Cranial Anatomy and Phylogenetic Position of the Titanosaurian Sauropod Bonitasaura salgadoi

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PABLO A. GALLINA and SEBASTIÁN APESTEGUÍA

Knowledge of titanosaurian cranial anatomy has improved substantially in the last decade because several skulls have come to light or were restudied. The discovery of *Bonitasaura salgadoi*, a partial titanosaurian skeleton including cranial bones, permitted the definitive recognition of square jaws in a titanosaurian sauropod as well as a peculiar skull morphology that increases the morphological diversity of the group. Here we present a full description and illustration of the skull material of *B. salgadoi*. Among cranial bones, the lacrimal, quadrate, and dentary exhibit apomorphic differences from those of other titanosaurians. Conversely, the frontal and parietal are more conservative. A phylogenetic analysis recovers *B. salgadoi* as a member of the Titanosauria, related to mid-sized to large titanosauroids from the Turonian–Campanian of South America, in contrast to a previous hypothesis that suggested a nemegtosaurid affinity. The skull reconstruction presented here shows that the skull of *B. salgadoi* is anteroposteriorly short and dorsoventrally high, contrasting with the elongate skull of *Rapetosaurus krausei*.

Key words: Sauropoda, Titanosauria, skull, Late Cretaceous, Río Negro, Argentina.

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Introduction

Titanosaurians were a successful group of sauropod dinosaurs that inhabited both Gondwanan and Laurasian landmasses probably since Middle–Late Jurassic times, when land connections still linked both megacontinents. Titanosaurians were also the only sauropod lineage that survived until the end of the Cretaceous (Day et al. 2002; Curry Rogers 2005). The bulk of the diversity of the group was historically concentrated on southern continents, especially in South America, where "land isolation" was the biogeographical scenario (Huene 1929; Bonaparte 1986; Powell 1986). Recent reinterpretations of some Mongolian sauropods as titanosaurians (Calvo 1994; Salgado and Calvo 1997; Wilson 1997; Curry Rogers and Forster 2001; Wilson 2002, 2005), and the study of new titanosaurians from Madagascar and South America (Curry Rogers and Forster 2001; Apesteguía 2004), led to the hypothesis that at least one group of titanosaurians, the Nemegtosauridae (Wilson 2005; contra Upchurch et al. 2004), achieved a more global distribution. However, this was little explored in a phylogenetic context (Curry Rogers 2005).

Most of the rich knowledge of titanosaurian diversity was historically based on postcranial evidence. In recent years, however, several skulls came to light or were restudied, reinvigorating an old debate about whether titanosaurian skulls more closely resembled short-snouted, domed skulls, such as that of *Camarasaurus*, or long-snouted, equine-like skulls, such as that of *Diplodocus*.

The first titanosaurian specimen that included both skull and postcranial material, *Antarctosaurus wichmannianus*, from Upper Cretaceous beds of north Patagonia (Wichmann 1916), was studied and named by Huene (1929). The particular jaw morphology of *A. wichmannianus*, with square corners and teeth restricted to the symphysial ramus, prompted an erroneous *Diplodocus*-like skull restoration (Huene 1929: 68). Some subsequent authors suggested the inclusion of *A. wichmannianus* in the Diplodocoidea based on this jaw morphology (Jacobs et al. 1993; Wilson and Sereno 1998; Wilson 1999). However, the undoubtedly titanosaurian postcranial skeleton and basicranial morphology (suggesting nemegtosaurid affinities sensu Wilson 2005), as well as the presence of square jaws in other published and unpublished titanosaurians (Apesteguía 2004; MPM-125R), demonstrate that *A. wichmannianus* is indeed a titanosaurian.

In the 1970s and 1980s, respectively, *Nemegtosaurus mongoliensis* and *Quaesitosaurus orientalis* from the Upper Cretaceous Nemegt Formation in the Nemegt Basin of Mongolia were described. Both taxa were originally assigned to the Dicraeosauridae and were, at that time, two of the most com-
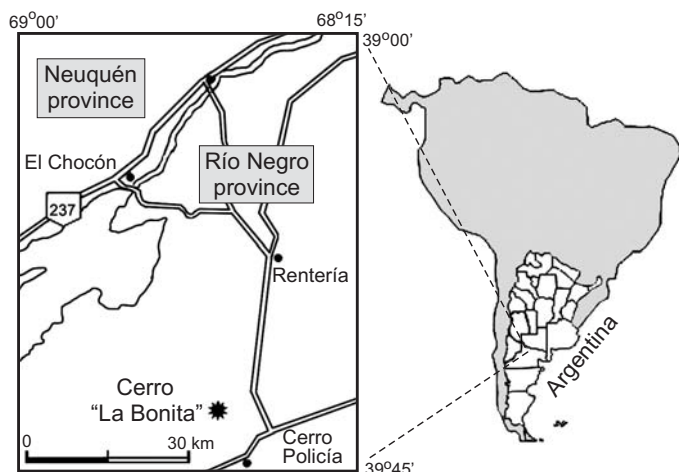
Fig. 1. Map location of La Bonita quarry (Upper Neuquén Group, Santonian–lower Campanian) in Río Negro province, northern Patagonia, where the holotype of *Bonitasaura salgadoi* was found.

plete Cretaceous sauropod skulls (Nowiński 1971; Kurzanov and Bannikov 1983). Later analyses supported their assignment to the Diplodocoidea (Yu 1993; Upchurch 1998, 1999; Upchurch et al. 2002, 2004), but more recently they have been recovered as titanosaurians (Calvo 1994; Salgado and Calvo 1997; Wilson 1997; Curry Rogers and Forster 2001; Wilson 2002, 2005). During the last decade, restudy of these Mongolian skulls, combined with new Gondwanan material of *Rapetosaurus krausei* and *Bonitasaura salgadoi*, substantially improved knowledge of titanosaurian cranial anatomy. In addition, numerous specimens from Patagonia have been reported recently, but remain undescribed.

The *Bonitasaura salgadoi* specimen was discovered early in the 1950s by shepherds in the foothills of La Bonita Hill, not far from the town of Cerro Policía (Fig. 1). However, because no paleontologists explored the area between 1922 and 1999, the exposed part of the skeleton remained untouched for almost half of a century. Successive fieldtrips to the area from 2003 to 2008 resulted in the collection of a relatively complete skeleton plus a few additional bones of a smaller specimen, as well as theropod and crocodylian teeth, turtle shells, and huge pterosaur wing bones. Here, we provide a detailed description of the skull of *B. salgadoi*, and analyze its phylogenetic position. In addition, we provide a skull reconstruction.

Institutional abbreviations.—CM, Carnegie Museum of Natural History, Pittsburgh, USA; DNM, Dinosaur National Monument, Jensen, USA; FMNH PR, Field Museum of Natural History, Chicago, USA; MCSPv, Museo de Cinco Saltos, Río Negro, Argentina; MGPIFD-GR, Museo de Geología y Paleontología del Instituto de Formación Docente Continua de General Roca, Río Negro, Argentina; MPCA, Museo Provincial Carlos Ameghino, Río Negro, Argentina; MPM, Museu de Paleontologia de Marília, Brasil; PVL, Collection of Vertebrate Paleontology of the Instituto Miguel Lillo, Tucumán, Argentina.

Geological setting

The "La Bonita" quarry, where the holotype of *Bonitasaura salgadoi* was found, exposes siliceous, continental rocks from the Upper Neuquén Group, including the Bajo de la Carpa and Anacleto formations (Santonian–lower Campanian) (Leanza et al. 2004). The lower Bajo de la Carpa Formation, from which the *B. salgadoi* holotype was recovered, is composed of sandstones and thin conglomerates alternating with pelites and wackestones. Conversely, the overlying Anacleto Formation is composed of sandy to pelitic levels. The sedimentation environment was controlled by a mid to low energy fluvial regime (Pérez et al. 2009).

Systematic paleontology

Saurischia Seeley, 1888

Sauropoda Marsh, 1878

Titanosauria Bonaparte and Coria, 1993

Titanosauroidea Upchurch, 1995

Bonitasaura salgadoi Apesteguía, 2004
Figs. 2–5.

Holotype: MPCA 460 (modified from the original description; see Comments below), consisting of a partially articulated, subadult skeleton.

Emended diagnosis.—*Bonitasaura salgadoi* differs from other titanosaurians in possessing the following unique combination of features: frontal outer rim straight (not sigmoid); thin and enlarged maxillary process of the lacrimal oriented downward and forward; posterior region of the dentary edentulous and bearing a sharp dorsal edge, with a profusely vascularized lateral surface; tongue-like process on spinoprezygapophyseal laminae of mid-cervical vertebrae; very robust, diagonal neural arch pillars and bulging neural spine summits on anterior dorsal vertebrae; longitudinal, paired fossae on the sides of the prespinal lamina in anterior dorsal vertebrae; circular, vertically oriented fossae aligned with the prespinal lamina in mid-dorsal vertebrae; thin, longitudinal laminae diverging from prespinal and postspinal laminae in anterior caudal vertebrae; anterior, longitudinal ridge of the tibia with marked promontory just over the anterior process of distal end.

Comments.—When the holotype was designated, the material included by Apesteguía (2004) was a left frontal, left parietal, right dentary with 15 teeth, two cervical, six dorsal and 12 caudal vertebrae, radius, metacarpal, femur, tibia, two metatarsals, two chevrons, and several cervical and dorsal ribs. The material assigned to this specimen has since been expanded.

Further preparation, plus new collecting trips to the quarry, added a right lacrimal, a left quadrate, an isolated tooth, the axis, 13 additional caudal vertebrae, three chevron bones, an incomplete humerus, two metacarpals, the left pubis, the left ischium, a fragmentary left fibula, both astragali, four metatar-
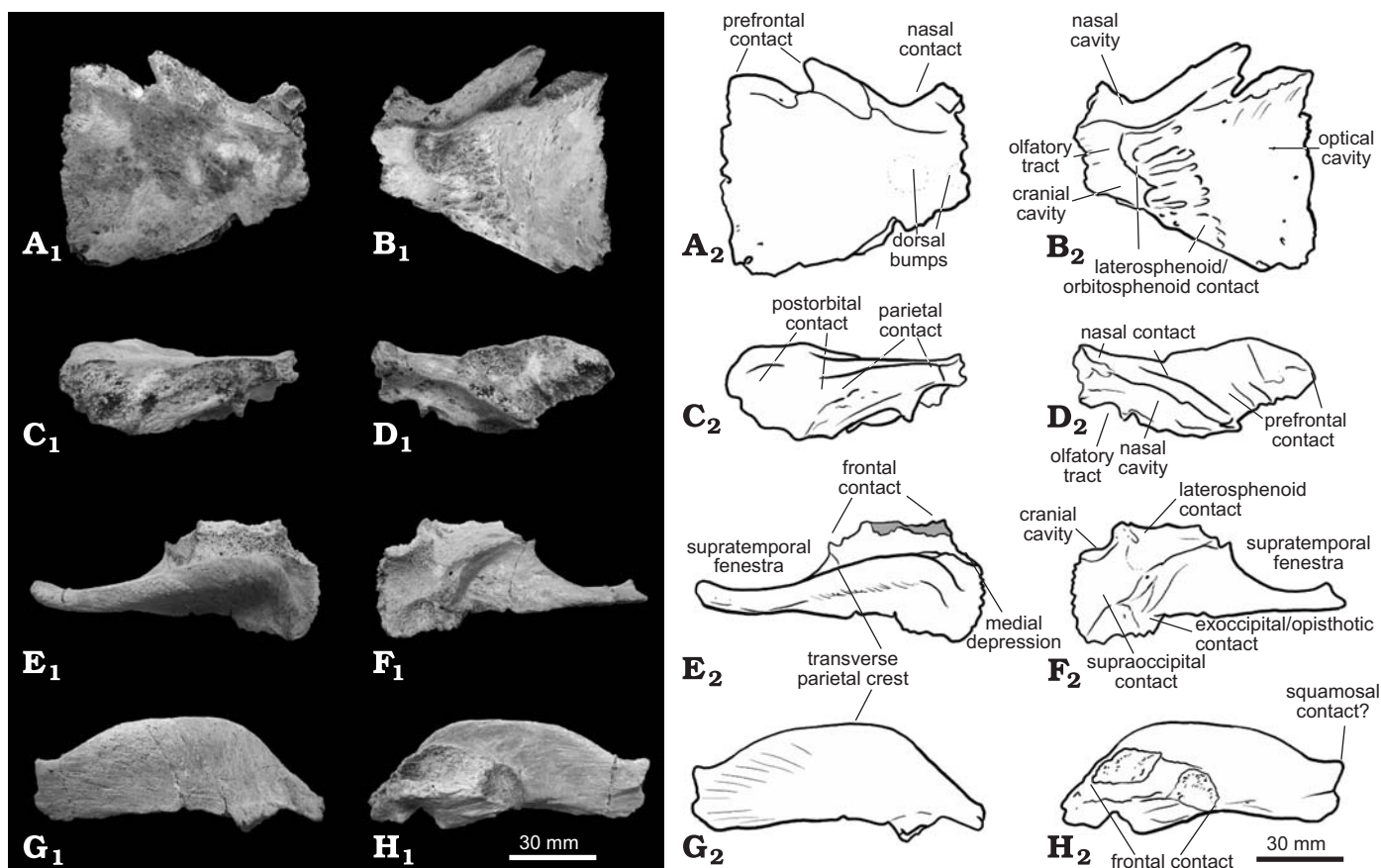
Fig. 2. Photographs and interpretive drawings of the titanosauroid *Bonitasaura salgadoi* Apesteguía, 2004 from the Upper Neuquén Group of Río Negro province, Patagonia, MPCA 460. **A–D**. Left frontal in dorsal (**A**), ventral (**B**), posterior (**C**) and anterior (**D**) views. **E–H**. Left parietal in dorsal (**E**), ventral (**F**), posterior (**G**), and anterior (**H**) views.

sals, two pedal phalanges, and an ungual phalanx. The radius mentioned by Apesteguía (2004) was actually a metacarpal I. All the cited material comes from the same quarry and pertains to the same individual (Pérez et al. 2009).

Stratigraphic and geographic range.—Bajo de La Carpa Formation (Santonian–lower Campanian), Upper Neuquén Group, Río Negro province, Argentina.

Description

The following description focuses only on the cranial elements; the postcrania will be described elsewhere (Gallina in

Table 1. Measurements (in cm) of skull elements of the holotype of the titanosauroid *Bonitasaura salgadoi* from the Upper Neuquén Group of Río Negro province, Patagonia. – not applicable measurement; * incomplete measurement.

	Bone elements					
	frontal	parietal	dentary	lacrimal	quadrate	teeth
Minimum width	8.5	9.9	–	0.4	–	–
Maximum width	–	–	7.3*	2.6	5	0.6
Minimum length	4.2	0.7	–	–	–	–
Maximum length	7.4	4.3	11.5*	15.5	24.5	3.8
Minimum height	0.5	2	–	–	–	–
Maximum height	2.4	3.4	4.2	7.3	6.5*	0.5

press; PAG and SA unpublished data). Measurements are listed in Table 1.

Frontal.—Only the left frontal was preserved (Fig. 2A–D). Although complete, it is damaged in the area that articulates with the parietal. The frontal forms the posterior part of the cranial roof, contacting the nasal and prefrontal anteriorly, the parietal and postorbital posteriorly, and the laterosphenoid–orbitosphenoid complex ventrally.

Though incomplete in its posteromedial corner, the large, flat bone is trapezoidal in dorsal view, as in *Antarctosaurus wichmannianus*, contrasting with the frontals of *Nemegtosaurus mongoliensis*, and *Phuwiangosaurus sirindhornae* (Suteethorn et al. 2009), which are more rectangular. The shorter, medial side contacts the opposite frontal and the longer, lateral side bounds the posterodorsal border of the orbit. In other titanosaurians (e.g., *Nemegtosaurus mongoliensis*, *Antarctosaurus wichmannianus*, *Rapetosaurus krausei*), and even diplodocoids (e.g., *Amargasaurus cazaui*, *Limaysaurus tessonei*, *Diplodocus longus*), this longer side is rather sigmoid, bearing a large, convex, posterior lobe that is slight in *N. mongoliensis* and *Saltasaurus loricatus*, oblique in *R. krausei* and *P. sirindhornae*, and strongly expanded in *Bonatitan reigi*. In contrast, in *Bonitasaura salgadoi* the lateral margin remains straight along its entire length; there is no

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posterior lobe. Because this trait is unknown in other sauropods, is considered here an autapomorphy of *B. salgadoi*. Although the frontal comes from a subadult specimen (Apesteguía 2004; Gallina in press), the size of this bone is similar to that of other known adult titanosaurians (e.g., *Antarctosaurus wichmannianus*, *Nemegtosaurus mongoliensis*, *Saltasaurus loricatus*, MGPIFD-GR 118).

Curry Rogers and Forster (2004) recognized only one large prominence on the skull roof in *Rapetosaurus krausei*. *Bonitasaura salgadoi*, however, bears three transversely aligned dorsal bumps (one and a half are preserved on the frontal, thus three are assumed for both frontals), as Powell (2003) noted for *S. loricatus*. The outer two correspond to the points of maximum doming of the cranial cavity, and actually represent the positions of the paired telencephalon lobes. The central prominence is located toward the posteromedial corner and is shared by both frontals. It represents part of an intense thickening of the suture area, a feature also documented by Paulina-Carabajal and Salgado (2007) in MGPIFD-GR 118, a titanosaurian braincase from the Allen Formation of Río Negro. A medial prominence was also recognized in *R. krausei* (Curry Rogers and Forster 2004), *A. wichmannianus* (Huene 1929), *S. loricatus* (Powell 1986, 2003), and *Bonatitan reigi* (Martinelli and Forasiepi 2004). Although the central prominence is only partially preserved, its original shape was probably round and not anteroposteriorly elongate, as in *A. wichmannianus*.

In ventral view, the frontal exhibits three concavities of different sizes and orientations, corresponding to the cranial, nasal, and orbital cavities, respectively. The orbital cavity is the largest, occupying the lateral half of the bone. The anteromedial part of the frontal houses the posterior part of the nasal cavity. These two cavities are separated by an oblique, osseous wall that originates on the laterosphenoid–orbitosphenoid articular surface and runs toward the anterolateral corner of the frontal. The frontal roofs the anterior part of the cranial cavity, covering the telencephalon. This part occupies the medial one-fourth of the frontal, posterior to the nasal cavity. The cranial and nasal cavities communicate with each other by means of a 1.1 cm-wide groove that housed the olfactory tract (CN I). The orbital and cranial cavities share a wide 2.3 cm rugose area that forms the oblique articular surface for the laterosphenoid–orbitosphenoid complex.

A faint, medially tapering articular facet for the postorbital embays the frontal in posterior view. This surface occupies about one-fourth of the lateral width of the frontal but it minimizes substantially the contribution of the frontal to the supratemporal fenestra, similar to the conditions in *A. wichmannianus*, in which the frontal is almost excluded from the fenestra, and *S. loricatus* (PAG personal observation) and *N. mongoliensis*, in which the frontal is completely excluded from the margin of the fenestra (contra Curry Rogers and Forster 2001). The opposite condition is present in *R. krausei* and *B. reigi*, in which the lack of an anteromedial projection of the parietal allows the frontal to form part of the supratemporal fenestra. The remaining medial three-fourths of the posterior side of the frontal forms the articulation with the parietal. Whereas the ventral portion of the frontal–parietal articular facet is very well preserved, its dorsal counterpart is heavily damaged.

In anterior view, the articular surfaces are visible for the nasal on the medial margin and the prefrontal on the lateral margin. The nasal articular surface is a long, deeply concave area; its ventral margin forms an anteriorly projecting shelf that contacted the expanded posterior region of the nasal. The articular facet is horizontally oriented and occupies half of the total width of the frontal. The articular facet for the prefrontal is a complex triangle composed of two parts divided by a conspicuous notch.

The arched and profusely rugose dorsal margin of the orbital cavity is visible in lateral view. A similarly ornamented orbital rim is present in *Camarasaurus*, *R. krausei*, *S. loricatus*, and *N. mongoliensis*. As in *R. krausei*, there is a small cleft toward the posterior border of the orbit. Using this as a basis the measurements of the preserved part of the orbital arch, coupled with other, recently published titanosaurian cranial reconstructions (e.g., Curry Rogers and Forster 2004; Wilson 2005), the complete orbital diameter for *B. salgadoi* is estimated to be about 14 cm. The highest point of the arch is located toward the anterior end of the orbit. The entire anterior border of the frontal is notably thickened: the prefrontal articular facet is about 1.5 times as thick as the postorbital facet.

In medial view, the interfrontal articulation is V-shaped and convolute. Although the primary proportions of the bone are similar to those of other adult sauropods, the presence of unfused frontals indicates that the specimen was immature. In this way, the convolute interfrontal suture resembles that of the juvenile specimen of *R. krausei* (FMNH PR 2185; Curry Rogers and Forster 2004: fig. 13).

Parietal.—Only the left parietal is preserved (Fig. 2E–H). Along with the frontal, it roofs the posterior part of the skull. This transversely elongate element, although obliquely positioned on the skull, is described here with its longer axis transverse to the sagittal plane. This way, its ventral side will be considered horizontal instead of oblique. The parietal meets the squamosal laterally and the supraoccipital and exoccipital–opisthotic complex posteriorly.

The bone is nearly complete, but all but a small, elongate portion of the fronto-parietal articular surface is lost. As also occurs in other titanosaurs, such as *R. krausei*, and also in diplodocoids, such as *Limaysaurus*, *Amargasaurus*, and *Dicraeosaurus*, there is a medial depression (parietal fontanelle) along the fronto-parietal suture, though it is not nearly as pronounced as in *Amargasaurus* or *Dicraeosaurus*. Posterior to this region, the dorsal surface rises as a vertical wall, forming a sharp, sigmoid, transverse parietal crest as in *B. reigi*, *R. krausei*, *S. loricatus*, and MGPIFD-GR 118. The medial one-third of this crest curves posteriorly as it approaches the midline, turning slighter and bounding the medial depression. Before reaching the interparietal contact, the crest splits into two parts: an anterior part that runs medially to meet its counterpart, and a posterior part that runs postero-
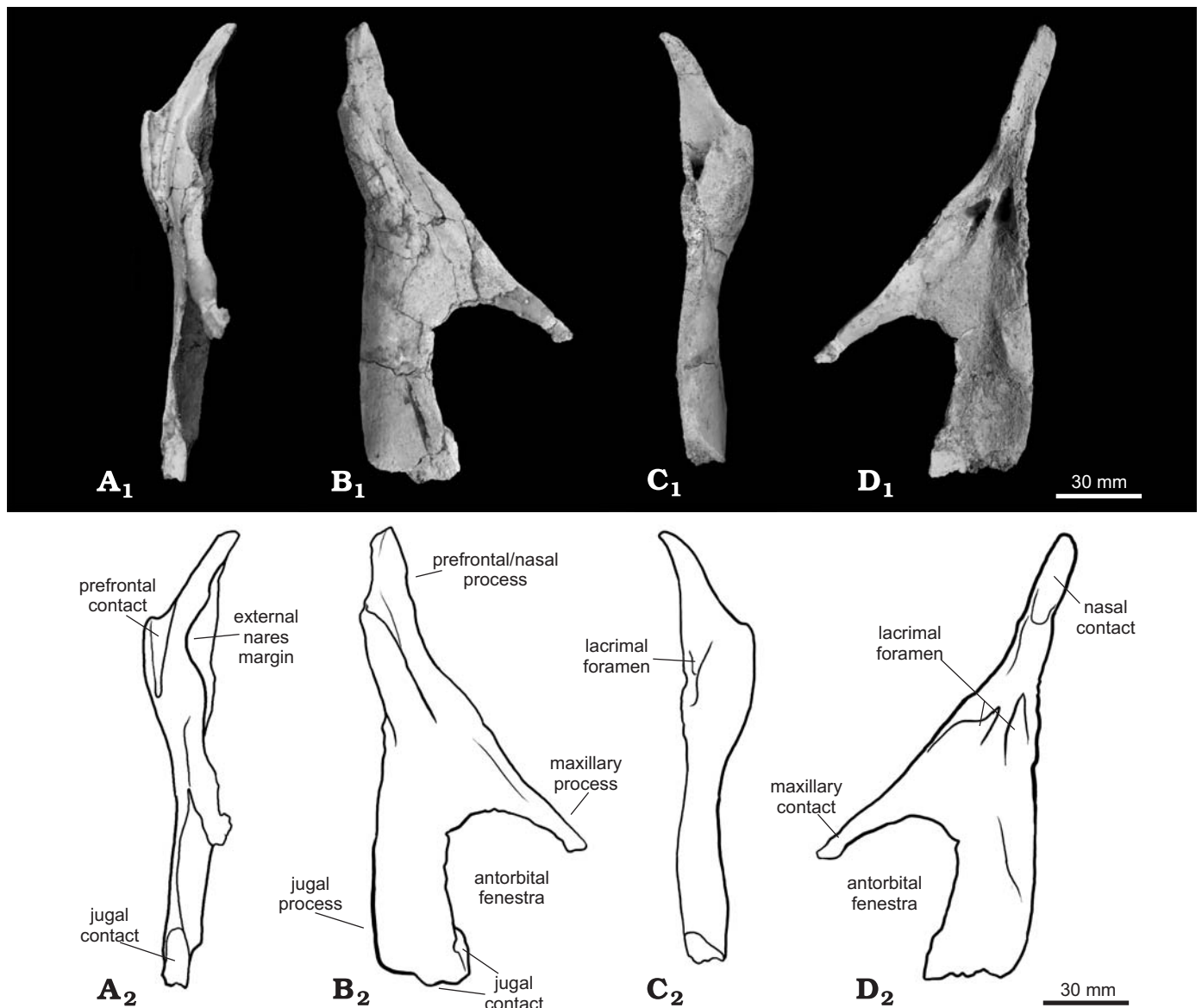
Fig. 3. Photographs and interpretive drawings of the titanosauroid *Bonitasaura salgadoi* Apesteguía, 2004 from the Upper Neuquén Group of Río Negro province, Patagonia, MPCA 460. Right lacrimal in anterior (**A**), lateral (**B**), posterior (**C**), and medial (**D**) views.

medially to meet the supraoccipital, similar to the condition in *S. loricatus*.

The lateral half of the parietal is a long, slightly anteriorly concave, squamosal process that ends in the articulation with the squamosal. The anterior side of this process plunges ventrally, forming a smooth posterior border of the supratemporal fenestra. This oval-shaped fenestra, which is oriented oblique to the sagittal plane, is about 50 mm in its longest dimension. In ventral view, the contact for the laterosphenoid lies close to the level of the crista antotica.

On the medial surface of the parietal there are three concave surfaces, one of which corresponds to the posterior portion of the cranial cavity and the other two are the articular contact for the supraoccipital. Lateral to the supraoccipital contact is an articular surface for the exoccipital–opisthotic.

In posterior view, the smooth bone surface becomes slightly concave toward the ventromedial border, at the level of the supraoccipital and exoccipital contacts. In contrast to the curved ventral border of the parietal in *Saltasaurus loricatus*, the ventral border of the parietal of *Bonitasaura salgadoi* is straight until its medial end, which projects ventrally.

In anterior view, the contact for the frontal is medially located; its dorsal surface is badly preserved. Laterally, on the anterior face of the squamosal process, there is a small, horizontal ridge. In medial view, the interparietal articular surface is convolute and anteroposteriorly enlarged.

Lacrimal.—A complete right lacrimal is preserved (Fig. 3). This bone forms the anterior border of the orbital cavity, contacting the prefrontal and the nasal dorsally. Along with the maxilla and jugal, the lacrimal frames the posterior border of the antorbital fenestra. The bone is largely laminar, but is triangular in cross section on its dorsal tip. As in *Nemegtosaurus*
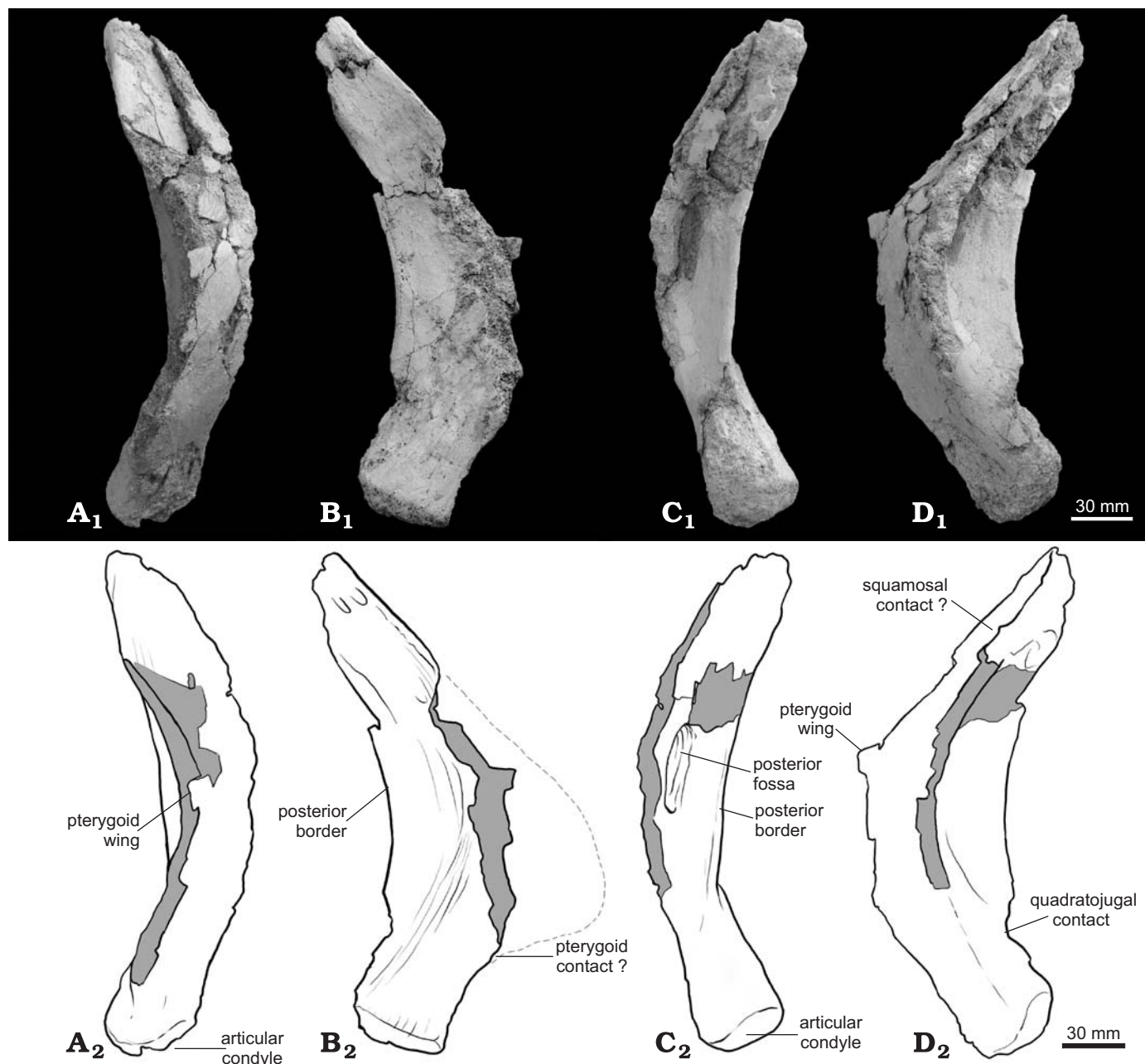
Fig. 4. Photographs and interpretive drawings of the titanosauroid *Bonitasaura salgadoi* Apesteguía, 2004 from the Upper Neuquén Group of Río Negro province, Patagonia, MPCA 460. Left quadrate in anterior (**A**), medial (**B**), posterior (**C**), and lateral (**D**) views.

mongoliensis, the lacrimal possesses three main processes: a posterodorsal prefrontal/nasal process and maxillary and jugal processes, both of which project anteroventrally. The prefrontal/nasal process is elongated and slightly concave medially. The similarly large maxillary process becomes thinner distally, in contrast to the broad maxillary process of *Rapetosaurus krausei*. The jugal process is flat and broad along its entire length, and bears two well-defined surfaces at 75° to each other (one on the anterior surface of the process, the other on the ventral surface) that housed a dorsal portion of the jugal.

The posterior portion of the antorbital fenestra, bounded by the maxillary and jugal processes, is ovoid, subtending a nearly 50° angle much less sharp than that of *R. krausei*.

Conversely, the posterior portion of the antorbital fenestra is much more acuminate in *Brachiosaurus*, *Camarasaurus*, and diplodocoids.

The prefrontal articular surface is concave and triangular in anterior view. The anterior opening of the lacrimal foramen opens medially, as in *N. mongoliensis*, but is divided by a thin bony septum. The posterior opening is posteriorly located and opens into the orbital cavity, unlike its homolog in *R. krausei*, which opens laterally.

In dorsal view, a marked embayment is evident on medial side of the prefrontal/nasal process. This is the lateral-most extent of the external nares, a situation shared only with *R. krausei*, unlike the condition in diplodocoids and basal macro-
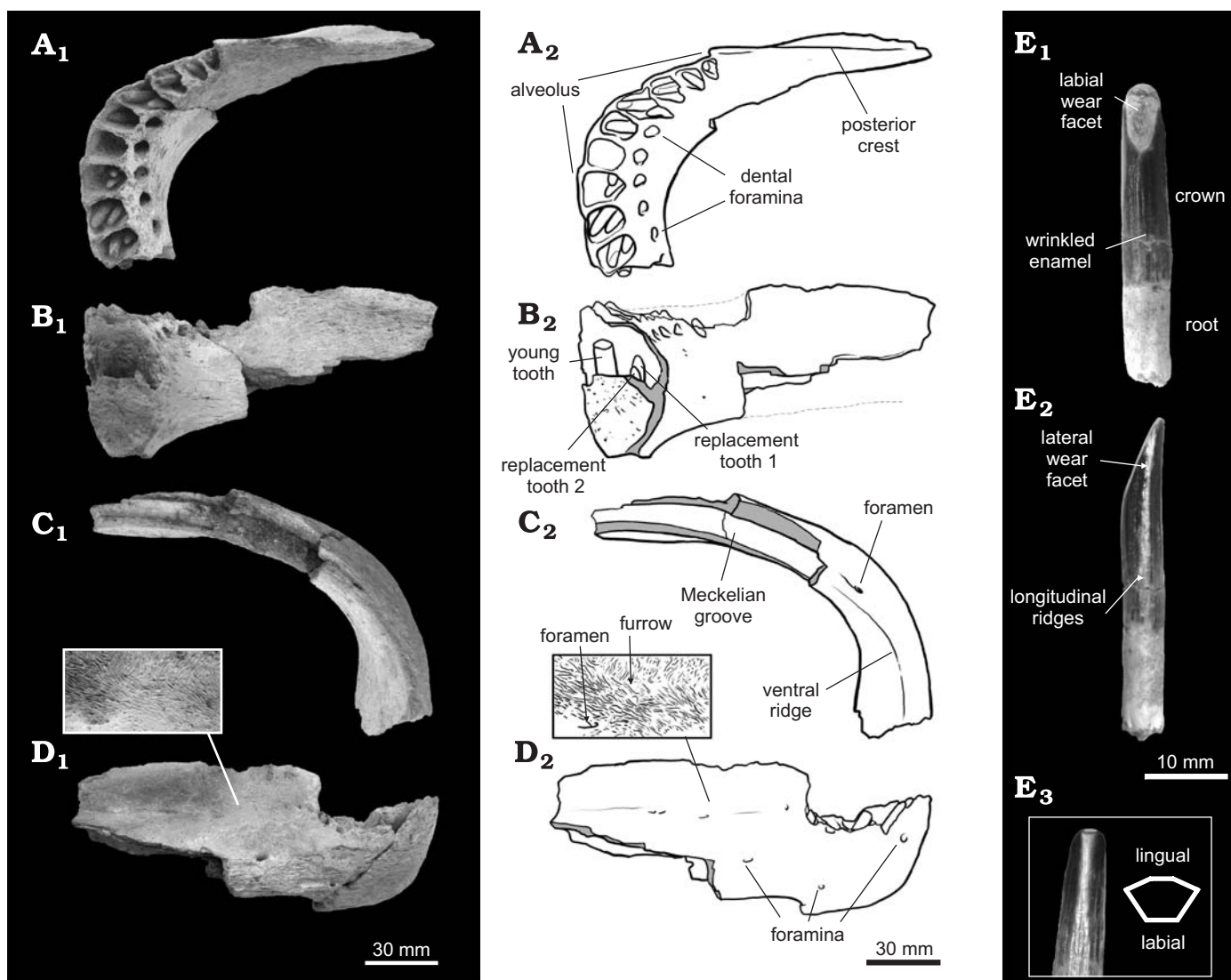
Fig. 5. Photographs and interpretive drawings of the titanosauroid *Bonitasaura salgadoi* Apesteguía, 2004 from the Upper Neuquén Group of Río Negro province, Patagonia, MPCA 460. **A–D**. Right dentary in dorsal (**A**), medial (**B**), ventral (**C**), and lateral (**D**) views. **E**. Isolated tooth in labial (E₁) and lateral (E₂) views; lingual view detail and schematic cross section showing hexagonal faceting (E₃).

narians in which the lacrimal is excluded from the narial opening (see Discussion, below).

Quadrate.—An incomplete left quadrate was recovered (Fig. 4); it lacks its pterygoid wing and posterolateral border. Its squamosal head is damaged. The element is dorsoventrally tall and laterally compressed.

In anterior view, the bone is curved, with its concave side oriented medially, as in *Malawisaurus dixeyi* and *Apatosaurus*. The base of the missing pterygoid wing is craniomedially oriented, differing from the more cranial orientation observed in *Rapetosaurus krausei*, *M. dixeyi*, and in diplodocids such as *Apatosaurus*.

Both the squamosal head and articular condyle point posteromedially, similar to *Phuwiangosaurus sirindhornae*. Due to poor preservation, the pterygoid contact is not evident under the pterygoid wing.

As in most titanosaurians, a vertically elongate fossa is vis-ible in posterior view, similar to those seen in *Antarctosaurus wichmannianus*, *M. dixeyi*, *P. sirindhornae*, *R. krausei*, and a new, as-yet undescribed form from Rincón de Los Sauces, Neuquén (Filippi et al. 2009). The depth and shape of the fossa cannot be estimated because of a broken lateral border, obfuscating comparison with other titanosaurians. The posterior border consists of a 4 mm thick lamina that thickens ventrally to a width of 11 mm. This lamina is oblique when viewed posteriorly, extending from the medial side of the squamosal head to the lateral side of the articular condyle. The squamosal head is badly preserved, but its triangular cross section seems similar to that of *R. krausei*. The articular condyle has a rugose, ovoid proximal surface, which differs from the kidney-shaped surface seen in *N. mongoliensis* and *P. sirindhornae*.

The quadratojugal contact, although damaged, can be discerned dorsal to the articular condyle in posterolateral view. However, there is no V-shaped scar as in *R. krausei*.

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Dentary.—An almost complete right dentary is preserved (Fig. 5A–D). Both the symphyseal end and the posterior ramus of the dentary are lost, making rendering description of the nature of the articulations with other mandibular elements difficult.

In dorsal view, the dentary is L-shaped (providing the "square jaw" morphology) with a straight anterior margin, as in *Antarctosaurus wichmannianus*, MPM-125R, and some diplodocoids (e.g., *Nigersaurus* [Sereno et al. 1999] and *Diplodocus*). There are 10 alveoli, although because other titanosaurians—particularly those that have square jaws—have more (e.g., *Rapetosaurus krausei*: 11; *Nemegtosaurus mongoliensis*: 13; MPM-125R: 14; *A. wichmannianus*: 16), others may have been present on the missing symphyseal ramus. All alveoli are subequal in size and quadrangular along the front of the jaw. Posterior to the jaw angle, the alveoli become smaller and more triangular in section. Within the broken, mesial-most alveolus, one newly-erupted and two unworn replacement teeth are visible, indicating that *Bonitasaura salgadoi* had a minimum of three teeth per alveolus. Alveoli 2, 3, 4, and 7 each contain two unerupted teeth; alveoli 6, 8, 9, and 10 each contain one unworn tooth. Alveolus 5 is empty. Except for the last two alveoli, dental foramina on the lingual surface of the dentary are associated with each alveolus. These foramina form an oblique line that angles toward the ventral corner of the symphysis.

The posterior ramus extends 6.5 cm behind the last alveoli but is incomplete. This small segment, about 2 cm tall, has a distinctive lateral surface riddled with dense concentrations of very small, randomly distributed furrows as well as oblique foramina. The bony cores of extant bovid artiodactyl horns and bird and turtle beaks exhibit a similar condition (Hieronymus et al. 2009). The thinner, taller bone behind the tooth row forms a sharp, straight, anteroposteriorly oriented border. A similar structure, albeit shorter and devoid of foramina and furrows, is seen in *R. krausei*, *Quaesitosaurus orientalis*, *A. wichmannianus*, and *N. mongoliensis*. This surface was proposed to have been covered in vivo with a keratinous sheath that functioned as an oral "guillotine" with a counterpart on the maxilla (Apesteguía 2004).

A partially filled Meckelian groove can be observed in ventral view on the dentary ramus; it reaches the mandibular angle, where it connects to the external surface via a series of foramina. The anterior region of the dentary is crossed by a pronounced ventral ridge, which is also present but less well developed in *A. wichmannianus*. Whereas the outer surface is profusely sculptured, the inner surface of the dentary is completely devoid of ornamentation.

The mandibular angle ("chin") is dorsoventrally constricted in lateral view. Nutrient foramina are present under the tooth row and separated from one another by distances equivalent to three alveolus widths. The ventral part of the posterior ramus of the dentary is incomplete and full length cannot be estimated.

In medial view, the intermandibular symphysis is D-shaped, with the labial side almost flat and the lingual side remarkably convex.

Teeth.—Dental material of *Bonitasaura salgadoi* includes 15 unworn teeth in different stages of growth in the dentary, plus one isolated, worn tooth (Fig. 5E). The dentary bears no functional teeth, presumably a function of a particular stage in the replacement pattern (see Discussion, below). The following description focuses primarily on the worn tooth.

The isolated tooth is large, narrow, and labiolingually compressed. The crown has wrinkled enamel, mostly at its base. The ratio of the crown/root height is 2:1, as in *N. mongoliensis* and *R. krausei*. The tooth slenderness index is about 5.3, as in other titanosaurians.

A distinct hexagonal "faceting" is evident in all crowns, as in *Clasmodosaurus* (Huene 1929), but remarkably, this faceting is observed in the fully grown teeth (Fig. 5E$_3$) and the largest unerupted tooth, which is in the symphyseal alveolus. The other unerupted dentary teeth have sub-elliptical cross-sections and two longitudinal ridges delimiting the labial and lingual faces. Although a thickness disparity between labial and lingual enamel is not as pronounced as in *Nigersaurus* (Sereno and Wilson 2005; Sereno et al. 2007), the labial enamel seems to be thinner than the lingual.

Unworn crowns taper distally to a point, but the mature crown has a high-angle, labial wear face, as in others titanosaurians like *R. krausei*, as well as dicraeosaurids. On this wear facet are long, parallel, and very thin scratches. A diminutive, worn surface is also present on the lingual face, in contrast to the more substantial lingual facet in basal macronarians as well as basal titanosaurians. In addition, two narrow, longitudinal wear facets are located on the lateral margin of the tooth, demonstrating that *Bonitasaura* used some form of tooth-to-tooth lateral contact, different from that which formed V-shaped facets in *N. mongoliensis*. On these lateral wear surfaces are many thin, randomly placed scratches.

Phylogenetic position of *Bonitasaura*

The phylogenetic position of *Bonitasaura salgadoi* is assessed here in order to test the original hypothesis of Apesteguía (2004) that it is a member of the Nemegtosauridae. The matrix used is based on those of previous analyses, such as Calvo et al. (2007a) and Gonzalez-Riga et al. (2009), but four new cranial and postcranial characters, as well as some additional taxa, are included. The new characters added are: #3. Frontal, dorsal texture: smooth (0); rugose (1); #10. External nares, configuration of lateral margin: lacrimal excluded, maxilla-nasal contact (0); lacrimal participates, separates maxilla and nasal (1); #17. Mandible, dorsal shape: U-shaped (0); L-shaped (1); and #33. Anterior dorsal vertebrae, infrapostzygapophyseal fossa: absent (0); present, not divided (1); present, divided in two subtriangular fossae (2).

Table 2. Character re-scoring of the present phylogenetic analysis.

Character	Taxon	Scoring	
		Previous analysis	Present analysis
7	*Camarasaurus*	0 (Calvo et al. 2007a)	1
	Brachiosaurus	0 (Calvo et al. 2007a)	1
	Rapetosaurus	1 (Calvo et al. 2007a)	0
8	*Camarasaurus*	0 (Calvo et al. 2007a)	1
	Brachiosaurus	1(Calvo et al. 2007a)	0
	Rapetosaurus	0 (Calvo et al. 2007a)	1
	Muyelensaurus	0 (Calvo et al. 2007a)	1
	Saltasaurus	0 (Calvo et al. 2007a)	1
13	*Muyelensaurus*	1 (Calvo et al. 2007a)	?
54	*Rinconsaurus*	0 (Calvo et al. 2007a)	1
	Muyelensaurus	0 (Calvo et al. 2007a)	1
57	*Malawisaurus*	0 (Calvo et al. 2007a)	1
65	*Ligabuesaurus*	0 (Gonzalez-Riga et al. 2009)	?
75	*Ligabuesaurus*	0 (Gonzalez-Riga et al. 2009)	1
77	*Futalognkosaurus*	? (Calvo et al. 2007a)	0
	Epachthosaurus	? (Calvo et al. 2007a)	0
	Opisthocoelicaudia	? (Calvo et al. 2007a)	0

Characters 7, 8, 13, 54, 57, 65, 75, and 77 were rescored (Table 2). The terminal taxa include those of Calvo et al. (2007a), with the addition of *Ligabuesaurus leanzai* (Bonaparte et al. 2006), *Nemegtosaurus mongoliensis* (Nowiński 1971), *Antarctosaurus wichmanianus* (Huene 1929), and *Bonitasaura salgadoi* (Apesteguía 2004). The data matrix, composed of 77 characters and 22 taxa, was analyzed using TNT v. 1.1 (Goloboff et al. 2008) (Appendices 1 and 2). *Camarasaurus* was used as the outgroup and multi-state characters were treated as unordered. The search, performed using 1000 replicates of Wagner trees, found seven equally most parsimonious trees with relatively high indices (143 steps, consistency index: 0.66, retention index: 0.71). The best score was obtained in 81% of the replicates. The strict consensus tree (Fig. 6A) collapsed node B, which includes the Turonian–Coniacian titanosaurians *Mendozasaurus neguyelap*, *Futalognkosaurus dukei*, *Rinconsaurus caudamirus*, *Muyelensaurus pecheni*, and the Santonian–Campanian *B. salgadoi* and *A. wichmannianus*, into a polytomy. In order to examine the collapse of node B, all taxa involved were removed individually for the consensus and reincluded one at a time for the final analysis. Only the exclusion of *A. wichmannianus* resolved the polytomy at node B (Fig. 6B). In this cladogram, *B. salgadoi* is sister taxon to the Lognkosauria (*M. neguyelap* + *F. dukei*); this clade is united by six synapomorphies (character states 25.1, 28.1, 29.2, 34.0, 44.1, 69.2). The node-based Lognkosauria, defined as the most recent common ancestor of *Mendozasaurus*, *Futalognkosaurus*, and all of its descendants, was supported by five synapomorphies in the original analysis of Calvo et al. (2007b). However, only one of them (30.2) was retained in our analysis; the others have broader distributions. In our analysis, *R. caudamirus* and *M. pecheni* do not form a

monophyletic clade (contra Calvo et al. 2007a). The positions of *M. neguyelap* and *F. dukei* are more derived than in previous analyses. Neither *Bonitasaura salgadoi* nor *A. wichmannianus* are closely related to the Nemegtosauridae (*N. mongoliensis* + *R. krausei*) (contra Apesteguía 2004 and Wilson 2005). However, they share a more distant common ancestor and are included in an unnamed taxon (node A, Fig. 6A). Although weakly supported by only one ambiguous synapomorphy (54.1), all trees recover an unusual position for *Malawisaurus dixeyi* as the sister taxon of *Andesaurus delgadoi*. In this regard, the node-based Titanosauria (defined as *Andesaurus*, *Saltasaurus*, their most recent common ancestor, and all of the descendents of that common ancestor; Salgado et al. 1997; Wilson and Upchurch 2003) is basically the same as the node-based Lithostrotia (defined as *Malawisaurus*, *Saltasaurus*, their most recent common ancestor, and all of the descendents of that common ancestor; Upchurch et al. 2004). Similarly, the node including the rest of titanosaurians, which is supported by five synapomorphies (35, 36, 43, 49, and 65), corresponds to the stem-based Titanosauroidea (all titanosaurians closer to *Saltasaurus* than to *Andesaurus*; Upchurch 1995; Salgado 2003), not the Titanosauridae, which actually has different definitions and is the subject of some nomenclatural controversy (see Salgado [2003] and Upchurch and Wilson [2003] for discussion). Finally, both *Epachthosaurus sciutoi* and *Lirainosaurus astibiae* have similar positions to those found by Gonzalez-Riga et al. (2009), with *L. astibiae* a basal member of the Titanosauroidea and *E. sciutoi* the sister taxon of node A.

Discussion

Titanosaurian skull morphology has been the focus of serious discussion for only the past few decades. The first titanosaurian skull restoration was made by Huene (1929) based on *Antarctosaurus wichmannianus* material, which included a braincase, a quadrate, a quadratojugal, squamosal, and a partial lower jaw. His restoration was heavily influenced by well-known *Diplodocus* skulls from the Upper Jurassic Morrison Formation of western North America. The similarities between the two, today recognized as convergences, lie primarily in the posterior skull region but also include similarities in lower jaw morphology and peculiar tooth arrangement.

During the last decade, successive phylogenetic analyses have supported a strong relationship between titanosaurians and other well-known, non-diplodocoid, Jurassic taxa, nesting them within a larger clade that also includes *Camarasaurus* (Camarasauromorpha; Salgado et al. 1997) and *Brachiosaurus* (Macronaria; Wilson and Sereno 1998). This was followed by a change in titanosaurian skull reconstructions to more closely match the taller skulls of *Camarasaurus* and *Brachiosaurus*, as portrayed by Salgado and Calvo (1997). However, the discoveries of *R. krausei*, and skull restorations of *N. mongoliensis* (Wilson 2005), have shown that the skulls of at least some titanosaurians varied markedly from the pur-
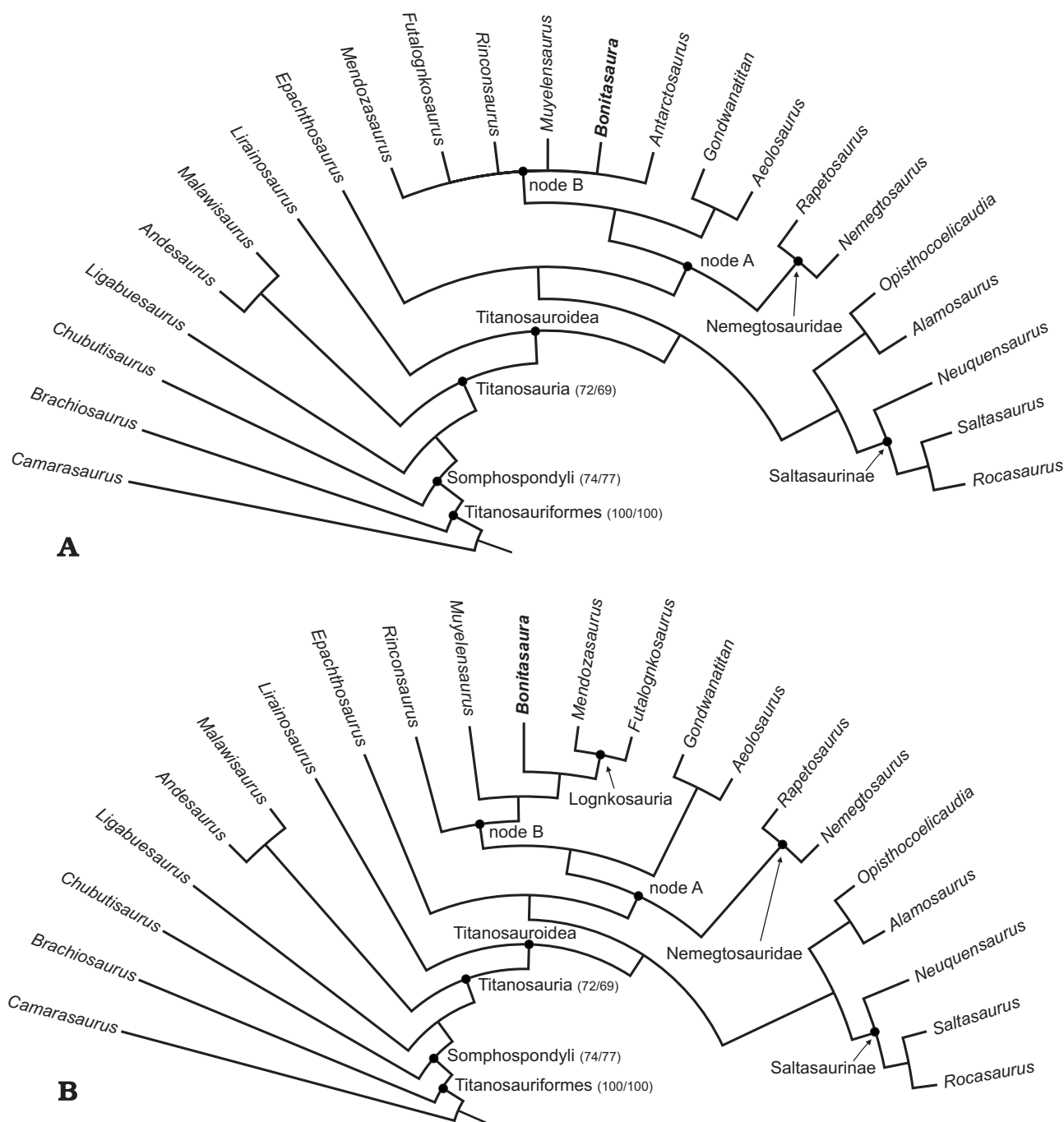
Fig. 6. Cladograms showing the phylogenetic relationships of *Bonitasaura salgadoi*. **A**. Strict consensus of seven most parsimonious trees (144 steps, consistency index: 0.66, retention index: 0.71). Nodes A and B are discussed in the text. **B**. Strict consensus of the same seven most parsimonious trees excluding *Antarctosaurus wichmannianus*. Bootstrap and Jackknife values up to 50% indicated in brackets.

ported low-domed, long-snouted *Brachiosaurus*-type skull. Curiously, the fossils resemble, in many ways, intermediate skull morphologies between the extremes of *Diplodocus* and *Camarasaurus*.

Cranial material of *Bonitasaura salgadoi* adds substantially to knowledge of titanosaurian skull morphology, and enables us to provide a new reconstruction for *Bonitasaura* (Fig. 7). This reconstruction resembles those of *Rapetosaurus krausei* and *Nemegtosaurus mongoliensis* (from Wil-

son 2005), but has several notable differences. The supratemporal fenestra is ovoid, as in other sauropods, but the small contribution of the frontal to its border differs from the condition in *N. mongoliensis*, in which parietals exclude the frontal from such a contribution. Despite the fact that the postorbital and squamosal are unknown for *Bonitasaura*, a postorbital–squamosal contribution to the supratemporal fenestra is assumed because it occurs in *R. krausei* and other titanosaurians, with the exception of *N. mongoliensis* and
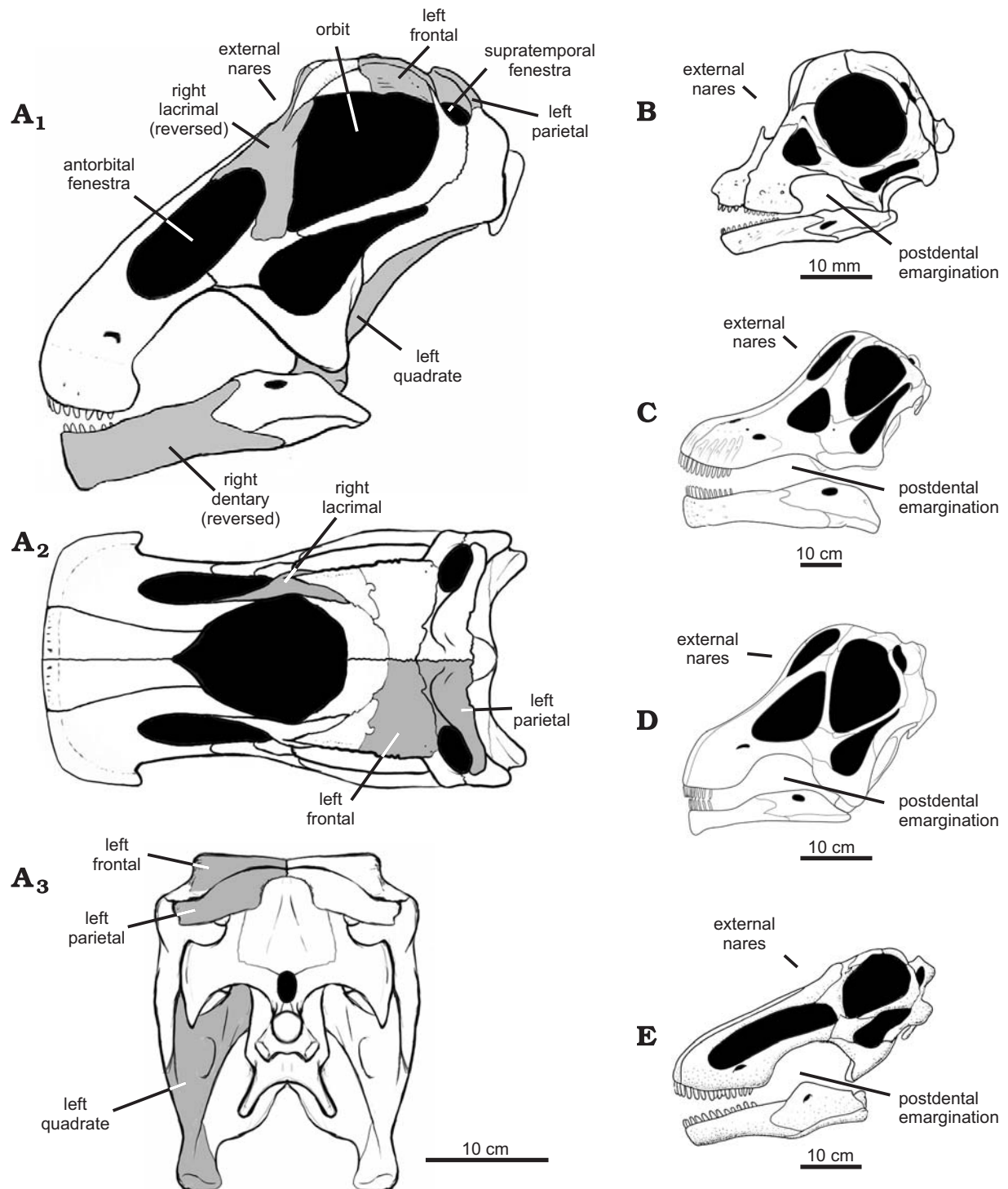
Fig. 7. Skull recontructions of *Bonitasaura* and other titanosaurians. **A**. *Bonitasaura salgadoi* (Upper Neuquén Group of Río Negro province, Patagonia) in lateral (A$_1$), dorsal (A$_2$) and posterior (A$_3$) views (preserved bones in grey). **B**. Embryonic skull reconstruction based on Auca Mahuevo titanosaurian embryos (Upper Neuquén Group of Neuquén province, Patagonia) in lateral view (modified from Salgado et al. 2005). **C**. *Nemegtosaurus mongoliensis* (Nemegt Formation, Gobi desert, Mongolia) in lateral view (modified from Wilson 2005). **D**. *Antarctosaurus wichmannianus* (Upper Neuquén Group of Río Negro province, Patagonia) in lateral view (Adam Yates, personal communication 2008). **E**. *Rapetosaurus krausei* (Maevarano Formation, Madagascar) in lateral view (modified from Curry Rogers and Forster 2004).

Quaesitosaurus orientalis. In the latter, the squamosal is excluded from the posttemporal fenestra by a laterally-oriented postorbital–parietal contact. In *Bonitasaura salgadoi*, the flat contact surface on the squamosal process of the parietal points ventrolaterally, suggesting a squamosal contact and hence a contribution to the posterior part of the fenestra.

One of the main controversies concerning titanosaurian skulls has been the position of the external naris: most pub-

lished cranial material (even in the most complete specimens, like *Nemegtosaurus mongoliensis* and *Quaesitosaurus orientalis*) did not preserve the mid-dorsal regions of the skulls. The bones that frame the external nares in non-titanosaurian sauropod skulls are the nasal dorsally and premaxilla and maxilla ventrally. Both the Nowiński (1971: fig. 2) and Upchurch (1999) restorations of the Mongolian taxa show the lacrimal participating in the narial opening, and hence the reconstructions maintain retracted dorsal narial positions. However, in Wilson (2005: fig. 16), the lacrimal is excluded from the narial opening due to the badly preserved lateral process of the nasal and dorsal process of the maxilla. On the other hand, both *Rapetosaurus krausei* and *Bonitasaura salgadoi* have notably smooth embayments on the dorsal aspects of the lacrimal, indicating that they contributed to the narial openings in each. The lacrimal contribution to the nares is more posteriorly located in *B. salgadoi* than in *R. krausei*, but the fact that the lacrimal contributes to the external nares in both taxa (plus, albeit more ambiguously, *N. mongoliensis*) suggests a condition widely distributed within the Titanosauria.

Additional information is supplied by the lacrimal concerning the shape of the posterior border of the antorbital fenestra. As in *R. krausei*, the antorbital fenestra is large and ovoid, in contrast with the triangular-shape restored in *N. mongoliensis* and the Auca Mahuevo embryos (Chiappe et al. 2001). However, in *B. salgadoi* it is anteroventrally projected at 45°, contrasting with the nearly horizontal position observed in *R. krausei*. These peculiar orientations of the antorbital fenestra and the maxillary process suggest a short snout configuration. Though no maxilla was recovered for *B. salgadoi* (rendering a reconstruction speculative), the anterior border of the antorbital fenestra is restored as round based on both *R. krausei* and the *Ampelosaurus* specimen exhibited at the Musée des Dinosaures of Espéraza, France (SA personal observation), as well as in the new form from Rincón de los Sauces (Filippi et al. 2009).

Chiappe et al. (2001) reported the presence of a ventral notch in the posterior regions of the maxillae of the Auca Mahuevo sauropod embryos. This structure, which is caudally bounded by the jugal and the quadratojugal, was considered by the authors as "similar" to the notch present in *R. krausei*. Salgado et al. (2005) considered this notch homologous to the preantorbital fenestra of adult neosauropods (e.g., *Diplodocus*, *Camarasaurus*, *Brachiosaurus*) and proposed closure during the course of ontogeny (Salgado et al. 2005: 90 fig. 6). However, they did not discard that at least "…a portion of this ventral notch corresponds to the space enclosed by the highly arched postdentigerous portion of the maxilla in adult titanosaurian skull". García (2007) reinforced the original interpretation of Chiappe et al. (2001), analyzing in detail the maxillae of the embryos and correlating both lateral and medial structures. His study revealed that the preantorbital fenestra was located anterior to the ventral notch of the maxilla as it occurs in adult skulls. This postdental notch is considered a possible synapomorphy of

Titanosauria (García et al. in press) and thus is represented in the reconstruction of the skull of *B. salgadoi*.

One purported synapomorphy shared by *N. mongoliensis* and *Q. orientalis* is the presence of rugose and sculptured elements bordering the orbital region (frontals, postorbitals, and prefrontals; Wilson 2002, 2005). The presence of this condition in *B. salgadoi* led Apesteguía (2004) to suggest a nemegtosaurid affinity for the species. However, as mentioned above, a sculptured orbital dorsal rim is clearly recognizable both in basal macronarians, such as *Camarasaurus* (CM 11338, DNM 975), and derived macronarians, such as *Saltasaurus loricatus* (PVL-4017-162). The broad distribution of this condition suggests it is not a synapomorphy of the Nemegtosauridae.

Wilson (2005) recognized a partially fused coronoid (= intercoronoid) in the lower jaw of *N. mongoliensis*, just posterior to the tooth row. Wilson (2005) claimed a similar situation was also present in *B. salgadoi*, but a careful examination of the original material has shown that this is incorrect: the posterior region of the preserved dentary includes neither any independent postdentary elements nor sutures or contact lines. This entire segment, with a sharp and straight border, is part of the dentary. This interpretation is reinforced by a comparison with the original lower jaw of *A. wichmannianus*, in which an edentulous segment, about the same length as that in *B. salgadoi*, is present and entirely composed by the dentary. Posterior to this zone, the coronoid as well other postdentary elements are present in *A. wichmannianus*, strongly suggesting the same condition existed in *B. salgadoi*.

Finally, *B. salgadoi* adds important data concerning titanosaurian tooth replacement. Previously, titanosaurian tooth replacement has been described only for two premaxillae from Salta and Río Negro provinces in Argentina (Powell 1979; Coria and Chiappe 2001). In both specimens, up to three replacement teeth are present, covered by one functional, labially located tooth. This condition changes in the lower jaw, where one newly-erupted unworn and two replacement teeth were found in the innermost dentary alveolus of *B. salgadoi* and also in the last frontal alveolus before the dentary corner of *A. wichmannianus*. A similar situation is also present in the fragmentary dentary of the titanosaur MCSPv-061 (García and Cerda 2010). Thus, it can be said that the condition in the dentary, for at least these three South American specimens, involves just up to three teeth per alveolus (one functional and two unworn teeth for replacement), not four as found in the two titanosaurian premaxillae mentioned above. This particular condition shows an apparent replacement rate differentiation between upper and lower teeth. Moreover, it must be noted that the presence of three unerupted teeth in the innermost alveolus, and two and one unerupted teeth in the outermost alveoli, show also a replacement rate differentiation along tooth row of *B. salgadoi* similar to the "replacement wave," noted by Nowiński (1971) for *N. mongoliensis*.

Conclusions

Skull material of *Bonitasaura salgadoi* represents new evidence and important information concerning titanosaurian skull morphology. The skull of *B. salgadoi* is anteroposteriorly short and dorsoventrally high, contrasting with the elongate skulls of *Rapetosaurus krausei* and diplodocoids. However, it is similar to the latter in possessing a single external narial opening and enlarged antorbital fenestra. Frontal and parietal proportions suggest a wide skull roof, as in other titanosaurians. The morphology of the lacrimal and its relationships to neighboring bones indicates a wide narial opening, as in *R. krausei* and diplodocoids.

Square jaws and a large number of alveoli in the titanosaurian *B. salgadoi* permitted the definitive recognition of this jaw morphology as a trait not exclusive to diplodocoids. The number of replacement teeth in the dentary is up to three, as has been reported for other titanosaurians, showing differences beetween upper and lower tooth replacement rate. The edentulous posterior border of the dentary in *B. salgadoi* does not include a fused coronoid, which was presumably located more posteriorly, as in *Antarctosaurus wichmannianus*.

Phylogenetic analysis recovers *B. salgadoi* as a titanosaurian, related to other mid-sized to large titanosaurians from the Turonian–Campanian of South America, such as *Mendozasaurus neguyelap*, *Futalognkosaurus dukei*, *Rinconsaurus caudamirus*, *Muyelensaurus pecheni*, and *A. wichmannianus*. Previous hypotheses relating *Bonitasaura salgadoi* to nemegtosaurids are not supported by the phylogenetic analysis, as well as the presence of the family in South America.

Increasing knowledge of titanosaurian anatomy is the result of a substantial number of new discoveries in the last two decades, with more than ten new taxa. However, few of them include cranial bones. Therefore, the cranial remains of *B. salgadoi* contribute substantially to titanosaurian skull reconstructions and increase the known range of morphological diversity for the group.

Acknowledgements

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Appendix 1

Data matrix

Camarasaurus	0010001100	1000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000
Brachiosaurus	0000011000	0000010101	1000001001	0100010000	0000000001	0000000000	0000000001	01110?0
Chubutisaurus	??????????	??????????	??????????	?????2?000	1?0??00001	?????0??0	0???0????	??111??
Andesaurus	??????????	??????????	??????????	?1??011101	1?0?000101	0001000?0	?????1110?	??01???
Malawisaurus	0???11??0?	????000201	?11000?00?	?11?011111	1??1000201	00?11010??	?1110??10?	????1?1
Ligabuesaurus	??????????	??????1?1	?000101010	?111011111	1????????	???????10	?????0????	??1110?
Mendozasaurus	??????????	??????????	??1010?122	?120?2??11	1?11000211	0011100010	1111?1????	??01111
Futalognkosaurus	??????????	??????????	2110101122	21?0?2??11	1111?0?2?1	??1??0????	?????1121	11????0
Epachthosaurus	??????????	??????????	??????????	?101121101	111?000221	0001100010	111??11??1	1101110
Rapetosaurus	1111110111	1111110221	201000100?	1121121111	11?0000221	0010?00010	1110??1101	1101?11
Nemegtosaurus	101111010?	1110110221	??????????	??????????	??????????	??????????	??????????	??????
Lirainosaurus	??????????	?????0?2?1	??????????	?10?121111	1?11?00221	00000000?0	1?101?????	???1??1
Rinconsaurus	??????????	??????211	?010001011	?101121111	11??00221	0011101110	1110111111	1101???
Muyelensaurus	?1?1??11??	?1?111?211	?11000?011	?121121111	11?0?00221	0021101110	1110?11111	11011??
Bonitasaura	?11111?1?1	??????1211	??1?101121	?120121111	1?11000221	0011101110	1?1??1112?	??0110?
Antarctosaurus	?101?111??	?110201211	??????????	??????????	??????????	???????10	11???1????	??0111?
Gondwanatitan	??????????	??????????	??????????	?1?1121111	111??1222	01002001?0	??????011	1???1??
Aeolosaurus	??????????	??????221	??????????	?1???2????	??30?01222	01102001?0	1?10?1101?	???11??
Opisthocoelicaudia	??????????	??????????	??????????	1001121011	1121100001	0020000011	1110111111	1101110
Alamosaurus	??????????	??????22?	?010001001	?1??120011	1131100221	0020000010	1111111121	11011??
Neuquensaurus	??????????	??????????	?011001012	?101121111	1131?10221	1020000010	111011?121	11?11?1
Saltasaurus	?11??111??	?01011?221	?001011012	?111121111	1110?10221	1020010011	2110111121	11011?1
Rocasaurus	??????????	??????????	??????01?	?101121111	1?????10221	10?00100??	?????1121	11?1???

Appendix 2

Character list

1. Short deep snout: present (0); absent (1) (modified from Upchurch 1998 by Curry Rogers 2005).
2. Frontal contribution to supratemporal fossa: absent (0); present (1) (Wilson and Sereno 1998).
3. Frontal, dorsal texture: smooth (0); rugose (1).
4. Parietal occipital process, dorsoventral height: deep, nearly twice the diameter of the foramen magnum (0); short, less than the diameter of the foramen magnum (1) (Wilson 2002).
5. Parietal, elongate lateral process: absent (0); present (1) (Curry Rogers 2005).
6. Parietal, cranial inclination with wide caudodorsal exposure of crest: absent (0); present (1) (Salgado and Calvo 1997).
7. Parietal, contribution to post-temporal fenestra: absent (0); present (1) (Wilson 2002).
8. Parietal, distance separating supratemporal fenestrae: less than (0); or twice (1); the long axis of supratemporal fenestra (Wilson 2002).
9. Ascending process of premaxilia: directed dorsally (0); directed caudo dorsally (1) (Gauthier 1986).
10. External nares, configuration of lateral margin: lacrimal excluded, maxilla-nasal contact (0); lacrimal participates, separates maxilla and nasal (1)
11. Preantorbital fenestra: absent (0); present (1) (Wilson and Sereno 1998).
12. Supraoccipital, height: twice (0); subequal (1); or less (2) than height of foramen magnum (Wilson 2002).
13. Paroccipital process, ventral non-articular process: absent (0); present (1) (Wilson 2002).
14. Longitudinal groove on the supraoccipital: absent (0); present (1) (Curry Rogers 2005).
15. Basipterygoid processes, angle of divergence: approximately 45° (0), less than 30° (1), over 45° (2) (Wilson 2002).
16. Basal tubera, craniocaudal depth: aprox half dorsoventral height (0); sheetlike 20% dorsoventral height (1) (Wilson 2002).
17. Mandible shape: U shape (0); L shape (1).
18. Tooth shape: spoon-like (0); compressed cone chisel-like (1); pencil chisel-like (2) (modified from Calvo 1994 by Calvo and González Riga 2003).
19. Tooth crowns, cross-sectional shape at mid-crown: D-shaped (0); subcylindrical with smooth crest (1); cylindrical (2) (modified from Wilson and Sereno 1998).
20. Wear facets of teeth sharply inclined: absent (0); present (1) (Salgado and Calvo 1997).
21. Cervical vertebrae, number: 12 (0); 13 (1); 14 or more (2) (Upchurch 1998).
22. Pleurocoels in anterior and middle cervical vertebrae: present (0); absent (1) (modified from Calvo and Salgado 1995).
23. Cervical pleurocoel divided by lamina or septa: present (0); absent (1) (Upchurch 1998).
24. Cervical prezygapophyses, relative length: articular facets that surpass (0); or not surpass (1) the centra (Salgado et al. 1997).
25. Posterior cervical neural spines lateraly expanded and wider than the centra: absent (0); present (1) (González Riga 2005).
26. Neural spines in cervical vertebrae: tall (0); small (1) (modified from Calvo and Salgado 1995).

27. Anterior cervical neural spines: bifid (0); single (1) (Upchurch 1998).
28. Posterior cervical vertebrae, proportions: ratio total height/ centrum length: less (0); or more (1) than 1.5 (modified from Calvo and Salgado 1995 by González Riga 2005).
29. Supradiapophyseal fossa in posterior cervical vertebrae: absent (0); shallow or reduced (1); deep and extended (2) (González Riga 2005).
30. Posterior cervical centra, proportions: ratio anteroposterior length/ height of posterior face: >3 (0); between 2.5 and 1.5 (1); less than 1.5 (2) (modified from Wilson 2002).
31. Dorsal vertebrae, number: 12 (0); 11 (1); 10 or fewer (2) (Wilson and Sereno 1998).
32. Anterior dorsal neural spines, shape: bifid (0); single (1) (McIntosh 1990).
33. Anterior dorsal vertebrae, infrapostzygapophyseal fossa: absent (0); present not divided (1); present divided in two subtriangular fossa (2).
34. Anterior dorsal neural spines inclined posteriorly more than 20 degree from vertical: absent (0); present (1) (modified from Wilson and Sereno 1998).
35. Posterior dorsal neural spines, dorsal development: more (0); or less (1) than 20 percent of the total height of the vertebra (modified from Sanz et al. 1999 from González Riga 2003).
36. Prespinal lamina in dorsal vertebrae: absent (0); present in the distal end of neural spine (1); present all along the neural spine (2) (Salgado et al. 1997).
37. Centroparapophyseal lamina in posterior dorsal vertebrae: absent (0); present (1) (Bonaparte and Coria 1993).
38. Ventrally widened or slightly forked centrodiapophyseal laminae in posterior dorsal vertebrae: absent (0); present (1) (Salgado et al. 1997).
39. Hyposphene-hypantrum articulation in dorsal vertebrae: present (0); absent (1) (Salgado et al. 1997).
40. Pleurocoels in dorsal vertebrae shape: circular or elliptical (0); posteriorly acuminate (1) (Salgado et al. 1997).
41. Camellate or somphospondylous types of internal structures of presacral vertebrae: absent (0); present (1) (modified from Wilson and Sereno 1998 by González Riga 2003).
42. Sacral vertebrae, number: five (0); six or more (1) (McIntosh 1990).
43. First caudal vertebrae, type: platycoelous (0); procoelous (1); opisthocoelous (2); biconvex (3) (Salgado et al. 1997).
44. Wide and deep interzygapophyseal cavity in caudal vertebrae: absent (0); present (1) (Calvo et al. 2007a)
45. Caudal transverse processes: disappear by caudal 15 (0); disappear by caudal 10 (1) (Wilson 2002).
46. Anterior and middle caudal centra, proportions: as high as wide (0); depressed, wider than high (1) (Salgado et al. 1997).
47. Mid caudal centra with the anterior face strongly inclined anteriorly: absent (0); present (1) (Franco-Rosas et al. 2004).
48. Articular face shape on anterior caudal centra: non-procoelous (0); slightly procoelous (1); strongly procoelous with prominent condyles (2) (modified from Salgado et al. 1997 by González Riga 2003).
49. Articular face shape on middle caudal centra: non-procoelous (0); slightly procoelous with reduced condyles (1); strongly procoelous with prominent condyles (2) (modified from Salgado et al. 1997 by González Riga 2003).
50. Neural arch in anterior caudal vertebrae: placed in the middle of the centrum (0); anteriorly (1); on the anterior border (2) (Salgado et al. 1997).
51. Anterodorsal border of neural spine in middle caudal vertebrae located posteriorly with respect to anterior border of the postzygapophyses: absent (0); present (1) (Salgado et al. 1997).
52. Anteriorly directed anterior caudal neural spine: absent (0); present (1) (Calvo et al. 2007a)
53. Shape of the section of neural spines in most anterior caudal vertebrae in dorsal view: axially elongated (0); transversely elongated (1); quadrangular (2) (Calvo et al. 2007a)
54. Neural spine in middle caudal vertebrae, shape: short anteroposteriorly (0); laminated and anteroposteriorly elongated (1) (modified from González Riga 2003 by Bonaparte et al. 2006).
55. Length proportions of prezygapophyses with respect to the centrum length in middle caudal vertebrae: shorter than 50% (0); between 40 to 50% (1); longer than 50% (2) (modified from González Riga 2003).
56. Ventral depression divided by a longitudinal septum in anterior and middle caudal vertebrae: absent (0); present (1) (Salgado and Azpilicueta 2000).
57. Postzygapophyseal process in middle caudal vertebra: absent (0); present (1) (Calvo et al. 2007a)
58. Well developed interprezygapophyseal lamina in middle caudal vertebrae: absent (0); present (1) (Calvo et al. 2007a)
59. Scapular glenoid orientation: relatively flat (0); strongly beveled medially (1) (Wilson and Sereno 1998).
60. Humerus, breadth of proximal end with respect to the total length: less (0); or more (1) than the 50% (González Riga 2003).
61. Humerus, type of proximal border: strongly curved (0); straight or slightly curved (1); sigmoidal (2) (modified from Upchurch 1998 by González Riga 2002).
62. Ulnar olecranon process, development: prominent, projecting above proximal articulation (0); rudimentary, level with proximal articulation (1) (Wilson and Sereno 1998).
63. Sternal plates, shape: suboval (0); semilunar (1) (Salgado et al. 1997).
64. Semilunar sternal plate with straight posterior border: absent (0); present (1) (González Riga 2003).
65. Coracoid, shape: suboval (0); quadrangular (1) (Salgado et al. 1997).
66. Metacarpals, distal phalangeal articular facets: present (0); absent (1) (Salgado et al. 1997).
67. Pubis, length with respect to ischium length: shorter or equal (0); longer (1) (Salgado et al. 1997).
68. Ischium, posterior process twice or more the length of pubis articulation: present (0); absent (1) (modified from Salgado et al. 1997 by Calvo and González Riga 2003).
69. Ischium, iliac pedicel: short and poorly developed (0); slender and well developed (1); wide and well developed(2) (Calvo and González Riga 2003).
70. Shape of preacetabular lobe of ilium: moderately expanded (0); broadly expanded and directed upward (1) (Salgado et al. 1997).
71. Orientation of preacetabular lobe of ilium: nearly vertical (0); nearly horizontal and laterally projected (1) (Salgado et al. 1997).
72. Relative orientation of the pubic peduncle of ilium: angled (0); perpendicular with respect to the sacral axis (1) (Salgado et al. 1997).
73. Humerus/femoral ratio of 0.90 or more: absent (0); present (1) (McIntosh 1990).
74. Lateral bulge of femur, below the greater trochanter: absent (0); present (1) (McIntosh 1990).
75. Distal end of tibia broader transversely than anteroposteriorly: absent (0); present (1) (Salgado et al. 1997).
76. Metatarsal I, length: shortest metatarsal (0); metatarsal V shorter tan metatarsal I (1) (Curry Rogers 2005).
77. Osteoderms: absent (0); present (1) (Sanz et al. 1999).