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Skull anatomy of *Mussaurus patagonicus* (Dinosauria: Sauropodomorpha) from the Late Triassic of Patagonia

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Abstract
The skull anatomy of *Mussaurus patagonicus* from the Upper Triassic Laguna Colorada Formation is described based on a revision of the type material and several recently found specimens. The studied material include two distinct size classes of individuals. The type material consists of extremely young individuals whereas the new specimens are interpreted as juvenile or subadult individuals. The latter are significantly larger, having a skull approximately three times longer than the type material. The skull anatomy of this taxon shows derived characters shared with some basal sauropodomorphs and eusauropods, which are absent in other basal sauropodomorphs (e.g. *Thecodontosaurus*, *Plateosaurus*). These include the presence of an extension of the infratemporal fenestra ventral to the orbit, dorsal and anterior rami of quadratojugal subperpendicular to each other, dorsoventral expansion of dentary at mandibular symphysis, slightly procumbent teeth with broad serrations restricted to the apical region (absent in some teeth). Differences among the studied specimens helps to understand the early ontogenetic changes occurring in this basal sauropodomorph, revealing major changes in the rostral and temporal regions.

Keywords: *Sauropodomorpha, Prosauropoda, Sauropoda, ontogeny*

Introduction

Basal sauropodomorphs from South America are, so far, exclusively recorded in Upper Triassic beds from three different basins (Paraná, Villa Unión-Ischigualasto, and El Tranquilo) in the southern part of the continent. The first of these basins is located in southern Brazil and has recently yielded remains of two sauropodomorphs: the plesiomorphic form *Saturnalia tupiniquim* from the Santa Maria Formation (Langer et al. 1999; Langer 2003, 2005) and *Unaysaurus tolentinoi* from the Caturrita Formation (Leal et al. 2004). Basal sauropodomorphs from the Villa Unión-Ischigualasto Basin (northwestern Argentina) are known from Los Colorados Formation and three different taxa have been recognized: *Riojasaurus incertus* (Bonaparte 1971), *Coloradisaurus brevis* (Bonaparte 1978), and *Lessemsaurus sauropoides* (Bonaparte 1999). Finally, a single basal sauropodomorph was

previously described from Patagonia (southern Argentina): *Mussaurus patagonicus* (Bonaparte and Vince 1979). This taxon was found in the Laguna Colorada Formation (El Tranquilo Group).

The type material upon which *Mussaurus patagonicus* was described includes remains of eight extremely young individuals. Some of these specimens are articulated and remarkably complete and all of them were found in close association. Additionally two complete eggs and eggshell fragments were found close to them. Bonaparte and Vince (1979) briefly described this material and discussed several aspects of its anatomy that suggested prosauropod affinities, although they also noted some similarities with the derived condition present in skulls of Sauropoda. Here, we further describe the skull anatomy of *Mussaurus patagonicus* and discuss its ontogenetic changes based on additional material recently found in the Laguna Colorada Formation, as well as several

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specimens from the PVL collection (Instituto Miguel Lillo, Tucumán). The new material consists of seven partially articulated skeletons found closely associated to each other. These are significantly larger than the type material, although they are interpreted as an association of juvenile specimens.

Systematic palaeontology

Saurischia Seeley 1887
Sauropodomorpha Huene 1932
Mussaurus patagonicus Bonaparte and Vince 1979
(Figures 1–7)

Holotype

PVL 4068, articulated skeleton of a post-hatchling individual.

Referred material

PVL 4208, skull lacking the rostral region with articulated cervicodorsal vertebrae, scapula, humerus, radius, ulna, and disarticulated hindlimb elements of a post-hatchling individual; PVL 4209, partial skull and lower jaws of a post-hatchling individual associated with partially articulated postcranial material, including dorsal vertebrae, femur, tibia, fibula, and metatarsals; PVL 4210, almost complete skull associated with postcranial remains of a post-hatchling individual. The postcranium includes scapulae, humeri, ulna, and an articulated series of posterior dorsal vertebrae, pelvis, and hindlimb; PVL 4211, remains of a post-hatchling individual including incomplete skull and mandibles and several disarticulated postcranial remains; PVL 4212, partially articulated postcranial skeleton of a post-hatchling individual; PVL 4213, disarticulated postcranial remains of post-hatchling individuals; PVL 4587, partially articulated skeleton belonging to, at least, two different individuals. Including cervicodorsal vertebrae, hindlimb, forelimb remains; PVL 5865, articulated skeleton and almost complete skull of a post-hatchling individual; MPM-PV 1813/1, skull articulated with cervicodorsal series; MPM-PV 1813/2, isolated skull; MPM-PV 1813/4, skull articulated with a cervicodorsal series, scapular girdle and forelimbs.

Locality and horizon

Laguna Colorada, Santa Cruz Province, Argentina. The MPM specimens were closely associated to each other and were collected on the southern margin of Laguna Colorada. These sediments belong to the Laguna Colorada Formation, El Tranquilo Group (Herbst 1965; Jalfin and Herbst 1995). In addition to basal sauropodomorphs this unit has yielded remains of a heterodontosaurid ornithischian (Baez and Marsicano 2001). The age of this formation is usually considered to be Late Triassic (Norian; Jalfin and Herbst 1995) based on the *Dicroidium* flora found below and above the horizon in which the *Mussaurus* remains were found (Jalfin and Herbst 1995; Gnaedinger and Herbst 1998a,b, 1999). Furthermore, El Tranquilo Group is intruded by the granitoids of La Leona Formation (Chebli et al. 1976). Radiometric dating (whole rock Rb-Sr) of these granitoids yielded an age of 203 ± 2 Ma (Pankhurst et al. 1993; Rapela and Pankhurst 1996), providing an upper bound for the age of El Tranquilo Group (Stipanicic and Marsicano 2002).

Emended diagnosis

The following diagnosis is emended from the original one (Bonaparte and Vince 1979) based on the cranial material described here. Characters indicated with an asterisk are a combination of characters exclusively found in the post-hatchling individuals (e.g. type material of *Mussaurus*) and the new juvenile specimens described here (PVL 4587 and MPM material). As this combination of characters is unique among sauropodomorphs, it forms the basis upon which the juvenile specimens are referred to *Mussaurus*
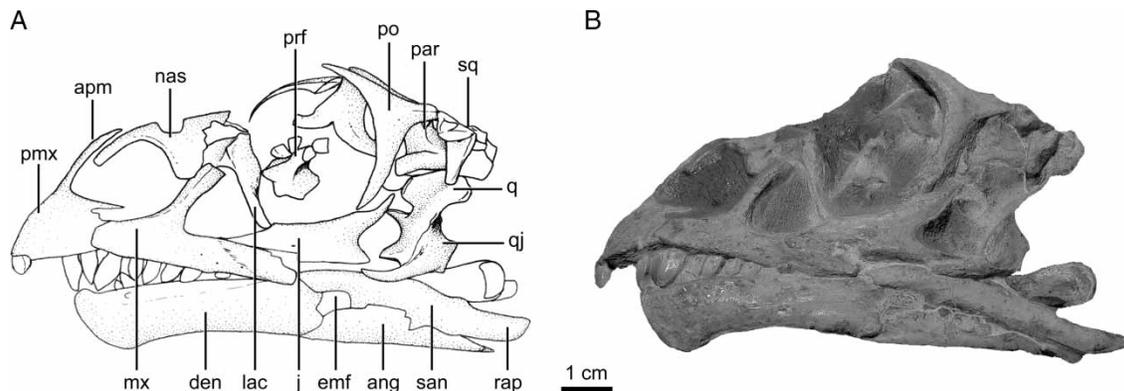

Figure 1.   Skull and mandible of *Mussaurus patagonicus* (MPM-PV 1813/4) in left lateral view. See abbreviations in Appendix.
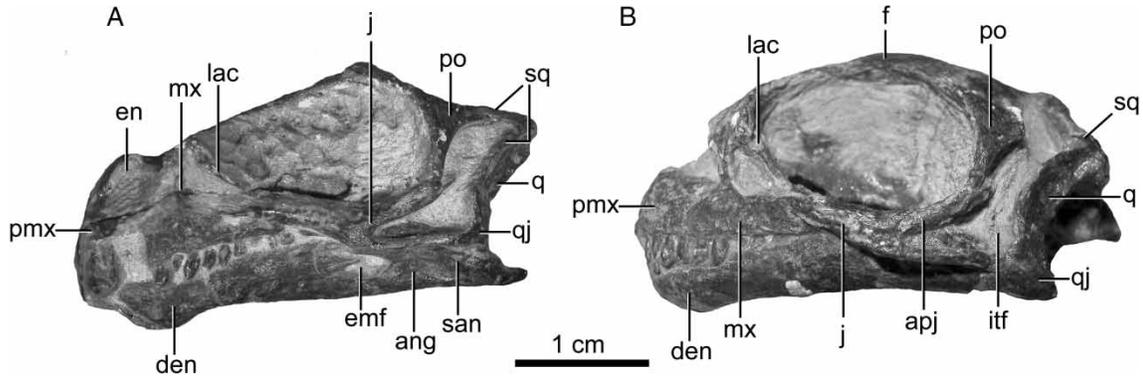
Figure 2.   Post-hatchling specimens of *Mussaurus patagonicus*. A, skull of PVL 5865 in left lateral view; B, skull of PVL 4210 in lateral view, inverted right side. See abbreviations in Appendix.

patagonicus. The postcranial characters included in the original diagnosis of this taxon (Bonaparte and Vince 1979) are subject to ontogenetic change and therefore cannot be considered as diagnostic of this taxon. The postcranial morphology of *Mussaurus* and a revision of its diagnostic features will be treated elsewhere.

Basal sauropodomorph with the following unique combination of characters: anterior margin of the premaxilla directed posterodorsally, forming an angle of 45° with the alveolar margin; main body of premaxilla anteroposteriorly shorter than deep*; ventral ramus of lacrimal straight and anteroposteriorly narrow*, markedly constricted at mid-height; absence of lateral (superficial) lamina of lacrimal covering the posterodorsal region of antorbital sinus; presence of a thin ridge along the entire ventral ramus of the lacrimal; ventral end of descending process of postorbital straight; rostral extension of the infratemporal fenestra underneath the orbit*; anterior and dorsal rami of quadratojugal subperpendicular to each other*; presence a dorsally projected peg-like process on the anterior tip of the dentary (immediately anterior to the first mandibular tooth)*; low and elongated caudal end of mandibular rami (posterior to the external mandibular fenestra) with only gently sigmoid dorsal margin*; dorsoventrally expanded anterior end of mandibular symphysis*; premaxillary teeth and anterior maxillary teeth with sigmoid distal margin lacking serrations on their margins (or having weakly developed broad denticles at the apical region); posterior maxillary teeth lanceolate with serrations on part of their anterior and posterior margins.

Description

Skull

The skull description is largely based on the most complete subadult specimen, MPM-PV 1813/4.
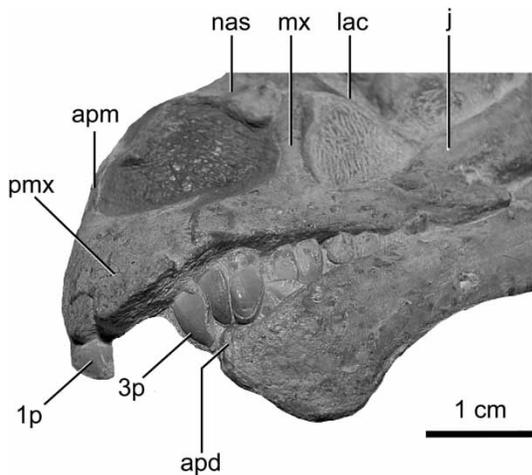

Figure 3.   Anterolateral view of the snout and mandible of *Mussaurus patagonicus* (MPM-PV 1813/4). See abbreviations in Appendix.
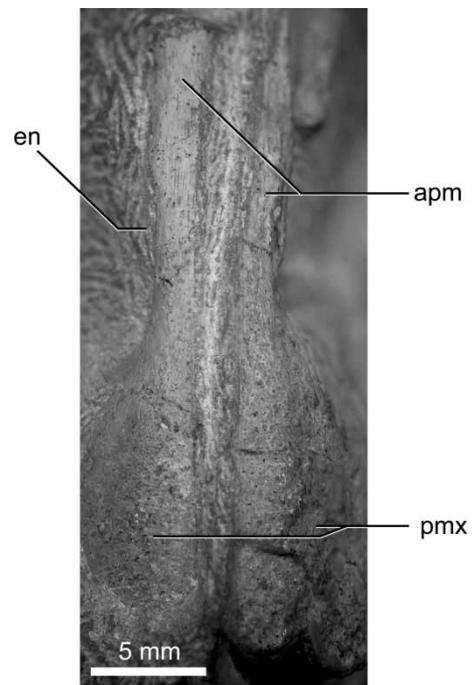

Figure 4.   Rostral end of *Mussaurus patagonicus* in anterior view (MPM-PV 1813/4). See abbreviations in Appendix.
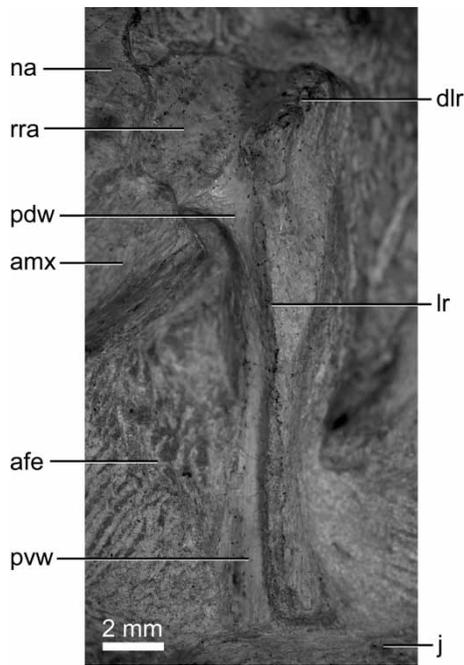
Figure 5.   Lacrimal of *Mussaurus patagonicus* (MPM-PV 1813/4) in lateral view. See abbreviations in Appendix.

However, some characters were better observed on the three other subadult specimens (MPM-PV 1813/1, MPM-PV 1813/2, PVL 4587) or the post-hatchling specimens described by Bonaparte and Vince (1979). In such cases, the collection number is explicitly indicated; otherwise the description corresponds to the morphology observed in MPM-PV 1813/4.

The skulls of the juvenile specimens have a relatively short and high rostrum (50% of the total skull length; Figure 1). The snout continuously increases its dorsoventral height towards the orbits. The skull reaches its maximum dorsoventral depth at the posterior margin of the orbits, tapering posteriorly along the temporal region. The external nares are notably large and are enclosed by the premaxillae, nasals, and maxillae (as in most sauropodomorphs). Their anteroposterior length is subequal to their dorsoventral depth and is approximately 55% the length of the orbit (Figure 1). The antorbital fenestra is rather small and subtriangular and lacks a well-developed fossa on its anterior and posterior margins. The orbits are notably large, occupying approximately 30% of the total skull length. This ratio is larger than in other sauropodomorphs, although this may just represent evidence for the subadult ontogenetic stage of these specimens (since the orbital length is subject to negative allometry respect to the skull length during development). The post-hatchling specimens originally described by Bonaparte and Vince (1979) have an orbital length of approximately 45% of the total skull length (Figure 2). The infratemporal fenestra is hourglass shaped and is almost as dorsoventrally high as the orbit. The dorsal end of this opening is mildly

expanded and is bordered by the postorbital and squamosal. The ventral end is also expanded, its anteroventral region extending underneath the orbit (Figures 1 and 2). The supratemporal openings are partially preserved in the specimens MPM-PV 1813/1 and PVL 4587, having preserved only their anterior region. These openings are large and dorsally exposed, in contrast to the condition of the post-hatchling specimens described by Bonaparte and Vince (1979), in which the openings are narrower and exposed laterodorsally (PVL 4210). Unfortunately, none of the available specimens have preserved a complete palate or occiput. The mandibles have a small external mandibular fenestra enclosed between the dentary, surangular, and angular.

The lateral surface of the left premaxilla is well exposed in the specimen MPM-PV 1813/4. The anterior margin of the premaxilla of *Mussaurus patagonicus* is directed posterodorsally, forming an angle of 45 degrees with the alveolar margin. Thus, the anteroventral tip of the snout is remarkably acute and pointed (Figures 1 and 3). This condition resembles the morphology of the *Yunnanosaurus huangi* (Young 1942; NGMJ V 116 [V20]), but differs from all other basal sauropodomorphs (in which this margin forms an angle of 60 to 90 degrees with the alveolar margin). The post-hatchling specimens of *Mussaurus* have a significantly larger angle (Figure 2), varying between 63 degrees (PVL 4068) and 71 degrees (PVL 4210).

The main body of the premaxilla (i.e. the laterally exposed surface located anterior to the posterior process and ventral to the ascending nasal process) is shorter than high, in contrast with the low and elongated condition of other basal sauropodomorphs (e.g. *Anchisaurus polyzelus* (Galton 1976; YPM 1883), *Efraasia minor* SMNS 1268, *Plateosaurus engelhardti* SMNS 13200, *Yunnanosaurus huangi* NGMJ V 116 [V20]). Interestingly, its proportions approximate those of a subadult specimen of *Massospondylus carinatus* (BPI/1/4376; Gow et al. 1990; Sues et al. 2004). In adult specimens of *Massospondylus carinatus* (e.g. BPI/1/5241) and *Coloradisaurus brevis* (PVL 3967), the main body of the premaxilla is subquadrangular (i.e. longer than in the juvenile BPI/1/4376, but shorter and higher than in other basal sauropodomorphs). The main body of the premaxilla of *Mussaurus patagonicus* lacks a well developed narial fossa, in contrast with the condition of *Plateosaurus engelhardti* (SMNS 13200) and related forms (e.g. *'Plateosaurus' gracilis* GPIT18318a, *Efraasia minor* SMNS 12216) in which a sharp ridge delimits a depressed narial fossa. The lateral surface of the premaxilla bears five neurovascular foramina scattered from the anteroventral margin of the external nares to the alveolar margin. Four of these foramina are notably small whereas one of them, located at the dorsoventral midpoint of this region, is three times larger.
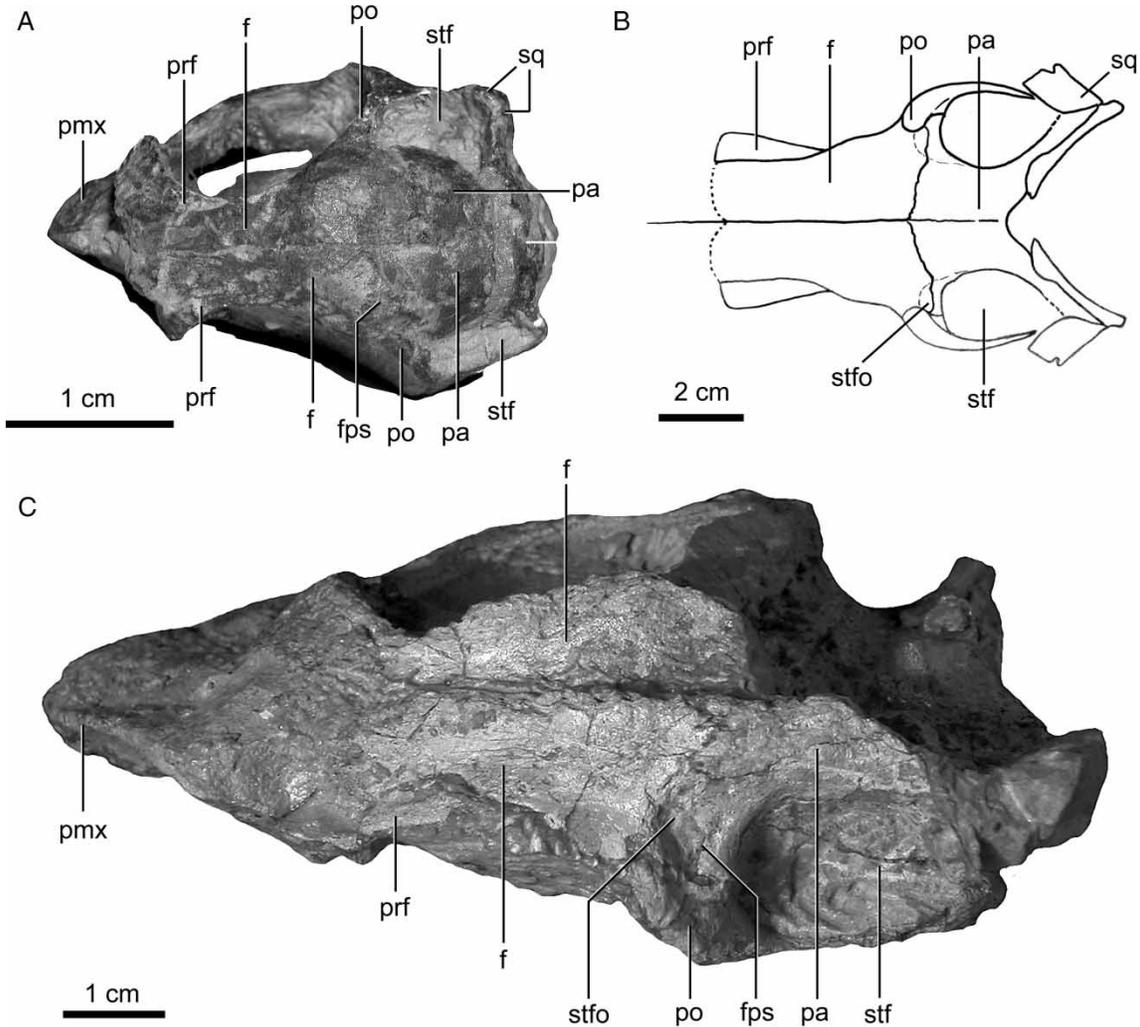
Figure 6.   Skull of *Mussaurus patagonicus* in dorsal view. A, post-hatchling specimen PVL 4210; B, reconstruction of supratemporal region based on specimens PVL 4587 and MPM-PV 1813/1; C, subadult specimen PVL 4587. See abbreviations in Appendix.

The ascending nasal process of the premaxilla forms the ventral half of the anterior margin of the external nares. This process has an almost constant latero-medial width along its length and does not seem to

Figure 7.   Left infratemporal region of *Mussaurus patagonicus* (MPM-PV 1813/4) in lateral view. See abbreviations in Appendix.

taper gradually (Figure 4), resembling the condition of most other non-eusauropod sauropodomorphs (Sereno 1999). Dorsally, this process is laterally overlapped by the descending process of the nasal. The posterior process of the premaxilla forms the ventral margin of the external nares and borders dorsally the anterior process of the maxilla. These two elements are slightly displaced from their natural contact, so it is not possible to determine the presence of a subnarial foramen in *Mussaurus patagonicus*.

The maxilla of *Mussaurus patagonicus* is triradiate, as in other basal sauropodomorphs. Its rostral ramus contacts the premaxilla, an ascending ramus forms the anterior edge of the antorbital fossa, and a posterior process extends along the ventral margin of the antorbital region. The rostral ramus is anterior to the ascending ramus and forms a tabular process (Figure 1). This process overlaps laterally the premaxilla and tapers abruptly at its anterior end.

The ascending ramus of the maxilla is subvertically oriented, forming an angle with the alveolar margin of
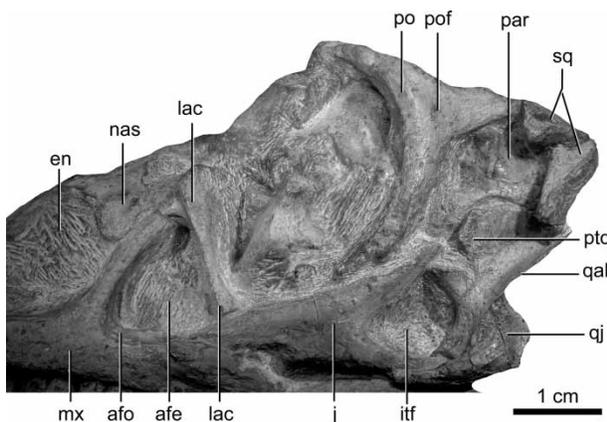
approximately 75 degrees (Figure 1). In the post-hatchling specimens however, this angle is close to 90 degrees and forms the anterior margin of the antorbital opening (Figure 2). This process is deflected posteriorly along the dorsalmost fifth of the dorsoventral height of the antorbital fossa. The nasal laterally overlaps this deflected region. A similarly oriented ascending ramus of the maxilla is also present in *Massospondylus carinatus* (BPI/1/5241) and *Coloradisaurus brevis* (PVL 3967). In contrast, in most basal sauropodomorphs (e.g. *Anchisaurus polyzelus* YPM 1883, *Lufengosaurus huenei* IVPP V 15 (Young 1941; Barrett et al. 2005), *Melanorosaurus readi* NMQR 3314, *Plateosaurus engelhardti* SMNS 13200, '*Plateosaurus*' *gracilis* GPIT 18318a, *Efraasia minor* SMNS 12216) the ascending ramus is deflected at the dorsoventral midpoint of the antorbital fossa (or even ventral to this point). The lateral surface of the ascending ramus is markedly narrow. This differs from the condition of most basal sauropodomorphs in which the external surface of this region is anteroposteriorly broad. However, this character state could reflect the subadult status of these specimens of *Mussaurus patagonicus* since the same morphology is present in young individuals of *Massospondylus carinatus* (BPI/1/4367) but not in adult specimens (e.g. BPI/1/5241). The ascending ramus of the maxilla extends dorsally as a lamina forming the anteromedial wall and floor of the antorbital fossa. As in other basal sauropodomorphs (except for *Plateosaurus engelhardti* SMNS 13200), this medial wall forms a strongly concave anterior margin of the antorbital fenestra and is markedly narrow anteroposteriorly (Figure 1). The dorsal end of this medial wall is slightly expanded posteriorly contacting the lacrimal at the posterodorsal corner of the antorbital fossa.

The posterior ramus is a low tabular process extending towards the anterior orbital margin. Its dorsal margin forms the ventral limit of the antorbital fossa while its ventral margin forms the alveolar margin of the maxilla. The lateral surface of this process is pierced by six moderately large neurovascular foramina. The most posterior of these openings is approximately twice the size of the preceding foramina and continues into a shallow groove directed posteriorly, as in other basal sauropodomorphs (Sereno 1999). Posterior to this opening, the posterior process of the maxilla overlaps laterally the anteroventral end of the jugal. At this point, the maxilla of specimen MPM-PV 1813/4 is slightly damaged and precise information on the sutural contact with the jugal cannot be observed, but this region is well preserved in the juvenile PVL 4587. The dorsal margin of the posterior process of the maxilla forms a sharp ventral edge of the antorbital fossa. Medial to this ridge, basal sauropodomorphs usually have a narrow groove through which would have passed the maxillary nerve and associated vessels

(Witmer 1997). Unfortunately, details on this structure are not currently available in any of the specimens of *Mussaurus patagonicus*.

The nasals are exposed in lateral view in MPM-PV 1813/4 and PVL 4587 (Figure 1), however, some information can be gathered from MPM-PV 1813/2. The nasal forms the anterior half of the dorsal surface of the snout. Anteriorly, the nasal extends as an acute process that covers the lateral surface of the nasal process of the premaxilla, forming the dorsal half of the anterior margin of the external nares. The ventral margin of the main body of the nasal forms the rounded dorsal margin of the narial opening. Posterior to this point, the nasal sends a broad descending process that overlaps laterally the ascending ramus of the maxilla and forms the dorsal half of the posterior margin of the external nares. In most basal sauropodomorphs, this region of the nasal is extended ventrally as a slender process that contacts the posterior process of the premaxilla, excluding the maxilla from the margin of the external nares. None of the other available specimens of *Mussaurus patagonicus* has this splint-like extension, although this could have been broken off during preservation. The posterior margin of the broad descending process of the nasal is sutured to the anterior margin of the dorsal surface of the lacrimal. Due to the reduced anteroposterior extension of the dorsal apex of the antorbital fossa, the nasal of *Mussaurus patagonicus* has only a marginal participation in its dorsal edge as in *Lufengosaurus huenei* (IVPP V 15; Barrett et al. 2005) and *Massospondylus carinatus* (BPI/1/4934). This contrasts with the condition of *Plateosaurus engelhardti* SMNS 13200, '*Plateosaurus*' *gracilis* GPIT 18318a, and *Efraasia minor* SMNS 12216, in which the nasal contributes significantly to the subhorizontal dorsal margin of the antorbital fossa. The dorsal surface of the nasal is markedly convex and extends posteriorly on the dorsal surface of the snout. Unfortunately, no details on the posterior dorsal surface of the nasals and the nasal-frontal suture can be observed in the available specimens of *Mussaurus patagonicus*.

As in most basal sauropodomorphs, the lacrimal is an L-shaped bone mostly exposed on the lateral surface of the skull (Figure 1). The lacrimal has a short and dorsoventrally broad rostral process that contacts the ascending ramus of the maxilla and the nasal and forms the dorsal apex of the triangular antorbital fossa (Figure 5).

The lateral surface of the rostral ramus is flat and smooth anteriorly and is bordered posterolaterally by a dorsal crest oriented oblique to the longitudinal axis of the skull. The development of this ridge resembles the dorsolateral ridge described for *Massospondylus carinatus* (Sues et al. 2004). The dorsomedial margin of the rostral ramus of the lacrimal is unfortunately missing, and therefore the lacrimal-prefrontal contact cannot be observed. This missing surface was

probably exposed on the dorsal surface of the skull, as in other basal sauropodomorphs.

The lacrimal's ventral ramus is anteroposteriorly narrow and straight, and forms the entire posterior margin of the antorbital fenestra. It is oriented obliquely, forming an angle of 60 degrees with the maxillary alveolar margin (Figure 1) and its ventral margin is sutured to the jugal. Although the maxilla is slightly displaced, the lacrimal does not seem to contact this element. The posterior surface of the lacrimal's ventral ramus is flat and faces posteriorly. The lacrimal opening, however, cannot be observed in any of the available specimens of *Mussaurus patagonicus*. The lateral surface of the ventral ramus of the lacrimal is markedly narrow anteroposteriorly at its midpoint and slightly flares at its dorsal and ventral ends. Along this region, the lacrimal bears a sharp ridge along its entire length. Anterior to this ridge, the lacrimal extends a reduced medial wall that forms the posterior floor of the antorbital fossa. This medial wall is moderately developed at the postero-ventral corner of the antorbital fossa (Figure 5) but is absent at the lacrimal's midheight and most of its dorsal region. Only at the dorsal end of the lacrimal there is an extremely reduced medial wall extending into the antorbital fossa (Figure 5). This area is exposed laterally as the lacrimal lacks the lateral (superficial) lamina that covers the posterodorsal corner of the antorbital sinus in other basal sauropodomorphs.

In comparison with other basal sauropodomorphs (e.g. *Plateosaurus engelhardti* SMNS 13200, '*Plateosaurus*' *gracilis* GPIT 18318a, *Efraasia minor* SMNS 12684, *Lufengosaurus huenei* IVPP V 15), in *Mussaurus patagonicus* the lacrimal's ventral ramus differs in being, straight, anteroposteriorly narrow, poorly expanded at its ventral and dorsal ends, and lacking a lateral (superficial) lamina over the posterodorsal corner of the antorbital sinus. In some of these characters the lacrimal resembles the condition found in *Anchisaurus polyzelus* YPM 1883, although the absence of a medial wall on the posteroventral corner of the antorbital fossa might be due to preservational biases (Fedak, in press).

Interestingly, the morphology of the lacrimal ventral ramus varies significantly in the above-described characters among the individuals referred to *Massospondylus carinatus* (e.g. BPI/1/4376, BPI/1/4934, BPI/1/4779, BPI/1/5241). If these specimens actually belong to a single species as most authors have recently considered (Gow et al. 1990; Sues et al. 2004) the noted variation seems to represent either individual variation or sexual dimorphism, since changes in these characters lack correlation with the specimen's size. Thus, the phylogenetic information of this variation is at the moment difficult to interpret given the limited sampling of well preserved lacrimals for most other taxa.

The left prefrontal of MPM-PV 1813/4 was preserved in disarticulation, inside the orbital opening (Figure 1). This element is triradiate as in other basal sauropodomorphs. Its dorsal surface is preserved in PVL 4587 (Figure 6C) and is flat and narrow, not as expanded as in *Plateosaurus engelhardti* (Galton 1984; AMNH 6810) or *Massospondylus carinatus* (BPI/1/5241). The descending process that covers the caudal surface of the lacrimal's ventral ramus was only partially preserved seems to be rather narrow and bears a slightly developed crest at its origin. The anterior process is not completely exposed but seems to taper anteriorly. The posterior process that would form the dorsal margin of the orbital opening was only partially preserved in MPM-PV 1813/4. Therefore, its sutural contact with the frontal cannot be determined. However, in the specimens MPM-PV 1813/1 and PVL 4587, the posterior tip of the right prefrontal is in articulation with the frontal. In this specimen, the prefrontal almost reaches the anteroposterior mid-point of the orbit. In the post-hatchling specimens (PVL 4210) the posterior process is relatively shorter and extends just up to the anterior third of the orbit (Figure 6).

Both frontals are well preserved in MPM-PV 1813/1 and some of the post-hatchling specimens (e.g. PVL 4210). These elements are longer than wide and subtriangular, having their maximum lateromedial width at the caudal end (Figure 6). Their dorsal surface is flat and smooth, except for the central region that is slightly bowed dorsally. The shape and extension of the frontals of the subadult specimen MPM-PV 1813/1 differ markedly from the condition of the post-hatchling individuals (which have rather narrow and short frontals, markedly bowed dorsally on their posterior half; Figure 6A). From these specimens, it seems that during ontogeny, the posterior end of the frontals of *Mussaurus patagonicus* expand transversely with respect to the anterior end (Figure 6). Consequently, the posterior end of the frontal enters the supratemporal fossa in the subadult specimens (MPM-PV 1813/1, PVL 4587) but is excluded from this depression in the post-hatchling individuals (PVL 4210). Interestingly, the exclusion of the frontals from the supratemporal opening is one of the recognized sauropod synapomorphies (Wilson and Sereno 1998; Wilson 2002), which underscores the problems of considering the type specimens for evaluating the phylogenetic relationships of *Mussaurus patagonicus*.

The frontal's articulation with the postorbital is moderately concave, rather than slot-like as in most basal sauropodomorphs (e.g. *Anchisaurus polyzelus* YPM 1883, *Massospondylus carinatus* BPI/1/5241, *Plateosaurus engelhardti* SMNS 13200). It is interesting to note that the specimen PVL 4587 seems to have a slightly more developed notch in the frontal (Figure 6C), although this region is not perfectly

preserved and it may have been accentuated by preservational causes. The fronto-parietal suture runs transversely for most of its length. *Massospondylus carinatus* (BPI/1/5241) and *Anchisaurus polyzelus* (YPM 1883) have a posteriorly oriented V-shaped fronto-parietal suture, but this suture is transversely oriented and interdigitated in *Thecodontosaurus caducus* (Yates 2003), *Plateosaurus engelhardti* (SMNS 13200), *Coloradisaurus brevis* (PVL 3967), and *Yunnanosaurus huangi* (NGMJ V 116 [V20]).

The anteriormost region of the frontals cannot be observed in any of the subadult specimens of *Mussaurus patagonicus*. In the post-hatchling specimens (PVL 4210), the frontal narrows progressively and is loosely sutured to the nasals at the level of the anterior orbital margin. The lateral edge of the frontals forms the posterior half of the dorsal orbital margin (Figure 6), as in most basal sauropodomorphs (except for *Thecodontosaurus caducus* (Yates 2003) which has a reduced posterior extension of the prefrontal).

The anterior halves of the parietals of MPM-PV 1813/1 are preserved in articulation with the frontals. There are no signs of a fronto-parietal fenestra in either the post-hatchling or the subadult specimens, which seems to be present in embryonic sauropod material (and some adult eusauropods; Salgado et al. 2005). They are strongly sutured to each other and have a narrow dorsal surface bounded by slightly developed ridges on either side. These ridges are more developed on the anterior region and delimit the medial and anterior margins of the supratemporal openings. Lateral to these edges, the parietal is ventrally and laterally deflected forming the medial floor (or wall) of the supratemporal fossa. The morphology of the parietals of the post-hatchling specimens of *Mussaurus patagonicus* is strikingly different. In PVL 4210, the parietals are notably expanded and dorsally bowed (Figure 6A). The dorsal surfaces of these elements have a similar width than the dorsal surface of the frontals (while in the subadult specimens each parietal is approximately one fifth of the frontal's width). The contribution of the parietals to the medial floor of the supratemporal fossa also changes markedly during development. In the specimen PVL 4210, this surface is enlarged and markedly convex, while in the subadult specimens is reduced and slightly concave (Figure 6).

The posterolateral wing of the parietals is poorly preserved in the subadult specimens. In the specimen MPM-PV 1813/1, this process is narrow and elongated and it is oriented posterolaterally forming an angle of 45 degrees with the longitudinal axis of the skull, resembling the condition of most basal sauropodomorphs. The morphology of this process in the post-hatchling specimen PVL 4210 also differs markedly, being proportionately shorter and oriented transversely rather than posterolaterally (Figure 6).

The postorbital is a slender triradiate element (Figure 7), having an anteromedial process (sutured to the frontal), a descending process (contacting the jugal), and a posterior process (sutured to the squamosal). The postorbital of most basal sauropodomorphs is a much more robust element with broader descending and posterior processes. The postorbital of specimen MPM-PV 1813/4 resembles in its general shape the proportions found in *Anchisaurus polyzelus* YPM 1883 or *Thecodontosaurus caducus* (Yates 2003; BMNH P24). However, in the different specimens of *Massospondylus carinatus* the robustness of the postorbital shows a marked correlation with specimen size. Thus, these differences probably represent the immature ontogenetic status of specimen MPM-PV 1813/4 (as is probably the case for YPM 1883 and BMNH P24). The main body of the postorbital is smooth and bears a large foramen, associated with a significantly smaller foramen on its lateral surface (Figure 7).

The anteromedial process is laterally bowed and extends onto the dorsal surface of the skull. In the specimen MPM-PV 1813/4, the left postorbital is slightly disarticulated from the frontal and, consequently, the distal end of this process was not preserved. In comparison with the post-hatchling specimens of *Mussaurus patagonicus* (PVL 5865), the anteromedial process of MPM-PV 1813/4 is proportionately more robust, longer, and distally broader. The anterior edge of this process forms the rounded posterodorsal margin of the orbit while its posterior edge forms the anterolateral margin of the supratemporal fossa. The distal tip of this process is straight, in contrast to the condition of *Plateosaurus engelhardti* (SMNS 13200) and *Coloradisaurus brevis* (PVL 3967) in which this end is medially recurved.

The descending process of the postorbital is also laterally bowed and its lateral surface is slightly convex (Figure 7). Its dorsoventral length is approximately twice as long as the anteromedial process. In post-hatchlings both processes are almost equal in length (PVL 4209). The anterior edge of the descending process forms most of the posterior margin of the orbital opening, being continuous with the anterior edge of the anteromedial process. Ventrally, this process tapers markedly and is posterolaterally overlapped by the ascending process of the jugal. At this end, the descending process of *Mussaurus patagonicus* is not abruptly deflected anteriorly, as in *Lufengosaurus huenei* (IVPP V 15), *Yunnanosaurus huangi* (NGMJ V 116 [V20]), and *Massospondylus carinatus* (BPI/1/5241).

The posterior process is broader and shorter than the descending process of the postorbital and its lateral surface is distinctly flat (Figure 7). The distal end of this process was not preserved in the specimen MPM-PV 1813/4, but is preserved in the subadult PVL 4587, where it overlaps the anterior process of

the squamosal. In the post-hatchling specimens (PVL 5865 and PVL 4210), the posterior end of this process fits into an anteriorly opened V-shaped facet on the squamosal (Figure 2).

The jugal of *Mussaurus patagonicus* is a triradiate element composed by an anterior suborbital process (articulating with the maxilla and lacrimal), an ascending process (articulating with the postorbital), and a posterior infratemporal process (articulating with the quadratojugal).

The suborbital process of the specimen MPM-PV 1813/4 occupies approximately two thirds of the anteroposterior extension of the jugal (Figures 1 and 5). This ratio would probably be smaller in the adult condition since the size of the orbit usually shows a negative allometry with respect to total skull length during development. This proportion in young specimens of other basal sauropodomorphs (e.g. *Thecodontosaurus caducus*) and the post-hatchling specimens of *Mussaurus patagonicus* is approximately 0.75 (Figure 2). The suborbital region of the jugal is dorsoventrally high in the subadult specimens (MPM-PV 1813/4 and PVL 4587; Figure 1), having a dorsoventral depth that is approximately 25% the total anteroposterior length of the jugal. In the post-hatchling specimens (PVL 4210 and PVL 5865) the suborbital region of the jugal is dorsoventrally low and elongated, forming a thin suborbital bar (Figure 2). The ventral margin of the suborbital region of the jugal has a distinct step at the posterior end of the caudal process of the maxilla (Figure 1). Its dorsal margin is slightly concave and forms the anteroventral and anterior edges of the orbital opening. The lateral surface of the jugal is pierced by a small foramen located close to the posterior margin of the orbital opening. Anterior to the orbit, the jugal tapers gradually, wedging between the lacrimal and maxilla (laterally overlapping the latter element). The anterior end of the jugal reaches the posteroventral edge of the antorbital fossa.

The ascending process of the jugal is relatively short and tapers rapidly along the sutural contact with the postorbital (Figures 1 and 5). The ventral half of this process faces laterally and projects posterodorsally oriented forming an angle of 45 degrees with the buccal margin of the jugal. Its dorsal half, instead, faces posterolaterally and is slightly deflected dorsally covering the posterior surface of the descending process of the postorbital. Ventral to the ascending process, the jugal is markedly incised, producing an elongated anteroventral corner of the infratemporal fenestra that extends underneath the orbit. A similar condition is also present in *Massospondylus carinatus* (BPI/1/5241), *Lufengosaurus huenei* (IVPP V 15), *Yunnanosaurus huangi* (NGMJ V 116 [V20]), *Riojasaurus incertus* (Bonaparte and Pumares 1995; ULR 56), *Melanorosaurus readi* (NMQR 3314), and sauropods, but not in other basal sauropodomorphs

(e.g. *Plateosaurus engelhardti* SMNS 13200, '*Plateosaurus*' *gracilis* GPIT 18318a, *Coloradisaurus brevis* PVL 3967). Interestingly, the extension of the infratemporal fenestra underneath the orbit is even more pronounced in the post-hatchling specimens (e.g. PVL 4209, 4210, 5865), showing that the development of this character decreases during the ontogeny of *Mussaurus patagonicus* (Figure 2).

The posterior process is markedly short and tapers posteriorly. Although this region is disarticulated from its natural contact with the quadratojugal in the specimen MPM-PV 1813/4, it seems that the extension of the jugal on the infratemporal bar of *Mussaurus* is not as developed as in some basal sauropodomorphs (e.g. *Plateosaurus engelhardti* SMNS 13200, *Massospondylus carinatus* BPI/1/5241). Derived eusauropod taxa have an extreme reduction of the posterior branch of the jugal and the quadratojugal forms most of the ventral margin of the infratemporal fenestra.

The quadratojugal is partially preserved in of MPM-PV 1813/4 and PVL 4587, lacking in the former the dorsal end of the ascending process, and disarticulated from the quadrate (Figure 1). The anterior jugal process of the quadratojugal and the ascending process are oriented to each other at an angle of approximately 80 degrees (in both the subadult and post-hatchling specimens; Figures 1 and 2), as in *Riojasaurus incertus* (ULR 56), *Melanorosaurus readi* (NMQR 3314), and sauropods. In these forms, the posteroventral corner of the infratemporal fenestra is not posteriorly extended as in *Plateosaurus engelhardti* (SMNS 13200) and *Coloradisaurus brevis* (PVL 3967), in which the ascending and jugal processes of the quadratojugal are subparallel to each other. Other basal sauropodomorphs, such as *Massospondylus carinatus* (BPI/1/5241) or *Lufengosaurus huenei* (IVPP V 15), have an intermediate morphology, with an angle of approximately 50–60 degrees and the posteroventral corner of the infratemporal fenestra only slightly extended posteriorly.

The anterior process is a splint-like projection that would extend along most of the ventral margin of the infraorbital fenestra (Figure 1), although the anterior portion of it would have been partially overlapped by the posterior process of the jugal. The main body of the quadratojugal is wide and its lateral surface is slightly concave. Its anterior margin forms the rounded posteroventral margin of the infratemporal fenestra. The ascending process is wide at its base and, in the post-hatchling specimens (e.g. PVL 5865) it tapers abruptly at the level of the anterior expansion of the quadrate. The ascending process is attached to the anterior margin of the quadrate and seems to end at the dorsoventral midpoint of the infratemporal fenestra. In the post-hatchling specimens, this process does not seem to contact the descending process of the

squamosal (although this may be due to preservational causes).

The quadrate of MPM-PV 1813/4 is disarticulated from the quadratojugal and squamosal and is exposed on anterior view (Figure 7). Its dorsal half is composed of two laminae set perpendicular to each other, the anteromedial or pterygoid wing and the anterolateral wing that articulates with the ascending process of the quadratojugal and descending process of the squamosal. The ventral half of the quadrate forms a stout process that bears the articular condyles on its distal end.

The pterygoid wing of the quadrate is subrectangular, having its major axis oriented dorsoventrally and its ventral margin perpendicular to the main axis of the quadrate (Figure 7). This contrasts with the semicircular or subtriangular condition present in *Thecodontosaurus caducus* (Yates 2003). The pterygoid wing occupies approximately 65% of the total quadrate length, being more restricted than in the most basal sauropodomorphs, in which it exceeds 70% of the quadrate length (e.g. *Saturnalia tupiniquim*, *Thecodontosaurus caducus*; Yates 2003). Unfortunately, the precise contact with the pterygoid is not exposed in any of the available specimens of *Mussaurus patagonicus*.

The anterolateral wing of the quadrate is less dorsoventrally extensive than the pterygoid wing (only extending along the dorsal half of the quadrate's dorsoventral extension). Its ventral margin is gently concave and is located dorsal to the corresponding edge of the anteromedial lamina. The anterolateral wing is also less developed anteriorly and narrower than the pterygoid wing. Its caudal surface is not exposed in the specimen MPM-PV 1813/4 but is well preserved in some of the post-hatchling specimens (e.g. PVL 5865). In this specimen the caudal surface of the anterolateral wing is slightly concave and is sutured anteroventrally to the ascending process of the quadratojugal and anterodorsally to the descending process of the squamosal. Unfortunately, none of the available specimens of *Mussaurus patagonicus* preserve the quadrate foramen, which varies in its location among basal sauropodomorphs (either enclosed within the anterolateral wing of the quadrate or located at the quadrate-quadratojugal suture).

The ventral half of the quadrate is a robust process lateromedially wide and anteroposteriorly flattened (Figure 7). Its anterior surface is slightly concave while its posterior surface (exposed in PVL 5865) is convex, bearing a slightly marked dorsoventral ridge. This process extends vertically, continuous with the dorsal half of the quadrate, instead of being posteriorly deflected as in *Plateosaurus engelhardti* (SMNS 13200) and *Coloradisaurus brevis* (PVL 3967). This character is probably correlated with the posterior extension of the posteroventral corner of the infratemporal fenestra present in the latter forms.

The squamosal of *Mussaurus patagonicus* is fragmentary in MPM-PV 1813/4. Among basal dinosaurs, this process is usually tetraradiate, however, in this specimen only two rami have been preserved. Fortunately, these two processes are complete on two of the post-hatchling specimens (PVL 4068 and PVL 5865). In these specimens the anterior and descending rami of the squamosal form an angle of approximately 40 degrees (Figure 6A).

In MPM-PV 1813/4, the anterior branch of the squamosal forms the posterolateral edge of the supratemporal opening and the posterior region of the dorsal margin of the infratemporal fenestra (Figure 1). This process is disarticulated from the posterior process of the postorbital and has a lateromedially broad dorsal surface. Its anterior end seems to be broken in this specimen. In the post-hatchling specimens, this process is complete and extends anteriorly along the dorsal margin of the infratemporal fenestra. The posterior process of the postorbital overlaps the dorsal surface of the squamosal along most of length of this process. Thus, only an elongated and dorsoventrally narrow surface of the anterior process of the squamosal is exposed (along the dorsal margin of the infratemporal fenestra).

In the specimen MPM-PV 1813/4, the descending process of the squamosal is broad, short, and has two distinct facets on its lateral surface divided by dorsoventrally extended ridge (Figure 7). The posterior surface is laterally concave and slightly broadens ventrally. This region would have been overlapped by the dorsal end of the anterolateral lamina of the quadrate. The anterior surface would thus correspond to the laterally exposed region of the descending process of the squamosal when these two bones were in articulation. This surface is smooth, slightly concave laterally, and tapers ventrally (Figure 7). As preserved in the specimen MPM-PV 1813/4, the anterior region of the descending process of the squamosal is proportionally short in dorsoventral extension and broad at its dorsal end (its dorsoventral length is approximately 25% of the anteroposterior extension of its dorsal end). This proportion differs from that of other basal sauropodomorphs, in which a slender and narrow descending process extends down to the dorsoventral midpoint of the posterior margin of the infratemporal fenestra. Only theropods (e.g. *Herrerasaurus ischigualastensis*) and sauropods (e.g. *Shunosaurus*, *Omeisaurus*) show a similarly short and broad descending process of the squamosal. However, it must be noted that this character state in *Mussaurus patagonicus* (based on the preserved squamosal fragment in MPM-PV 1813/4) might have been affected by the disarticulation of the elements of the infratemporal region (i.e. squamosal, quadrate, quadratojugal). Similarly, the preserved remains of the squamosal and quadratojugal do not seem to contact each other in the specimen MPM-PV

1813/4 (a condition traditionally regarded as a sauropod synapomorphic character). In the holotype of *Mussaurus patagonicus* (the post-hatchling specimen PVL 4068), the descending process is also quite short, although its base is proportionately narrower than in the subadult specimen. However, the other post-hatchling specimen in which this region has been preserved (PVL 5865) has an elongated descending process of the squamosal that reaches the dorsoventral midpoint of the posterior margin of the infratemporal fenestra (resembling the generalized condition of basal sauropodomorphs). Most probably, the differences in this character among the specimens of *Mussaurus patagonicus* are due to preservational problems in MPM-PV 1813/4 and PVL 4068.

The pterygoids (as well as all palatal bones) are only partially exposed in the post-hatchling specimen PVL 4210. As in other basal sauropodomorphs, the pterygoid is a complex bone, consisting of three main branches. The anterior ramus (laterally sutured to the palatine), the transverse flange (contacting the ectopterygoid), and the posterolaterally directed quadrate ramus.

The quadrate ramus is broad at its base (as preserved in the right pterygoid) and bears on its posterior margin a posteriorly opened notch that articulates with the distal end of the basipterygoideal processes. A similarly developed semicircular facet that 'hooks' around these processes is commonly present in dinosaurs, except for eusauropods (Upchurch 1995, 1998; Wilson and Sereno 1998; Wilson 2002) and the basal sauropodomorph *Thecodontosaurus caducus* (Yates 2003). Lateral to this facet, the quadrate ramus of the pterygoid is markedly narrow lateromedially and extends posterolaterally to contact the rostromedial flange of the quadrate. Unfortunately, in the specimen PVL 4210 this contact cannot be observed.

The anterior ramus of the pterygoid is triangular and extends anteriorly reaching the level of the rostral half of the orbital opening. The ventral exposure of this ramus is broader and shorter than in *Plateosaurus engelhardti* (SMNS 12949), resembling more the condition of *Massospondylus carinatus* (BPI/1/4779) and *Melanorosaurus readi* (NMQR 3314). The medial edges of the anterior ramus lie close to each other but do not seem to contact in the specimen PVL 4210. The lateral margins are bordered by the medial surface of the palatines (along the entire preserved length). Its anterior end and the choanal opening cannot be observed in this specimen.

The transverse process extends lateroventrally and its ventral exposure is significantly reduced due to the extensive posteromedial region of the ectopterygoid (as in *Massospondylus carinatus* BPI/1/4779). Its posterior margin is slightly anteriorly deflected and delimits the ventrally exposed surface of the transverse process and the posteroventrally exposed surface of the base of the quadrate process of the pterygoid. Thus, these two branches of the pterygoid are adjacent to each other as in most basal sauropodomorphs (e.g. *Plateosaurus engelhardti* SMNS 12949, *Massospondylus carinatus* BPI/1/4779, *Thecodontosaurus caducus* (Yates 2003), *Melanorosaurus readi* NMQR 3314), rather than being well separated from each other as in sauropods (e.g. *Shunosaurus lii* (Chatterjee and Zheng 2002)).

The medial process of the left ectopterygoid is exposed on the palate of the post-hatchling specimen PVL 4210. Its ventral surface is extensive, reducing the extension of the suborbital fenestra. The posterior margin of the ectopterygoid lies close to the posterior margin of the transverse process of the pterygoid, reducing the ventral exposure of the latter element. From this point, the ectopterygoid sends a well developed anteromedial projection, the medial margin of which borders the lateral margin of the anterior pterygoid branch. The lateral margin of this ante-romedial extension of the ectopterygoid is laterally convex and its anterior end seems to contact the posteromedial branch of the palatine. Thus, the pterygoid is excluded from the reduced suborbital fenestra.

A similarly expanded ectopterygoid sutured to the palatines (and the consequent reduction of the suborbital fenestra extension) is also present in *Massospondylus carinatus* (BPI/1/4779) and *Melanorosaurus readi* (NMQR 3314). The medial process of the ectopterygoid of these forms differs markedly from the condition of *Plateosaurus engelhardti* (SMNS 12949) and *Thecodontosaurus caducus* (Yates 2003), in which the anteromedial extension of the ectopterygoid is absent and its anterior margin is straight or concave. Consequently in these two taxa, the suborbital fenestra is notably large and the ectopterygoid-palatine contact is absent. Interestingly, the palate of sauropods also has an ectopterygoid-palatine contact and a reduced (or completely obliterated) suborbital opening.

The left palatine of the post-hatchling specimen PVL 4210 is exposed in ventral view (Figure 2). This element is oriented oblique to the longitudinal axis of the skull and its shaft is markedly constricted (with respect to the lateral and medial expansions). The anteroposterior extension of the palatine shaft is approximately 40% the length of the medial expansion. This condition resembles that of *Massospondylus carinatus* (BPI/1/4779), but differs from other basal sauropodomorphs (e.g. *Plateosaurus engelhardti* SMNS 13200) in which the shaft is more than half the length of the medial expansion. The anterior margin of the palatine is strongly concave and probably delimited the posterior edge of the choanal opening. Its posterior edge is gently concave and forms the anterior and anteromedial margins of the reduced suborbital opening.

The maxillary process is directed anterolaterally and seems to be moderately expanded anteroposteriorly. Unfortunately, further details of this region cannot be observed since it is only partially exposed in the specimen PVL 4210. The medial end of the palatine is markedly expanded anteroposteriorly. The anterior half of this expansion is a lateromedially narrow, acute, and elongated process. The posterior half of the medial expansion of the palatine is triangular and lateromedially broad (approximately twice as wide as the anteromedial process).

Braincase elements of the available specimens of *Mussaurus patagonicus* are missing in most of the specimens. Only parts of the basipterygoid processes of the basisphenoid were preserved in the post-hatchling specimen PVL 4210. These are slender and elongated processes that extend ventrolaterally from the main body of the basisphenoid. The two basipterygoid processes are set at a right angle to each other. The distal ends of these processes are rounded and slightly expanded with respect to the basipterygoid shaft. This articular surface fits into the hook-like facet on the medial region of the base of the pterygoid's quadrate process. Unfortunately, no details of the rest of the basisphenoid–parasphenoid complex can be observed in the available specimens of *Mussaurus patagonicus*.

The occipital region is also poorly represented in the available specimens of *Mussaurus patagonicus*. Only the post-hatchling specimen PVL 4210 has exposed most of the supraoccipital. This element has two distinct surfaces divided by a slightly developed sagittal ridge. These surfaces are slightly concave and face posterolaterally on the occiput. The entire posterior surface of the supraoccipital is subrectangular, being twice as wide as high. The dorsal margin is only slightly arched, lacking the acute dorsal process that extends on the sagittal plane in other sauropodomorphs (e.g. *Plateosaurus engelhardti* AMNH 6810; *Shunosaurus lii* (Chatterjee and Zheng 2002)), except for *Thecodontosaurus caducus* (Yates 2003). Anterior to this margin, a slit-like fontanelle is present between the supraoccipital and the parietal, being anteroposteriorly narrow and lateromedially wide. This opening could reflect the early ontogenetic stage of the specimen PVL 4210, although it is present in adult specimens of several basal sauropodomorphs (e.g. *Riojasaurus incertus* ULR 56, *Coloradisaurus brevis* PVL 3967, *Plateosaurus engelhardti* SMNS 13200, *Massospondylus carinatus* BPI/1/5241, *Anchisaurus polyzelus* YPM 1883).

Mandible

The lower jaw is completely preserved in several specimens of *Mussaurus patagonicus*. The specimen MPM-PV 1813/4 has a complete lower jaw slightly displaced posteriorly with respect to the skull (Figure 1). Most of the following description is based on its morphology. This specimen and most of the available material, however, have the mandible exposed in lateral view, precluding the observation of some elements (e.g. splenial, articular), which only can be partially observed in the post-hatchling specimen PVL 4210.

The anterior half of the lower jaw is rather short and high in comparison with other basal sauropodomorphs (e.g. *Thecodontosaurus caducus* (Yates 2003), *Plateosaurus engelhardti* SMNS 13200, *Massospondylus carinatus* BPI/1/4934, *Yunnanosaurus huangi* NGMJ V 116 [V20], *Riojasaurus incertus* ULR 56). The posterior half, instead, is lower and more elongated than in other forms (*Plateosaurus engelhardti* AMNH 6810, *Massospondylus carinatus* BPI/1/4779), except for *Thecodontosaurus caducus* (Yates 2003) and *Riojasaurus incertus* (ULR 56).

The dentaries of *Mussaurus patagonicus* are notably different from those of other basal sauropodomorphs, and resemble in several characters the condition present in eusauropods (as noted by Bonaparte and Vince (1979) for the post-hatchling specimens). The dentary is proportionately short and high, particularly at its anterior end. The minimum dorsoventral depth of the dentaries is approximately 24% of its anteroposterior length (measured at the anteroposterior midpoint of the tooth row). The maximum dorsoventral depth of the dentaries (measured either at the symphyseal tip or at the level of the anterior edge of the external mandibular fenestra) is approximately 30% of its anteroposterior length (Figure 1). These ratios are larger than those found in other basal sauropodomorphs (including *Tazoudasaurus naimi*; Allain et al. 2004), even in comparison with those having relatively short and high dentaries such as *Thecodontosaurus caducus* (Yates 2003) and *Thecodontosaurus antiquus* (Riley and Stutchbury 1836; Benton et al. 2000). Interestingly, the proportionally high and short condition of the dentaries of *Mussaurus patagonicus* seems to increase in later ontogenetic stages of the available specimens (Figures 1 and 2). The post-hatchling specimen PVL 5865 has a proportionally lower dentary; maximum and minimum dorsoventral depths are 27% and 17% of the anteroposterior length, respectively. In ventral view, the mandibular rami of the dentaries of *Mussaurus patagonicus* (PVL 5865) meet at the symphysis forming an angle of approximately 43 degrees, resembling the condition of most basal sauropodomorphs. This condition contrasts with the strong medial curvature along the anterior region of the dentaries in eusauropods that produce a broad U-shaped symphysis (Upchurch 1995, 1998; Wilson and Sereno 1998).

The dentaries are remarkably expanded at their symphyseal region and bear a peg-like process at their anterodorsal margin (Figures 1 and 3). This small

process extends dorsally and is located just anterior to the first mandibular tooth. Thus, the first dentary tooth is displaced posteriorly from the rostral margin of the symphysis, as in most basal sauropodomorphs (except for *Saturnalia tupiniquim* and *Anchisaurus polyzelus*; Yates 2004). The dorsoventral extension of the symphyseal rostral end is approximately 1.4 times the dorsoventral height of constricted region of the dentaries (measured perpendicular to the tooth row axis at each point). This condition might be slightly less developed in fully mature specimens, since the dorsoventral expansion of the symphyseal region seems to decrease slightly along the ontogeny of *Mussaurus patagonicus* (relative to the dorsoventral expansion of the rest of the dentary); in the post-hatchling specimen PVL 5865 this ratio of symphyseal expansion is 1.5. A dorsoventral expansion of the symphyseal end of the dentaries was previously known only in *Riojasaurus incertus* (ULR 56) and eusauropods (e.g. *Shunosaurus lii* (Chatterjee and Zheng 2002), *Omeisaurus* (Tang et al. 2001), *Brachiosaurus*, *Diplodocus*, *Camarasaurus*). However, the proportional expansion of the symphysis in *Riojasaurus incertus* is less developed (i.e. 1.25) than in *Mussaurus patagonicus* and basal eusauropods (ranging between 1.4 and 1.44). The ventral margin of the symphyseal region is markedly curved ventrally. This condition is also found in some basal sauropodomorphs (e.g. *Plateosaurus engelhardti* SMNS 13200, '*Plateosaurus*' *gracilis* GPIT 18318a, *Coloradisaurus brevis* PVL 3967, *Massospondylus carinatus* BPI/1/4934), but absent in others (e.g. *Riojasaurus incertus* ULR 56, *Melanorosaurus readi* NMQR 3314, *Thecodontosaurus caducus* (Yates 2003), *Efraasia minor* SMNS 12684, *Saturnalia tupiniquim* MCP 3845).

The lateral surface of the dentaries is smooth and slightly convex and bears six large neurovascular foramina anteroposteriorly aligned below the tooth row. Along the posterior half of the tooth row, the lateral surface of the dentary is longitudinally divided by a slightly marked ridge located close to the alveolar margin (Figures 1 and 3). Below this ridge, the lateral surface of the dentaries is smooth and flat, although it becomes slightly concave towards the posterior end. Above the longitudinal ridge, the dentary is laterodorsally exposed, leaving the tooth row slightly inset from the lateral edge of this bone. This condition is commonly present in basal sauropodomorphs (*Thecodontosaurus caducus* (Yates 2003), *Efraasia minor* SMNS 12684, *Plateosaurus engelhardti* SMNS 13200, *Coloradisaurus brevis* PVL 3967, *Riojasaurus incertus* ULR 56, *Anchisaurus polyzelus* YPM 1883).

The posterior third of the dentary slightly expands dorsoventrally and has a concave lateral surface (Figure 1). The posterodorsal end of the dentary is laterally overlapped by the surangular. As preserved in the specimen MPM-PV 1813/4, this branch would not extend posteriorly to form the dorsal margin of the external mandibular fenestra as in other basal sauropodomorphs. This morphology, however, is probably a preservational artefact since the post-hatchling specimen PVL 5865 has a posteriorly extended posterodorsal process of the dentary that forms the anterior third of the dorsal margin of the external mandibular fenestra. The posteroventral end of the dentary overlaps laterally the angular. The posteriormost end of the ventral process seems to be missing from the specimen MPM-PV 1813/4, since the angular has a concave acute articular facet extending posteriorly from the preserved end of the dentary. In the post-hatchling specimen PVL 5865 and PVL 4209, the posteroventral process of the dentary is much more extensive, forming the anterior half of the ventral margin of the external mandibular fenestra.

Between the posterodorsal and posteroventral processes, the dentary forms a straight and subvertical anterior margin of the external mandibular fenestra.

The surangular of *Mussaurus patagonicus* is a low and elongated element that forms the dorsal margin of the posterior half of the mandibular ramus (Figures 1 and 6). The anterior end of this element overlaps the posterodorsal process of the maxilla, reaching the level of the anteroposterior midpoint of the orbital opening.

The surangular dorsal margin is gently sigmoid, being convex anteriorly (from its anterior margin to the level of the posterior surangular foramen). This condition resembles that of the most basal sauropodomorphs (e.g. *Thecodontosaurus caducus* (Yates 2003), *Efraasia minor* SMNS 12684). In contrast, a strongly bowed surangular, having a developed coronoid process above the mandibular fenestra, is present in *Plateosaurus engelhardti* (AMNH 6810), *Coloradisaurus brevis* (PVL 3967), *Anchisaurus polyzelus* (YPM 1883), and to a lesser degree, *Massospondylus carinatus* (BPI/1/4779) and *Yunnanosaurus huangi* (NGMJ V 116 [V20]). A dorsally bowed surangular is also present in some eusauropods such as *Omeisaurus maoianus* (Tang et al. 2001) and reaches an extreme degree of development in macronarian sauropods (Wilson and Sereno 1998). The posterior half of the dorsal margin of the surangular of *Mussaurus patagonicus* is gently concave (Figure 8), instead of being strongly concave as in those forms with a well developed coronoid process. In this region, the dorsal margin of the surangular has a slightly developed bulge located four millimetres posterior to the posterior surangular foramen (Figure 8). This point probably represents the level of the craniomandibular articulation, since a similar structure is present at this articulation in *Plateosaurus engelhardti* (AMNH 6810). Based on this interpretation, the craniomandibular articulation of the specimen MPM-PV 1813/4 would be located ventral to the longitudinal axis of the tooth row, as in most basal sauropodomorphs (except for *Thecodontosaurus caducus* (Yates 2003) and
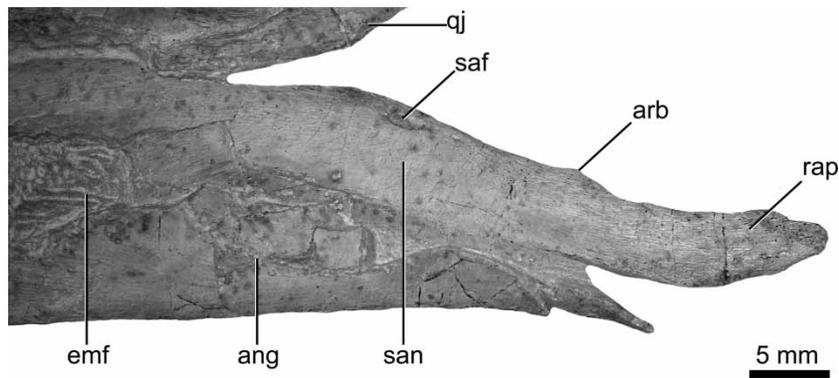
Figure 8. Posterior region of left mandibular ramus of *Mussaurus patagonicus* (MPM-PV 1813/4) in lateral view. See abbreviations in Appendix.

Riojasaurus incertus ULR 56). In the post-hatchling specimen PVL 5865 the lower jaw is in natural articulation and its articular surface also lies well below the tooth row.

In the specimen MPM-PV 1813/4, the ventral margin of the surangular extends posteroventrally along its suture with the dentary and forms most of dorsal margin of the external mandibular fenestra (Figure 8). As noted above, in the post-hatchling specimen PVL 5865, the surangular is restricted to the posterior two thirds of the dorsal margin of the external mandibular fenestra. Posteriorly, the surangular forms the rounded posterodorsal margin of this opening (Figure 8) and extends ventrally down to the dorsoventral midpoint of the posterior margin of the external mandibular fenestra (where it contacts the angular). Posterior to this opening, the ventral margin of the surangular is overlapped by the angular along a posteroventrally directed suture. The posterior end of this suture almost reaches the posterior tip of the retroarticular process, as in *Massospondylus carinatus* (BPI/1/4779).

The lateral surface of the surangular is flat and occupies the dorsal half of the mandibular ramus. A noticeable posterior surangular foramen is located at the anteroposterior midpoint of the surangular, close to its dorsal margin (Figure 8). The large anterior surangular foramen located above the external mandibular fenestra in other basal sauropodomorphs (e.g. *Massospondylus carinatus* BPI/1/4779. *Efraasia minor* SMNS 12684, *Anchisaurus polyzelus* YPM 1883) seems to be absent in *Mussaurus patagonicus*. Posterior to the craniomandibular articulation, the surangular covers the lateral surface of the entire retroarticular process. Along this region, the surangular is slightly deflected dorsally and its lateral surface is markedly convex.

The angular of *Mussaurus patagonicus* is low and elongated (Figures 1 and 6). Anteriorly, this element is overlapped by the posteroventral process of the dentary and forms part of the ventral margin of the external mandibular fenestra. The angular contacts the surangular at the posterior edge of this opening, forming its the ventral half. Posterior to this opening, the dorsal margin of the angular overlaps laterally the surangular. This margin is only slightly convex, in contrast to the strongly bowed condition of *Massospondylus carinatus* (BPI/1/4934). Along this region, the angular forms the ventral half of the mandibular ramus in MPM-PV 1813/4. The post-hatchling specimens have a much more reduced exposure of the angular on the lateral surface of the lower jaw. A similar ontogenetic change is seen in the referred specimens of *Massospondylus carinatus* (BPI/1/4376, BPI/1/4779, and BPI/1/5241). As noted above, the posterior tip of the angular almost reaches the caudal end of the retroarticular process. Unfortunately, none of the available specimens of *Mussaurus patagonicus* have exposed their articular, prearticular, splenial, or coronoid bones.

Dentition

The dentition of *Mussaurus patagonicus* shows a unique combination of characters among basal sauropodomorphs. Most of the lower dentition is hidden by the premaxillary and maxillary tooth row. Several teeth of the upper tooth row are well preserved in the subadult specimens, but only a few teeth of the post-hatchling specimens are well preserved (e.g. PVL 4210). All the preserved teeth are notably constricted at their base, a synapomorphic character of Sauropodomorpha (Gauthier 1986). The total upper dentition would have had between 13 and 15 elements. Other basal sauropodomorphs have larger numbers of dental elements (except for *Anchisaurus polyzelus* YPM 1883, and probably *Saturnalia tupiniquim* MCP 3845).

The premaxillary tooth row of PVL 4587 and MPM-PV 1813/4 seems to be complete, although its is not clear if there were four or five elements in the premaxilla (due to missing teeth in MPM-PV 1813/4 or poor preservation in PVL 4587). Four premaxillary teeth are preserved in the post-hatchling specimens (PVL 5865 and PVL 4210), which is the most

common condition among basal sauropodomorphs (only *Plateosaurus engelhardti* SMNS 13200, and '*Plateosaurus*' *gracilis* GPIT 18318a have five premaxillary teeth). All these elements are slightly procumbent, a condition also present in *Massospondylus carinatus* (BPI/1/5241) and eusauropods (Gauthier 1986).

The first premaxillary tooth of the specimen MPM-PV 1813/4 is dislocated from its alveolus and only the apical region of its crown is exposed (Figure 3). This element is rather large in comparison with the posterior maxillary teeth and is covered with a thick enamel layer. Its mesial margin is slightly convex and lacks the serrations commonly present in non-eusauropod sauropodomorphs. Its distal margin is markedly convex at the crown's base and seems to be nearly straight towards the crown's apex. The second premaxillary tooth is missing from the specimen MPM-PV 1813/4. In the post-hatchling specimen PVL 4210 this tooth is partially erupted, so the base of the crown is not exposed. The axis of this element is slightly recurved at the apical region, which ends in a sharp apex. The labial surface has a central thickening. The mesial margin lacks serrations, but the apical portion of distal margin has four broad serrations.

The third premaxillary tooth is well preserved in the specimen MPM-PV 1813/4. The crown is markedly constricted at its contact with the root, and is notably expanded along its proximal half (Figure 3). The apex of the third premaxillary tooth tapers rapidly, having a noticeable asymmetry between its mesial and distal margins. The mesial margin is gently convex along the crown's height and seems to lack serrations (as in the first premaxillary tooth). The distal margin of this tooth also lacks serrations, however, in the specimen PVL 4587 this margin has two small and rounded serrations, located distally to the crown's apex. Only in the specimen MPM-PV 1813/4 the distal margin is complete, and shows a notably different profile in comparison with the mesial edge. The distal margin is sigmoid in shape, being markedly convex proximally and gently concave towards the crown's apex. This asymmetry contrasts with the generalized condition of basal sauropodomorphs, which have a symmetrical leaf-shaped premaxillary crown. The lateral surface of the third premaxillary tooth is markedly convex and is covered by a thick layer of enamel that is faintly wrinkled (Figure 3). Interestingly, a wrinkled enamel surface was previously considered to be exclusively in eusauropods (Wilson and Sereno 1998; Wilson 2002) although these taxa have a much more developed condition with coarser rugae and sulci on the enamel surface (present even in embryonic material of *Camarasaurus*; Britt and Naylor 1994). Among basal sauropodomorphs, *Anchisaurus polyzelus* YPM 1883 was noted to have wrinkled enamel (Yates 2004).

The fourth premaxillary tooth is similar in size to the preceding element. Unfortunately, this tooth is slightly damaged in PVL 4587 and only partly exposed in the specimen MPM-PV 1813/4 (since the third premaxillary tooth crown laterally overlaps the anterior region of this element; Figure 3). The distal margin of the fourth premaxillary tooth is also sigmoid in shape, although its proximal convexity and its apical concavity are less pronounced than in the third premaxillary tooth. At the crown's apex, this element has three extremely weak, broad serrations (present in the specimens MPM-PV 1813/4 and PVL 4587). The presence of serrations restricted to the apical region of the crowns is present in *Anchisaurus polyzelus* (YPM 1883), *Massospondylus carinatus* (BPI/1/4779), and basal eusauropods (Yates 2003).

The maxillary dentition is only partially exposed in the available specimens of *Mussaurus patagonicus* (Figure 1). The specimen MPM-PV 1813/4 has six preserved elements, while the most complete maxillary dentition in the post-hatchling specimens consists of nine teeth (on the left maxilla of PVL 5865). The posteriormost element in this post-hatchling specimen is located close to the posterior margin of the maxilla. The complete maxillary dentition could have had more elements but probably not more than one or two additional teeth. The crowns of these teeth decrease in height posteriorly, although their mesiodistal extension remains similar. Thus, these crowns become more blunt and robust along the maxillary tooth row. In the specimen MPM-PV 1813/4 and the post-hatchling specimen PVL 5865, all maxillary teeth are slightly procumbent (except for the two posteriormost elements). This condition was also previously considered to be present exclusively in *Anchisaurus polyzelus* (YPM 1883) and eusauropods (Gauthier 1986; Yates 2004).

The three anteriormost maxillary teeth of the specimen MPM-PV 1813/4 are similar in shape, having only a slight difference in size. Their mesial and distal margins lack serrations and resemble in shape the posterior premaxillary teeth (Figure 1). However, the distal margin of the second maxillary tooth of the subadult specimen PVL 4587 seems to have small blunt serrations. The maxillary elements have a less pronounced asymmetry between the mesial and distal margins. In particular, the proximal half of the distal margin is only slightly convex and its apical half is straight rather than concave. The lateral surface of these crowns is also convex and their enamel layer seems to be thinner than in the premaxillary elements. The posterior elements are poorly preserved in all the available specimens of *Mussaurus patagonicus*. However, an erupting fourth maxillary tooth of the specimen MPM-PV 1813/4 shows that the posterior maxillary teeth had well-developed and acute serrations oriented at approximately 45 degrees from the tooth's margin, as in all other sauropodomorphs
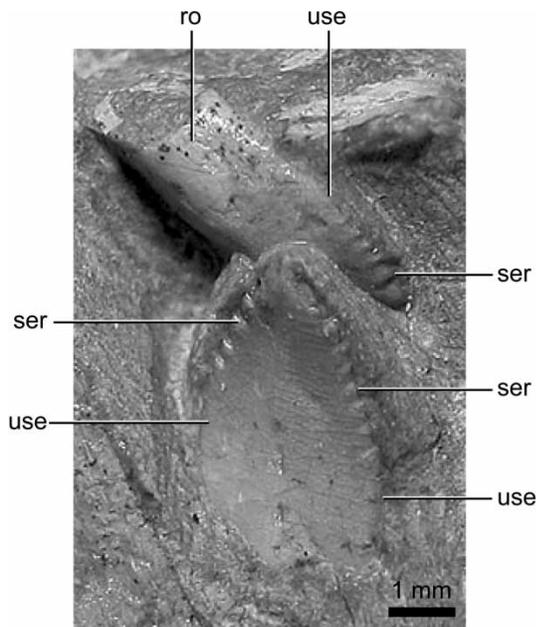
Figure 9. Posterior maxillary tooth of *Mussaurus patagonicus* (MPM-PV 1813/2). See abbreviations in Appendix.

(Benton et al. 2000). Two isolated teeth of the specimen MPM-PV 1813/2 also bear serrated margins (Figure 9). In these elements the denticles are restricted to the apical region of the crown, being absent from the basal region where the leaf-shaped crown reaches its maximum mesio-distal width. A similar morphology is present in the posterior maxillary teeth of the post-hatchling specimen PVL 4211.

Discussion

The material described here includes two main classes of skull size that shed some light on several ontogenetic changes occurring during the development of this taxon. The first class of specimens is represented by the 'post-hatchling' specimens, with a skull length of approximately 3 cm. These specimens were found in close association with two unhatched eggs and eggshell fragments (Bonaparte and Vince 1979). The individual age of these specimens has not been well established, but they have been usually interpreted as extremely young individuals rather than as embryos (Bonaparte and Vince 1979; Weishampel and Horner 1994). This interpretation is mainly based upon the assumption that the associated eggs belong to this species (since the skeletons are significantly larger than the unhatched eggs).

The specimen PVL 4587 and the MPM material belong to a larger class of specimens, the skulls of which are approximately 10 cm long. The material catalogued as PVL 4587 was found closely associated with the post-hatchling specimens and the eggs and comprises a skull and postcranial remains (represent-ing at least two different individuals due to repetition of elements). The MPM material was found in the same locality and includes seven partially articulated skeletons (three of them with skulls) that were found in close association with each other. Several characters preliminary found in the available postcranial material of the MPM material indicate these specimens are not adult forms: lack of fusion between the vertebral centra and neural arches along the entire column, lack of complete ossification on the distal and proximal ends of humeri, femora, and tibiae.

In addition to these specimens, large fragmentary skull remains of a basal sauropodomorph were found in the same locality. This material and some postcranial elements were referred by Casamiquela (1980) to cf. *Plateosaurus*. This material is significantly larger than the MPM skulls and could represent the adult form of *Mussaurus*. Unfortunately, the overlapping material is restricted to a few fragments and these cranial remains cannot be confidently assigned to *Mussaurus* at the moment. The postcranial material is more complete and may provide the necessary information to determine if these adult specimens belong to *Mussaurus patagonicus*.

Ontogenetic changes

The available material of *Mussaurus patagonicus* allows examining some of the early ontogenetic changes occurring from the condition of the extremely young individuals to the recently collected juvenile speci-mens. The skull anatomy shows remarkable changes in the rostral and temporal region, which commonly vary during the ontogeny of dinosaurs and other archosaur reptiles (Dodson 1975; Carpenter 1994; Horner and Currie 1994; Norell et al. 1994; Varrichio 1997; Chiappe et al. 2001; Rauhut and Fechner 2005; Salgado et al. 2005).

The rostrum in the subadult specimens is relatively longer than in the post-hatchling specimens, with a relative enlargement of the premaxilla, maxilla, and nasal bones respect to the total skull length. Similarly, the relative size of the external nares and antorbital fenestra increases during ontogeny of *Mussaurus*, as recently noted for the basal sauropodomorph *Massos-pondylus carinatus* from the Early Jurassic of South Africa (Sues et al. 2004; Reisz et al. 2005).

The temporal region of the skull increases in its height and length during the ontogeny of *Mussaurus patagonicus*, although its lateromedial width decreases relative to the skull length. The supratemporal openings are narrow and laterodorsally exposed in the post-hatchling specimens (PVL 4210) but become broader and dorsally exposed in the subadult individuals. The changes in this region markedly affect the morphology of the parietal. This element is expanded and dorsally bowed in the post-hatchling specimens but becomes dorsally flattened and

relatively narrow in the subadult specimens. The parietal of the subadult specimens of *Mussaurus patagonicus*, however, does not have a sharp emargination along the edge of the supratemporal fossa noted in the development of *Massospondylus carinatus* (Reisz et al. 2005), although this could be due to non-adult condition of the *Mussaurus* material described here. The frontal also shows changes in its shape, proportions, and in its participation in the supratemporal fossa. In the post-hatchling specimens the frontal seems to be excluded from the incipient supratemporal fossa (PVL 4210). In the subadult specimens the frontal participates in this depression and is emarginated forming a sharp anterior edge of the supratemporal fossa, as also noted for *Massospondylus carinatus* (Reisz et al. 2005).

Other changes, however, may be more specific of the ontogenetic development of *Mussaurus*. This includes the changes on the anterior margin of the premaxilla, which is remarkably more vertical in the post-hatchling specimens than in the subadults (changing from 63 to 71 degrees to 45 degrees). Similarly, the ascending ramus of the maxilla changes its orientation (changing the angle with the alveolar margin from 90 to 75 degrees), the prefrontal extends posteriorly reaching the anteroposterior midpoint of the orbit, the descending process of the postorbital increases its length, and the infratemporal fenestra reduces its extension underneath the orbit, the dentary becomes proportionately shorter and higher (e.g. minimum height relative to anteroposterior length from 17% to 24%), and the angular increasingly overlaps the surangular on the lateral surface of the mandibular ramus, posterior to the external mandibular fenestra.

Relationships of Mussaurus

The relationships of *Mussaurus patagonicus* need to be re-evaluated through a phylogenetic analysis including the specimens described herein. This point lies outside the scope of this contribution, but we will briefly comment on some characters potentially relevant to this topic. The new information on the skull anatomy of this taxon shows the presence of several derived characters present in sauropods but absent in other basal sauropodomorphs (e.g. *Plateosaurus engelhardti*, *Thecodontosaurus caducus*). Some of these include the presence of the ascending process of the jugal posterodorsally directed forming an acute extension of the infratemporal fenestra ventral to the orbit, the dorsal and anterior branches of the quadratojugal forming an angle of approximately 90 degrees, broad anteromedial extension of ectopterygoid reducing the development of the suborbital fenestra, dorsoventral expansion of anterior end of the dentary at the mandibular symphysis, slightly procumbent premaxillary and maxillary teeth with faint enamel wrinkling, serrations on mesial and distal margins of tooth crowns absent or restricted to the apical region. Other basal sauropodomorphs (e.g. *Massospondylus carinatus*, *Lufengosaurus huenei*, *Yunnanosaurus huangi*, *Anchisaurus polyzelus*, *Melanorosaurus readi*) share the presence of at least some of these characters with *Mussaurus* and derived sauropodomorphs.

Other characters of the skull of *Mussaurus patagonicus*, instead, show the plesiomorphic condition present in most basal sauropodomorphs instead of the derived eusauropod (or neosauropod) condition. Among these we can note the presence of anteriorly located external nares, a (reduced) antorbital fossa surrounding the antorbital fenestra, a subcircular orbit with an extensive infraorbital region of the jugal separating the antorbital and infratemporal openings, the frontal forming at least half of the orbital rim and extending posteriorly into the supratemporal fossa, a dorsoventrally narrow anterior branch of quadratojugal that reaches the midpoint of the infratemporal opening (lacking a contact with the maxilla), an enlarged supratemporal fenestra, the semicircular facet that 'hooks' around the basipterygoid processes, the mandibular rami meeting at an acute angle rather than forming a broad U-shaped symphysis, and the surangular dorsal margin poorly bowed dorsally.

Conclusions

Numerous authors have underscored the importance of understanding ontogenetic changes due to the ubiquity of heterochrony in the origin of evolutionary novelties (e.g. McKinney and McNamara 1991; Shubin 1994). In particular, these processes have been suggested to play an important role in the evolution of several dinosaur groups (Weishampel and Horner 1994; Long and McNamara 1995, 1997; Rauhut and Fechner 2005), including Sauropodomorpha (Bonaparte and Vince 1979; Reisz et al. 2005; Chiappe et al. 2001; Salgado et al. 2005).

The study of different growth stages of *Mussaurus patagonicus* shows numerous skull characters that are subject to strong ontogenetic change. Some of these characters show a 'sauropod-like' condition in the post-hatchling specimens but a plesiomorphic condition in the subadult specimens (e.g. anterior margin of premaxillae subvertically oriented, lateral surface of maxilla below narial region and antorbital opening proportionately short and high, ascending process of the jugal forming a lower angle with the posterior process of the jugal producing an extensive projection of the infratemporal fenestra underneath the orbit, participation of the frontal on the supratemporal fossa, temporal region of the skull lateromedially wide respect to its anteroposterior length, posterolateral processes of parietal oriented transversally to the longitudinal axis of the skull). These characters fit the

hypothesis that major features of the sauropod skull morphology could have been originated through paedomorphic processes, as first proposed by Bonaparte and Vince (1979) due to some similarities in the skull morphology of the *Mussaurus* holotype and *Camarasaurus* (e.g. short premaxilla and maxilla, dorsoventrally high antorbital fenestra, expanded mandibular symphysis, and enlarged teeth).

Other characters, however, seem to have an opposite developmental trend, showing a plesiomorphic-like condition in the post-hatchlings and a more derived condition in the subadult skulls (e.g. relative enlargement of the descending process of the postorbital, the increase in the posterior extension of the posterodorsal process of the prefrontal along the orbital rim, infraorbital region of the jugal decreasing its anteroposterior extension and increasing its dorsoventral depth relative to the anteroposterior extension of this bone, increase in dorsoventral height of dentary at mandibular symphysis relative to the anteroposterior extension of this element). A similar pattern of conflicting developmental trends was recently noted in the ontogeny of derived neosauropods (Salgado et al. 2005), suggesting that heterochronic processes underlying the evolution of sauropodomorph skulls may be more complex than previously thought.

The cranial morphology of the adult stage in *Mussaurus* is currently unknown and new materials are needed in order to understand the late ontogenetic changes of this taxon. Such remains will also be critical to appropriately test the phylogenetic relationships of *Mussaurus patagonicus* since many of the characters subject to ontogenetic change in this taxon have been previously interpreted as varying phylogenetically among basal sauropodomorphs and Sauropoda (Galton 1990; Upchurch 1995, 1998; Wilson and Sereno 1998; Sereno 1999; Wilson 2002; Galton and Upchurch 2004; Yates 2004). Understanding the pattern of ontogenetic changes in sauropodomorphs would not only be useful to test the relationships of *Mussaurus* but also to explore the role and influence of non-mature individuals in phylogenetic analysis of basal sauropodomorphs. This issue could be of critical importance since several basal sauropodomorphs are primarily known from specimens that are suspected to be juveniles such as *Anchisaurus polyzelus* and *Thecodontosaurus caducus* (Yates 2003; Fedak 2005).

Acknowledgements

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Appendix

Institutional abbreviations

AMNH   American Museum of Natural History, New York, USA
BMNH   The Natural History Museum, London, England
BPI   Bernard Price Institute, Johannesburg, South Africa
GPIT   Institut und Museum für Geologie und Paläontologie, Universitat Tübingen, Tübingen, Germany
IVPP   Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China
MACN   Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
MCP   Museu Pontificia Universidade Catolica, Porto Alegre, Brazil
MPM   Museo Regional Provincial Padre M. J. Molina, Rio Gallegos, Argentina
NGMJ   Provincial Geological Museum, Nanjing, China
NMQR   National Museum, Bloemfontein, South Africa
PVL   Instituto Miguel Lillo, Tucumán, Argentina

SAM   Iziko—South African Museum, Cape Town, South Africa
SMNS   Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany
ULR   Museo Ciencias Naturales, Universidad La Rioja, La Rioja, Argentina
YPM   Yale Peabody Museum, New Haven, USA.

Anatomical abbreviations

1p   first premaxillary tooth
3p   third premaxillary tooth
afe   antorbital fenestra
afo   antorbital fossa
amx   ascending process of maxilla
ang   angular
apd   anterior process of dentary
apj   ascending process of jugal
apm   ascending process of premaxilla
arb   articular bulge of surangular
den   dentary
dlr   lacrimal dorsolateral ridge
emf   external mandibular fenestra
en   external nares
fps   frontoparietal suture
f   frontal
itf   infratemporal fenestra
j   jugal
lac   lacrimal
lr   lacrimal lateral ridge
mx   maxilla
nas   nasal
par   parietal
pdw   posterodorsal medial wall of antorbital fossa
pmx   premaxilla
po   postorbital
pof   foramen on lateral surface of postorbital
prf   prefrontal
ptq   pterygoid wing of quadrate
pvw   posteroventral medial wall of antorbital fossa
q   quadrate
qal   quadrate anterolateral wing
qj   quadratojugal
rap   retroarticular process
ro   tooth root
rra   lacrimal rostral ramus
saf   surangular foramen
san   surangular
se   serrations on crown's margin
sq   squamosal
stf   supratemporal fenestra
stfo   supratemporal fossa
use   unserrated portion of crown's margin