Osteology of the sauropod embryos from the Upper Cretaceous of Patagonia

LEONARDO SALGADO, RODOLFO A. CORIA, and LUIS M. CHIAPPE

Exceptionally well-preserved embryonic skulls of Upper Cretaceous (Campanian Anacleto Formation) sauropods from Auca Mahuevo (Neuquén Province, Argentina) provide important insights into the ontogeny and evolution of titanosaurian neosauropods. The most important cranial modifications occurring during titanosaurian ontogeny appear to be centered on the infraorbital and narial regions, which exhibit a substantial degree of "mosaic" evolution. On one hand, the Auca Mahuevo embryos show a large jugal that forms part of the lower margin of the skull and unretracted external nares, as indicated by the position and orientation of the lacrimals as well as the anterior extension of the frontals. Both of these features are ancestral for neosauropods, being present in prosauropods. On the other hand, the embryonic skull exhibits a large ventral notch, tentatively interpreted as homologous to the neosauropod preantorbital fenestra, that opens ventral to the jugal and between the maxilla and the quadratojugal, and a temporal region that closely resembles the adult neosauropod condition. This mosaic of character states indicates that different regions of the skull of titanosaurian neosauropods acquired their characteristic morphology at substantially different rates during their ontogenetic development.

Key words: Titanosauria, sauropod embryos, cranial anatomy, ontogenetic development, Anacleto Formation, Upper Cretaceous, Auca Mahuevo, Patagonia.

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Introduction

The recent discovery of numerous *in ovo* remains of Late Cretaceous sauropods from the Argentine locality of Auca Mahuevo (Neuquén Province, Patagonia) has given new impetus to studies of sauropod biology and evolution (Chiappe et al. 1998, 2001). These embryos are contained within mudstones of the Anacleto Formation, a fluvial sedimentary unit whose age is regarded as early Campanian (Dingus et al. 2000; Leanza and Hugo 2001).

Initial studies (Chiappe et al. 1998) assigned the Auca Mahuevo embryos to Neosauropoda (the clade containing the most recent common ancestor of *Diplodocus* and *Saltasaurus* and all of its descendants), based primarily on the similarity between the dentition of the embryos and those of both diplodocoids and many titanosaurians (somphospondylians closer to *Saltasaurus* than to *Euhelopus*). Moreover, these works argued that the embryos possibly pertained to Titanosauria given the fact that only these sauropods have been recorded from the Anacleto Formation. This initial assignment was subsequently supported by discoveries of better preserved embryos (Chiappe et al. 2001). Herein we provide a more detailed description of these embryos and discuss within a phylogenetic context a number of characters

that change during the prenatal ontogeny of neosauropods, particularly titanosaurians. Specifically, the embryos from Auca Mahuevo provide an opportunity to test previous hypotheses regarding neosauropod phylogeny, for instance, the alleged correlation between different characters expressed in adult skulls.

Institutional abbreviations.—MCF-PVPH, Vertebrate Paleontology collection of the Museo Municipal de Plaza Huincul, "Carmen Funes," Plaza Huincul, Argentina; GIN, Geological Institute of the Mongolian Academy of Sciences, Ulaanbataar, Mongolia.

Material examined

MCF-PVPH-263: A nearly complete skull, exposed on its left side, partially damaged in the narial region (Fig. 1).

MCF-PVPH-272: Nearly complete skull, partially deformed, and broken in the supraorbital and rostral areas (Fig. 2).

MCF-PVPH-250: Both premaxillae, maxillae, and articulated nasals (the left exposed on its internal surface); two series of sclerotic rings, each belonging to a different orbit, one

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formed by at least five plates, the other by at least three plates; an incomplete frontal; a complete right parietal; a postorbital; a possible squamosal; an incomplete mandible, possibly a dentary, dorsally exposed; over 30 variably preserved, scattered teeth; and many unidentified appendicular elements (Fig. 3).

MCF-PVPH-113a: Part of a nasal; a possible prefrontal; a lacrimal; both frontals fused after death by diagenetic processes; unidentified long bones.

MCF-PVPH-113b: ?Left premaxilla and maxilla; part of the left jugal; a possible squamosal articulated to a quadrate (possibly the left); and possible fragments of the right squamosal and quadrate (though parts of the parietal and postorbital could also be present).

MCF-PVPH-264: Both maxillae, the left articulated to its corresponding premaxilla; both frontals; part of a parietal; both jugals; an articular; and unidentified bones.

MCF-PVPH-262: Right premaxilla; both maxillae, though fragmentary, one of them with at least four teeth implanted; nasals; frontal; a possible postorbital; right jugal; squamosal; unidentified bones.

MCF-PVPH-147: Complete skull, somewhat deformed.

Description

The embryonic skull is dorsoventrally high and anteroposteriorly short, roughly triangular in lateral view (Figs. 1, 2). Due to the incompleteness of MCF-PVPH-272, MCF-PVPH-263, and MCF-PVPH-147 (the best-preserved specimens) some measurements were obtained through a combination of all specimens. Accordingly, the dorsoventral skull height, measured through the middle of the orbit, ranges from approximately 57% (MCF-PVPH-263) to 51% (MCF-PVPH-272) the anteroposterior length of the skull. These proportions roughly match those in *Camarasaurus* (greater than 55%) and contrast those in *Diplodocus* (less than 45%). In spite of the fact that the holotype of *Nemegtosaurus mongoliensis* is an essentially complete skull (Nowiński 1971), this ratio cannot be established for this specimen, because the quadratojugal is somewhat displaced from its original position (Salgado and Calvo 1997). However, in GIN 100/402, a skull assigned to *Nemegtosaurus* that is housed in Ulaanbataar, Mongolia, the length from the anterior end of the snout to the posterior margin of the paraoccipital process is ~570 mm, and the height at the middle of the orbit is ~240 mm (personal observation); this is less than 50% the length. This ratio is somewhat lower than in the embryos from Auca Mahuevo. Although the skull of *Rapetosaurus* is incomplete, it appears proportionally similar to the embryos described herein, the skull height being 54% its length (Curry Rogers and Forster 2001: fig. 1).

The orbit of the titanosaurian embryos is large, comprising more than one-third of the skull length, as seen in MCF-PVPH-263, 272, and 147. The roughly triangular antorbital fenestra is bordered anteriorly by the maxilla, and ventrally and posteriorly by the jugal and lacrimal, respectively (Figs. 1, 2). The orbit is enclosed ventrally by the jugal, anteriorly by the lacrimal, dorsally by the frontal, and posteriorly by the postorbital. Although the prefrontal cannot be definitively distinguished within the available specimens, a bone that could be identified as such is present in MCF-PVPH-272 (Fig. 2) and MCF-PVPH-250 (Fig. 3). If correctly identified, the prefrontal would have contributed to the anterodorsal margin of the orbit. The infratemporal fenestra is defined by the postorbital anteriorly, the quadratojugal ventrally and the squamosal and quadrate posteriorly. The supratemporal fenestra is anteromedially delimited by the parietal, laterally by the postorbital, and posteriorly by the squamosal (MCF-PVPH-263 and MCF-PVPH-272) (Figs. 1, 2).

Premaxilla.—Specimens MCF-PVPH-250, 263, 113b, 272, 262, and 147 provide detailed information on the premaxilla. The proportions of this bone are similar to the premaxilla of *Nemegtosaurus* and the specimen from Salitral Moreno (Río Negro Province, Argentina) described by Coria and Chiappe (2001). The premaxilla is relatively mediolaterally wide and subtriangular in lateral view. The angle formed between the medial and lateral margins is greater than 25°, similar to the condition in *Brachiosaurus* (30°) and differing from diplodocids (10°) and *Nemegtosaurus* (18°) (Upchurch 1999).

As shown in MCF-PVPH-113b (Fig. 4D) and MCF-PVPH-262 (Fig. 4E), the dentigerous margin of the premaxilla bears four alveoli, as in all sauropods. In medial view, on the maxillary margin, a distinct cotylar surface is developed near the dorsoventral midline of the element (Fig. 4D, E). The anteromedial process of the maxilla articulates on this cotylus, as seen in MCF-PVPH-113b (Fig. 4D) and less clearly in MCF-PVPH-147. To the best of our knowledge, such a cotylar structure of the premaxilla has not been reported in any other sauropod, although it seems to be present in some basal sauropodomorphs (e.g., *Mussaurus*, Bonaparte and Vince 1979: fig. 2).

Many specimens preserve disarticulated premaxillae. In MCF-PVPH-263 (Fig. 4B), MCF-PVPH-147 (Fig. 4C), MCF-PVPH-113b (Fig. 4D), and MCF-PVPH-272 (Fig. 2), the premaxilla and maxilla are preserved in articulation. In lateral view, the anterior margin of the premaxilla is sigmoid, or "stepped", as termed by Wilson and Sereno (1998) (this "step" cannot be observed in MCF-PVPH-147, Fig. 4C). As shown by MCF-PVPH-250 (Fig. 3), the posterodorsal process of the premaxilla appears shorter and less developed than in *Camarasaurus*, *Nemegtosaurus* (MGI 100/402), and *Diplodocus* (Wilson and Sereno 1998).

Maxilla.—The maxilla is one of the largest bones of the skull and perhaps the best represented within the studied sample. This bone has two ascending processes. The posterior one, well-preserved in MCF-PVPH-264 (Fig. 4A), MCF-PVPH-263 (Fig. 4B), MCF-PVPH-147 (Fig. 4C), MCF-PVPH-113b (Fig. 4D), MCF-PVPH-250 (Fig. 4F), and partially in MCF-PVPH-272 (Fig. 2), is larger. This process bounds the
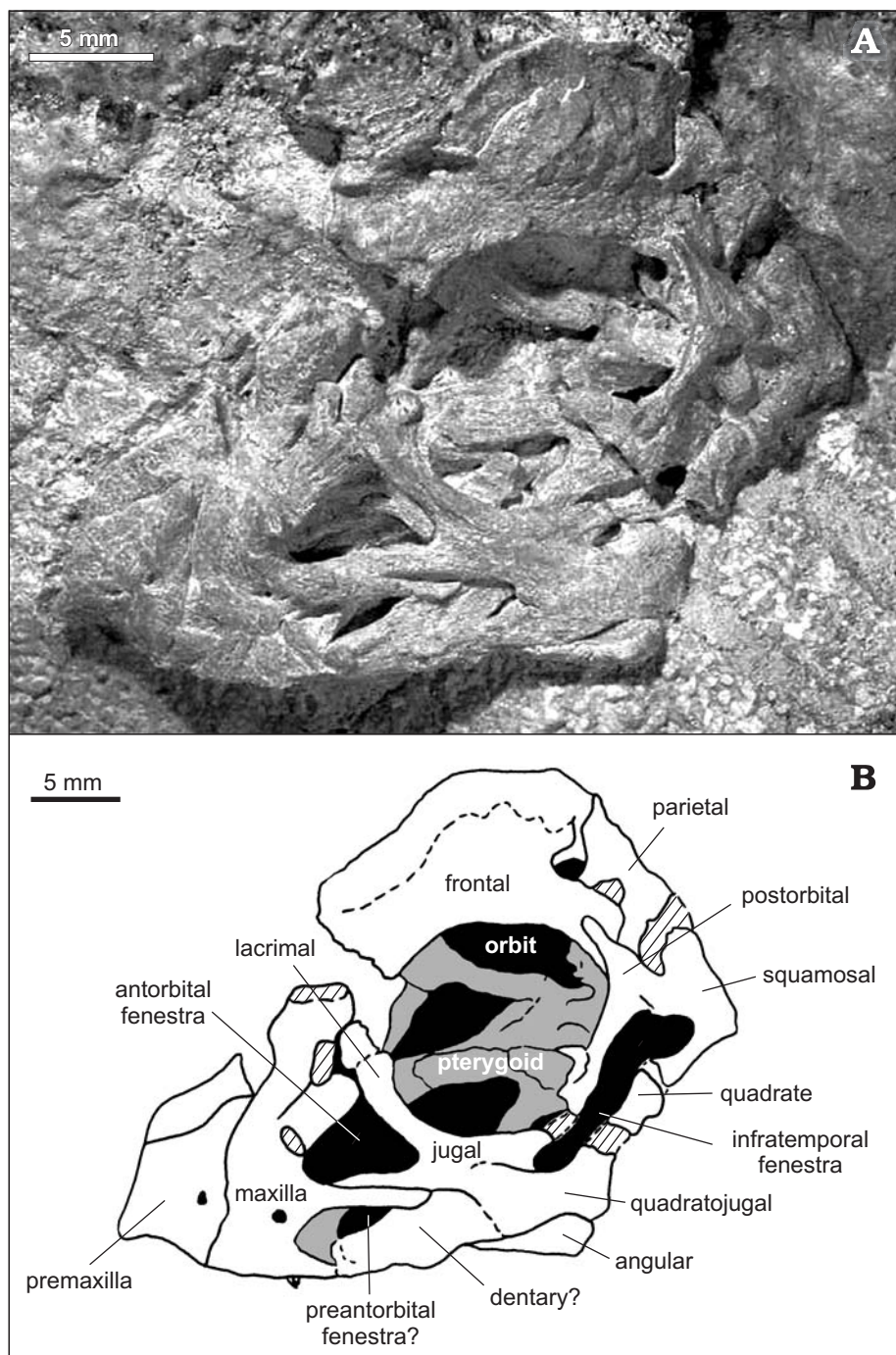
Fig. 1. Titanosaurian sp. indet. MCF-PVPH-263, photograph (**A**) and interpretative drawing (**B**) in left lateral view.

antorbital fenestra anteriorly. Identifying the correct homology between these processes and the structures present in adult sauropod maxillae is difficult. We tentatively identify the posterior process as the homologue of the single ascending process of the adult sauropod maxilla, as both of these structures bound the antorbital fenestra anteriorly. If this interpretation is correct, then the embryonic anterior process can be interpreted as homologous to the floor of the narial fossa in adult skulls. The main body of the maxilla has two other posteriorly directed processes. As is seen in MCF-PVPH-264 (Fig. 4A), the dorsal process is longer. In MCF-PVPH-263, the dorsal process has an extensive dorsal contact with the anterior process of the jugal, virtually excluding the maxilla from the ventral margin of the antorbital fenestra (Fig. 1). Both posterior processes of the maxilla are connected anteriorly by a thin lamina. In the laterally exposed maxillae of MCF-PVPH-263 (Fig. 4A) and MCF-PVPH-263 (Fig. 4B), these posterior processes define a space, which we interpret as homologous to the preantorbital fenestra of adult neosauropods (Witmer 1997: fig. 17). However, we do not discard that at least a portion of this ventral notch corresponds to the space enclosed by the highly arched post-
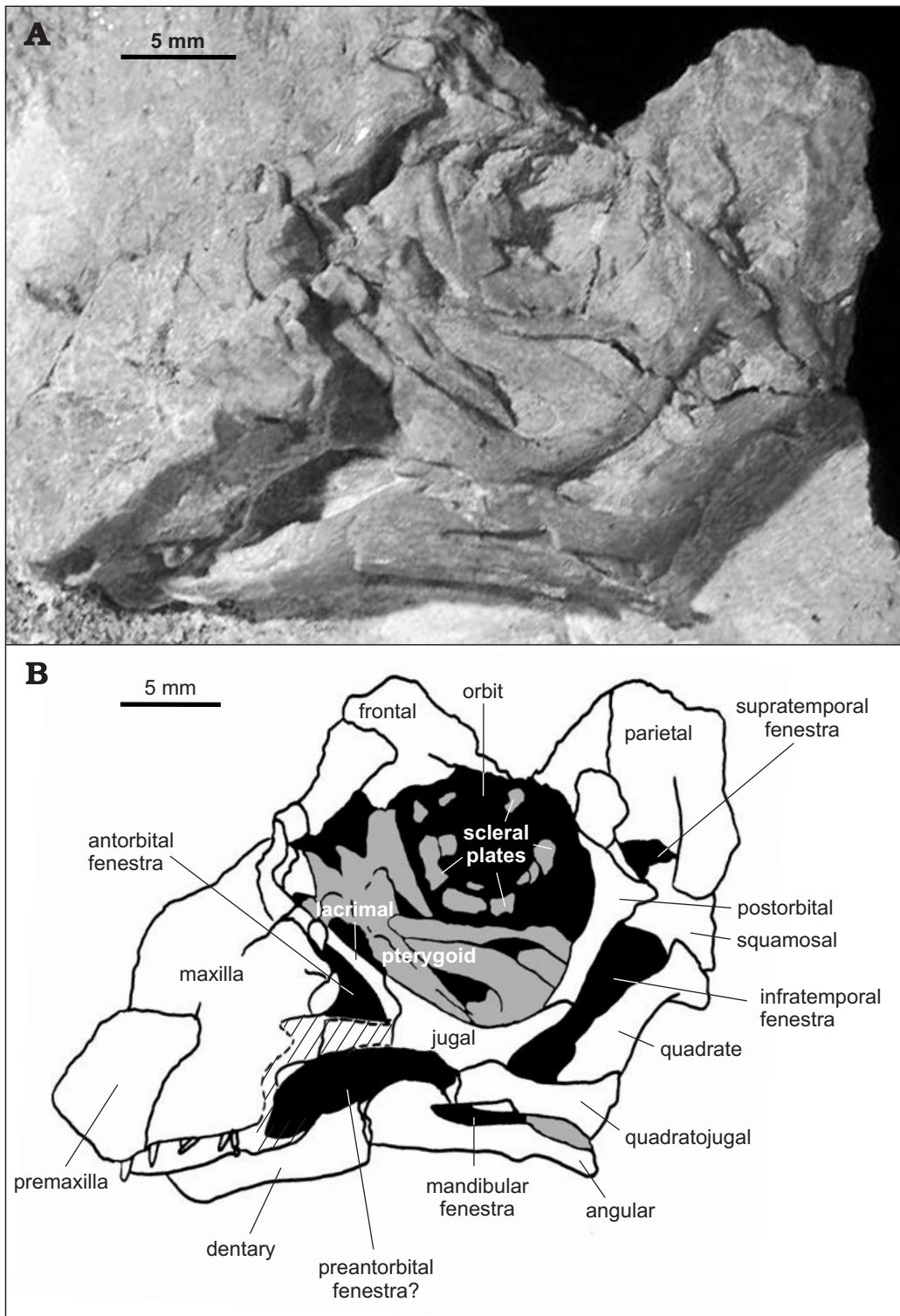
Fig. 2. Titanosaurian sp. indet. MCF-PVPH-272, photograph (**A**) and interpretative drawing (**B**) in left lateral view.

dentigerous portion of the maxilla in adult titanosaurian skull (Chiappe et al. 2001). Unlike the diplodocids *Diplodocus* and *Apatosaurus*, the embryonic specimens MCF-PVPH-250, MCF-PVPH-264, and MCF-PVPH-113b do not show any trace of maxillary processes that articulate tightly with the vomer (Berman and McIntosh 1978).

The maxilla has an anterior projection that can be seen in MCF-PVPH-264 (Fig. 4A), MCF-PVPH-113b (Fig. 4D), and MCF-PVPH-250 (Fig. 4F). In the cases in which the maxilla has been preserved articulated to the premaxilla, this projection is only observed in medial view, e.g., MCF-PVPH-113b (Fig. 4D). Although the surface ventral to the level of the anterior projection varies in size in different specimens, e.g., it is greater in MCF-PVPH-113b (Fig. 4D) than in either MCF-PVPH-250 (Fig. 4F) or MCF-PVPH-264 (Fig. 4A), it cannot be determined whether this variation is taxo-

nomic, ontogenetically related or due to preservational artifacts.

In MCF-PVPH-250, the medial surface of the maxilla is exposed. On the posterior half of the bone, there is a longitudinal ridge, oblique to the anteroposterior axis (Fig. 4F) that possibly corresponds to the "processus palatinus" for articulation with the palatines (Witmer 1997). However, this ridge cannot be observed on the medial face of the left maxilla in MCF-PVPH-264.

The maxilla of MCF-PVPH-272 shows five teeth and enough space anteriorly to accommodate two or three more (Fig. 2). Five teeth are also present in a bone that appears to be the maxilla of MCF-PVPH-262. In MCF-PVPH-263, two small teeth are placed just anterior to the anterior margin of the structure interpreted as the preantorbital fenestra (Fig. 1). In MCF-PVPH-250, the ventral margin of the left maxilla has at least five alveoli posterior to the base of the posterior ascending process (Fig. 4F). This feature indicates that the maxillary tooth row would have extended posterior to the anterior margin of the antorbital fenestra. This condition is comparable to that in *Shunosaurus*, *Camarasaurus*, and *Euhelopus* but differs from the condition in diplodocoids and adult titanosaurians (e.g., *Nemegtosaurus*), in which the teeth are confined to an area anterior to the anterior margin of the antorbital fenestra (Coria and Salgado 1999). The antorbital fenestra of *Rapetosaurus* is uniquely expanded over the tooth row (Curry Rogers and Forster 2001: 530).

Nasal.—The nasals are relatively well-represented. In MCF-PVPH-250 (Fig. 3), both nasals have been preserved in articulation with the premaxillae. Anteriorly, these bones bend ventrally, whereas posteriorly, they are rather straight.

Although the narial region is not preserved in any of the specimens, it is possible to infer that the external nares were not retracted above the orbits, given the strong forward inclination of the lacrimal (MCF-PVPH-263 [Fig. 1], MCF-PVPH-272 [Fig. 2], and MCF-PVPH-147) that usually contacts the posterior end of the nasals, and the anterior extension of the frontals over the anterodorsal margin of the orbit.

Prefrontal.—Probable prefrontals are observed in specimens MCF-PVPH-113a, MCF-PVPH-250 (Fig. 3), and MCF-PVPH-272 (Fig. 2). These bones are placed in a more anterior position than in other sauropods.

Lacrimal.—The lacrimal is a long bone that forms the anteroventral corner of the orbit. The dorsal and ventral ends are somewhat anteroposteriorly expanded, MCF-PVPH-263 (Fig. 1) and MCF-PVPH-272 (Fig. 2). The articulations of the lacrimal cannot be established in any of the specimens. As mentioned above, the lacrimal forms the posterodorsal margin of the antorbital fenestra. Ventrally, it articulates with the corresponding process of the jugal.

Sclerotic ring.—Remains of scleral ossicles are seen in MCF-PVPH-250 (Fig. 3) and in MCF-PVPH-272 (Fig. 2). The scleral ossicles are quadrangular and at least some of them are partially imbricated. In MCF-PVPH-250, two series

of scleral ossicles are preserved, one formed at least by five elements, and the other at least by three (Fig. 3).

Frontal.—The frontals are well-represented in MCF-PVPH-263 (Fig. 1), MCF-PVPH-113a, and MCF-PVPH-264. Like the parietals, they are relatively mediolaterally wide but narrow dorsal to the orbital margin, e.g., MCF-PVPH-263, MCF-PVPH-113a, and MCF-PVPH-264. A parietal fenestra opens between the frontal and parietal in MCF-PVPH-263 (Fig. 1). This condition is likely an ontogenetically variable feature.

Parietal.—In dorsal view, the parietal is posteriorly broad. The descending process for the squamosal is robust, and it posteriorly encloses the supratemporal fenestra. The anterolateral process of the parietal anteriorly surrounds the supratemporal fenestra, MCF-PVPH-250 (Fig. 3). Posteriorly, the parietal thickens dorsoventrally at the interparietal suture, as in other sauropods (Salgado and Calvo 1992).

Postorbital.—The postorbital has an inverted L- shape, with the ventral end directed slightly anteriorly, MCF-PVPH-263 (Fig. 1), 272 (Fig. 2), and 147. This inclination, however, is less marked than that in adult sauropods. This morphology positions the anteroventral extreme of the infratemporal fenestra ventral to the posterior portion of the orbit. The process for the jugal is long and narrow. The posterior process articulates with the squamosal, as seen in MCF-PVPH-263 (Fig. 1) and MCF-PVPH-272 (Fig. 2). The postorbital articulates with the frontal anteriorly (MCF-PVPH-263).

Jugal.—The jugal is a relatively long bone that dorsoventrally narrows near its anteroposterior midline (Fig. 5). It is tetraradiate, with two anterior and two posterior processes. The anterodorsal process articulates with the posteroventral corner of the lacrimal, as shown in MCF-PVPH-272 (Fig. 2). The anteroventral or anterior process of this bone articulates with the posterodorsal process of the maxilla (Fig. 1) and the jugal posterodorsal process articulates with the postorbital (Fig. 2). The posteroventral process appears to have contacted the quadratojugal, as suggested by MCF-PVPH-263 (Fig. 1) and MCF-PVPH-272 (Fig. 2). The jugal process for the lacrimal is shorter than its process for the maxilla. In MCF-PVPH-264, an element is present close to the right maxilla that we interpret as a right jugal. It preserves the short process for the lacrimal and the longer, anteriorly expanded anterior process for the maxilla (Fig. 5A). Both the main body of the jugal and its process for the lacrimal form the ventral margin of the orbit. In turn, the anterior process of the jugal delineates the ventral margin of the antorbital fenestra, located ventral to the ventral margin of the orbit. In contrast to the condition in adult sauropods, the jugal of these embryonic titanosaurians forms part of the ventral margin of the skull, because the maxilla and quadratojugal do not contact each other ventral to the orbit (Chiappe et al. 2001).

Quadratojugal.—As in other dinosaurs, the quadratojugal forms the posteroventral corner of the skull (Figs. 1, 2). The anterior end of this bone is somewhat expanded, a condition
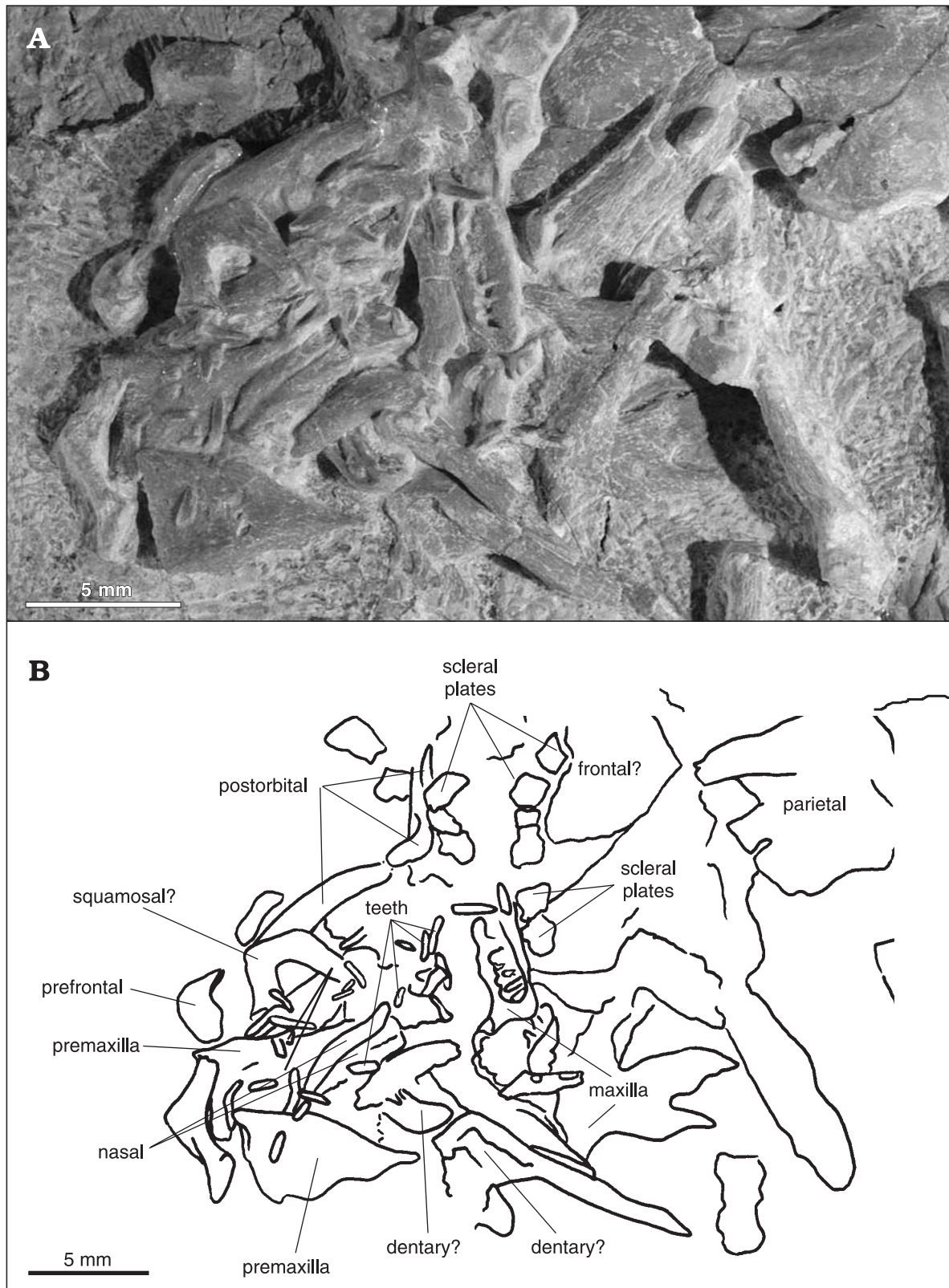
Fig. 3. Titanosaurian sp. indet. MCF-PVPH-250, photograph (**A**) and interpretative drawing (**B**).

synapomorphic of eusauropods (Wilson and Sereno 1998). As observed in MCF-PVPH-272 (Fig. 2) and less clearly in MCF-PVPH-263 (Fig. 1) and MCF-PVPH-147, the quadrato-

jugal does not extend anteriorly beyond the middle of the orbit, a condition shared with *Nemegtosaurus* and that contrasts the condition in diplodocids (Wilson and Sereno 1998, fig.

6A). The anterior articulation of the quadratojugal is obscured due to the poor preservation of this portion of the skull in most specimens. The dorsal process of the quadratojugal is short and does not contact the squamosal, as is evident in MCF-PVPH-263 (Fig. 1) and MCF-PVPH-272 (Fig. 2).

Quadrate.—The quadrates are represented in MCF-PVPH-263 (Fig. 1), MCF-PVPH-272 (Fig. 2), and possibly in MCF-PVPH-113b. The lack of contact between the squamosal and quadratojugal exposes the quadrate in the lateral view. This bone is somewhat anteroventrally-posterodorsally inclined, with its posterodorsal end anteroposteriorly expanded, as can be seen in MCF-PVPH-272 (Fig. 2). In this specimen, the pterygoid wing of the quadrate is apparently less developed than in other sauropods (Wilson and Sereno 1998: figs. 6, 7).

Squamosal.—The squamosal is a well-ossified, L-shaped bone that articulates anteriorly with the parietal and the postorbital and ventromedially with the quadrate. There is no contact between the squamosal and the quadratojugal. As can be seen in MCF-PVPH-272 (Fig. 2), the squamosal posteriorly bounds the supratemporal fenestra, contacting the posterolateral processes of the parietal.

In MCF-PVPH-262, there is a well-preserved left squamosal, medially exposed. Both the articulation for the postorbital and the longitudinal groove for the quadrate can be clearly seen. In this specimen, the ventral process of the squamosal is relatively long and distally robust, as is also the case in MCF-PVPH-263 (Fig. 1). In MCF-PVPH-113b both squamosals appear to be preserved in articulation with the quadrates.

Palate.—Through the orbits of MCF-PVPH-263 (Fig. 1), MCF-PVPH-272 (Fig. 2), and less clearly in MCF-PVPH-147, some palatal elements can be observed. Bones that are interpreted as pterygoids are long and anteriorly directed, curving and expanding posteriorly. Part of the pterygoid wing for the ectopterygoid is seen in MCF-PVPH-263 (Fig. 1).

Mandible.—The mandible is poorly represented. In MCF-PVPH-250, there are some elongate bones that are interpreted to be parts of the lower jaw (Fig. 3). One of these, possibly a right dentary, possesses a series of three alveoli. Another, posteriorly flat element of MCF-PVPH-250 resembles the dentary of *Antarctosaurus wichmannianus*. In MCF-PVPH-263, there is a bone placed between the maxilla and the quadratojugal that is interpreted as a dentary, broken and dorsally displaced (Fig. 1). In MCF-PVPH-272, the lower jaw, though incomplete, is articulated to the skull (Fig. 2). In general, the mandible is low, as has been described for some titanosaurians (Huene 1929; Powell 1986; Coria and Salgado 1999). The number and placement of the dentary teeth remain unknown.

A large external mandibular fenestra is partially visible in MCF-PVPH-272 (Fig. 2). The retroarticular process appears to be short, as suggested by MCF-PVPH-263 (Fig. 1), 264, and 272 (Fig. 2), unlike the condition in some adult titanosaurians (Coria and Salgado 1999).

Dentition.—All teeth of the embryos studied herein are narrow and subcylindrical (Chiappe et al. 1998). Their different thicknesses are interpreted as an indication of their differing positions in the jaws. As in other neosauropods, the crowns are devoid of marginal denticles (Chiappe et al. 1998; Wilson and Sereno 1998). Although their total number remains unknown, more than 30 scattered teeth are preserved in MCF-PVPH-250 (Fig. 3).

Appendicular bones.—Although in most studied specimens, appendicular elements are preserved in addition to portions of the skull, the anatomical information provided by the former is minimal. In general, postcranial elements present a lesser degree of ossification than the skull bones. In MCF-PVPH-250, there are seven preserved limb bones that remain unidentified. The longest bones show unossified, slightly expanded extremities.

Discussion

The morphology of bones represented in more than one specimen (premaxillae, maxillae, nasals, parietals, postorbitals, and jugals) is essentially constant; the minor differences observed among these elements can be explained in terms of their differing degrees of preservation. The three complete skulls available (MCF-PVPH-147, 263, and 272) are identical in their basic morphology, having the same proportions and similarly oriented fenestrae delimited by the same elements. Although the range of intraspecific variation in titanosaurian skulls is unknown, we believe that the embryonic evidence does not indicate the presence of more than one sauropod species at Auca Mahuevo.

All the embryos present the same degree of ontogenetic development. In general, periosteal bone is well-developed in the skull, whereas it is poorly preserved in the limb bones. Bellairs and Osmond (1998) stated that, in chickens, vertebral ossification initiates by day 13 of embryonic development, whereas skull (day 9) and limb bones begin to ossify earlier. At approximately the 14th day, roughly one day after the onset of vertebral ossification, "most of the skull bones have undergone at least some ossification" (Bellairs and Osmond 1998: 95); the shafts of the limb bones are also well-ossified at this stage. The sclerotic ring, in turn, is ossified by day 12. If the relative timing of ossification in the Auca Mahuevo embryos is similar to that in chickens, we are forced to conclude that these titanosaurian embryos died after their skulls and limb bones had reached a substantial degree of ossification, but before their vertebral columns became ossified to any appreciable degree.

The fact that the nares are not retracted and that the quadrates are anteroventrally inclined suggests that these characters are phylogenetically independent, as claimed by Upchurch (1999) (*contra* Salgado and Calvo 1997).

Britt and Naylor (1994) described materials assigned to *Camarasaurus*, which they interpreted as embryonic based
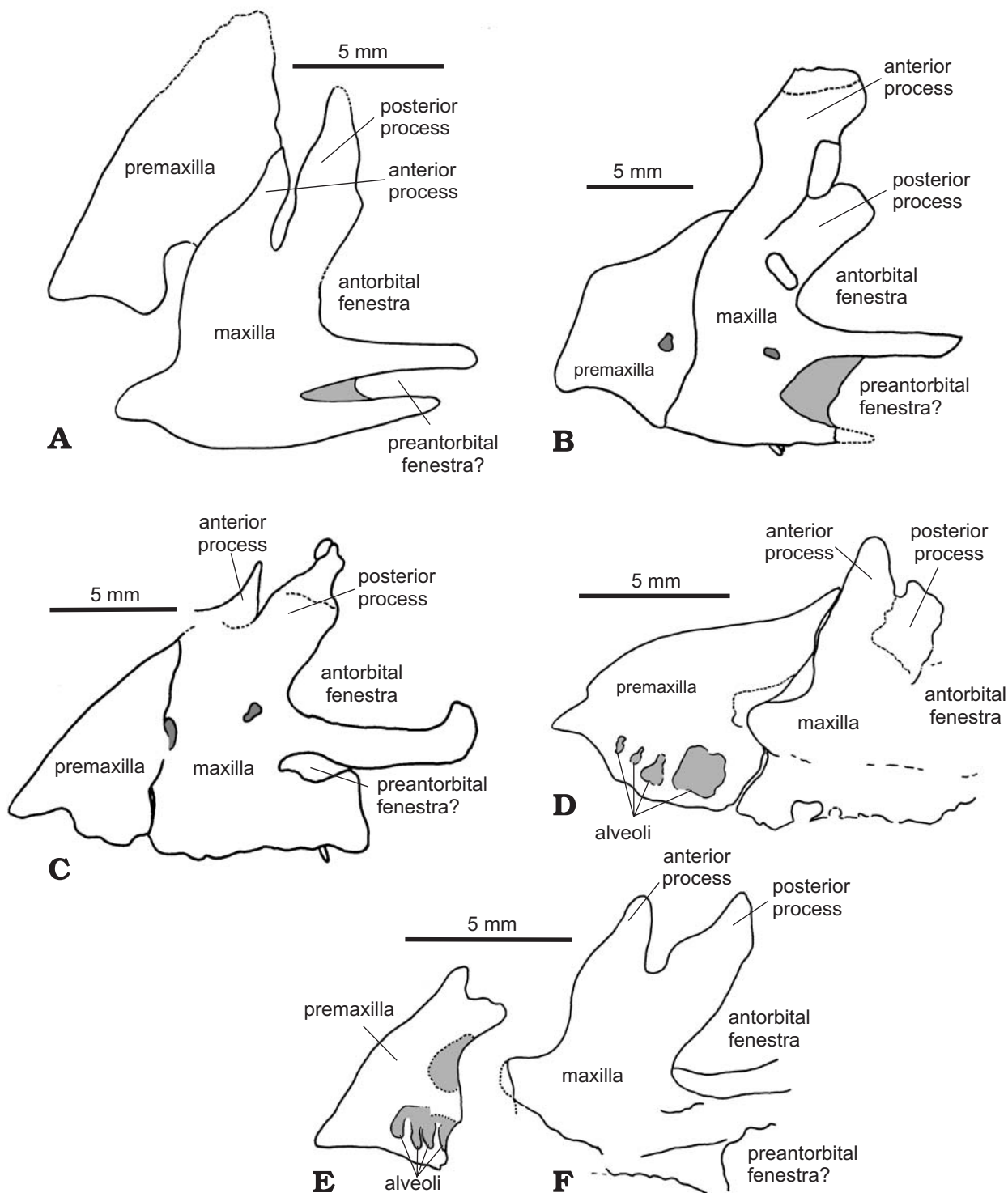
Fig. 4. Titanosaurian embryonic premaxilla-maxilla complex. **A**. MCF-PVPH-264 (reversed). **B**. MCF-PVPH-263. **C**. MCF-PVPH-147 (reversed). **D**. MCF-PVPH-113b. **E**. MCF-PVPH-262. **F**. MCF-PVPH-250 (reversed).

primarily on the presence of unerupted teeth. Nonetheless, the unquestionably embryonic materials described herein show that, at least in some titanosaurians, the teeth erupted prior to hatching.

Interestingly, in addition to juvenile characters, the embryos from Auca Mahuevo display a mosaic of features that

have been recognized as synapomorphies of groups of varying degrees of inclusiveness. Below, we examine each character from a phylogenetic standpoint. For the purposes of the present discussion, we have ordered the series of characters as follows: (1) characters attesting to the juvenile condition of the embryos, (2) characters absent in adult sauropodo-

morphs, (3) eusauropod synapomorphies, (4) characters absent in adult eusauropods, (5) neosauropod synapomorphies, (6) characters absent in adult neosauropods, (7) titanosaurian synapomorphies, and (8) characters absent in adult titanosaurians.

Characters attesting to the juvenile condition of the embryos

Parietal fenestra.—In MCF-PVPH-263, there is an opening (that is certainly not the result of a fracture) between the parietal and the frontal, which is more elongate mediolaterally than rostrocaudally (Fig. 1). The existence of a frontoparietal opening in sauropods has been previously discussed by a number of authors. It existence has been proposed in *Diplodocus* (Holland 1924), *Camarasaurus* (White 1958), *Dicraeosaurus*, and *Amargasaurus* (Salgado and Calvo 1992), but only in the last two genera does the fenestra remain open in adults. In the other taxa it is apparently only present in immature individuals.

Relatively large orbit.—In juvenile dinosaurs, as in most vertebrates, the orbit is proportionally large with respect to the skull length. In the studied embryos, the specimens preserving the skull show orbits with sizes at least 50% of the skull length.

Incomplete ossification of the periosteum.—This is particularly evident in the long bones, whose periosteum exhibits the porous appearance typical of embryonic and neonate archosaurs (Bennett 1993; Sanz et al. 1997; Horner 2000; Ricqlès et al. 2000).

Characters absent in adult sauropodomorphs

Jugal participation in the rim of the antorbital fenestra.— The extensive participation of the jugal in the antorbital fenestra embryos described herein is unusual in adult sauropodomorphs, only present apomorphically in diplodocids (Wilson and Sereno 1998: fig. 6). Apparently, the maxillary process of the jugal, well-developed in the titanosaurian embryos, is reduced during ontogeny. A less likely explanation is that the elongate anterior process of the jugal is an autapomorphy of the Auca Mahuevo titanosaurian.

Eusauropod synapomorphies

Jugal process of the postorbital much longer than the anteroposterior extent of its dorsal end.—The embryos from Auca Mahuevo have a postorbital with a long jugal process. The plesiomorphic condition, typical of basal sauropodomorphs, is a short jugal process of the postorbital. Although Gauthier (1986) proposed a long jugal process as a sauropod synapomorphy, the absence of cranial material in *Vulcanodon karibaensis* necessitates that it is an eusauropod synapomorphy (Wilson and Sereno 1998).

Snout with stepped anterior margin.—Wilson and Sereno (1998) and Wilson (2002) proposed the character "snout with stepped anterior margin" as a synapomorphy of the Eusauropoda. They suggested that the "step" would have become more pronounced during ontogeny. In fact, in some adult titanosaurians, the "step" is conspicuous (Coria and Chiappe 2001), but it is moderately developed or even nonexistent in other species (e.g., *Malawisaurus* and *Rapetosaurus*) (Wilson and Sereno 1998; Curry Rogers and Forster 2001: 531). The "step" is present in the embryos MCF-PVPH-263, MCF-PVPH-272, and less clearly in MCF-PVPH-250 and MCF-PVPH-262.

Squamosal-quadratojugal contact absent.—Wilson and Sereno (1998) interpreted this condition as a synapomorphy of the Eusauropoda, although a squamosal-quadratojugal contact is present in *Camarasaurus*, *Nemegtosaurus*, and, possibly *Brachiosaurus* (Upchurch 1999).

In some adult titanosaurians, e.g., *Rapetosaurus* (Curry Rogers and Forster 2004) and *Nemegtosaurus*, whose phylogenetic placement varies according to different authors, from Diplodocoidea (Upchurch 1995, 1999) to Titanosauria (Salgado and Calvo 1997; Curry Rogers and Forster 2001, 2004), the contact is definitely present. A lack of contact between the quadratojugal and jugal in the adult stage of some reptiles has been interpreted as a paedomorphic trait (Rieppel 1993). Similarly, the loss of the squamosal-quadratojugal contact in some adult sauropods may be paedomorphic.

Anterior ramus of quadratojugal elongate, distally expanded.—In MCF-PVPH-263 (Fig. 1) and MCF-PVPH-272 (Fig. 2), the quadratojugal is extended and anteriorly expanded. This has been proposed as a synapomorphy of the Eusauropoda (Wilson and Sereno 1998; Wilson 2002).

Antorbital fossa absent.—This condition, synapomorphic for the Eusauropoda according to Wilson and Sereno (1998) and Wilson (2002), is present in the embryos studied herein. There is no evidence of a smooth, inset surface along most of the border of the external antorbital fenestra in these specimens.

Characters absent in adult eusauropods (plesiomorphic for Eusauropoda)

Extensive participation of the frontal in the orbital rim.— In adult eusauropods, the frontals form less than 20% of the orbital margin. This condition differs from that observed in the embryos. In the latter, as in basal sauropodomorphs (Galton 1990), primitive theropods (Chure 1998), and therizinosauroids (Barsbold and Maryańska 1990), the prefrontal and postorbital are distant from one another, and the frontal forms most of the dorsal rim of the orbit. To what extent this character is related to the juvenile condition of the Auca Mahuevo embryos remains unknown. Juvenile dinosaurs have relatively large orbits (see above), which positions the highest point of the skull dorsal to the orbits (Long and McNamara 1995: fig.
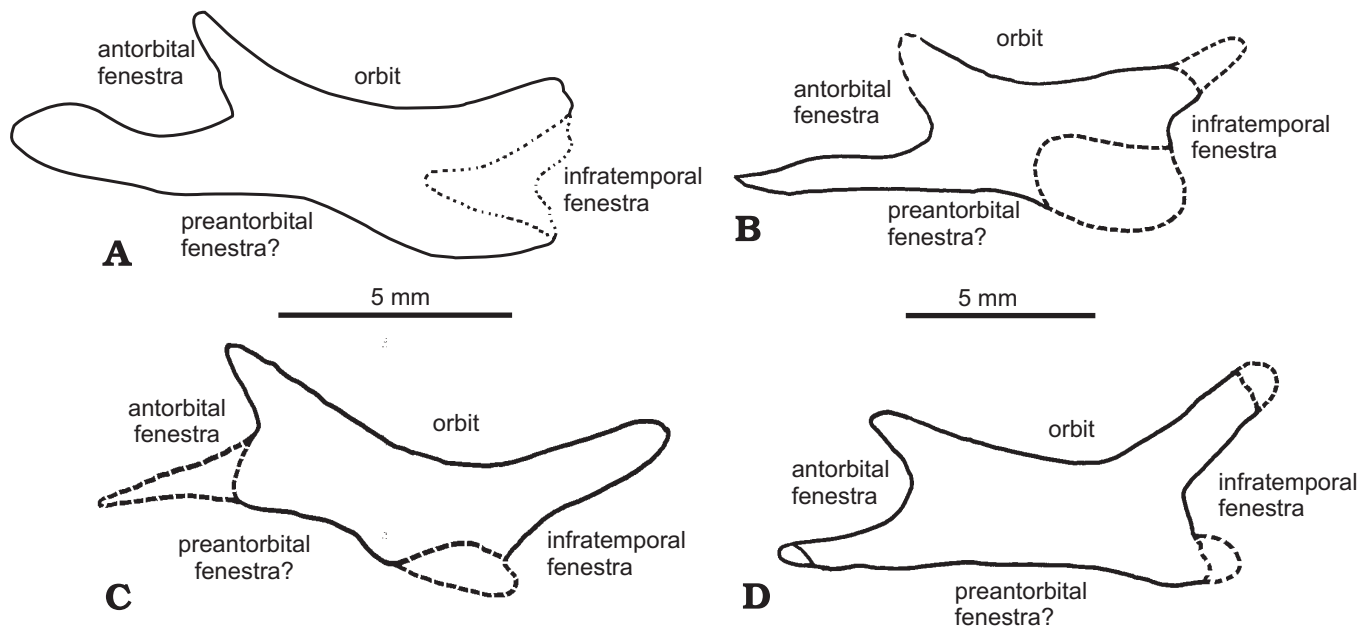
Fig. 5. Titanosaurian embryonic jugal. **A**. MCF-PVPH-264 (reversed). **B**. MCF-PVPH-263. **C**. MCF-PVPH-272. **D**. MCF-PVPH-262 (reversed).

4) and determines that the frontal has greater participation in the orbital rim. The contribution of the frontal to the orbit could reduce during eusauropod ontogeny, as the orbits proportionally decrease in size. In this case, ontogeny would coincide with eusauropod phylogeny.

Non-retracted external nares.—Upchurch (1995), Wilson and Sereno (1998), and Wilson (2002) stated that the partial retraction of the nares is a synapomorphy of eusauropods. In the studied embryos, although the narial opening cannot be clearly seen, we consider the nares to be non-retracted, given the probable placement of the nasals, the strong anterodorsal inclination of the lacrimal, and the anterior extent of the frontal.

Our understanding of the condition in adult titanosaurians is limited; furthermore, we do not know if all titanosaurians possessed the same narial configuration. Salgado and Calvo (1997) judged, based on an isolated premaxilla, from Los Blanquitos, Salta Province, Argentina (Powell 1979), and the premaxillae of *Malawisaurus dixeyi* (Jacobs et al. 1993), that titanosaurian nares would not have been fully retracted, displaying a "camarasauroid" configuration. Conversely, Curry Rogers and Forster (2001, 2004) interpreted that the external nares of *Rapetosaurus krausei* were fully retracted. Regardless of the narial condition in adults of the Auca Mahuevo titanosaurian (partially or fully retracted), it is probable that the nares would have migrated posterodorsally during ontogeny, from a non-retracted to a partially or fully retracted state.

Absence of external narial fossa.—Upchurch (1999: 111) stated that the narial fossa is a synapomorphy of the Eusauropoda, possibly linked to the partial retraction of the nares. Although the condition in adult titanosaurians has not been established, Upchurch (1999) argued that, at least in *Malawisaurus*, such a fossa was present.

In the embryos described herein, on the medial face of the maxilla, the maxillary shelf, which forms the floor of the external narial fossa in eusauropods, does not seem to be present.

Subcircular orbital margin.—Character 25 of Wilson and Sereno (1998: 35) "infraorbital region of cranium shortened anteroposteriorly" encompasses two different features that are thought to be correlated (see Wilson and Sereno 1998: 67, "Characters Ordered by Anatomical Region"): "shape of the orbital margin" and "anteroventral extension of the laterotemporal (= infratemporal) fenestra."

According to these authors, the shortening of the infraorbital area of the skull positions the laterotemporal and antorbital fenestrae close to one another. In this way, the orbit becomes subtriangular in shape with the anteroventral margin acute, and the laterotemporal fenestra extends anteroventrally partially under the orbit, forcing the reduction of the jugal and its exclusion from the ventral margin of the skull. This is the condition in all eusauropods, except in "*Rebbachisaurus*" *tessonei*, wherein the orbit is apomorphically subcircular (Wilson 2002).

In the studied embryos, the orbit is subcircular and the jugal is anteroposteriorly elongate. This bone, which participates in the ventral margin of the skull, forms the majority of the ventral rim of the orbit. Nevertheless, the anteroventral portion of the laterotemporal fenestra is clearly positioned ventral to the posterior part of the orbit. For this reason, we interpret that the extension of the laterotemporal fenestra ventral to the orbit has not resulted in the exclusion of the jugal from the ventral margin of the orbit nor the skull. According to our interpretation, the exclusion of the jugal from the ventral margin of the skull inferred in adult titanosaurians (if, in fact, this is the case, as the quadratojugal of *Rapeto-*

saurus krausei is unknown) is caused by the posterior expansion of the maxilla. Moreover, the posterior extension of the maxilla would cause the enclosure and partial or complete obliteration of the preantorbital fenestra within the maxillary body, a condition seen in adult neosauropods.

This peculiar cranial morphology does not have a correlate in titanosaurian phylogeny, since there are no known adult eusauropods with a partially enclosed, ventrally open preantorbital fenestra.

Quadratojugal does not contact the maxilla.—In eusauropods, the quadratojugal and the maxilla are in contact or at least very close to each other. As a possible consequence of this, the jugal is displaced dorsally from the ventral margin of the skull. In the studied embryos, the jugal is displaced dorsally, but the lack of contact between the maxilla and quadratojugal necessitates that the jugal still participates in the ventral margin of the skull. The anteroposteriorly extensive embayment enclosed by the maxilla, jugal, and quadratojugal is thought to be homologous to the preantorbital fenestra.

Neosauropod synapomorphies

Crown denticles absent.—Wilson and Sereno (1998) proposed this character as a synapomorphy of neosauropods. Chiappe et al. (1998) pointed out that the teeth of the Auca Mahuevo embryos do not have serrations, which confirms their affiliation to that group of sauropods. All teeth in the embryos examined, MCF-PVPH-113b, 250, and 272 have the same morphology as those mentioned by Chiappe et al. (1998).

Presence of preantorbital fenestra.—This character was considered by Wilson and Sereno (1998, character 74) as a synapomorphy of the Neosauropoda, or of *Jobaria + Neosauropoda*, according to Wilson (2002: character 4). Upchurch (1999), in contrast, claimed that the preantorbital fenestra was present only in the diplodocids *Diplodocus* and "*Barosaurus*" *africanus*, and *Nemegtosaurus*, a taxon he purported to be included in Diplodocoidea. In the latter genus, however, he recognized that in the original description Nowiński (1971) had considered the absence of that opening.

In the described embryos, the large opening that is enclosed anteriorly by the posterior processes of the maxilla, dorsally by the jugal, and posteriorly by the quadratojugal (clearly seen in MCF-PVPH-263 and MCF-PVPH-147) is interpreted as homologous to the preantorbital fenestra. If accurately interpreted, the existence of this opening would be demonstrated in the embryos of titanosaurians, although we are uncertain if it persisted in adults, because of the dearth of adult skulls of undoubted titanosaurians (it is apparently present in *Rapetosaurus krausei*, Curry Rogers and Forster 2004). Wilson and Sereno (1998) mentioned that the fenestra is not present in adult *Camarasaurus*, but is present in subadults. The presence of a possible preantorbital fenestra in specimens MCF-PVPH-263 and MCF-PVPH-147 would confirm that

such an opening was present in embryos of at least one non-diplodocoid sauropod lineage (Fig. 6).

Given the lack of contact between the quadratojugal and maxilla, it is possible that the supposed preantorbital fenestra remained ventrally open. This interpretation is supported by the morphology of the maxilla in MCF-PVPH-264, where the maxillary posteroventral process is relatively short, and in MCF-PVPH-272, wherein the morphology of the quadratojugal is well known.

Wilson and Sereno (1998) and Salgado (1999) considered that the preantorbital fenestra is not a mere subdivision of the antorbital fenestra but rather an evolutionary novelty. Contrarily, Witmer (1997) and Upchurch (1999) believed that the osseous bar separating the antorbital fenestra from the preantorbital fenestra is the novel character, at least in diplodocoids. Our interpretation of the evidence provided by the embryos from Auca Mahuevo supports the first hypothesis.

Ventral process of the postorbital broader mediolaterally than anteroposteriorly. —Wilson and Sereno (1998) established this character as a synapomorphy of Neosauropoda (character 75), while Wilson (2002: character 16), hypothesized it as a synapomorphy of *Jobaria + Neosauropoda*. As seen in MCF-PVPH-263, the postorbital is wide mediolaterally, at least as much as it is broad anteroposteriorly.

Long axis of the supratemporal fenestra oriented transversely.—This character was mentioned by Wilson and Sereno (1998) and Wilson (2002) as a synapomorphy of *Omeisaurus + Neosauropoda*. This is the condition in the embryos from Auca Mahuevo, according to what is observed in MCF-PVPH-250 (Fig. 3) and MCF-PVPH-272 (Fig. 2).

Characters absent in adult neosauropods (plesiomorphic for Neosauropoda)

Mandible with short articular glenoid.—Upchurch (1999: 116) stated that the quadrate articulation of the articular was elongate in most neosauropods, except *Brachiosaurus*. This author supposed that this character was reversed in this titanosauriform genus. Apparently, the embryos show the plesiomorphic condition, as seen in MCF-PVPH-264 where the articular has been preserved in dorsal view. Given the paucity of adult titanosaurian mandibles, it is not possible to establish whether this condition varied during ontogeny or if it represents a reversal within the clade Titanosauriformes (*Brachiosaurus*, *Saltasaurus*, their most recent common ancestor and all of its descendants, Salgado et al. 1997).

Titanosaurian synapomorphies

Skull proportionally wide posteriorly.—In *Camarasaurus* and *Brachiosaurus*, the transverse width of the skull is approximately 50% of its anteroposterior length. In *Diplodocus* and *Nemegtosaurus*, it is 40%. There are few complete indisputably titanosaurian skulls. One of them comes from Rincón de los Sauces, Neuquén, Argentina. According to Coria and
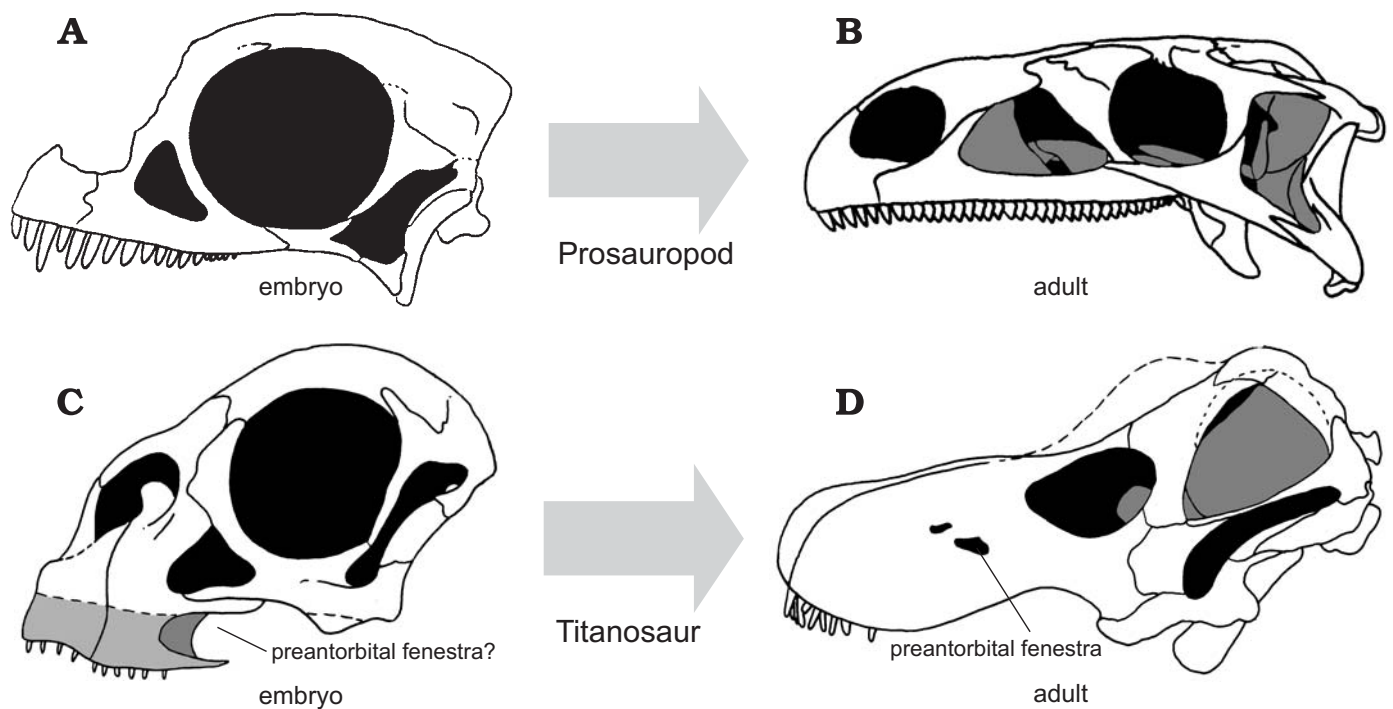
Fig. 6. Ontogenetic evolution of the sauropodomorph skull. The prosauropod skulls are based on *Mussaurus* embryo (**A**) and *Plateosaurus* adult (**B**). The titanosaurian skulls are based on the embryos from Auca Mahuevo (**C**) and *Nemegtosaurus* adult (**D**). Note the ventral expansion of the premaxilla and maxilla of the titanosaurian embryo (shaded area), which enclose the preantorbital fenestra in the adult stage.

Salgado (1999), this skull is 25 cm wide and 45 cm long, which corresponds to a width/length ratio of 55.55%. In the embryonic specimen MCF-PVPH-272, the width of the skull is more than the half of its length, a similar proportion to that observed in the titanosaur from Rincón de los Sauces. Although a proportionally wide skull has never been formally proposed as a titanosaurian synapomorphy, we propose it as a synapomorphy of at least a subgroup of Titanosauria.

Low mandible.—Some titanosaurians, such as *Antarctosaurus wichmannianus* (Huene 1929; Powell 1986) and the titanosaur from Rincón de los Sauces (Coria and Salgado 1999), have a mandible that is extremely dorsoventrally low anteriorly. In MCF-PVPH-272 (Fig. 2), the proportions of the lower jaw seem to agree with those titanosaurian taxa.

Characters absent in adult titanosaurians (plesiomorphic for titanosaurians)

Supratemporal fenestra well-developed.—Salgado and Calvo (1997: 38) pointed out that *Saltasaurus*, *Antarctosaurus*, *Quaesitosaurus*, and *Nemegtosaurus* possess a reduced, transversely narrow supratemporal fenestra. They stated that this character could be a synapomorphy of the Titanosauridae (defined as the most recent common ancestor of *Epachthosaurus*, *Malawisaurus*, and *Saltasaurus* and all of its descendants).

Nevertheless, Powell (1986, 1992) considered a reduced supratemporal fenestra as diagnostic of *Antarctosaurus wich-*

mannianus and *Saltasaurus loricatus*. The titanosaurian from Rincón de los Sauces has a anteroposteriorly reduced fenestra which resembles those of *Antarctosaurus* and *Saltasaurus* (Coria and Salgado 1999). Upchurch (1999), however, argued that a small supratemporal fenestra is a character convergent between titanosaurians and diplodocoids.

In the embryos from Auca Mahuevo, the supratemporal fenestra is well-developed (MCF-PVPH-250 and MCF-PVPH-272). Hence, this character is plesiomorphic in the embryos.

Tooth row posteriorly surpasses the anterior margin of the antorbital fenestra.—Since the original description of *Antarctosaurus* (Huene 1929), it has been suspected that at least some titanosaurians have teeth that are restricted to the anterior region of the snout. This condition has been recently confirmed by the discovery of the titanosaurian specimen from Rincón de los Sauces, the teeth of which are limited to the anterior ends of the mandibles (Coria and Salgado 1999).

In contrast, in MCF-PVPH-263 (Fig. 1) and MCF-PVPH-272 (Fig. 2), the tooth row extends posteriorly at least to the anterior margin of the antorbital fenestra. Furthermore, in MCF-PVPH-147, there is a tooth that is placed posterior to the anterior margin of the antorbital fenestra. In MCF-PVPH-250 (Fig. 4F), the ventral margin of the maxilla houses at least five alveoli, the posteriormost of which lies ventral to the antorbital fenestra. In the embryos from Auca Mahuevo, the teeth are not limited to the tip of the snout, as in adults of some titanosaurians.

In *Rapetosaurus krausei* and in embryos from Auca Mahuevo, the maxillary teeth extend ventral to the antorbital fenestra. This character constitutes a marked difference with the Diplodocoidea (Wilson 2002) and possibly with the titanosaurian from Rincón de los Sauces. However, the anterior extension of the antorbital fenestra dorsal to the tooth row has been included in the diagnosis of *Rapetosaurus krausei* by Curry Rogers and Forster (2001). As such, these authors did not view the posterior extension of the tooth row as a plesiomorphy, but rather as the result of an apomorphic lengthening of the antorbital fenestra.

Conclusion

Comparisons between the embryonic skulls from Auca Mahuevo and the best-preserved skulls of adult sauropods exhibiting titanosaurian similarities (i.e., *Nemegtosaurus* and *Rapetosaurus*) indicate that dramatic transformations took place during the early ontogeny of these dinosaurs (Fig. 6). For instance, the frontals and parietals were greatly reduced in relative size and migrated dorsally to the posterodorsal region of the orbit. The orbit became ventrally constricted and adopted an inverted tear-shaped contour. Furthermore, the rostrum became substantially enlarged, probably as a consequence of maxillary expansion, and the maxilla expanded posteriorly, establishing a connection with the quadratojugal. As such, the maxilla excluded the jugal from the ventral margin of the skull and possibly enclosed the preantorbital fenestra within its body (Fig. 6). In addition, the external nares likely expanded in size and migrated posterodorsally to a position dorsal to the orbits. Apparently, the temporal region of the skull (as known in other sauropods) experienced less dramatic changes during its early ontogeny. The most profound of these transformations undoubtedly affected the infraorbital and narial areas.

From the study of the embryos it can be concluded that the skull changes that occurred during the early ontogeny of titanosaurians do not exactly reflect the transformations that seem to have occurred during the evolution of the clade. Thus, although the developmental pathway illustrated by the embryos follows an overall "Haeckelian" pattern, it does not conform to this pattern in all details. The character combination observed in the studied embryos is unknown for any adult eusauropod. Such a difference may well be the result of different portions of the skull developing at different rates.

The exclusion of the jugal from the ventral margin of the skull in adult neosauropods seems to be a two-fold change. The first step of this transformation probably involved the ventral expansion of the maxilla and premaxilla, while the second step is manifested in the subsequent expansion of the posterior processes of the maxilla, which enclosed and in some cases obliterated the preantorbital fenestra in the adult stage (Fig. 6). This two-part change likely occurred early during development. If a series of successive sister-taxa of adult sauropodomorphs is considered (e.g., *Plateosaurus*, *Shunosaurus*, *Omeisaurus*, and *Camarasaurus*) these changes are not evident. They possibly took place in a neosauropod ancestor, because a rudimentary, almost obliterated preantorbital fenestra became characteristic of the adult neosauropod skull (Wilson 2002).

Acknowledgements

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