, which has a value of 7.8 (Prieto-Márquez and Wagner, 2013).

Ilium—Specimen MPCA-Pv SM2/49 is an almost complete right ilium with an anteroposterior length of 750 mm (Fig. 8A, B, G). The ilium has a ratio between the maximum dorsoventral depth of the caudal end of the preacetabular process and the dorsoventral distance from the pubic peduncle to the dorsal margin of the ilium of less than 0.50, as is the case in several non-hadrosauroid iguanodontians and basal hadrosauroids (Xing et al., 2014). The preacetabular process is broken in its more proximal part. It is robust with a small ventral deflection; the angle between the preacetabular process and the body of the ilium is greater than 150°, as occurs in *Sahaliyania elunchunorum* Godefroit, Hay, Yu, and Lauters, 2008, and *K. nagorny*, and unlike in other hadrosaurids, which have an angle of less than 150° (Godefroit et al., 2012; Xing et al., 2014). The lateral side is somewhat eroded, flat, and presents one gentle crosswise ridge similar to *W. salitralensis* and ‘*K.*’ *australis*, unlike *S. koerner* and other hadrosaurines. In *Bo. rionegrensis*, the ridge runs parallel to the dorsal border of the preacetabular process in lateral view, unlike *W. salitralensis* and ‘*K.*’ *australis*, where it runs divergently (Prieto-Márquez and Salinas, 2010). The preacetabular notch is slightly more open than in *W. salitralensis* and ‘*K.*’ *australis* (Prieto-Márquez and Salinas, 2010; Juárez Valieri et al., 2010). The ventral border of the process is lateromedially narrow, and the dorsal border is very wide due to the presence of a strong longitudinal ridge for attaching the transverse processes of the sacral vertebrae on the medial side. The ridge extends all along the preacetabular process and the iliac blade, until it passes the ventral apex of the pubic peduncle posteriorly. Due to this ridge, the transverse section is of an inverted-‘L’ shape.

The iliac blade is anteroposteriorly longer than dorsoventrally high. In lateral view, the dorsal side is strongly concave above

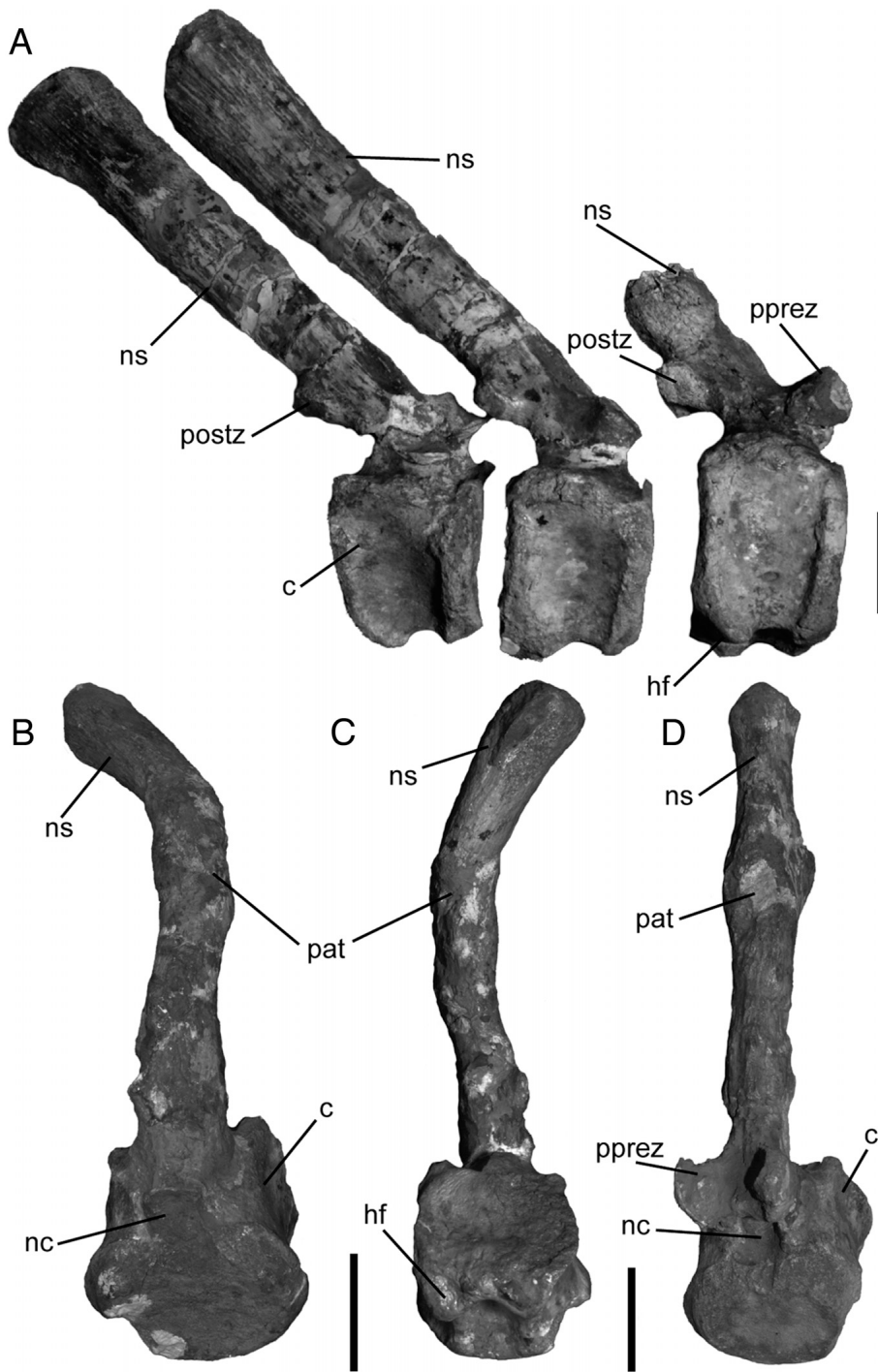


FIGURE 5. *Bonapartesaurus rionegrensis*, caudal vertebrae. **A**, MPCA-Pv SM2/14–24, middle caudal in lateral view. **B**, anterodorsal and **C**, posteroventral views of MPCA-Pv SM2/17, pathological caudal vertebra. **D**, MPCA-Pv SM2/19, pathological caudal vertebra in anterodorsal view. **Abbreviations:** **c**, centrum; **hf**, hemapophyseal facets; **nc**, neural canal; **ns**, neural spine; **pat**, pathology; **postz**, postzygapophysis; **pprez**, prezygapophysis; **tp**, transverse process. Scale bar equals 5 cm.

the supraacetabular process, as in hadrosaurids (Horner et al., 2004). This concavity is more pronounced than in *W. salitralensis* (Juárez Valieri et al., 2010). The supraacetabular process is well developed dorsoventrally and projects laterally. It shows an asymmetrical 'V' shape, as seen, for example, in the hadrosaurines *Prosaurolophus maximus* Brown, 1916, *Br. canadensis*, *W. salitralensis*, and '*K.*' *australis* (Juárez Valieri et al., 2010; Prieto-Márquez and Salinas, 2010; Godefroit et al., 2012). Its anteroposterior length is more than half the anteroposterior length of the iliac blade. Its ventral apex is located anterodorsally to the ventral apex of the posterior tuberosity of the iliac peduncle. In

dorsal view, the supraacetabular process shows an extreme lateral development that contrasts with the moderate lateral development of '*K.*' *australis* and the lesser lateral development of *W. salitralensis* (Juárez Valieri et al., 2010; Prieto-Márquez and Salinas, 2010). The iliac portion of the acetabulum is anteroposteriorly wider than in *W. salitralensis* (Juárez Valieri et al., 2010). The pubic and ischial peduncles are well developed. The pubic peduncle is relatively short and triangular in lateral view, as in hadrosaurids (Horner et al., 2004). Its articular face is a plane, in contrast to the convex face of *W. salitralensis* (Juárez Valieri et al., 2010). The ischial peduncle is composed of two knobs of



FIGURE 6. *Bonapartesaurus rionegrensis*, pectoral elements. **A**, MPCA-Pv SM2/46, right scapular blade in lateral view. **B**, MPCA-Pv SM2/47, distal fragment of the left humerus in anterior view. **Abbreviations:** **sb**, scapular blade; **uc**, ulnar condyle. Scale bar equals 5 cm.

similar size separated by a shallow embayment, as in *Hadrosaurus foulkii* Leidy, 1858, *Gilmoresaurus mongoliensis* Brett-Surman, 1979, hadrosaurines, and lambeosaurines (Xing et al., 2014). The dorsal knob is more vertical than in '*K.* *australis*' (Prieto-Márquez and Salinas, 2010). The postacetabular process is rectangular with a marked ventral deflection for half of its length, similar to *Edmontosaurus regalis* Lambe, 1917, except that the posterior end of the process is dorsoventrally wider in *Bo. rionegrensis* than in *E. regalis* (Campione, 2014). This shape of the postacetabular process is also different from '*K.* *australis*', where the process rises dorsally, and from *W. salitralensis*, whose process has a sharp profile posteriorly (Juárez Valieri et al., 2010; Prieto-Márquez and Salinas, 2010). The postacetabular process is almost half of the dorsoventral height of the iliac blade, differentiating it from *W. salitralensis* and '*K.* *australis*', which have a lower process (Juárez Valieri et al., 2010; Prieto-Márquez and Salinas, 2010). It has a triangular cross-section. In

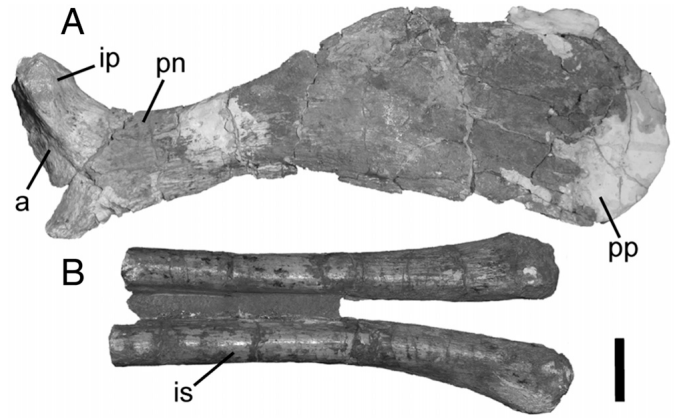


FIGURE 8. *Bonapartesaurus rionegrensis*, pelvic elements. **A**, MPCA-Pv SM2/50, left pubis in lateral view. **B**, MPCA-Pv SM2/51, distal fragments of ischia in ventral view. **Abbreviations:** **a**, acetabulum; **ip**, iliac peduncle; **is**, ischial shaft; **pn**, prepubic neck; **pp**, prepubic process. Scale bar equals 5 cm.

dorsal view, the postacetabular process looks like a club distally, as does that of '*K.* *australis*', with the only difference being that in MPCA-Pv SM2/49 it is asymmetrical, with the medial border convex and the lateral border more or less straight (Prieto-Márquez and Salinas, 2010). The axis of the postacetabular process is strongly twisted along its length, so that its medial side progressively faces dorsolaterally, as in '*K.* *australis*' and contrary to *S. koeneri* and *W. salitralensis* (Juárez Valieri et al., 2010; Prieto-Márquez and Salinas, 2010). In ventral view, however, the postacetabular process is similar to '*K.* *australis*'.

Pubis—Specimen MPCA-Pv SM2/50 is an almost complete left pubis (Fig. 9A). This conserves completely the prepubic process and the iliac peduncle. The prepubic process is rectangular and longer anteroposteriorly than wide dorsoventrally, similar to *Maiaasaura peeblesorum* Horner and Makela, 1979, *Br. canadensis*, and *K. nagorny* (Godefroit et al., 2012). In lateral view, the dorsal and ventral sides are slightly divergent due to the fact that the ventral margin is slightly more expanded. In lateral view, the anterior side has a circular form, like in some hadrosaurines (Xing et al., 2014). The prepubic neck of the blade is strongly constricted and is very long, with the dorsal side nearly straight, as in hadrosaurine taxa (Gates et al., 2011). The maximum width of the prepubic blade is more than double the maximum width of the prepubic neck, as in *Gryposaurus latidens* Horner, 1992, *Lambeosaurus lambei* Parks, 1923, and *Corythosaurus casuarius* Brown, 1914 (Evans and Reisz, 2007; Prieto-Márquez, 2012). The long and rectangular shape of the prepubic process is similar to those of *E. regalis*, *S. australis*, *Gryposaurus* spp., *P. maximus*, and *Saurolophus* spp. (Prieto-Márquez and Salinas, 2010; Campione, 2014), but is differentiated from them by its round anterior margin. With respect to the South American taxon *S. australis*, MPCA-Pv SM2/50 further differs in that it presents a shorter prepubic process and a less massive iliac peduncle (Prieto-Márquez and Salinas, 2010). The iliac peduncle is long, robust, and anteriorly directed and has a triangular cross-section. It projects anterodorsally, and its articular face has a triangular shape. The anterior side of the iliac peduncle is slightly concave, and the preserved part of the posterior side is almost straight. In lateral view, there are some strong muscular marks on the anterior side of the iliac peduncle, probably for the *M. ambiens*, and on the ventral side of the prepubic neck, probably for the *M. obliquus abdominis internus* and *externus* and the *M. transversus abdominis* (Dilkes, 2000). It is similar to the type 1 pubis (*Edmontosaurus* and *Gilmoresaurus*) of Brett-Surman and

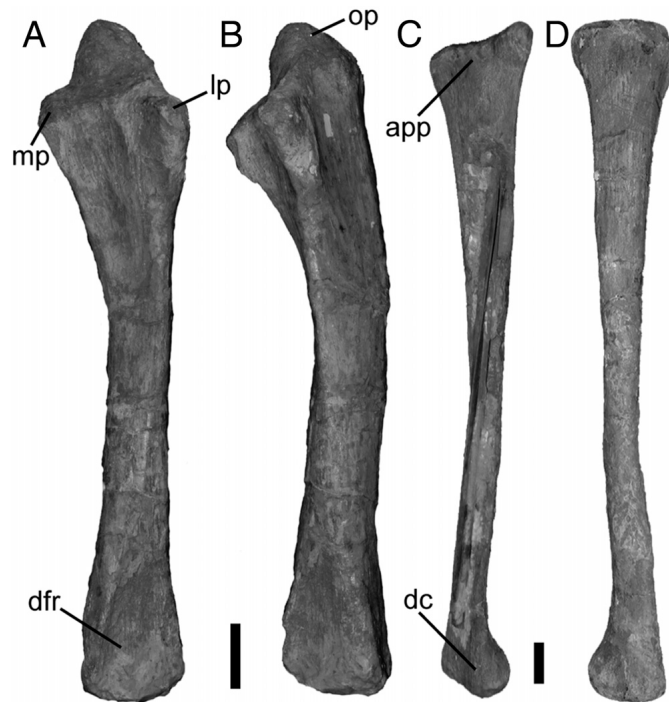


FIGURE 7. *Bonapartesaurus rionegrensis*, appendicular elements. MPCA-Pv SM2/48, left ulna in **A**, anterior and **B**, lateral views. MPCA-Pv SM2/56, left fibula in **C**, medial and **D**, lateral views. **Abbreviations:** **app**, anterior peg process; **dc**, distal condyle; **dfr**, distal face for radius; **lp**, lateral process; **mp**, medial process; **op**, olecranon process. Scale bar equals 5 cm.

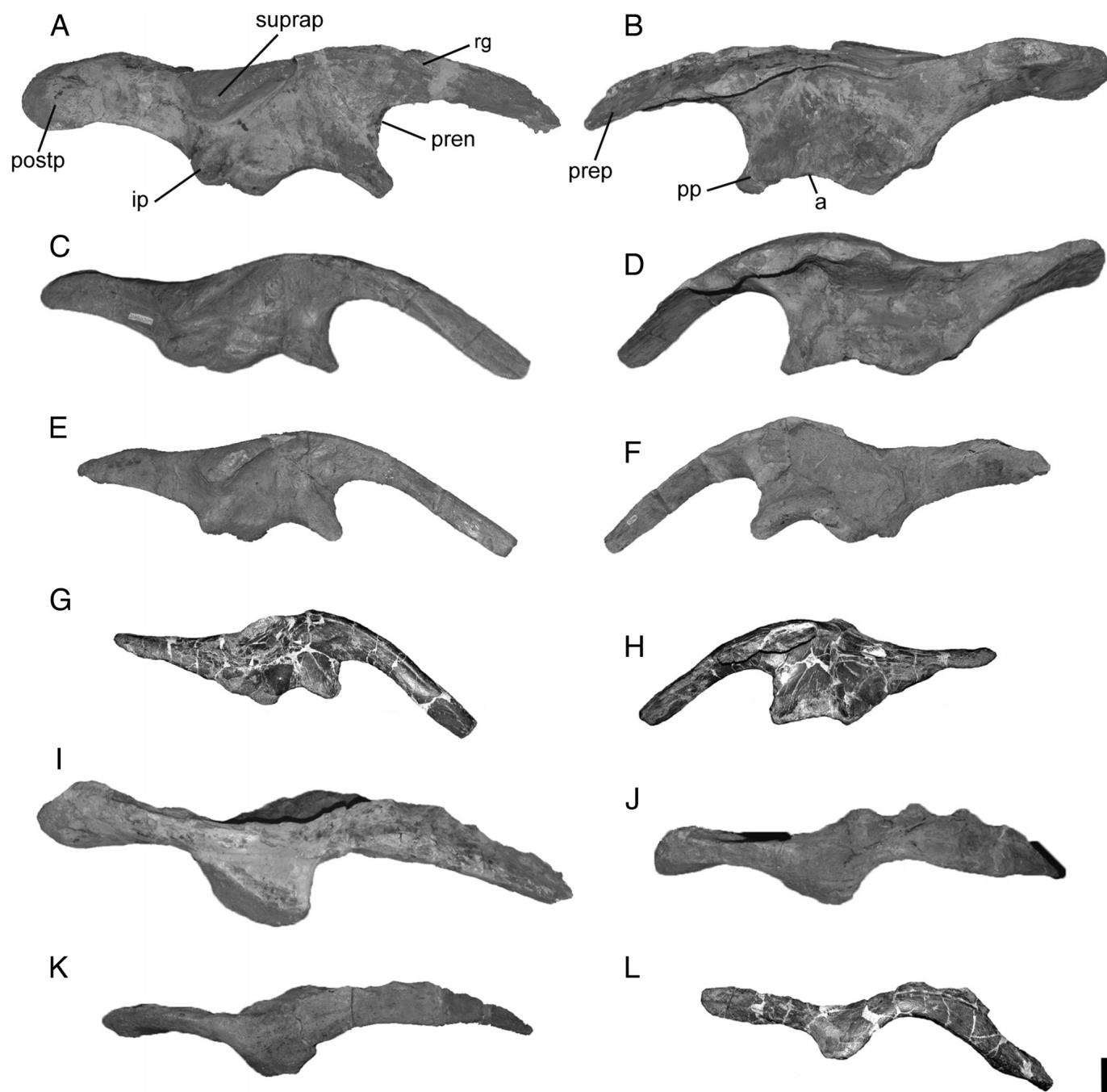


FIGURE 9. **A, B, I**, MPCA-Pv SM2/49, right ilium of *Bonapartesaurus rionezensis*. **C, D, J**, MACN-RN-02, left ilium of '*Kritosaurus*' *australis*. **E, F, K, M**, MPCA-Pv SM2/51, left ilium of '*Willinikaqe salitralensis*.' **G, H, L**, FMNH P13423, right ilium of *Secernosaurus koeneri*. The ilia of '*Kritosaurus*' *australis* and '*Willinikaqe salitralensis*' are reversed in lateral, medial, and dorsal views for comparative purposes. **A, C, E, G** in lateral, **B, D, F, H** in medial, and **I, J, K, L** in dorsal views. **Abbreviations:** **a**, acetabulum; **ip**, ischial peduncle; **postp**, postacetabular process; **pp**, pubic peduncle; **pren**, preacetabular notch; **prep**, preacetabular process; **rd**, ridge; **suprap**, supraacetabular process. Scale bar equals 5 cm.

Wagner (2007), with a shorter neck, and to state 1 of character 252 of Prieto-Márquez (2010).

Ischium—The distal parts of both ischia have been collected, MPCA-Pv SM2/51 (Fig. 9B). Their transverse section is subcircular. On the lateral side, the ischia are straight, and on the medial side, they are convex. Their ends have a knob-like outline, unlike in the lambeosaurines (Horner et al., 2004), and they are deflected ventrally.

Femora—Both femora (MPCA-Pv SM2/52–53; Fig. 10A–C) have been preserved completely. They have a length of 960 mm and have the typical hadrosaurid form (Horner et al., 2004). The shaft is straight and massive with a rectangular cross-section. They are mediolaterally narrow. The femoral head and greater trochanter are separated by a wide groove. The greater trochanter and lesser trochanters are joined. Below the lesser trochanter, there is a slight insertion mark for the *M. puboischiofemoralis internus* 2

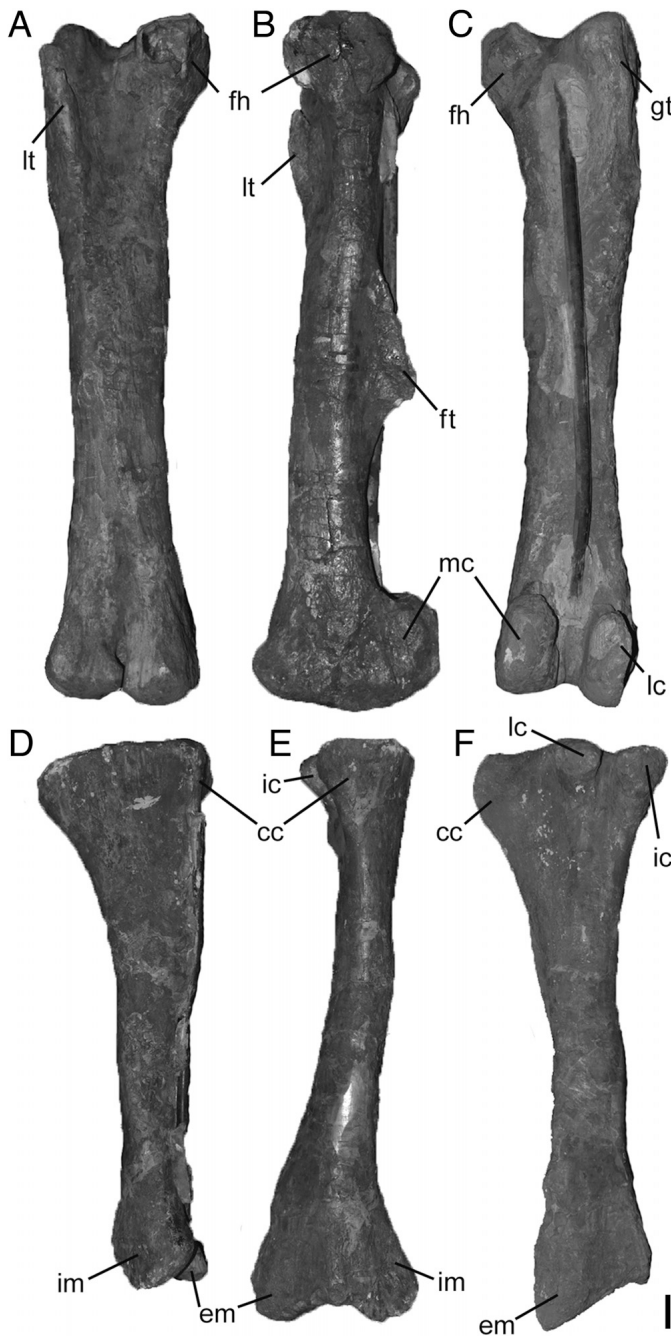


FIGURE 10. *Bonapartesaurus rionegrensis*, hind limb elements. MPCA-Pv SM2/53, right femur in **A**, anterior, **B**, medial, and **C**, posterior views. MPCA-Pv SM2/54, left tibia in **D**, anterior, **E**, medial, and **F**, lateral views. **Abbreviations:** cc, cnemial crest; em, external malleolus; fh, femoral head; ft, fourth trochanter; gt, greater trochanter; ic, internal condyle; im, internal malleolus; lc, lateral condyle; lt, lesser trochanter; mc, medial condyle. Scale bar equals 5 cm.

(pars dorsalis) (Dilkes, 2000). The fourth trochanter is triangular in shape, with the proximal side longer than the distal side, and mediolaterally narrow. The distal condyles are more expanded anteroposteriorly than proximodistally and lateromedially. The intercondylar extensor groove is practically closed in both femora, forming a funnel (Horner et al., 2004).

Tibiae—Both tibiae are completely preserved (MPCA-Pv SM2/54–55; Fig. 10D, E). These are robust and have a length of around

800 mm. The tibial shaft is long, straight, and ovoid in cross-section. The proximal head of the tibia is wide lateromedially and enlarged anteroposteriorly. The medial side of the head is convex, and in lateral view the cnemial crest, the lateral condyle, and a prominent internal condyle are visible. The cnemial crest has the typical wing shape, is strongly deflected laterally, and is short proximodistally as in *Wulagasaurus dongi* Godefroit, Hay, Yu, and Lauters, 2008 (Godefroit et al., 2008), and unlike the rest of the hadrosaurids (Xing et al., 2014). In lateral view, the crest forms a broad and deep cavity where it is possible to make out the insertion marks of the ligaments of M. ilio-tibialis (Godefroit et al., 2004). The internal condyle is separated from the lateral condyle by a deep and narrow groove. In proximal view, it can be seen that the internal condyle is narrower anteroposteriorly than the lateral condyle, which is more robust. The lateral condyle is deflected towards the medial condyle, so that the groove separating the condyles closes slightly. The distal head of the tibia is nearly as wide lateromedially as its proximal head. The external malleolus is more prominent distally than the internal malleolus, which is more prominent medially. The articular surface of the external malleolus is turned toward the posteromedial side of the tibia, and the articular surface of the internal malleolus is turned toward the anterolateral side of the tibia. Both malleoli form a pronounced concavity by the joint of the astragalus.

Fibulae—Both complete fibulae have been collected (MPCA-Pv SM2/56–57; Fig. 7C, D). The left fibula is straight, whereas the right fibula is deformed and shows a marked concavity of the anterior side in lateral view. The length of the left fibula is approximately 95% of the length of the tibia. Both fibulae are slender, and their proximal end is transversely compressed and moderately widened anteroposteriorly, forming an anterior peg process. This projection is strongly developed, as in *Ba. johnsoni* (Godefroit et al., 1998), but not as much as in *G. latidens* (Prieto-Márquez, 2012). As is usual in hadrosaurids, the diameter of the fibula decreases progressively distally and the minimal anteroposterior constriction of the shaft is below its midpoint (Horner et al., 2004). The shaft is twisted laterally, and its distal third lies against the anteroposterior surface of the tibia. The distal end of the fibula is less expanded anteriorly than the proximal end, and it is a rounded, club-shaped condyle. The size of this distal expansion is comparable to that of *Charonosaurus jiajinensis* Godefroit, Zan, and Jin, 2000 (Godefroit et al., 2001). The flattened distal surface of the fibula fits against the dorsal surface of the calcaneum.

Astragalus—Specimen MPCA-Pv SM2/58 is a complete left astragalus (Fig. 11A, B). It is wider lateromedially than anteroposteriorly, in dorsal view giving a rectangular appearance similar to *C. jiajinensis* (Godefroit et al., 2001). In ventral view, the lateral side is convex and the medial side straight. In anterior view, it looks like a right triangle, as in other North American hadrosaurids (Brett-Surman and Wagner, 2007). The articular surface for the internal malleolus of the tibia is wide, occupying more than half of the dorsal side; this surface is slightly concave and faces anteromedially. The articular surface for the external malleolus of the tibia is concave and faces laterally. A low, oblique, and round ridge separates the two articular surfaces that join together the posterior and anterior ascending processes. The medially set posterior process is elongated, rounded, and low. The anterior ascending process is sharp and higher than in *Amurosaurus riabinini* (Godefroit et al., 2004). The ventral side of the astragalus is regularly convex craniocaudally and concave mediolaterally.

Calcaneum—The right calcaneum, MPCA-Pv SM2/59, is almost complete (Fig. 11C, D). It is stout and subtrapezoidal, being slightly more elongated craniocaudally than mediolaterally. Its ventral side is regularly rounded. It is located between the anterolateral side of the distal tibia, the distal expansion of the fibula, and the lateral side of the astragalus. The calcaneum

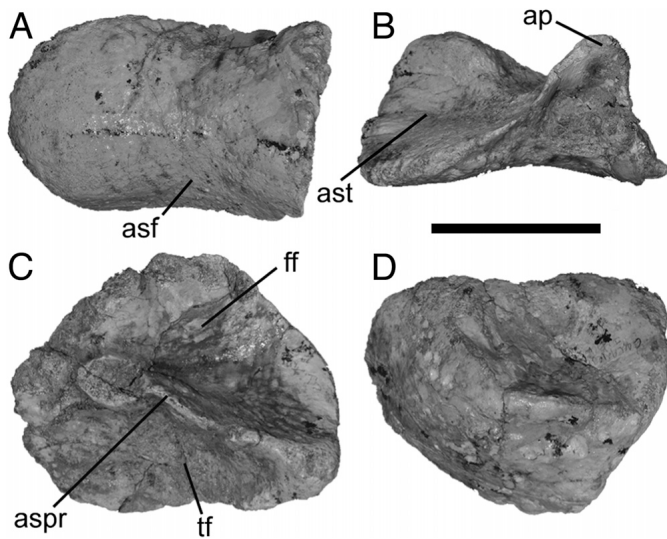


FIGURE 11. *Bonapartesaurus rionegrensis*, tarsal elements. MPCA-Pv SM2/58, left astragalus in **A**, dorsal and **B**, anterior views. MPCA-Pv SM2/59, left calcaneum in **C**, dorsal and **D**, ventral views. **Abbreviations:** **ap**, ascending process of the astragalus; **aspr**, ascending process of the calcaneum; **ast**, articular surface of tibia; **ff**, fibular facet; **tf**, tibial facet. Scale bar equals 5 cm.

does not come into contact with the astragalus due to the fact that it presents a taphonomic break. An oblique transverse ridge separates the two articular surfaces from each other. The cranial articular facet for the fibula is very slightly larger anteroposteriorly and narrower mediolaterally than the posterior articular surface for the tibia. The ascending process is prominent. In lateral view, the lateral side of the calcaneum is trapezoidal.

Pes—Specimen MPCA-Pv SM2/60–69 is an almost complete, articulated left pes (Fig. 12A). This has preserved every

metatarsal and most of the phalanges except 3, 4, and 5 of each toe. It can only be observed in dorsal view because the ventral side remains in the rock matrix. Metatarsal I is absent, as is common in the clade Hadrosauridae (Horner et al., 2004). Metatarsal II shows a considerable growth of pathological bone, which covers it almost completely except for the proximal and distal ends. Metatarsal III is robust, the longest and straightest of the metatarsals. It has a proximodistal length/mediolateral width ratio at the midshaft of up to 4.5 (Xing et al., 2014). The proximal articular surface of metatarsal III is slightly concave and triangular, whereas the distal articular surface is rectangular and saddle shaped. The intercondylar groove is well developed and divides the distal articular surface into two subequal parts. Metatarsal IV is longer than metatarsal II but no larger than metatarsal III. It has a proximal articular surface that is triangular and concave. On the medial side of metatarsal IV, there is a process that underlaps the lateral margin of metatarsal III. The first phalanges of digits II, III, and IV are longer than wide, as in other hadrosaurids (Horner et al., 2004). Pedal phalanx II-2 has a proximodistal length that is slightly less than the mediolateral width at the midshaft, as occurs in basal hadrosaurids and hadrosaurines (Xing et al., 2014). The second phalanges on digits III and IV are dorsoventrally compressed and wider than long.

PHYLOGENETIC ANALYSIS

In this paper, we follow the definition of Sereno (1998) for the clade Hadrosaurinae, which is ‘all hadrosaurids closer to *Saurolophus* than to *Parasaurolophus*,’ and for Lambeosaurinae, which is ‘all hadrosaurids closer to *Parasaurolophus* than to *Saurolophus*.’ Within Hadrosaurinae, there are four widely recognized lineages: Brachylophosaurini, Kritosaurini, Edmontosaurini, and Saurolophini (Sereno, 2005; Gates et al., 2011; Prieto-Márquez, 2014; Prieto-Márquez et al., 2014). Brachylophosaurini was defined by Gates et al. (2011) as taxa more closely related to *Brachylophosaurus*, *Maiasaura*, and *Acristavus* than *Gryposaurus* or *Saurolophus*. Kritosaurini was defined by Prieto-Márquez (2014) as the most exclusive clade of

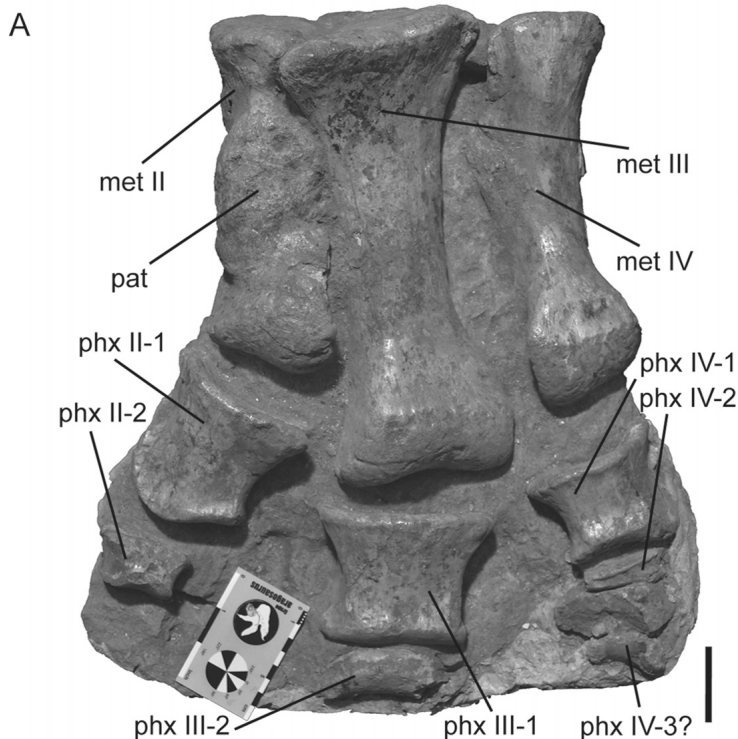


FIGURE 12. *Bonapartesaurus rionegrensis*, MPCA-Pv SM2/60–69, left pes in dorsal view. **Abbreviations:** **met II**, metatarsal II; **met III**, metatarsal III; **met IV**, metatarsal IV; **pat**, pathology; **phx II-1**, phalanx II-1; **phx II-2**, phalanx II-2; **phx III-1**, phalanx III-1; **phx III-2**, phalanx III-2; **phx IV-1**, phalanx IV-1; **phx IV-2**, phalanx IV-2; **phx IV-3?**, possible phalanx IV-3. Scale bar equals 5 cm.

hadrosaurids containing ‘*Kritosaurus*’ *navajovius* Brown, 1910, *Gryposaurus* *notabilis* Lambe, 1914, and *Naashoibitosaurus* *ostromi* Hunt and Lucas, 1993. Edmontosaurini was defined by Sereno (2005) as the most inclusive clade containing *Edmontosaurus* *regalis* Lambe, 1917, but not *Maiasaura* *peeblesorum* Horner and Makela, 1979, *Saurolophus* *osborni* Brown, 1912. Saurolophini was defined by Prieto-Márquez et al. (2014) as saurolophine hadrosaurids more closely related to *Saurolophus* *osborni* than to *Kritosaurus* *navajovius*, *Edmontosaurus* *regalis* Lambe, 1917, *Brachylophosaurus* *canadensis* or *Lambeosaurus* *lambei* Parks, 1923.

To assess the phylogenetic relationships of the Argentinean hadrosaurines, we have included these taxa in the matrix proposed by Xing et al. (2014) (see Supplementary Data S1, S2, and S3). In addition, we have revised the previously published data on the character coding of *Arenysaurus* *ardevoli* Pereda-Suberbiola, Canudo, Cruzado-Caballero, Barco, López-Martínez, Oms, and Ruiz-Omeñaca, 2009, in the matrix of Xing et al. (2014) and corrected several errors. We have removed the taxa *W. salitralensis*, which was coded by Prieto-Márquez (2010) as Salitral Moreno OTU and is at present considered a nomen vanum (Cruzado-Caballero and Coria, 2016), and *S. koernerii*, due to the differences observed between this and ‘*K.*’ *australis* (see Description). The character distribution was analyzed with Mesquite 2.75 (Maddison and Maddison, 2010). The resulting matrix included 62 species-level taxonomic units (four iguanodontians outside Hadrosauroida and 58 hadrosaurids) coded across 346 equally weighted characters and was run with TNT 1.1 (Goloboff et al., 2008). The non-hadrosauroid iguanodontian *Ouranosaurus* *nigeriensis* Taquet, 1976, was the outgroup.

Prior to the traditional search, 10,000 trees were set as maximum trees in memory. A heuristic search with 1000 replicates of Wagner trees using random addition sequences was performed, followed by TBR branch swapping, holding 1000 trees per replicate. Bremer support and bootstrap values were calculated for each branch to assess its robustness.

Three hundred and twenty-four equally most parsimonious trees were obtained. They have a length of 1008 steps, a consistency index (CI) of 0.498, and a retention index (RI) of 0.862. The strict consensus tree is presented in Figure 13. In contrast to Xing et al. (2014), we have not deleted *H. foulkii* a posteriori. The resulting topology resembles previously published hypotheses, with the exception of the appearance of several polytomies among several basal taxa (clade 65: *Prothadros* *byrdi* + *Probactrosaurus* *gobiensis* + *Jintasaurus* *meniscus* + *Eolambia* *caroljonesa*; clade 64: *Levnosovia* *transoxiana* + *Tanius* *sinensis*; clade 70: *Shuangmiaosaurus* *gilmorei* + *Nanningsaurus* *dashiensis* + *Claosaurus* *agilis*), hadrosaurines (clade 76: *Hadrosaurus* *foulkii* + *Wulagasaurus* *dongi* + *Acristavus* *gagslarsoni*; clade 85: *Gryposaurus* *notabilis* + *Gryposaurus* *monumentensis* + *Gryposaurus* *latidens* + *Gryposaurus* *incurvimanus*), and lambeosaurine taxa (clade 104: due to the disappearance of the *Parasaurolophus* clade; clade 107: due to the disappearance of the *Hypacrosaurus* clade), and with *Bo. rionegrensis* nested between *Prosaurolophus* *maximus* and the *Saurolophus* clade.

Previous analyses by Prieto-Márquez (2010) reported *Bo. rionegrensis* as a sister taxon of *S. koernerii* with the *Kritosaurus*-*Gryposaurus* clade, and with an unnamed hadrosaurid (UTEP Big Bend OTU) from Big Bend National Park (Texas) as the closest sister taxon to the South American clade. Prieto-Márquez (2010) encoded *Bo. rionegrensis* on the basis of the remains deposited at the Museo Carlos Ameghino in Cipolletti (Río Negro Province, Argentina) and the abstract of Powell (1987). In a recent review of the remains deposited at this museum, Cruzado-Caballero and Coria (2016) described two different morphotypes and proposed *W. salitralensis* to be a nomen vanum. Accordingly, the phylogenetic position of *B. rionegrensis* (*W.*

salitralensis to Prieto-Márquez, 2010) in Prieto-Márquez (2010) is the result of a chimera comprising specimens of different ontogenetic stages, different morphotypes, and different taxa. The position of *B. rionegrensis* as a sister taxon of the *Kritosaurus*-*Gryposaurus* clade in Prieto-Márquez (2010) was supported by characters 33 (dentary: ratio between the length of the proximal edentulous slope of the dentary and the distance between the rostral-most tooth position and the caudal margin of the coronoid process: less than 0.20, sample mean ratio of 0.11), 34 (dentary: angle between the dentary proximal-most edentulous slope and the horizontal: less than 150°, sample mean angle of 144°), and 36 (dentary: angle of deflection of the rostral ventral margin of the dentary: greater than 25°, sample mean angle of 33°). Between *Bo. rionegrensis* and *W. salitralensis*, only *W. salitralensis* preserves cranial remains; all of them belong to juvenile individuals, and in the case of the dentary, two morphotypes have been described (Cruzado-Caballero and Coria, 2016). The same applies to the coracoid, which is only present in *W. salitralensis* and belongs to a juvenile individual. As regards the ilium, several differences between the two taxa have been observed (see Ilium). The more inclusive position as a sister taxon of *S. koernerii* was supported by the height of the neural spine relative to that of the centrum of the tallest posterior dorsal or sacral vertebrae (in adults; character 200:1); the angle between the lateral margins of the facet for scapular articulation and the glenoid of the coracoid (character 207:0); the asymmetry of the lateral profile of the supraacetabular process of the ilium (character 238:0); the demarcation of the posterodorsal margin of the lateroventral rim of the supraacetabular process of the ilium (character 240:0); and the dorsoventral thickness of the midshaft of the ischium (character 270:2). In this case, as stated above, the coracoid belongs to a juvenile individual; we have observed differences in the ilia (see Ilium); moreover, either the two taxa have not preserved the ischium or it is incomplete.

In our analysis, *Bo. rionegrensis* holds a position within the Saurolophini tribe as a sister taxon of *Saurolophus* spp., with *Prosaurolophus* *maximus* as the closest outgroup taxon. Although the six synapomorphies of Saurolophini cannot be coded for *Bo. rionegrensis*, it shares the following characters with the genus *Saurolophus*: (1) the ratio between the proximo-distal length of the ulna and the anteroposterior width of this element at the midshaft is less than 10 (character 274:0) and (2) the general shape of the distal end of the fibula in lateral view is club-shaped, forming a greatly expanded anteriorly fibular distal end (character 336:1). Nevertheless, *Bo. rionegrensis* is well differentiated from all other members of Saurolophini in (1) the ratio between the height of the neural spines and that of the centrum of the sacral vertebrae: greater than 3.5 (character 245:2); (2) the degree of ventral deflection of the iliac preacetabular process: slight, with the angle greater than 150° (character 287:0); (3) the ratio between the maximum dorsoventral depth of the posterior end of the preacetabular process and the dorsoventral distance from the pubic peduncle to the dorsal margin of the ilium: less than 0.50 (character 289:0); (4) the ratio between the dorsoventral height and anteroposterior length of the iliac central plate: 0.8 or greater (character 290:0); (5) the symmetry of the lateral profile of the supraacetabular process absent (character 295:0); (6) the mediolateral thickening of the posterior portion of the iliac postacetabular process: present, the caudal portion of the postacetabular process markedly thickening mediolaterally as a result of the dorsomedial twist of the postacetabular process (character 303:1); (7) the morphological character of the cnemial crest of the tibia: presence of a cranially expanded cnemial crest restricted to the proximal end of the tibia (character 335:0); and (8) the degree of development of the articular surface of the astragalus for the internal malleolus of the tibia: moderately expanded medially, articulating with only part of the ventral surface of the tibial internal malleolus (character 338:1).

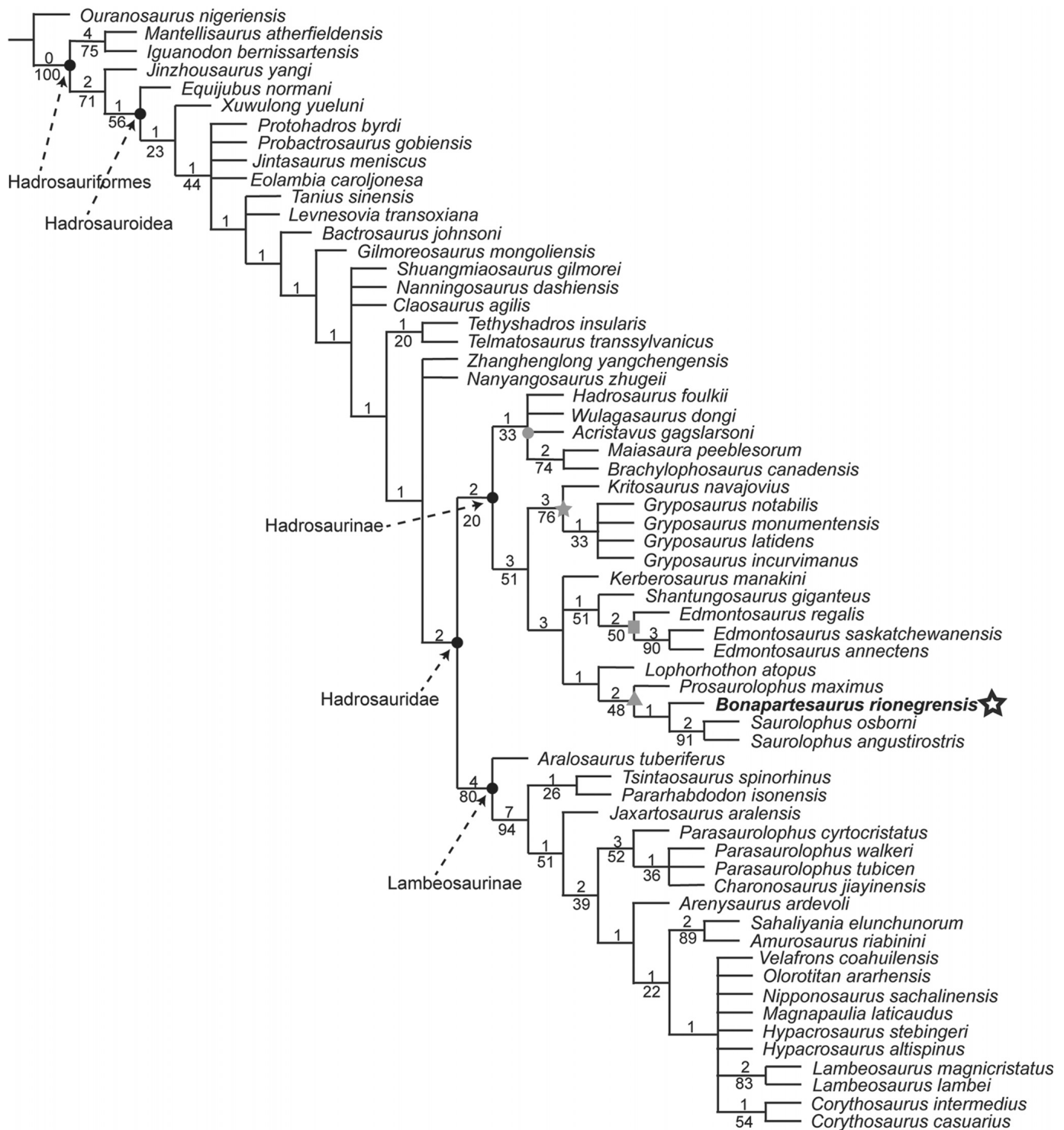


FIGURE 13. Strict consensus of 323 most parsimonious trees resulting from the maximum parsimony analysis implemented in TNT, showing the suggested systematic position of *Bonapartesaurus rionegrensis* within Hadrosauridae. Numbers above the branches are Bremer support values and numbers under the branches represent bootstrap values after 1000 replicates. Bootstrap values lower than 20 are not shown. Gray symbols represent the lineages within the clade Hadrosaurinae: circle, Brachylophosaurini; star, Kritosaurini; square, Edmontosaurini; triangle, Saurolophini.

DISCUSSION

Paleobiogeographic Implications

There have been numerous studies of the origin and paleobiogeographic distribution of the clade Hadrosauridae (Brett-

Surman, 1979; Milner and Norman, 1984; Horner et al., 2004; Sues and Averianov, 2009; Prieto-Márquez, 2010; Xing et al., 2014), all of which have focused on Laurasian remains. In South America, research on the arrival of this clade was originally carried out by Casamiquela (1964) and Bonaparte et al. (1984), and

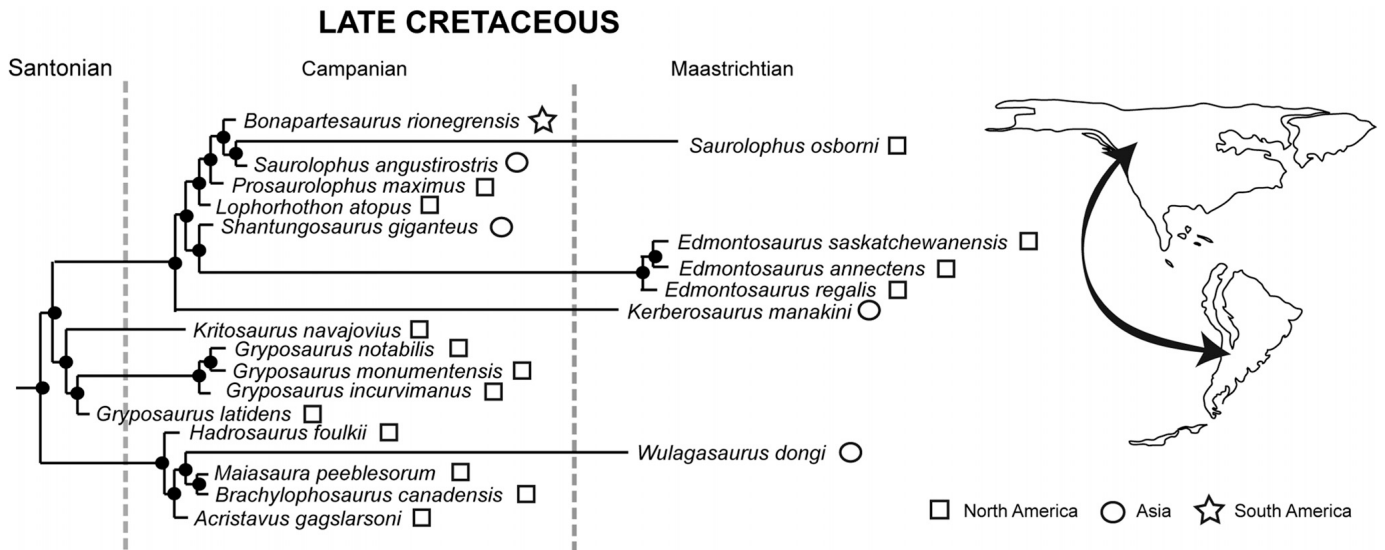


FIGURE 14. Phylogeny and temporal and geographical occurrences of Hadrosaurinae. Time-calibrated phylogeny of hadrosaurines using the maximum-agreement subtree 143 of 323 most parsimonious trees calculated in TNT. Arrow represents the Gondwanan dispersal episode.

more recently by Salinas et al. (2006), Coria (2009, 2013), and Prieto-Márquez and Salinas (2010).

The origin of this clade in the South American continent has been explained by many authors as being a result of geodispersal from North America during the Late Cretaceous (Casamiquela, 1964; Bonaparte, 1984; Bonaparte et al., 1984; Prieto-Márquez and Salinas, 2010; Coria, 2013). According to Prieto-Márquez and Salinas (2010), this geodispersal event would have occurred no later than the late Campanian. This is supported by Pough et al. (2004), who confirm the existence of a land connection between the two American continents during the Late Cretaceous, which would have been interrupted in the Maastrichtian (Pindell and Kennan, 2002).

Pascual (2006) refers to two episodes of faunal exchange between the Americas: the Gondwanan episode (Campanian) and the South American episode (Paleocene). During the Gondwanan episode, South America maintained bridges with Antarctica (Case et al., 2000) and North America. In the latter case, the presence of a connection was due to the subduction of the southern part of the North American plate under the eastward-moving Caribbean plate. These movements may have given rise to a Proto-Antillean volcanic arc (see references in Prieto-Márquez and Salinas, 2010). According to Coria (2013), the dispersal route used by the hadrosaurids as well as by other forms of vertebrates from the North American continent during the Gondwanan episode, although brief, allowed for bidirectional faunal exchange, as shown by the fossil record.

According to our analysis, the phylogenetic position of *B. rionegrensis* within the Saurolophini tribe and its relationships with the North American hadrosaurines *P. maximus* and *Lophorhothon atopus* Langston, 1960 (Fig. 14; Supplementary Data S4), suggest a possible dispersal event from North America to South America no later than the late Campanian, in accordance with Prieto-Márquez and Salinas (2010). Our time-calibrated phylogeny of hadrosaurines suggests the possibility that there were at least two geodispersal events. On this interpretation, in a first event, a group of *P. maximus* or its ancestors migrated from North America to Asia (*S. angustirostris*), and in a second event another group migrated from North America to South America (*Bo. rionegrensis*). The two events could have occurred at the same time, no later than the late Campanian, during the Gondwanan episode. It should be possible to test this interpretation

when the revised data of '*Kritosaurus*' *australis* and *Secernosaurus koeneri*, plus data from new Argentinean hadrosaurid remains, are included in new phylogenetic and biogeographic analyses.

CONCLUSIONS

The reassessment of the remains of *Willanakaqe salitralensis* has revealed that the paratype, MPCA-Pv SM2, belongs to a different taxon, *Bonapartesaurus rionegrensis*. This is a new hadrosaurine, which provides further data on a South America fauna that is poorly known and consists of two valid taxa, *Lapampasaurus cholini* and *Secernosaurus koeneri*. *Bonapartesaurus rionegrensis* is located within the Tribe Saurolophini, with *Prosaurolophus maximus* as the closest outgroup taxon and as a sister taxon of *Saurolophus* spp. This position contrasts with the original position, sensu Prieto-Márquez (2010), of *W. salitralensis* in the *Kritosaurus*-*Gryposaurus* clade. The differences in the analysis are because the initial assessment was based on a chimera comprising specimens of different ontogenetic stages, different morphotypes, and different taxa. The new position of *Bo. rionegrensis* is supported by the following characters shared with the genus *Saurolophus*: (1) the ratio between the proximodistal length of the ulna and the anteroposterior width of this element at the midshaft is less than 10 (character 274:0) and (2) the general shape of the distal end of the fibula in lateral view is club-shaped, forming a greatly expanded anteriorly fibular distal end (character 336:1). It differs from all other members of Saurolophini in (1) the ratio between the height of the neural spines and that of the centrum of the sacral vertebrae: greater than 3.5 (character 245:2); (2) the degree of ventral deflection of the iliac preacetabular process: slight, with the angle greater than 150° (character 287:0); (3) the ratio between the maximum dorsoventral depth of the posterior end of the preacetabular process and the dorsoventral distance from the pubic peduncle to the dorsal margin of the ilium: less than 0.50 (character 289:0); (4) the ratio between the dorsoventral height and anteroposterior length of the iliac central plate: 0.8 or greater (character 290:0); (5) the symmetry of the lateral profile of the supraacetabular process absent (character 295:0); (6) the mediolateral thickening of the posterior portion of the iliac postacetabular process: present, the caudal portion of the postacetabular process markedly thickens mediolaterally as a result of the dorsomedial twist of the

postacetabular process (character 303:1); (7) the morphological character of the cnemial crest of the tibia: presence of a cranially expanded cnemial crest restricted to the proximal end of the tibia (character 335:0); and (8) the degree of development of the articular surface of the astragalus for the internal malleolus of the tibia: moderately expanded medially, articulating with only part of the ventral surface of the tibial internal malleolus (character 338:1).

Biogeographically, *Bo. rionegrensis* provides new data on the occupation of South America by hadrosaurids no later than the late Campanian. This taxon suggests the possible occurrence of at least two dispersal events from North America within the Saurolophini tribe, one towards South America and another towards Asia.

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