

REVISITING THE HADROSAURID (DINOSAURIA: ORNITHOPODA) DIVERSITY OF THE ALLEN FORMATION: A RE-EVALUATION OF *WILLINAKAQE SALITRALENSIS* FROM SALITRAL MORENO, RÍO NEGRO PROVINCE, ARGENTINA

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REVISITING THE HADROSAURID (DINOSAURIA: ORNITHOPODA) DIVERSITY OF THE ALLEN FORMATION: A RE-EVALUATION OF *WILLINAKAQE SALITRALENSIS* FROM SALITRAL MORENO, RÍO NEGRO PROVINCE, ARGENTINA

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Key words. Hadrosauridae. Morphotype. Maastrichtian. Patagonia.

THE alpha taxonomic diversity of hadrosaurids in South America is modest compared with that of North America. Currently, it consists of three species: *Secernosaurus koeneri* Brett-Surman, 1979; Prieto-Márquez, 2010), *Willinakaqe salitranensis* Juárez Valieri, Haro, Fiorelli, Calvo, 2010 and *Lapampasaurus cholinoi* Coria, González Riga, Casadío, 2012. This diversity has been a matter of debate in later years (Prieto-Márquez and Salinas, 2010; Coria, 2014).

One of the most productive stratigraphical units with hadrosaurid bones is the late Campanian Allen Formation, widely exposed in northern Patagonia. The hadrosaurid *Willinakaqe salitralensis* (Juárez Valieri *et al.*, 2010) was described to include all hadrosaurid remains from that unit, based on information gathered from both associated and isolated specimens. Coria *et al.* (2012) later identified as a different taxon a specimen collected from the Allen Fm. in La Pampa Province and originally referred to *Willinakaqe*, *i.e.*, *Lapampasaurus cholinoi*. In a recent review of the South American hadrosaurid diversity, Coria (2014) casted some doubts on the taxonomic assignment of most of the material referred to *W. salitralensis*. He defined the holotype specimen (an incomplete premaxilla) as the only material representing that taxon. Here we analyze in detail the remains assigned to *W. salitralensis* and discuss the taxonomic status of this form.

Institutional abbreviations. **MPCA-Pv-SM**, Museo Provincial Carlos Ameghino, Paleontología de Vertebrados, Salitral Moreno, Cipolletti, Río Negro, Argentina; **ROM**, Royal Ontario Museum, Toronto, Ontario, Canada. **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
ORNITHISCHIA Seeley, 1887
ORNITHOPODA Marsh, 1881
HADROSAURIDAE Cope, 1870
SAUROLOPHINAE Brown, 1914
(*sensu* Prieto-Márquez, 2010)

Genus *Willinakaqe* Juárez Valieri, Haro, Fiorelli and Calvo, 2010

Type species. *Willanakaqe salitranensis* Juárez Valieri, Haro, Fiorelli and Calvo, 2010.

Original diagnosis. Premaxilla with a long and convex anterolateral surface anterior to the narial fossa (autapomorphy); narial fossa shallow, with a premaxillary foramen; posterodorsal and posterolateral processes of the premaxilla widely divergent; premaxillary denticles poorly de-

veloped; dorsal vertebrae with a shallow fossa located on the lateral surface of the neural arch upon the base of the transverse process (autapomorphy); eight sacral vertebrae in adults, the first with a ventral keel; high neural spines in sacral and proximal caudals, more than three times the height of the centrum; caudal neural spines showing a progressive distal expansion; dorsal border of the proximal section of the scapula straight; distal region of the postacetabular process of the ilium ventrally deflected (autapomorphy); femur without the enclosed cranial intercondylar groove.

Willinakaqe salitralensis was originally identified as a saurolophine (Juárez Valieri *et al.*, 2010) based upon remains collected in the early 1990s and housed in the Museo Carlos Ameghino in Cipolletti, Río Negro Province, Argentina. Although there is no certainty about the stratigraphical provenance of the remains, scientific personnel involved in the fieldwork reported that they were collected from at least two different bone-beds at Salitral Moreno (Río Negro Province) (García and Salgado, 2013). One of those bone-beds was dominated by remains of juvenile hadrosaurid specimens, whereas the other included hadrosaurid specimens of different ontogenetic stages associated with bones of other taxa such as titanosaur sauropods (*Rocasaurus muniozi* Salgado and Azpilicueta, 2000; *Aeolosaurus* sp. Powell, 1987b, saltasaurines indet.), ankylosaurs, non-avian and avian theropods, turtles, gastropods, and plants (Powell, 1987a; García and Salgado, 2013).

IS WILLINAKAQE PROPERLY DIAGNOSED?

The remains selected to diagnose *Willinakaqe salitralensis* are mostly isolated bones of juvenile, sub-adult and adult animals. One of the paratypes, MPCA-Pv-SM2, is a partial skeleton of an adult specimen provisionally housed in the collection of Vertebrate Paleontology of the University National of Tucumán and Fundación Miguel Lillo (Tucumán, Argentina). This material shows unique characteristics that potentially allow its taxonomic differentiation from *W. salitralensis* and other hadrosaurids (Cruzado-Caballero and Powell, in prep.).

Also, some specimens assigned to *W. salitralensis* (Juárez Valieri *et al.*, 2010) and deposited in the Museo Carlos Ameghino were misidentified either anatomically or taxonomically. The surangular MPCA-Pv-SM3 assigned to the paratype is actually the fragment of a cervical postzy-

gapophyseal process; MPCA-Pv-SM10 and MPCA-Pv-SM12, described as two left maxillae with teeth are actually from the right side; the cervical vertebra MPCA-Pv-SM11 is actually a titanosaurid caudal vertebra; and MPCA-Pv-SM26 corresponds to a sauropod dorsal rib.

The original diagnosis of *Willinakaqe salitralensis* included both autapomorphies and a combination of characters, and its holotype specimen (MPCA-Pv-SM8) is a premaxilla that was described as almost complete (Fig. 1). However, it only preserves its most anterior section, including part of the oral margin, the anterior and dorsal borders of the narial fossa and the base of the posterodorsal process. Juárez Valieri *et al.* (2010) did not consider the possible juvenile condition of MPCA-Pv-SM8, but its size is similar to that of the juvenile premaxillae studied by Campione *et al.* (2012). Therefore, we consider that MPCA-Pv-SM8 likely belongs to a juvenile individual.

OBJECTIONS TO THE DIAGNOSTIC FEATURES OF WILLINAKAQE

Premaxilla with a long and convex anterolateral surface anterior to the narial fossa (autapomorphy). A long anterolateral surface anterior to the narial fossa is also observed in *Maia-saura peeblesorum* Horner and Makela, 1979 (ROM 65035) and *Prosaurolophus maximus* Brown, 1916 (TMP 1983.064.03) (Horner, 1983; Campione *et al.*, 2012; Fig. 1). The *W. salitralensis* premaxilla could potentially show a convergent feature with those two North American forms, but Campione *et al.* (2012) and Prieto-Márquez (2014) have detected important morphological changes along the snout ontogeny of hadrosaurids. Juveniles tend to exhibit unique combinations of primitive and derived characters that are not present in adults due to ontogenetic and/or size-related variation. The morphology of this area in snouts of adult *W. salitralensis* is currently unknown.

Narial fossa shallow, with presence of a premaxillary foramen. The presence of a premaxillary foramen is a diagnostic feature of Saurolophine (Horner *et al.*, 2004).

Posterodorsal and posterolateral processes of the premaxilla widely divergent. This area of MPCA-Pv-SM8 is not preserved well enough to establish this characteristic (Fig. 1.1–4). Only the base of posterodorsal process is preserved, but its fragmentary condition prevents knowing whether or not they were divergent.

Premaxillary denticles not well developed. The occlusal area MPCA-Pv-SM8 is badly eroded (Fig. 1.2, 4). No denticles are observed in order to describe their development.

Dorsal vertebrae with a shallow fossa located on the lateral surface of the neural arch, upon the base of the transverse process (autapomorphy). This feature is described as widely

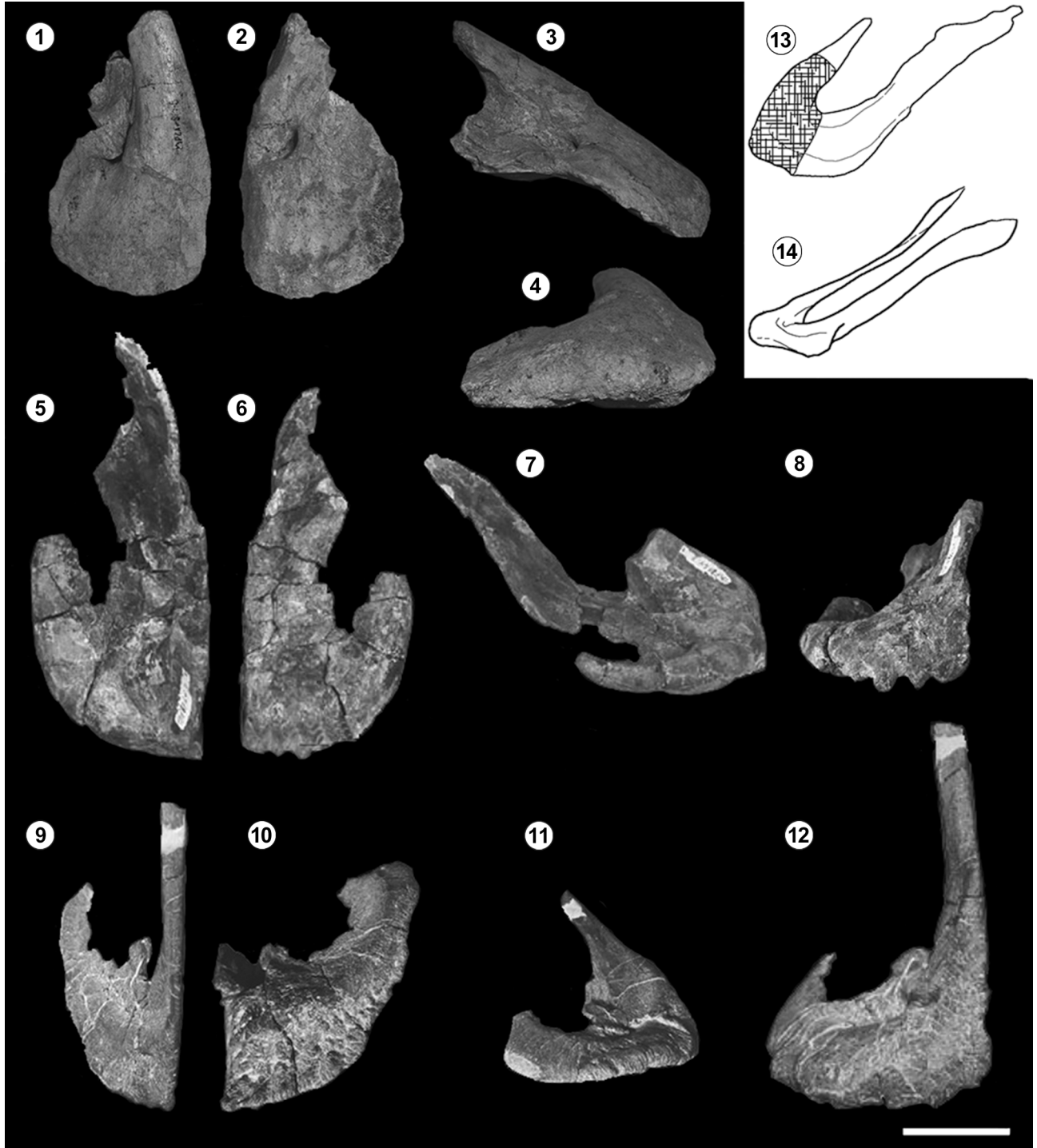


Figure 1. 1–4, premaxillae of MPCA-Pv-SM8; 5–8, *Prosaurolophus maximus* (TMP 1983.064.03) and 9–12, *Maiasaura peeblesorum* (ROM 65035). 1, 5, 9, dorsal view; 2, 6, 10, ventral view; 3, 7, 11, lateral view; 4, 8, 12, anterior view. 13, premaxillae of *Gryposaurus incurvimanus* (TMP 1980.022.000) and 14, *Lambeosaurus magnicristatus* (TMP 1066.004.000) in lateral view. Shaded area in 13 depicts what corresponds to what is preserved in MPCA-Pv-SM8. 5–12, taken from Campione *et al.* (2012). Scale bar= 5 cm.

distributed among Hadrosauridae (Horner *et al.*, 2004).

Eight sacral vertebrae in adults, the first with a ventral keel.

This feature is preserved only in the articulated specimen MPCA-Pv-SM2 briefly described by Powell (1987a). We consider this specimen as a different form, which will be discussed elsewhere.

High neural spines in sacral and proximal caudals, more than three times the height of the centrum.

In the studied sample, this character is only present in MPCA-Pv-SM2.

Caudal neural spines showing a progressive distal expansion.

This character is only seen in MPCA-Pv-SM2.

Dorsal border of the proximal section of the scapula straight.

This is a primitive feature present in basal hadrosaurids (Prieto-Márquez, 2010). In our opinion, this is the only valid unique character of *W. salitralensis*, although shared with the basal hadrosaurids *Bactrosaurus* Gilmore, 1933, and *Gilmoreosaurus* Brett-Surman, 1979, and the lambeosaurine *Nipponosaurus* Nagao, 1936 (Xing *et al.*, 2014).

Distal region of the postacetabular process of ilium ventrally deflected (autapomorphy).

This feature is only present in MPCA-Pv-SM2, and could represent a diagnostic feature of a new form (Cruzado-Caballero and Powell, in prep.).

Femur without enclosed cranial intercondylar groove. This is a feature that commonly occurs in adult individuals of several hadrosaurid taxa (Brett-Surman and Wagner, 2007).

COULD THE SPECIMENS ASSIGNED TO *WILLINAKAQE* REPRESENT MORE THAN ONE TAXON?

In a recent paper, Coria (2014) recognized two different humeral morphologies among the specimens assigned to *Willinakaqe salitralensis*. In addition to this, two morphotypes have also been observed in the dentaries and metatarsals. These morphotypes evidence the presence of robust and gracile hadrosaurid individuals among the specimens originally attributed to *W. salitralensis*. These morphotypes are found across different ontogenetic stages in juvenile to sub-adult individuals.

Morphotype 1 characterizes a robust form and it is represented by MPCA-Pv-SM7, a right dentary; MPCA-Pv-SM35, a left humerus; MPCA-Pv-SM56, a left metatarsal III; and MPCA-Pv-SM32, a right metatarsal IV (Figs. 2.3, 6, 3.5–8, 4.1, 3). On the other hand, morphotype 2 characterizes a gracile form and it is represented by MPCA-Pv-SM3 and MPCA-Pv-SM4, two right dentaries; MPCA-Pv-SM34, a left humerus; MPCA-Pv-SM29, a left metatarsal III; and MPCA-Pv-SM57, a right metatarsal IV (Figs. 2.1–2, 4–5, 3.1–4, 4.2, 4).

Dentaries (Fig. 2). Hadrosaurid dentaries are characterized by a large number of tooth positions, the deflection angle of the symphyseal portion, the position of the coronoid process relative to the dental battery, among other characters (Xing



Figure 2. Dentaries. 1–3, lateral and, 4–6, medial views. 3, 6, morphotype 1: right dentary MPCA-Pv-SM7; 1–2, 4–5, morphotype 2: right dentaries, 1, 4, MPCA-Pv-SM3; 2, 5, MPCA-Pv-SM4. Scale bar= 5 cm.

et al., 2014). Dentary morphology can be used to differentiate the two subfamilies of the clade, Saurolophinae and Lambeosaurinae. However, such a differentiation should be done upon adult individuals due to changes occurring during ontogeny. It should be noted that the dentaries MPCA-Pv-SM3, MPCA-Pv-SM4 and MPCA-Pv-SM7 belong to juvenile individuals, although MPCA-Pv-SM 7 is slightly larger.

The two dentary morphotypes differ in the number of tooth positions, width of the tooth positions and angle between the tooth row and the coronoid process. In MPCA-Pv-SM7 (morphotype 1) the dental battery has an anteroposterior length of 194.2 mm, which is longer than the 147.2 mm long dental battery of MPCA-Pv-SM3 (morphotype 2). Both dental batteries have 27 preserved tooth positions, but MPCA-Pv-SM7 seems to be missing at least five additional tooth positions. The tooth row is 40 mm wide in MPCA-Pv-SM7 and 35 mm in MPCA-Pv-SM3. According to Hubner and Rauhut (2010), McDonald *et al.* (2010), and Prieto-Márquez (2014) the number of tooth position in the dentary increases during ontogeny while the teeth suffers a reduction in width. In our case, MPCA-Pv-SM7 is slightly larger, has a higher estimated number of tooth positions and a greater tooth width if compared to MPCA-Pv-SM 3. Thus, although these characters depend on the ontogeny, but considering that both dentaries correspond to juvenile individuals, a taxonomic differentiation between these specimens cannot be ruled out. Moreover, the posterior end of the dental battery surpasses the posterior margin of the coronoid process in MPCA-Pv-SM7, whereas in MPCA-Pv-SM3 it is located more anteriorly. Finally, the coronoid process is more robust and more anteriorly projected in MPCA-Pv-SM7 than in MPCA-Pv-SM3 and MPCA-Pv-SM4. These differences are not likely to be explained by ontogenetic differences.

Humeri (Fig. 3). According to Egi and Weishampel (2002), the humeral morphology of hadrosaurids changes during ontogeny. The differences in the humeral shape between juvenile and adult lambeosaurines are clear, but not as clear in hadrosaurines. The humeral shapes are relatively similar between juvenile lambeosaurines and most juvenile hadrosaurines. Saurolophine humeri maintain a short deltopectoral crest that projects slightly from the shaft as compared with lambeosaurine humeri, and the deltopectoral crest of the latter is anteroposteriorly larger than the

diameter of the humeral shaft (Horner *et al.*, 2004). In saurolophines, the deltopectoral crest is almost three times as dorsoventrally long as it is transversely wide; the ventrolateral border is at, or just above, the midpoint of the humerus; and the overall aspect of the saurolophine humerus is long and slender compared to the thicker and more robust lambeosaurine humeri (Brett-Surmann and Wagner, 2007). Lastly, according to Prieto-Márquez (2014) the only humeral character that exhibits ontogenetic variation is the angulation of the ventral margin of the deltopectoral crest (*Edmontosaurus annectens*; Weishampel *et al.*, 1993: character 37).

MPCA-Pv-SM34 and MPCA-Pv-SM35 are two left humeri that, based on their size, correspond to the same

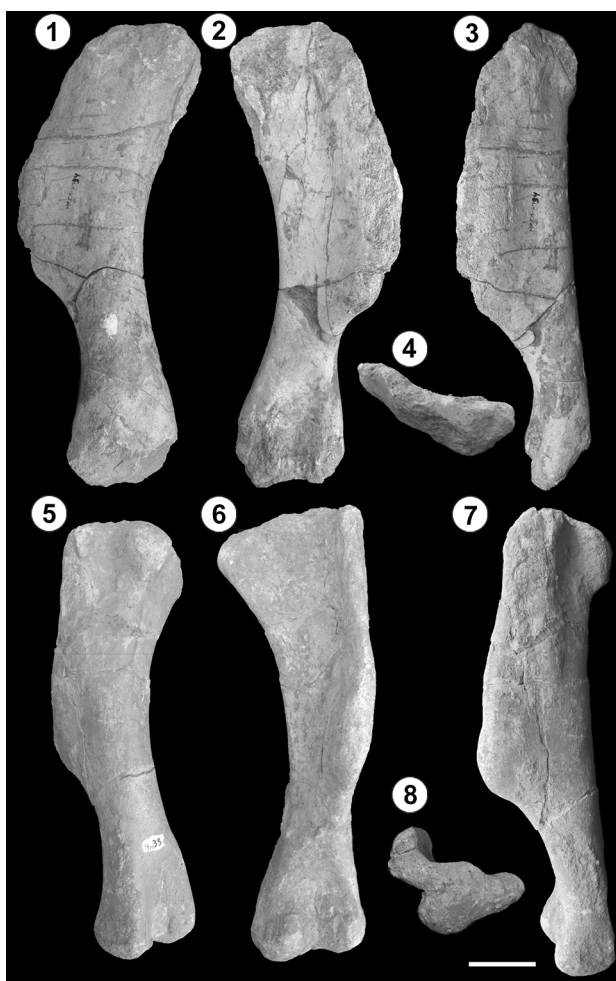


Figure 3. Humeri. 1, 5, lateroposterior view, 2, 6, medial view, 3, 7, lateral and, 4, 8, dorsal views. 5–8, morphotype 1: left humerus MPCA-Pv-SM35; 1–4, morphotype 2: left humerus MPCA-Pv-SM34. Scale bar= 5 cm.



Figure 4. Metatarsals in dorsal view. 1, 3, morphotype 1: 1, left metatarsal III MPCA-Pv-SM56; 3, right metatarsal IV MPCA-Pv-SM32. 2, 4, morphotype 2: 2, left metatarsal III MPCA-Pv-SM29; 4, right metatarsal IV MPCA-Pv-SM57. Scale bar= 5 cm.

ontogenetic stage, subadult or adult. The morphotype distinctions are based on the orientation and dimensions of the deltopectoral crest, and the development of the bicipital groove. Both humeri have a slightly similar proximodistal height (363 mm in MPCA-Pv-SM34 and 356 mm in MPCA-Pv-SM35), and the deltopectoral crest is slightly shorter in MPCA-Pv-SM34 than in MPCA-Pv-SM35 (209 mm and 219 mm, respectively). The crest is less projected anteromedially and wider anteroposteriorly (102.3 mm in MPCA-Pv-SM34 than in MPCA-Pv-SM35 (80.3 mm). Consequently, the bicipital groove in MPCA-Pv-SM35 is anteroposteriorly narrower and deeper than in MPCA-Pv-SM34.

Metatarsals (Fig. 4). According to Brett-Surman and Wagner (2007), hadrosaurid adult individuals show differences in the length/width ratio between metatarsal II and IV. Similarly, Prieto-Márquez (2010) claims that the length/width ratio of metatarsal III may indicate differences at a sub-familial level. The metatarsals III MPCA-Pv-SM29 and MPCA-Pv-SM56, and the metatarsals IV, MPCA-Pv-SM32 and MPCA-Pv-SM57, belong to individuals that, –based on their size– correspond to a similar ontogenetic stage (subadult or adult). The differences between length/width proportions indicate MPCA-Pv-SM56 and MPCA-Pv-SM32 are more robust than MPCA-Pv-SM29 and MPCA-Pv-SM57.

CONCLUSIONS

Willinakaqe salitralensis was based upon remains collected in an extensively outcropping formation and from several strata within it. The specimens belong to individuals

of different ontogenetic stages and include two different morphotypes. Also, the holotype specimen is very incomplete and too weathered to support a strong diagnosis. The immature nature of that individual could also lead to misidentification of unique features that could be modified throughout the ontogeny.

The differences found in the dentaries (number of tooth positions, width of the tooth positions, and position and angle between the tooth row and the coronoid process), humeri (orientation and dimensions of the deltopectoral crest and development of bicipital groove) and metatarsals (length/width proportions) indicate differences of taxonomic significance among the specimens assigned to *W. salitralensis*. In addition, the invalidity of all characters of the original diagnosis, lead us to consider *Willinakaqe salitralensis* as *nomina vanum*.

The hadrosaurids from the Allen Formation in the area of Río Negro Province likely include at least one taxon different from any other recorded hadrosaurid. Nonetheless, such taxonomic identification requires a more rigorous osteological analysis of all available evidence.

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