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***Bonitasaura salgadoi* gen. et sp. nov.: a beaked sauropod from the Late Cretaceous of Patagonia**

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Abstract Ornithischian and theropod dinosaurs were morphologically diverse during the Cretaceous. In contrast, sauropods were relatively more conservative. The anatomy of *Bonitasaura salgadoi*, a new 9-m titanosaurian sauropod from Upper Cretaceous beds of Patagonia, suggests that sauropod anatomical diversity would have included unexpected items. Its unusual, rectangular lower jaw possesses narrow, anteriorly restricted teeth and shows evidence of a sharp keratinous sheath over the non-dentigerous region that probably worked to guillotine plant material. This discovery definitely demonstrates that titanosaurs acquired a mandibular configuration similar to that of some basal diplodocoids, as had already been suggested by the lower jaw of the controversial genus *Antarctosaurus*. This oral configuration, plus the beak-like structure and the skull shape, resemble some traits more commonly seen in Laurasian ornithischians, mostly unexpressed in southern continents. A high sauropod morphological diversity seems to be in agreement with the poorly represented ornithischian clades of the southern hemisphere.

like' skulls, restriction of the cylindrical, narrow-crowned teeth to the anterior part of the snout, comb-like dentition (Coria and Chiappe 2001), squared symphysis, and nostrils retracted to the top of the head. The high femur/humerus ratio (a reversal) and an incipient whiplash tail could also be regarded as convergences. The lower jaw seems also to be problematic in titanosaur anatomy. Based on it, the Patagonian titanosaur *Antarctosaurus wichmannianus* (von Huene 1929), was interpreted as a chimera which included a diplodocoid lower jaw (Jacobs et al. 1993; Wilson and Sereno 1998; Upchurch 1999), and was later specified to be a rebbachisaurid (Sereno et al. 1999).

A new partially articulated sauropod titanosaur (Fig. 1c, d) was recovered in Santonian rocks of the Bajo de la Carpa Formation top (Hugo and Leanza 1999) at Río Negro Province, Argentina. Among the collected bones, a right dentary bearing several teeth provides new insights into the morphology of Late Cretaceous herbivorous dinosaurs on southern continents.

Introduction

After the purported global extinction of diplodocoid sauropod dinosaurs during the Cenomanian–Turonian (Bakker 1986), titanosaurs became the sole surviving latest Cretaceous sauropods. They successfully evolved in southern continents by radiating in a wide range of forms that later recolonized some Laurasian areas.

Derived titanosaurs are said to parallel diplodocoids (Salgado and Calvo 1997; Wilson 2002) in their 'horse-

Systematic paleontology

Saurischia Seeley 1888

- Sauropoda Marsh 1878
- Titanosauria Bonaparte and Coria 1993
- *Bonitasaura salgadoi* gen. et. sp. nov.

Etymology

The generic name is derived from the “La Bonita” hill, the name of the quarry, and *saura*, a female reptile. The species, *salgadoi*, honors Leonardo Salgado, the Argentinian paleontologist who gave new perspectives to sauropod research.

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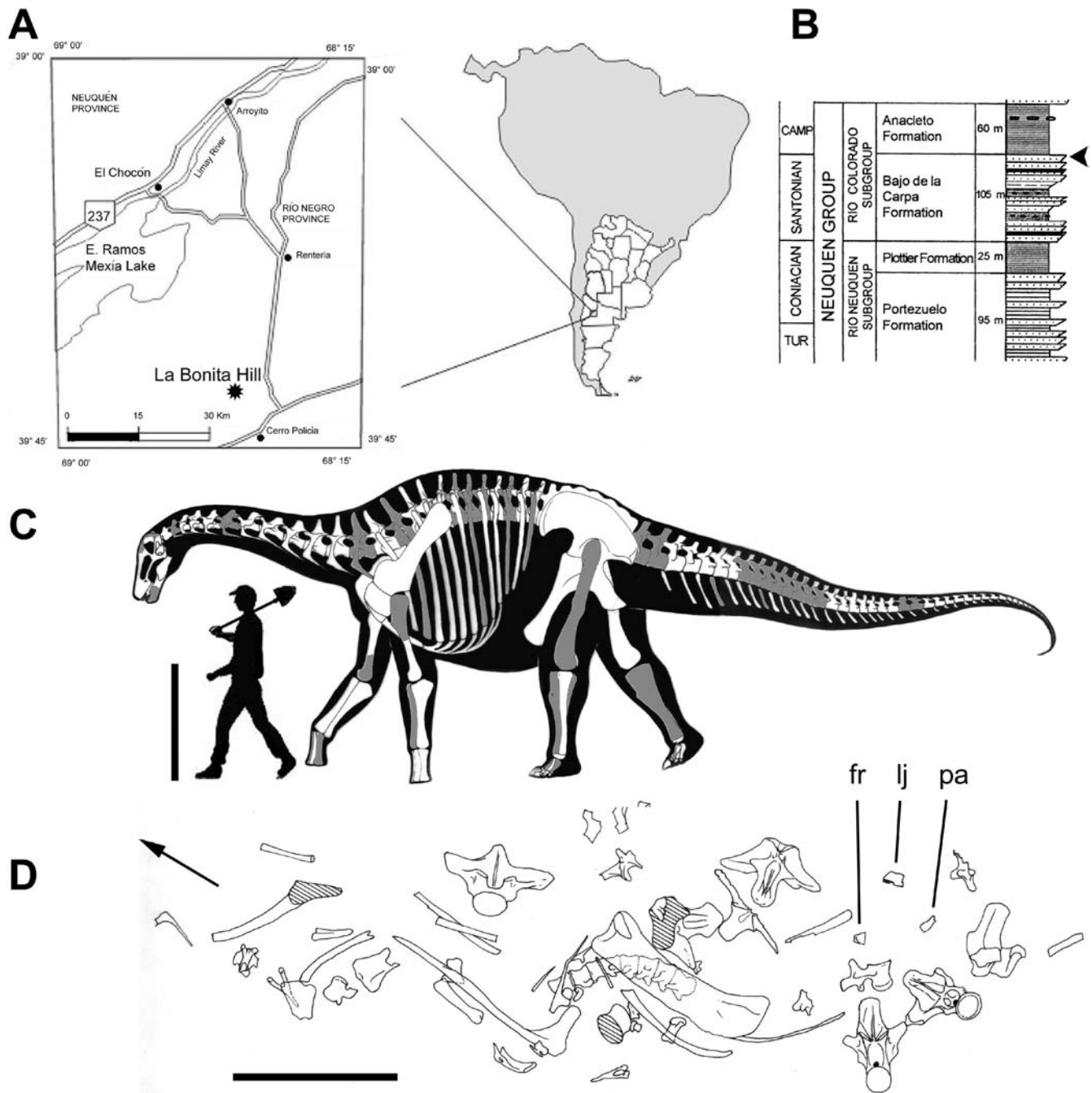


Fig. 1 A The 'La Bonita' hill, about 100 km south of Cipolletti, Argentina. B Stratigraphic position (arrow) of the fossil discovery. C Skeletal reconstruction and body shape of *Bonitasaura*. Preserved bones are indicated as dashed zones. The preserved dentary

is actually the right one. D Quarry map. Scale bars are 1 m in length. Arrow in D points north. Skull bones are labelled as *fr* (frontal), *lj* (lower jaw) and *pa* (parietal)

Holotype

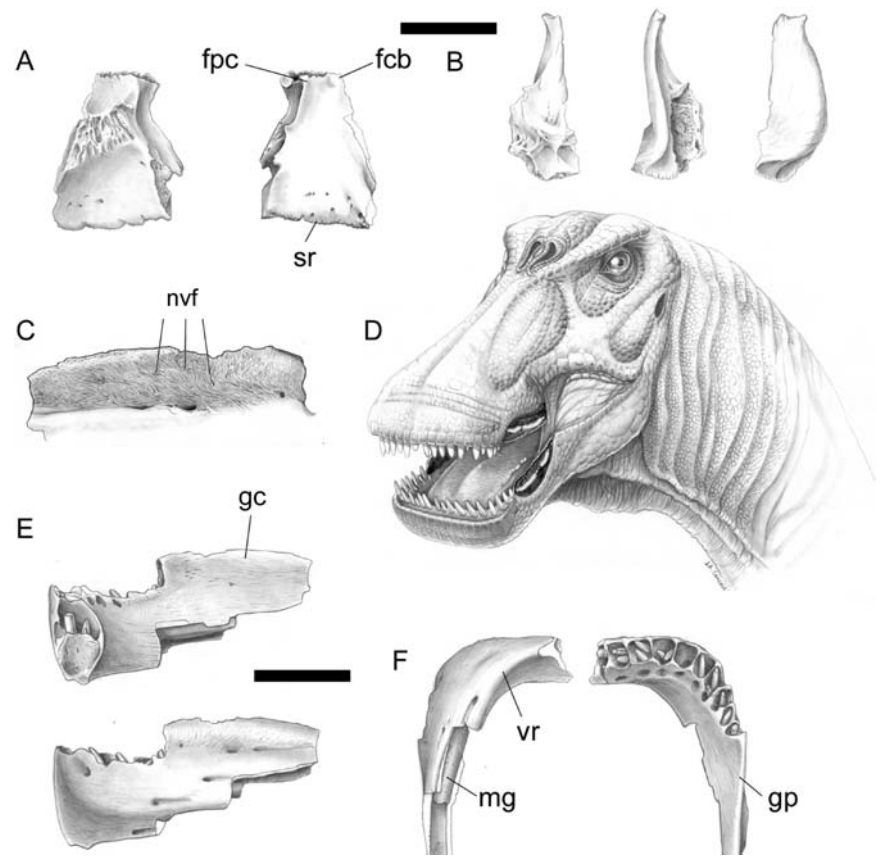
MPCA 300 (Museo Provincial "Carlos Ameghino", Cipolletti, Río Negro, Argentina), consists of a partially articulated, subadult skeleton (Fig. 1a–c). The material includes a left frontal, left parietal, right dentary with 15 teeth, lacking at least three or four alveoli distal to the symphysis, two cervical, six dorsal, and 12 caudal vertebrae, two chevrons, several cervical and dorsal ribs,

humerus, radius, two metacarpals, femur, tibia, two metatarsals.

Locality and geological setting

"La Bonita" hill fossil quarry, Cerro Policía, Río Negro Province, NW Patagonia, Argentina. The specimen was found in a fluvial sandstone (Hugo and Leanza 1999)

Fig. 2 *Bonitasaura*, MPC 300, holotype. **A** Right frontal in ventral and dorsal views. **B** Left parietal in anterior, dorsal and posterior views. **C** Labial view of the cutting mandibular crest on the posterior dentary and its densely pitted lateral surface. **D** Reconstruction of the head of *Bonitasaura* showing the position of the guillotine-like mandibular crest covered by a dark rhamphotheca. **E** Right dentary in lingual and labial (reversed) views. **F** Dentary in ventral and dorsal views. *Scale bars: A, B, E, F* 50 mm; *C* 30 mm. Abbreviations: *fc* frontal central “bump”; *fpc* frontoparietal concavity; *gc* guillotine crest; *mg* meckelian groove; *nvf* neurovascular foramina; *sr* sculptured rim; *vr* ventral ridge



which belongs to the uppermost layers of the Bajo de la Carpia Formation (Santonian; Hugo and Leanza 1999).

Diagnosis

Bonitasaura differs from other titanosaurs in the following combination of features: dentary alveoli reduced in number (three in the main ramus, one in the angle, and up to seven in the anterior region); middle and posterior region of the dentary edentulous and forming a sharp dorsal edge, with a profusely vascularized lateral side; very robust, diagonal neural arch pillars and bulging neural spine summits on anterior dorsal vertebrae. More diagnostic characters might emerge once all of the postcranial material has been prepared.

Description

The preserved skull remains of *Bonitasaura* include right frontal and parietal, and an incomplete lower jaw (Fig. 2a, b). However, only the latter will be described here. *Bonitasaura* (Fig. 2) bears an anteroposteriorly straight mandibular ramus that turns medially at almost a right angle to meet the opposite ramus in a transverse symphysis. The anteroventral margin of the dentary is vertical and lacks a chin-like process, thus differing from diplodocoids (Salgado and Calvo 1997; Upchurch 1999; Wil-

son 2002). The depth of the dentary is fairly homogeneous except for the posteriormost preserved region, but it is not possible to see whether it gradually deepens as in *Rapetosaurus* (Curry Rogers and Forster 2004). As in the latter, the lateral plate is substantially higher than the medial one. Although only ten complete alveoli were preserved, each ramus would have borne around 13 alveoli, which decrease in size posteriorly. All but the last two alveoli are associated with large neurovascular foramina. The anteriormost preserved alveolus bears up to three teeth, the same number as recorded for *Antarctosaurus* and other titanosaurs (Powell 1979; Coria and Chiappe 2001), whereas diplodocoids reached a higher number, as in the rebbachisaurid *Nigersaurus*, where up to seven narrow, striated replacement teeth are present (Sereni et al. 1999).

Posterior to the tooth-bearing region, the dorsal border of the jaw bears an abrupt elevation that terminates in a long, thin, horizontal edge, only preserved for its first 65 mm (Fig. 2c, e). The jaw widens ventrally up to three times. The upper 15 mm of this exquisitely preserved surface, especially on the labial side, is profusely pierced by small neurovascular foramina and furrows, as in the regions on bird dentaries sheathed by the rhamphotheca (Norell et al. 2001). This unusual morphology of the mid-to posterior region of the dentary, where bite-forces are higher, and its presumably keratinous cover, would have provided a strong cropping device for cutting tough plant material.

In contrast with primitive titanosaurs (Martínez 1998), which have broad-crowned, compressed cone-chisel-like teeth, *Bonitasaura* bear narrow, pencil-chisel-like teeth (Fig. 2), as in the derived titanosaurs *Rapetosaurus* (Curry Rogers and Forster 2004), *Antarctosaurus* (von Huene 1929), *Nemegtosaurus* (Nowinski 1971), and undescribed new forms from Patagonia. As in *Antarctosaurus*, *Rinconosaurus* (Calvo and González Riga 2003), and the isolated Patagonian premaxilla MPCA 79 (Coria and Chiappe 2001), these teeth have well-marked, non-denticulated carinae on their mesial and lateral edges that divide the labial and lingual sides. Although the teeth of MPCA 79 are slightly larger in diameter, this difference is expected to occur between upper and lower teeth in both diplodocoids and titanosaurs (Nowinski 1971; Holland 1906). *Rinconosaurus* carinae are more primitive in being larger and asymmetrically developed. These carinae fill a morphological gap between the broad two-winged basal macronarian teeth, the asymmetrically winged teeth of basal titanosauriforms, and the completely cylindrical teeth of advanced titanosaurs.

The abundant postcranial remains of *Bonitasaura* (MPCA 300) will be described elsewhere. However, *Bonitasaura* does not differ significantly in the postcranium from other derived titanosaurs (Apesteguía and Gallina 2002). The dorsal vertebrae bear a well-developed prespinal lamina. Both anterior and middle caudal vertebrae are strongly procoelous, while the distalmost caudals are long and biconvex. Metacarpals are relatively slender, in contrast to the short metatarsals. *Bonitasaura* differs from known titanosaur species in having anterior dorsals with robust, bulging neural spine summits, which are supported by remarkably robust bases.

Discussion

Although a detailed character analysis is beyond the scope of this work, available information suggests that *Bonitasaura* is closely related to the Late Cretaceous Malagasy titanosaur *Rapetosaurus* and the Mongolian taxa *Nemegtosaurus* and *Quaesitosaurus*. These four sauropods share sculptured frontal borders, a dentary symphysis that is almost perpendicular to the mandibular rami, and narrow, pencil-chisel-like teeth that are cylindrical in cross-section and mostly restricted to the anteriormost portion of the lower jaw. This set of characters may suggest that *Bonitasaura* is related to the Nemegtosauridae (Wilson 2002), which is defined as including all titanosaurs more closely related to *Nemegtosaurus* than to *Saltasaurus*.

Bonitasaura differs from *Antarctosaurus* in having the guillotine crest, a less straight angle of symphysis, and a rather flat instead sinuous posterior surface of the parietal. *Rapetosaurus* substantially differs in having a dentigerous region more extended backwards and an even more gently curved symphysis (Curry Rogers and Forster 2004). The presence in *Antarctosaurus* of an extensive edentulous region (although devoid of a tall crest) and the *Rapetosaurus* short, rugose postalveolar ridge and the bizarre

post-dentigerous corner of the maxilla, suggest that incipient guillotine-like structures could have been developed in other titanosaurs.

The unresolved phylogenetic relationships of *Antarctosaurus*, and the fact that the record of Late Cretaceous sauropods is only composed of derived titanosaurs and basal diplodocoids (i.e., Rebbachisauridae), led Upchurch (1999) to propose two possibilities for the status and evolutionary relationships of this species: a chimera of bones from different lineages, or a diplodocoid that acquired a postcranium largely convergent with that of derived titanosaurs. The discovery of *Bonitasaura* has shed light on the systematic affinities of *Antarctosaurus*, showing that its bizarre lower jaw features are not unusual in advanced titanosaurs, which can bear a squared snout convergent to that of diplodocoids, as originally proposed (see von Huene 1929; Calvo 1994; Salgado 2001). This is also supported by the clear titanosaur affinities of the remaining *Antarctosaurus* bones.

Wilson (2002) remarked on the morphological diversity acquired by sauropod dinosaurs. However, it is clear that their lineages were morphologically far less disparate than other dinosaurs (e.g., theropods include *Tyrannosaurus rex* and hummingbirds; ornithischians include large frilled ceratopsians as well as small and fast runners like *Othnielia*). Sauropod morphological variation is limited to changes in relative neck and limb proportions, loss of manual phalanges, muscular and pneumatic variation (inferred), armor, weapons and tail mobility, wide or narrow hip and limb gauges (Wilson and Carrano 1999), and some craniodental configurations. Several workers (e.g., Paul 1984) have already noted the possible possession of both beaks and teeth in prosauropods, their sister-group; a combination that is common in ornithischians, occasionally present in theropods, but was never suspected for derived sauropods.

The feeding mechanism proposed for derived titanosaurs (Calvo 1994) involves cutting and cropping of selected soft vegetation with the anteriormost teeth. The device exhibited by *Bonitasaura*, novel for sauropods, with the non-dentigerous zone of the dentary (and perhaps the maxilla) developed into a cutting surface, would have permitted effective slicing of tougher vegetation and minimized tooth wear. On the other hand, comb-like dental replacements have already been reported for advanced diplodocoids and purported titanosaurs (Coria and Chiappe 2001; Powell 1979; Holland 1906).

Most nemegtosaurids had a long, square-snouted, shoe-shaped, hadrosaur-like head (Curry Rogers and Forster 2004; Nowinski 1971), which could be present also in the Late Cretaceous rebbachisaurid diplodocoids. The new titanosaur *Bonitasaura* constitutes the first sauropod dinosaur yet recorded that not only possesses squared jaws, with narrow-crowned teeth arranged in continuous series that include at least three replacement elements per alveolus, but additionally also a keratinous beak to aid in cutting plant material. A keratinous cutting structure in addition to the aforementioned nemegtosaurid features has previously been reported only in

Late Cretaceous ornithischians, particularly hadrosaurs (Morris 1970), and has been proposed as an adaptive response to the rise and diversification of flowering plants (Bakker 1986; Salgado and Calvo 1997). However, the beak of ornithischians differs from that of *Bonitasaura* in that it is at the tip of the mouth, and there are teeth in the cheeks. Functional anatomical studies are necessary in order to evaluate how these differences reflect different ways of living in the two taxa. Furthermore, the dental mechanism seems to be less complex by far. The configuration shown by *Bonitasaura* is thus unique in having a posteriorly placed beak.

Interestingly, the similarities in mouth configuration and corporal mobility (i.e., loss of the hyposphene–hypantrum complex) among rebbachisaurid sauropods and derived titanosaurs suggest probable constraints on sauropod morphology that conditioned them to take advantage of a determinate resource. These constraints could be related to genetical or morphological limitations, environmental stasis, or the dominance of a particular vegetational food source.

Late Cretaceous sauropods in the southern hemisphere apparently entered new adaptative zones that were previously believed to have been occupied exclusively by ornithischians (Powell 2003). The unusual features exhibited by titanosaurs and rebbachisaurids suggest that some Late Cretaceous sauropods acquired a disparate morphological diversity. Although several ornithischian lineages were present at the same time, they were restricted to rare and small-sized forms when compared with other regions. This panorama changed when North American ornithischians entered South America by Late Campanian times. The morphological diversity of Late Cretaceous southern hemisphere sauropods and their adaptative capabilities may help to explain their persistence into the latest Cretaceous.

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