

A dentary of *Patagosaurus* (Sauropoda) from the Middle Jurassic of Patagonia

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Abstract. A sauropod dinosaur dentary from the Middle Jurassic (Callovian) of the Cañadón Asfalto Formation of southern Argentina is described. The dentary can be referred to *Patagosaurus fariasi* Bonaparte. Differences between several specimens referred to *Patagosaurus* indicate that more than one taxon of sauropod is represented in this material. A critical discussion of several new and previously used sauropod dentary characters is presented. On the basis of dentary and dental characters taken from published phylogenetic analyses, an advanced, non-neosauropodan eusauropodan position for *Patagosaurus* is indicated. Sauropod dentaries exhibit numerous characters of potential phylogenetic value, but more detailed investigations and new finds are necessary to explore their distribution and phylogenetic utility.

Resumen. UN DENTARIO DE *PATAGOSAURUS* (SAUROPODA) DEL JURÁSICO MEDIO DE PATAGONIA. Se describe un dentario de un dinosaurio saurópodo del Jurásico Medio (Calloviano) de la Formación Cañadón Asfalto en la provincia del Chubut, Argentina. El dentario puede referirse a *Patagosaurus fariasi* Bonaparte. Diferencias entre varios especímenes referidos a *Patagosaurus* indican que más de un taxón de saurópodo está representado en este material. Se presenta además una discusión crítica de varios caracteres para dentarios de saurópodos, algunos de ellos nuevos y otros previamente utilizados. Caracteres dentarios y de huesos dentarios, tomados de análisis filogenéticos publicados, indican que *Patagosaurus* ocupa una posición avanzada entre los eosaurópodos no-neosaurópodos. Los dentarios de saurópodos muestran numerosos caracteres con potencial valor filogenético, pero se necesitan más estudios detallados y nuevos hallazgos para explorar su distribución y utilidad filogenética.

Key words. Middle Jurassic. Patagonia. Sauropoda. *Patagosaurus*. Cañadón Asfalto Formation.

Palabras clave. Jurásico Medio. Patagonia. Sauropoda. *Patagosaurus*. Formación Cañadón Asfalto.

Introduction

Sauropod dinosaurs represent an important and well-known component of Mesozoic terrestrial vertebrate faunas. However, whereas Late Jurassic sauropods are well known from localities in North America, China and Tanzania (Weishampel, 1990), and our knowledge of the Cretaceous sauropods has been increasing rapidly in recent years, mainly to discoveries in South America and Africa, relatively little is still known about the early history of this group.

Although Middle Jurassic sauropods are known from a number of localities, including England (Phillips, 1871; Huene, 1927, 1932), Madagascar (Lydekker, 1895; Lavocat, 1955; Bonaparte, 1986a), Morocco (Lapparent, 1955; Monbaron *et al.*, 1999), eastern Australia (Longman, 1926, 1927), and Patagonia (Bonaparte, 1979, 1986b), our knowledge of sauropod diversity and evolution during this time is far

from complete, mainly owing to the fact that most of the known material is fragmentary or has not been described in detail yet. Virtually complete Middle Jurassic sauropods are only known from China (Dong, 1992). However, this area was geographically isolated from the rest of the world from the Middle Jurassic to the Lower Cretaceous (Russell, 1993), so that the Chinese sauropods may only give limited information concerning the evolution of sauropods in the Middle Jurassic in other parts of the world, whether they are interpreted as a monophyletic clade (Upchurch, 1995, 1998), or not (Wilson and Sereno, 1998).

Generally, many sauropod taxa are known only from fragmentary material (McIntosh, 1990). Thus, detailed character analyses of isolated elements are important to identify phylogenetically useful characters to help key in fragmentary specimens in phylogenies based on the complete skeletal evidence (e.g. Salgado *et al.*, 1997; Upchurch, 1998; Wilson and Sereno, 1998). Furthermore, skulls or even cranial elements are only known for rather few sauropods (McIntosh, 1990). Thus, the recent discovery of a sauropod dentary in the Middle Jurassic of Chubut, Argentina, is significant.

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Geological and paleontological context

The specimen comes from the Cañadón Asfalto Formation, a continental unit of mainly lacustrine sediments that has large exposures in the northern parts of Chubut province, Argentina (figure 1). Traditionally, all the Middle-Upper Jurassic sediments of these basins have been grouped together in the Cañadón Asfalto Formation, although two different sequences have been recognized (Figari and Courtade, 1993; Page *et al.*, 1999). Whereas the lower sequence (Cañadón Asfalto Formation *sensu stricto*) is mainly composed of lacustrine shales, limestones and marls, with rare intercalations of conglomerates and sandstones, the upper one starts with lacustrine shales, but is dominated by fluvial and overbank de-

posits. Furthermore, both sequences also differ significantly in their tectonic structure and their age. Thus, it might be justified to distinguish an Upper Jurassic (Kimmeridgian-Tithonian) Cañadón Calcáreo Formation from the Middle Jurassic (Callovian) Cañadón Asfalto Formation, as proposed by Proserpio (1987).

Several dinosaur taxa have been described from these units. Theropods are represented by the basal tetanuran *Piatnitzkysaurus* (Bonaparte, 1979, 1986b), while sauropods include the genera *Volkheimeria*, *Patagosaurus* (Bonaparte, 1979, 1986b) and *Tehuelchesaurus* (Rich *et al.*, 1999). However, although originally described as coming from the Cañadón Asfalto Formation, *Tehuelchesaurus* is actually derived from sediments that can be assigned to the

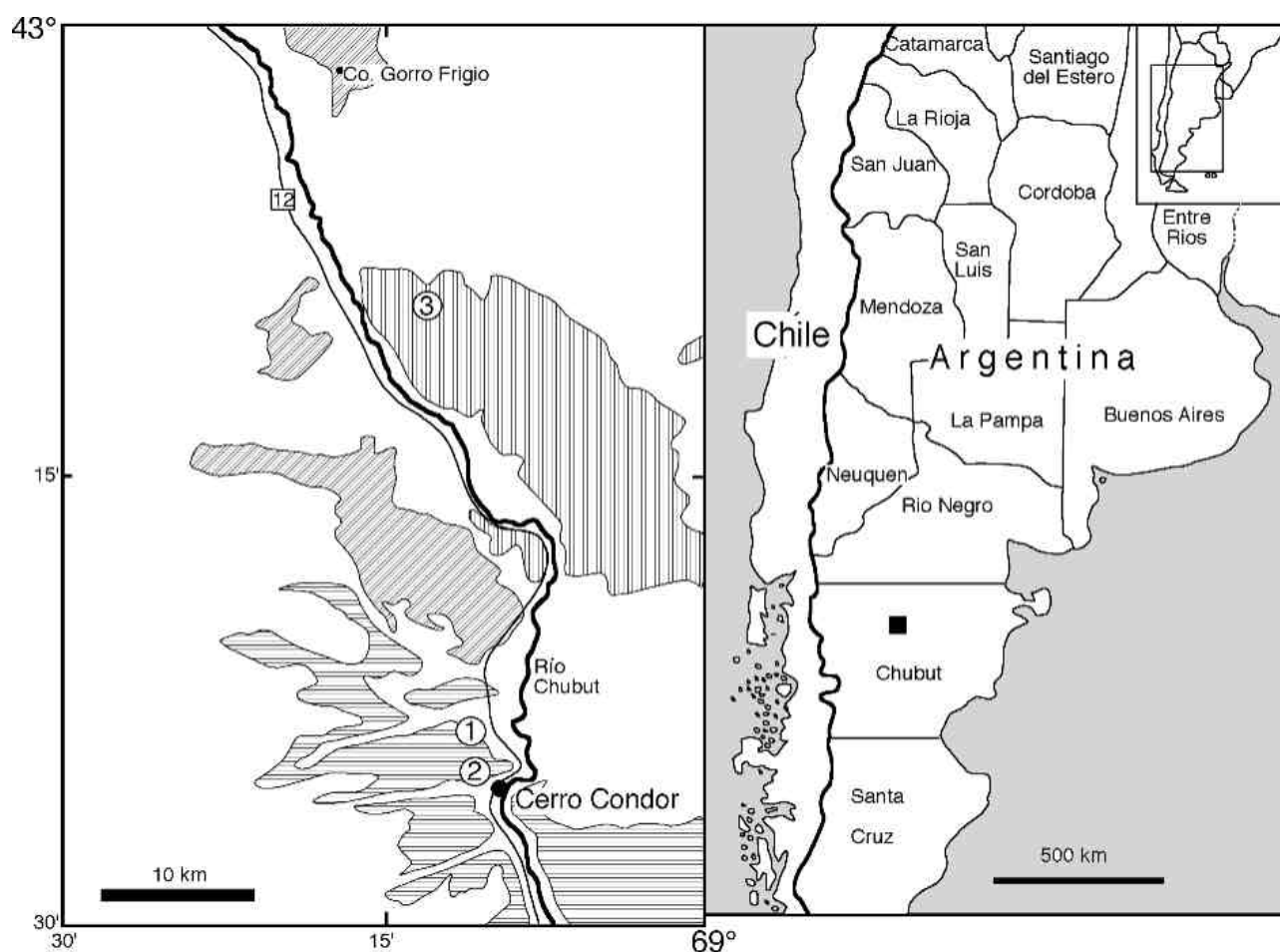


Figure 1. Outcrops of Middle and Upper Jurassic sedimentary rocks in the area between Cerro Condor and the Cerro Gorro Frigio in north-central Chubut, Argentina, and position of dinosaur localities. Horizontal hatching: outcrops of the Cañadón Asfalto Formation (Callovian); vertical hatching: outcrops of the Cañadón Calcáreo Formation (Kimmeridgian-Berriasian); cross-hatching: undifferentiated. 1. locality Cerro Condor North, type locality of *Patagosaurus*; 2. locality Cerro Condor, type locality of *Piatnitzkysaurus* and *Volkheimeria*, and locality of several specimens referred to *Patagosaurus*, including the dentary described in the present work; 3. Estancia Fernández, type locality of *Tehuelchesaurus*.

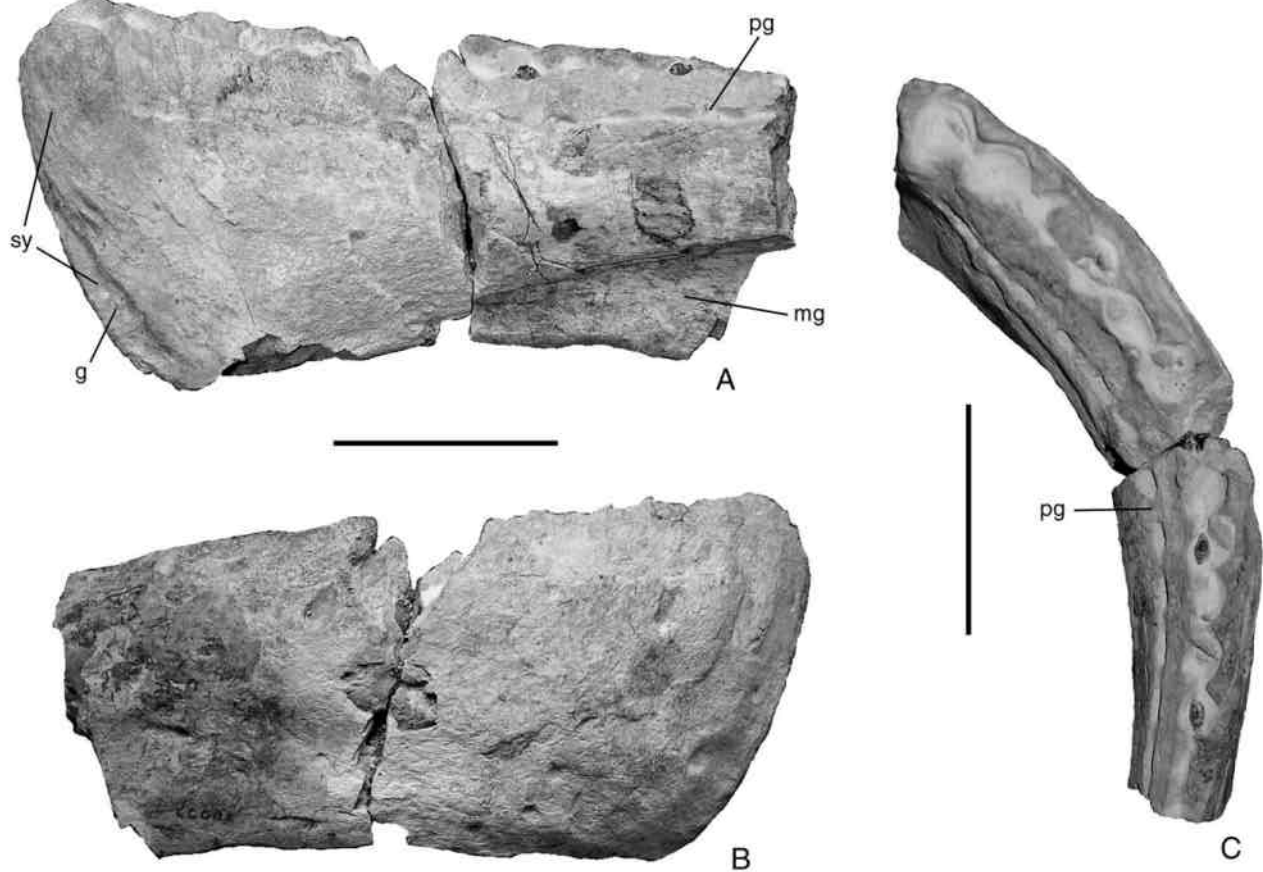


Figure 2. *Patagosaurus fariasi*, right dentary, MPEF-PV 1670. **A**, medial view. **B**, lateral view. **C**, dorsal (occlusal) view. Abbreviations: g, groove in the lower half of the symphysis; mg, Meckelian groove; pg, parodontal groove; sy, symphysis. Scale bars equals 5 cm.

Cañadón Calcáreo Formation (figure 1). Thus, the latter represents a member of a different, considerably younger fauna.

Recent fieldwork carried out by the Museo Paleontológico Egidio Feruglio in both the Cañadón Asfalto and Cañadón Calcáreo Formations has brought a wealth of new vertebrate fossils to light (Rauhut *et al.*, 2001, 2002; Rauhut and Puerta, 2001), including new dinosaur specimens. Among these specimens is the sauropod mandible described below.

Institutional abbreviations. MACN - Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MB - Museum für Naturkunde der Humboldt Universität, Berlin, Germany; MPEF - Museo Paleontológico Egidio Feruglio, Trelew, Argentina; PVL - Fundación Instituto Miguel Lillo, Tucumán, Argentina.

Systematic paleontology

DINOSAURIA Owen, 1842
SAURISCHIA Seeleg, 1887
SAUROPODOMORPHA Huene, 1932
SAUROPODA Marsh, 1878

Patagosaurus fariasi Bonaparte, 1979

Figures 2-5

Newly referred specimen. Isolated right dentary MPEF-PV 1670.

Description. The sauropod mandible comes from the locality of Cerro Cóndor, which was originally worked by Bonaparte (1979, 1986b). The bone bearing layers are conglomerates included in the Cañadón Asfalto Formation and are thus of Middle Jurassic age. The element was found in two pieces on the weathered surface, close to an old excavation site. The bone is generally well preserved, although the posteriormost part and parts of the alveolar border are missing (figure 2). No fully erupted teeth are preserved, but replacement teeth can be observed in several alveoli.

The dentary is relatively short and high and is curved medially in its anterior part (figure 2). As in most sauropods, the anterior end is slightly dorso-ventrally expanded. As preserved, the maximal length of the dentary is 148 mm, with the length in lateral view, measured parallel to the mandibular symphysis (ignoring the curvature of the jaw), being only 135 mm. Its maximum height anteriorly is 85 mm (the ventral border is slightly damaged) and

minimum height towards the posterior break is 68 mm. The body of the bone is massive (23 mm thick at the posterior break). The body of the dentary is slightly twisted; whereas posteriorly, the dorsal part and the alveolar border are slightly inclined medially, anteriorly the ventral part shows a slight curvature towards the medial side. Thus, the tooth row is anteriorly slightly antero-laterally inclined.

On the lateral side (figure 2.B), several large foramina are present below the tooth row. These foramina are widely spaced and closer to the alveolar border posteriorly than anteriorly.

Medially (figure 2.A), the alveolar border is slightly lower than laterally, more so in its anterior than its posterior part. It is formed by the fused interdental plates, which have a wavy dorsal margin, so that a small dorsal spur is present between each two teeth. The interdental plates are separated from the body of the dentary by a shallow paradental groove. Within this groove, a large, oval foramen is developed below each alveolus. Whereas the medial side of the dentary is almost a dorso-ventral plane in the symphyseal region, it is increasingly more convex posteriorly. In the posterior half of the dentary, the Meckelian groove is clearly set off from the body of the dentary by a pronounced step. It expands dorso-ventrally posteriorly and is not bound by the dentary ventrally. No trace of the Meckelian groove is found in the anterior half of the bone.

The symphysis is narrow and dorso-ventrally tall (figure 2.A). It is clearly set off from the medial side of the dentary at a wide angle of approximately 110°. The symphysis is flat and wide in its dorsal half and has a narrowing groove with sharply defined mar-

gins in its lower half. Four small, longitudinally arranged foramina are present within this groove, just in front of its posterior border.

Fourteen alveoli are preserved (figure 2.C) and only one or two might be missing posteriorly. The alveoli are round to slightly oval and gradually increase in size towards the front of the jaw. Replacement teeth are exposed in the 7th, 9th and 12th alveolus; due to the break in the middle of the element, the tooth in the 7th alveolus is exposed in its entire length in mesial view (figure 3.A). The teeth are elongate lanceolate in shape and bear several small, apically directed denticles in the apical third of the tooth margin (figure 3). Only very slight enamel ornamentations are present in the preserved teeth. It consists of small, longitudinal wrinkles in the basal part of the crown and very fine pitting in the apical part. On the broken surface, a further tooth germ is present medial to the erupting tooth.

At the posterior break, a channel is visible that extends antero-posteriorly through the body of the dentary laterally to the alveoli. It is situated just above the midline and is elongated oval in shape. The same channel can also be found in the break in the middle part of the dentary. Here it is situated almost exactly at mid-height of the bone and slightly narrower than in its posterior part. Although the channel lies ventral to the level of the lateral foramina, it seems most probable that it is connected with the latter. Furthermore, a small, matrix-filled opening in the ventralmost part of the broken surface of the anterior portion of the dentary is completely enclosed in bone and continues anteriorly along the ventralmost border of the bone.

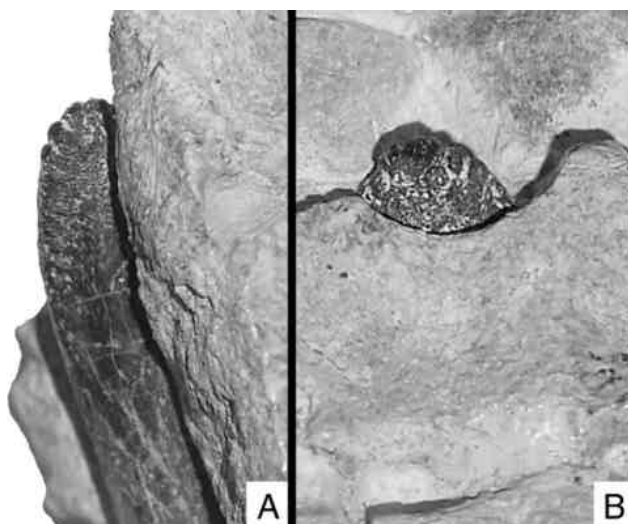


Figure 3. Erupting replacement teeth in A, the 7th alveolus and B, the 9th alveolus of MPEF-PV 1670. Note marginal denticles in the apical part of the crown.

Discussion

Taxonomic identity and sauropod diversity in the Cañadón Asfalto Formation

Of the two sauropods known from the Cañadón Asfalto Formation, cranial material has only been described for *Patagosaurus fariasi* (Bonaparte, 1986b).

Bonaparte (1986b) referred three cranial elements to *Patagosaurus*: a premaxilla (PVL 4076), maxillae (MACN CH 934; both left and right maxilla) and a partial juvenile mandible (MACN CH 933; figure 4). In direct comparison of MPEF-PV 1670 with the left dentary MACN CH 933, only minor differences are found. The two dentaries are very similar in their general shape and in many details, including the probably apomorphic characters of the structure of the symphysis and the lack of a Meckelian groove in the anterior half of the bone (see discussion below). Although the holotype of *Patagosaurus* (PVL 4170) does not have any cranial elements preserved, a com-

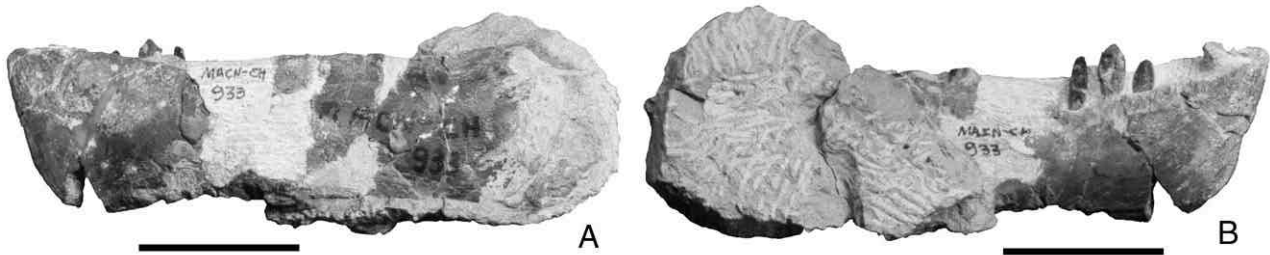


Figure 4. *Patagosaurus fariasi*, juvenile left dentary, MACN CH 933. **A**, lateral view. **B**, medial view. Scale bar equals 5 cm.

parison of the associated postcranium of MACN CH 933 with PVL 4170 confirms the identification of the former as *Patagosaurus fariasi*. Thus, a referral to *Patagosaurus* is supported by a direct comparison of comparable elements.

However, a comparison of the teeth in the dentaries with those found in the maxillae of MACN CH 934, a specimen that was also referred to *Patagosaurus*, reveal some differences. Most notably, all the replacement teeth found in the maxillae of MACN CH 934 lack marginal denticles. Although a few sauropods with generally smooth tooth margins occasionally show a few teeth with marginal denticles (e.g. Janensch, 1935-1936), it seems unlikely that this is the case here, since all preserved teeth of MPEF-PV 1670 and MACN CH 933 show serrated carinae, whereas none of the three preserved replacement teeth of MACN CH 934, which represents an animal of similar or slightly smaller size than MPEF-PV 1670 exhibit this character. Further differences between MACN CH 934 and *Patagosaurus* are found in the postcranial material associated with the maxillae. In the dorsal neural arches, differences include the shape of the neural canal, the inclination of the zygapophyses, and the presence of short spinodiapophyseal lamina in MACN CH 934. Furthermore, the ilium of this specimen is relatively lower than that of the holotype and differs in the relative length of the pubic peduncle and preacetabular blade. Thus, these differences indicate that more than one taxon of sauropod is present in the material referred to *Patagosaurus*. Therefore, the Middle Jurassic sauropod fauna of the Cañadón Asfalto Formation is more diverse than previously recognized; at least one additional taxon of sauropod is present. However, the formal description of the new taxon has to await a complete revision of *Patagosaurus*, which is currently being carried out by the author.

Implications for the morphology and ontogeny of the skull of Patagosaurus

The dentary described here gives some, admittedly limited, information about the skull morphology of *Patagosaurus*. In the articulated lower jaw, the dis-

tance between the two rami at the end of the tooth row is estimated to be 140-150 mm, and thus approximately as much as the length of the dentary tooth row (figure 5). The very short and high dentary furthermore indicates a relatively high and short skull. Thus, *Patagosaurus* seems to have had a rather short, broad muzzle, as is the case in most sauropods (Christiansen, 1999).

Although not derived from a fully adult individual, the dentary described here at least represents an old juvenile or subadult. Differences between this element and the smaller dentary MACN CH 933 may thus indicate ontogenetic differences. Most notably, MACN CH 933 is more slender and the anterior expansion of the bone less pronounced. Indeed, with an estimated maximum length of c. 120 mm for the part of MACN CH 933 that is comparable to MPEF-PV 1670, the former is not much shorter than the latter; it is, however, considerably less deep, with the anterior



Figure 5. Reconstruction of articulated dentaries of *Patagosaurus fariasi* in dorsal view (based on MPEF-PV 1670), illustrating the broadly arched shape of the muzzle in dorsal or ventral view.

expansion only reaching 50 mm. Other differences are clearly correlated with this difference in proportions, such as the relatively larger teeth and the alveolar part making up almost half of the height of the bone. Thus, it seems that the dentary of *Patagosaurus* exhibited a positive allometry in increase in dorsoventral height as compared to dentary length during ontogeny. This allometry was mainly expressed as an increase in the height and massiveness of the subalveolar dentary body.

Another possible ontogenetic change might be the number of teeth. Bonaparte (1986b) estimated the total number of teeth in MACN CH 933 as 13. Thus, with an estimated 15–16 alveoli in MPEF-PV 1670, it seems that the number of teeth in the dentary was slightly increased during sauropod ontogeny. This is in accordance with the pattern described in psittacosaur by Sereno (1990).

Dentary characters. The dentary and teeth described here exhibit several characters that might be of interest in establishing the phylogenetic position and ontogenetic changes in this bone in *Patagosaurus*. Unfortunately, however, a detailed analysis of dentary characters is made difficult by the few skulls known for sauropod dinosaurs and the even fewer detailed descriptions of dentaries available. Thus, first dentary characters used in the phylogenetic analyses of Upchurch (1998) and Wilson and Sereno (1998) are discussed, and then an analysis of other characters of potential phylogenetic value is presented.

Characters used by Upchurch (1998) and Wilson and Sereno (1998). Five dentary and six dental characters used by Upchurch (1998) and three dentary and three dental characters used by Wilson and Sereno (1998) can be evaluated in the dentary described here. Several of these characters are eusauropod or (under accelerated transformation) sauropod synapomorphies and are clearly present in MPEF-PV 1670 (figure 2): anterior end of dentary dorsoventrally expanded (Upchurch, 1998; Wilson and Sereno, 1998); shape of the anterior portion of the tooth rows broadly arched, U-shaped (Wilson and Sereno, 1998); enamel surface texture wrinkled (Wilson and Sereno, 1998); mid-crowns of teeth D-shaped in cross-section (Wilson and Sereno, 1998).

Other proposed synapomorphies at this level are somewhat problematic, either for establishing the systematic position of *Patagosaurus*, or in their interpretation within sauropod phylogeny. Upchurch (1995, 1998) noted the presence of a 'lateral plate' along the tooth rows in the tooth-bearing elements of the skull and lower jaws, which was interpreted as an eusauropod synapomorphy. Although the supposed apomorphic character state is present in MPEF-PV 1670 and, even more pronounced, in MACN CH 933,

it must be noted that their morphology in this respect is not significantly different from that in several theropods and prosauropods (e.g. *Plateosaurus*; MB R. 1937), in which the medial border of the alveoli, formed by the (plesiomorphically unfused) interdental plates, is lower than the lateral alveolar border. However, whereas the lateral plate in *Plateosaurus* remains of subequal height throughout the length of the jaws, it increases anteriorly in sauropods, and a lateral plate seems not to be present in all prosauropods (Upchurch, pers. com. 2002). This character needs more consideration to establish its distribution within saurischian phylogeny.

A further eusauropod synapomorphy proposed by Upchurch is the presence of prominent grooves near the mesial and distal margins on the labial side of the tooth crown as a synapomorphy of a clade including *Barapasaurus* and eusauropods. These grooves are absent in the only well-exposed replacement tooth of MPEF-PV 1670, which, given their broad distribution in other basal eusauropods, might be an autapomorphy of *Patagosaurus*.

Another proposed synapomorphy of eusauropods is the loss of denticles on the tooth crowns, although it was noted that it might be considerably homoplastic (Upchurch, 1998). The dentary described here clearly shows the plesiomorphic character state for this character. However, the fact that marginal denticles are present in the eusauropods *Mamenchisaurus* and *Omeisaurus* (Upchurch, 1998), the recognition of the presence of marginal denticles in *Patagosaurus*, and the recent discovery of other, clearly eusauropodan taxa that have marginal denticles (Monbaron *et al.*, 1999; Sereno *et al.*, 1999) indicates that the loss of denticles on the tooth crowns represents an apomorphic character on a higher node in the tree, probably on the level of Neosauropoda, as suggested by Wilson and Sereno (1998; see also Calvo and Salgado, 1995).

One other character used by Wilson and Sereno (1998), a reduction of the number of teeth in the dentary to 17 or less, seems also to be present in MPEF-PV 1670, although, as noted in the description, the tooth-row is slightly incomplete. According to Wilson and Sereno (1998), this character state is a synapomorphy of a clade containing *Omeisaurus* and neosauropods. However, it might even be synapomorphic at a slightly higher node, since the recently described *Jobaria*, which was regarded as the direct sister group to neosauropods, to the exclusion of *Omeisaurus*, probably has 20 tooth positions in the dentary (Sereno *et al.*, 1999).

Thus, the characters used by Upchurch (1998) and Wilson and Sereno (1998) indicate advanced non-eusauropodan eusauropod relationships for *Patagosaurus* on the basis of dentary characters, which is in

accordance with the result of the only phylogenetic analysis in which *Patagosaurus* has been included so far, that of Upchurch (1998). However, it must be noted that the analysis of Upchurch was based on the published description of this taxon (Bonaparte, 1986b), which includes material of at least two different taxa (see above). A revised analysis of the phylogenetic position of *Patagosaurus* on the basis of all the skeletal evidence has to await a complete revision of the material referred to this taxon.

Other characters of potential phylogenetic importance. Apart from the characters listed by Upchurch (1998) and Wilson and Sereno (1998), several other characters of the dentary might be found to be either autapomorphies of *Patagosaurus*, synapomorphies of some subset of sauropods, or ontogenetically variable characters, once mandibular material is known for more taxa.

1) Dentary symphysis with a pronounced longitudinal groove in its lower part (figure 2.A). As noted above, both MPEF-PV 1670 and MACN CH 933 have a ventrally widening groove developed in the lower half of the dentary symphysis. Such a structure is absent in theropods and sauropodomorphs ancestrally. It also seems to be absent in most sauropods, such as *Camarasaurus* (Madsen *et al.*, 1995), *Brachiosaurus* (Janensch, 1935-1936), *Barosaurus africanus* (Janensch, 1935-1936), *Dicraeosaurus* (Janensch, 1935-1936), and *Malawisaurus* (Jacobs *et al.*, 1993), and might thus represent an autapomorphy of *Patagosaurus*.

2) Meckelian groove restricted to the posterior half of the dentary. In theropods, prosauropods and several sauropods, including *Mamenchisaurus* (Russell and Zheng, 1993), *Camarasaurus* (Madsen *et al.*, 1995), *Brachiosaurus* (Janensch, 1935-1936), *Dicraeosaurus* (Janensch, 1935-1936), and *Malawisaurus* (Jacobs *et al.*, 1993), the Meckelian groove on the medial side of the dentary is wide posteriorly and narrows anteriorly. However, in these taxa, it persists to the anteriormost part of the dentary as a narrow, dorsally sharply bordered groove along the ventral edge. In MPEF-PV 1670 and MACN CH 933, no Meckelian groove can be found in the ventral part of the medial side of the anterior half of the bone (figure 2.A). Especially its absence in the small dentary MACN CH 933 is noteworthy, since the presence of a well-developed Meckel's cartilage is a juvenile character and thus one might expect the corresponding groove in the dentary to be better developed in juveniles. Given the distribution of this character, it seems probable that this is another autapomorphy of *Patagosaurus*.

3) Posterior part of the Meckelian groove not bordered ventrally by the dentary (figure 2.A). In theropods and prosauropods, the ventral border of the wide, posterior part of the Meckelian groove is

formed by a thin lamina of the dentary that expands medioventrally from the lateral side. In MPEF-PV 1670, no medioventral flange of the dentary is present; the lateral side terminates in a vertical plate, and thus, the Meckelian groove is open ventrally. In most sauropods, the situation is unclear, since this structure has seldom been described or illustrated in detail and is obscured by the splenial and angular in articulated mandibles. However, the derived character state is at least also present in the camarasauromorph sauropods *Camarasaurus* and *Brachiosaurus* (Carpenter, pers. comm. 2002), indicating that this is a possible apomorphy of some subclade of sauropods.

4) Denticles on teeth restricted to the apicalmost third of the crown (figure 3). In dinosaurs ancestrally and in prosauropods, denticles are usually found on at least half the length of the tooth crown mesially and along the entire carina posteriorly. As noted above, in neosauropods, marginal denticles are absent. In MPEF-PV 1670 and MACN CH 933, marginal denticles are small and restricted to the apicalmost part of the crown, even if well-developed crown margins extend over at least three fourths of the tooth crown. The presence of denticles in the apicalmost third of the crown of another basal eusauropod taxon, *Omeisaurus* (He *et al.*, 1984), indicates that this character state might be part of a transformation series of reduction of marginal denticles from the basis of the crown apically, culminating in the loss of denticles, in sauropod evolution.

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