

New information on the palate and lower jaw of *Massospondylus* (Dinosauria: Sauropodomorpha)

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Received 25 April 2005. Accepted 27 July 2005

Additional anatomical details of the palate and lower jaw of the prosauropod dinosaur *Massospondylus* Owen are documented on the basis of a previously undescribed skull from the upper Elliot Formation. The palate is generally similar to that of other early sauropodomorphs, but can be shown to differ from those of *Plateosaurus*, *Lufengosaurus* and *Thecodontosaurus* in several respects. For example, *Massospondylus* lacks the well-developed palatine boss seen in *Plateosaurus* and the pneumatic recess that is present on the ectopterygoid of *Thecodontosaurus*. In addition, *Massospondylus* possesses an expanded medioventral premaxillary process that is much larger than that of any other basal sauropodomorph.

Keywords: *Massospondylus*, upper Elliot Formation, Lower Jurassic, palate, mandible.

INTRODUCTION

The basal sauropodomorph (prosauropod) dinosaur *Massospondylus carinatus* Owen is represented by abundant material, including complete skeletons and skulls, from the upper Elliot, Clarens and Forest Sandstone formations of southern Africa (Owen 1854; Cooper 1981; Gow 1990; Gow *et al.* 1990; Sues *et al.* 2004). Indeed, material of this animal is so common that it was selected as the eponymous index taxon of a biostratigraphical unit dubbed the *Massospondylus* range zone (Kitching & Raath 1984), which is thought to be Lower Jurassic (?Pliensbachian and/or ?Toarcian) in age (Yates *et al.* 2004). Although *Massospondylus* was named a century and a half ago (Owen 1854), many aspects of the anatomy and taxonomy of this animal remain unclear. For example, new evidence suggests that some specimens previously ascribed to *Massospondylus* may pertain to another, potentially new, basal sauropodomorph taxon (Barrett 2004).

Cranial material of *Massospondylus* has been described in detail on the basis of a superb series of skulls housed in the collections of the Bernard Price Institute for Palaeontological Research, Johannesburg (Gow 1990; Gow *et al.* 1990; Sues *et al.* 2004). However, preservation and/or the stage of preparation of these specimens has prevented collection of anatomical data from various regions of the palate and from the medial surface of the lower jaw, with the result that these regions have not yet been fully described. In BP/1/4779, for example, the lower jaws are adhered to the skull and remain partly encased in matrix, obscuring the rostral part of the palate. The palates of basal sauropodomorphs are poorly known: only that of *Plateosaurus* has been described in its entirety (Galton 1984), though partial and/or brief descriptions do also exist for other taxa (e.g. *Lufengosaurus*: Young 1951, Barrett *et al.* 2005; *Thecodontosaurus*: Yates 2003; *Massospondylus*: Sues *et al.* 2004). Here, we provide a description of the palatal aspect of the skull and medial surface of the lower jaw of

Massospondylus based on a previously figured, but undescribed skull in the collections of the South African Museum, Cape Town (SAM-PK-K1314; Figs 1–4).

MATERIALS

In 1967, a joint expedition organised by the South African Museum, Yale University, Birkbeck College (University of London), and the British Museum (Natural History) (now the Natural History Museum, London) collected a variety of vertebrate fossils from the Stormberg Group of South Africa and Lesotho (Attridge & Charig 1967; see also Crompton 1968). During the course of this expedition, C.E. Gow collected an almost complete skeleton of *Massospondylus*, including an excellent skull (SAM-PK-K1314). This specimen pertained to the upper Elliot Formation of Blikana Mountain, Orange Free State (30°34'S, 27°37'E), from an horizon approximately 10–12 m below the contact with the overlying Cave Sandstone (J. Attridge, pers. comm., 2004).

The skull has been compressed dorsoventrally, resulting in midline separation of the palatal elements, some disarticulation of the suspensorial elements, and damage to the nasal region (Figs 1–3). The left mandible (Fig. 4) is essentially complete, but only the rostral part of the right dentary is present. In other respects, the skull is well preserved, with delicate structures such as the left stapes and right sclerotic ring preserved in their correct anatomical positions. SAM-PK-K1314 appears to have been a subadult individual, as evidenced by the presence of discernible sutures between the elements of both the braincase and skull roof.

Initially, preparation was carried out by Ione Rudner of the South African Museum, and was continued by William Amaral and Charles Schaff of the Museum of Comparative Zoology, Harvard University. The left-hand side of the skull has been almost completely prepared, revealing details of all available bone surfaces, whereas the interior of the right-hand side of the skull is still filled with matrix. Both lower jaws are prepared in the round

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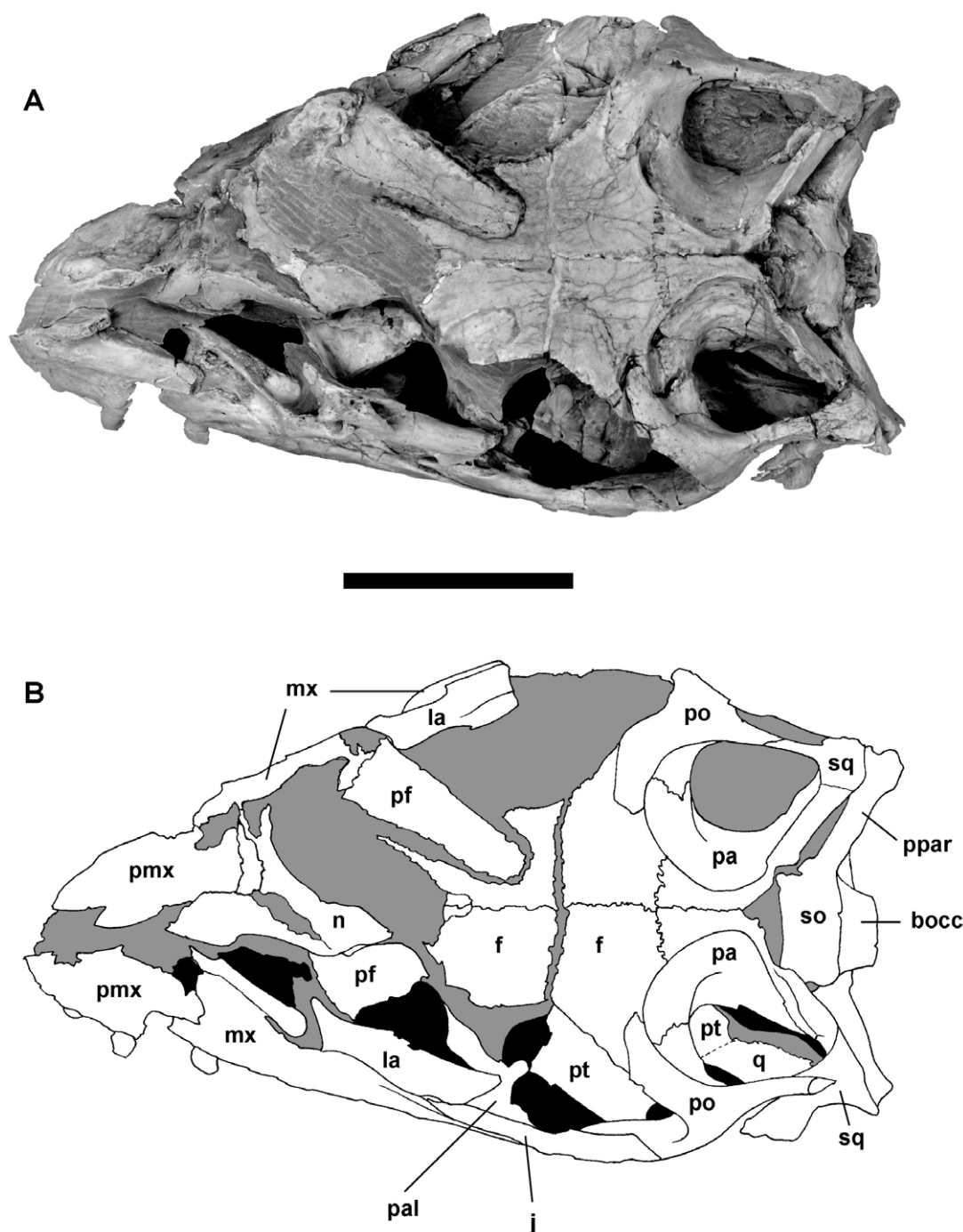


Figure 1. Skull of *Massospondylus carinatus* (SAM-PK-K1314). **A**, Photograph of skull in dorsal view. **B**, Interpretative drawing of the skull. Grey fill represents matrix and reconstruction; black fill represents voids within the skull. Scale bar equals 5 cm.

and are separated from the skull. Although the specimen has never been formally described, it has been figured (e.g. Cooper 1981: figs 1 & 2) and mentioned briefly in several papers (e.g. Attridge *et al.* 1985; Crompton & Attridge 1986). It also formed the basis for the skull reconstruction of *Massospondylus* proposed by Crompton & Attridge (1986: fig. 17.4).

Sues *et al.* (2004) have proposed an emended diagnosis for *Massospondylus* based on a series of cranial autapomorphies (e.g. presence of a lateral boss on the prefrontal and a distinct ridge on the lateral surface of the lacrimal) and a unique combination of other cranial characters (e.g. the combined presence of an ascending maxillary process that is tall, nearly vertical with a narrow medial sheet with

an elongate prefrontal). The majority of these features (see Sues *et al.* 2004, for a full list) are present in SAM-PK-K1314, indicating that the latter can be referred to *Massospondylus*, an identification confirmed by comparison with other skulls referred to this genus (e.g. BP/1/4376, BP/1/4779, BP/1/4934 and BP/1/5241).

This description is not intended to be exhaustive, but aims to supplement the recent account provided by Sues *et al.* (2004). In order to avoid excessive duplication of information, the lower jaw will be described in medial view only (Fig. 4), and we will concentrate on those areas of the palate (Fig. 3) that are either unprepared or damaged in the series of *Massospondylus* skulls described by Gow *et al.* (1990) and Sues *et al.* (2004).

A



B

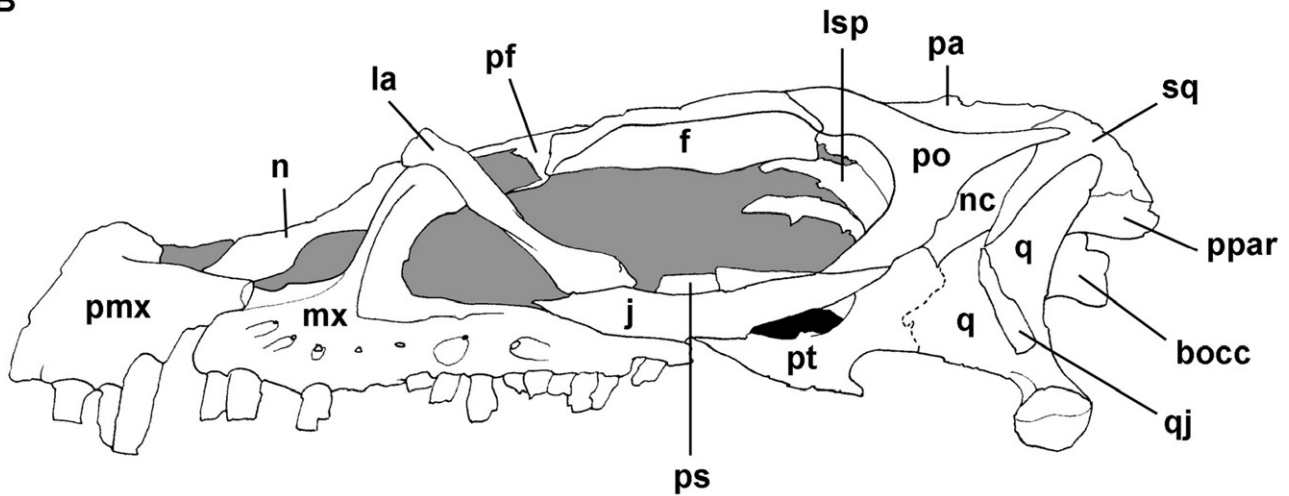


Figure 2. Skull of *Massospondylus carinatus* (SAM-PK-K1314). **A**, Photograph of skull in left lateral view. **B**, Interpretative drawing of the skull. Grey fill represents matrix and reconstruction; black fill represents voids within the skull. Note that breakage of the lower temporal bar reveals some details of the palate in lateral view. Although the braincase can be seen through the dorsal part of the lower temporal fenestra, no suture lines or foramina are discernible. Scale bar equals 5 cm.

DESCRIPTION

Palatal aspect of skull

Premaxilla

Four alveoli are present in each premaxilla, though only three teeth are preserved in life position (right teeth 2, 3 and 4). A sub-circular replacement foramen lies dorsal to each alveolus: the alveoli and replacement foramina were continuous with each other and were not separated by bars of bone. The conjoined replacement foramina/alveoli are separated from each other by rhomboidal interdental plates. The lateral wall of the dental parapet is dorso-ventrally deeper than the medial wall: this difference in height remains constant along the length of the premaxilla and the tooth crowns are not obscured in labial view.

The ventral surface of the premaxilla is strongly concave transversely and meets its counterpart at the midline to form a complete premaxillary secondary palate. The caudomedial corner of each premaxilla gives rise to a stout, triangular process that extends caudally parallel to the skull midline, tapering to a bluntly rounded point (referred to hereafter as the medioventral process). This process has a small contact with the rostral margin of the

vomer and probably made a small contribution to the rostromedial margin of the internal naris.

Maxilla

In ventral view, the maxilla is dorsoventrally tallest rostrally and tapers caudally to a narrow ramus with a sub-triangular transverse cross-section. A rostromedially directed, stout, cylindrical premaxillary process is present. The medial surface of the maxilla is gently concave dorsoventrally in its rostral part, becoming more planar in the middle section of the bone, before giving rise to a sharp ridge that extends along the caudalmost third of the tooth-bearing ramus, which divides the medial surface into a planar, horizontally oriented surface (lying ventral to the ridge) and a concave area above. This area displays a distinct, strap-like, striated articular surface for the reception of the maxillary process of the palatine.

Rostrally, the lateral margin of the dental parapet is dorsoventrally higher than the medial one. However, the height of the former decreases caudally, until the two margins reach the same height in the caudal third of the tooth-bearing ramus. Small sub-circular replacement foramina are confluent with the medial margins of the alveoli rostrally, but the foramina display a progressive

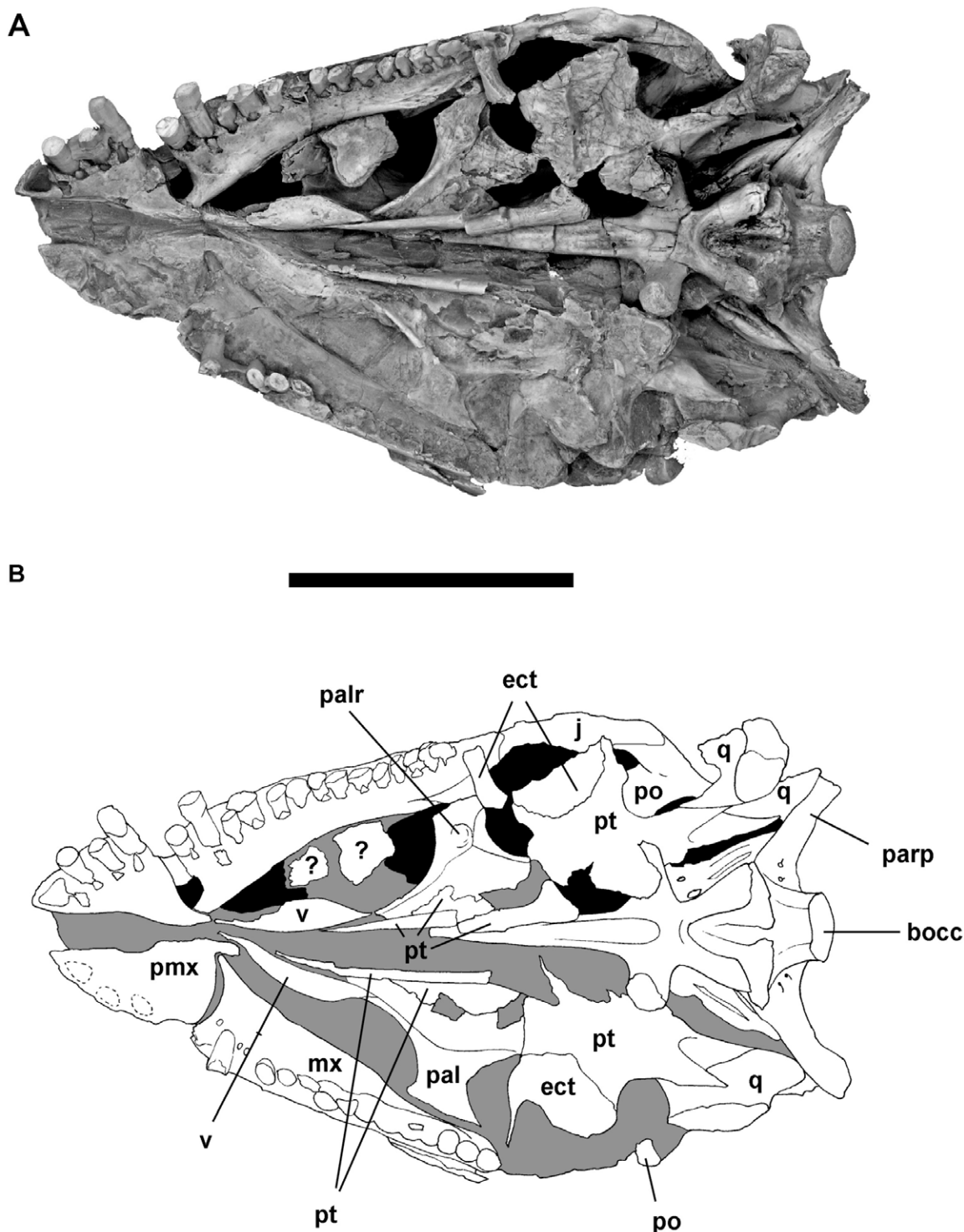


Figure 3. Skull of *Massospondylus carinatus* (SAM-PK-K1314). **A**, Photograph of skull in palatal view. **B**, Interpretative drawing of the skull. Grey fill represents matrix and reconstruction; black fill represents voids within the skull. Most of the braincase elements are unlabelled for clarity. See Gow (1990) and Sues *et al.* (2004) for details of braincase anatomy. Note that scale bar equals 5 cm.

decrease in size caudally, eventually becoming entirely confluent with the alveoli approximately halfway along the tooth row. Alveoli are separated from each other by small rhomboidal interdental plates. The gently concave medial margin of the maxilla would have formed the lateral margin of the large, sub-elliptical internal naris.

Sues *et al.* (2004) mentioned the presence of a small contact between the maxilla and vomer in BP/1/4779 but this contact is not visible due to the presence of matrix surrounding the vomers. There is a small sliver of bone

contacting the rostrolateral margin of the right vomer but this is most likely the medioventral process of the premaxilla. Furthermore there is no evidence of any contact between these elements in SAM-PK-K1314. The rostromedialmost part of the maxilla may have made a very small contribution to the secondary palate.

Vomer

The vomers are long, sinuous bones in ventral view, which are mediolaterally widest in their central portion

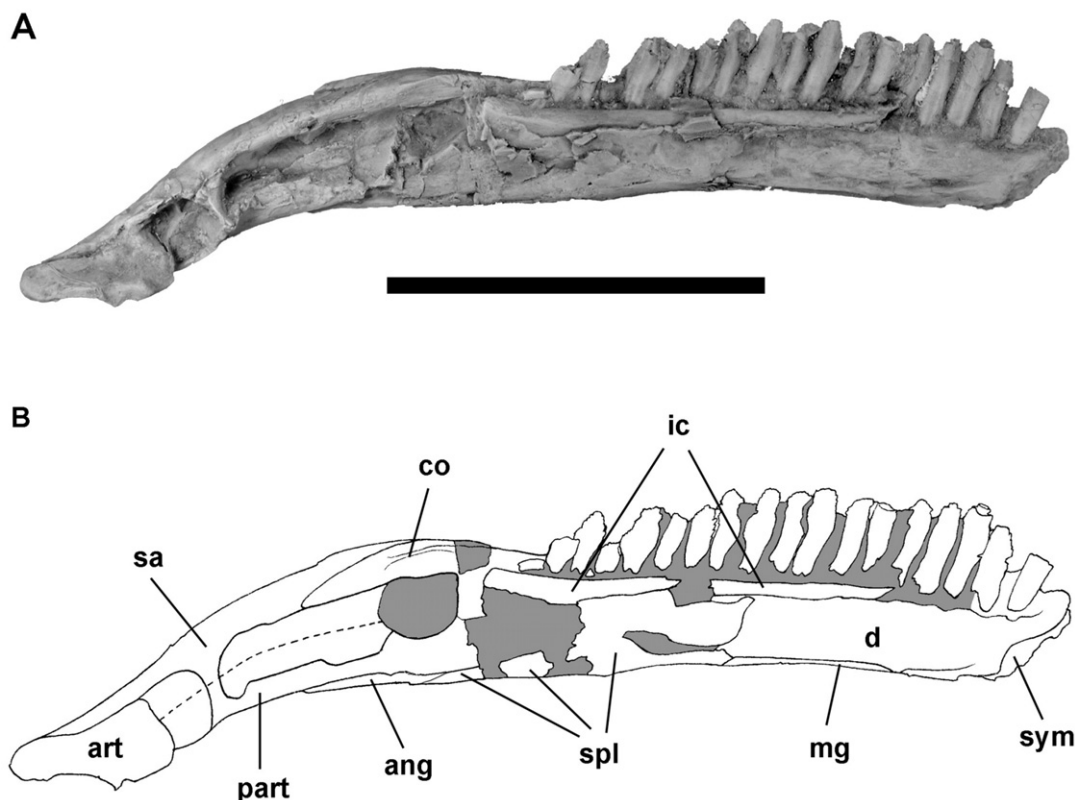


Figure 4. Left lower jaw of *Massospondylus carinatus* (SAM-PK-K1314). **A**, Photograph of lower jaw in medial view. **B**, Interpretative drawing of the lower jaw. Grey fill represents matrix and reconstruction. Dotted line represents the position of likely boundary between the prearticular and surangular. Scale bar equals 5 cm.

and taper both rostrally and caudally. Rostrally, the area that articulates with the premaxilla is flat ventrally, whereas the central and caudal sections of the bone, where the vomer articulates with the pterygoids and palatines (which are the portions visible in BP/1/4779) are transversely convex. The dorsal surfaces of the vomers are obscured by matrix.

Although the vomers have become separated, it is likely that they were in contact along the midline for much of their length, but were separated caudally by the intervention of a narrow rostral extension of the palatine process of the pterygoids. The rostral margin of the vomer and the medioventral process of the premaxilla met along a very short overlapping contact. Caudally, the vomer tapers to a fine point that is clasped between the pterygoid (medially) and palatine (laterally). The concave lateral margin of the vomer comprises the rostral half of the medial margin of the internal naris.

Palatine

There is a small, lightly rugose patch on the ventral surface of the palatine, immediately lateral to the apex of the triangular fossa that occupies the medial side of the ventral surface. This rugosity, which is also present in BP/1/4779, occurs in the same position as the palatine peg seen in *Plateosaurus* (Galton 1984). No other details can be added to the description of Sues *et al.* (2004).

Ectopterygoid

SAM-PK-K1314 permits one new observation on the ectopterygoid in addition to those provided by Sues *et al.*

(2004): namely, the ectopterygoid provides a relatively large contribution to the pterygoid flange, accounting for almost all of its lateral portion, or approximately one third of its total surface area.

Pterygoid

As in *Plateosaurus* (Galton 1984), the quadrate process of the pterygoid is subdivided. A long tapering dorsal ramus extends upward along the vertical part of the pterygoid wing of the quadrate and a shorter, stouter ventral ramus extends horizontally along the base of the pterygoid process: this feature is also visible in BP/1/4934 and BP/1/4779, although the distinction between the two rami is not as marked in the latter skull (Sues *et al.* 2004: fig. 5B; pers. obs.). This character cannot be seen in the other skulls in the Bernard Price Institute due to either damage or presence of surrounding matrix. No other details can be added to the descriptions provided by Sues *et al.* (2004).

Mandible

The caudal part of the left mandible has undergone torsion relative to the undeformed rostral part. In particular, the dorsal part of the coronoid eminence is rotated medially, so that in lateral view it appears to be much lower in height than it would have been originally. Also, the articular region has become depressed and rotated medially, so that the articular glenoid faces mainly medially, rather than dorsally, and the level of the craniomandibular joint is situated considerably further ventrally than it would have been in life. The external mandibular fenestra is matrix-filled; the internal mandib-

ular fossa is also partly obscured by matrix and by a small amount of restoration. The internal mandibular fenestra is large and is bounded by the surangular and angular laterally, the prearticular ventrally, the surangular caudo-dorsally and the coronoid rostrally, with small contributions from the intercoronoid and dentary rostrally. Eighteen tooth positions are present and 15 erupted teeth are preserved *in situ*.

Only the rostralmost part of the right mandible is preserved (from its rostral end up to approximately the level of the 12th tooth position). Its morphology agrees in all respects with that of the left mandible.

Dentary

The lateral dental parapet is higher than the medial one for almost the entire length of the dentary (though this discrepancy is reduced slightly near to the end of the tooth row). In medial view, immediately ventral to the row of alveoli, sub-circular replacement foramina are present, which are separated from each other by small rhomboidal interdental plates. The presence of these foramina can only be confirmed for the first five tooth positions; caudal to this, the region ventral to the tooth row is obscured by the intercoronoid. The symphysis is rostrocaudally narrow, rugose, and approximately elliptical in outline. A very shallow Meckelian groove extends along the ventral margin of the dentary from the base of the symphysis to the articulation with the splenial. Most of the caudal part of the dentary is obscured by contact with the splenial, intercoronoid and prearticular.

Splenial

The splenial is a thin, plate like element that covers much of the caudal part of the dentary in medial view. A sub-rectangular main body, which extends from the ventral margin of the mandible to the level of the intercoronoid, gives rise to a caudally tapering ventral process that extends along the ventral margin of the mandible, underlying the prearticular. The medial surface of the splenial is flat to very gently convex dorsoventrally. The caudoventral process wraps around the ventral margin of the mandible, overlapping the angular, so that a very small sliver of the splenial is visible in lateral view. A small rostral projection from the ventral part of the main body fits into the Meckelian groove that extends along the ventral surface of the dentary.

Intercoronoid

As preserved, the intercoronoid extends from a point level with the rostral margin of the coronoid eminence to the base of the fifth dentary tooth (though it is likely to have extended further rostrally in life). It lies parallel and ventral to the medial dental parapet. It is a dorsoventrally narrow, elongate, rod-like element, which is broken at its rostral and caudal terminals. The medial surface is very gently convex dorsoventrally. Caudally, the terminal part of the intercoronoid is slightly upturned relative to the rest of the bone. Rostrally, it contacts the dentary; in its midsection it also contacts the splenial (ventrally); and

caudally it develops an additional contact with the prearticular (ventrally). The intercoronoid may also have contacted the coronoid caudally, but this cannot be confirmed due to damage.

Coronoid

The coronoid is poorly preserved, but it appears to have been a relatively mediolaterally narrow, rostrocaudally short element that comprises the rostral margin of the coronoid eminence in medial view. It is broken rostrally, so it is not possible to determine its contacts with the prearticular, splenial and intercoronoid. It contacts the surangular laterally.

Preadicular

The prearticular is an elongate element with expanded rostral and caudal ends that are connected to each other via a narrow shaft. It forms the ventral margin of the internal mandibular fenestra. It is not possible to see if a foramen is present at the splenial/prearticular junction (as occurs in *Plateosaurus*: Galton 1984) due to crushing of this area and the presence of matrix.

Rostrally, the prearticular contacts the splenial and intercoronoid (in medial view) and dentary laterally. In its middle section, the prearticular contacts the angular and surangular laterally, and caudally it contacts the surangular laterally and the articular dorsally. The rostral expansion is plate-like and its dorsal margin curves caudoventrally to form the rostral margin of the internal mandibular fenestra. The bone narrows caudally before expanding again, both dorsoventrally and mediolaterally, to form the crest-like caudoventral margin of the internal mandibular fenestra (in combination with a medially directed process arising from the surangular). Caudal to this crest, the prearticular thins to form a transversely oriented sheet that contacts the surangular laterally forming a trough for reception of the articular. The prearticular forms the medioventral boundary of a shallow fossa, bounded caudally by the rostral margin of the articular and rostrally by the crest-like ridge marking the caudal margin of the internal mandibular fenestra. This fossa has an irregular surface and many have been filled with cartilage in life: the rostral margin of the articular is composed of smooth finished bone and is not likely to have extended any further forwards, nor has it been displaced caudally.

Surangular

The surangular is the largest post-dentary bone. In lateral view, it contacts the dentary rostrally (though the contact is not clear), the angular ventrally and forms the dorsal boundary of the external mandibular fenestra. Near to its caudal end, the contact with the articular can be seen, and the caudalmost part of the surangular extends almost to the tip of the retroarticular process. It is not possible to see if the large foramen usually present on the rostral surface of the coronoid eminence is present, due to damage. However, a small foramen is present on the lateral surface on the caudal border of the coronoid eminence; this is contiguous with a foramen visible on the

medial surface, which enters the internal mandibular fenestra.

In medial view, the surangular forms the lateral boundary of the internal mandibular fenestra and its thickened dorsal border. In the rostral part of this dorsal border, the surangular is overlapped by the coronoid. For most of its length the surangular forms an approximately flat plate (thickened along its dorsal margin, slightly convex laterally and slightly concave medially). It is not possible to determine whether there was any contact with the intercoronoid rostrally, due to damage in the intervening area. The ventral part of the surangular has an extensive contact with the prearticular. Caudally, the surangular thickens mediolaterally to form a medially oriented tapering process that arises at the border of the internal mandibular fenestra to contact the prearticular (forming the crest-like caudal margin of the fenestra, see above). Caudal to this crest, the surangular comprises the lateral boundary of the shallow fossa that lies in front of the articular (see above).

Angular

The angular comprises the caudoventral part of the lateral surface of the mandible and forms the ventral border of the external mandibular fenestra. It is sub-triangular in lateral view and contacts the surangular along its length, dorsally. Caudally, it does not extend as far back as the retroarticular process. At its caudalmost point it has a very small contact with the articular. Owing to the torsion of the mandible, the prearticular is visible ventral to the angular (in its caudal part) in lateral view. The lateral surface of the angular is flat to very gently convex, dorsoventrally.

The angular is overlapped medially by the prearticular, which largely obscures it. A very small part of the angular wraps around the ventral surface of the mandible and is visible between the prearticular and the splenial.

Articular

The articular comprises the articular glenoid of the mandible and the majority of the retroarticular process. It fits into a sulcus formed by the surangular and prearticular, which both contact the articular ventrally; in the case of the surangular, this contact continues for the length of the articular, whereas the prearticular terminates more rostrally (although broken in this specimen) allowing the articular to be seen in ventral view. The articular also contacts the angular at its ventrolateral margin. In dorsal view, the articular has a sub-elliptical outline and can be divided into two regions. Rostrally, the dorsal surface is mildly concave both rostrocaudally and mediolaterally and this area represents the glenoid for reception of the quadrate condyle. The glenoid is defined rostrally and medially by the thickened margins of the articular and laterally by the surangular. Caudally, the glenoid boundary is not marked by a ridge, but by a distinct change of slope as the articular curves slightly dorsally to form its second region, the retroarticular process. The glenoid is of approximately the same length as the quadrate condyle. A distinct notch is present medial to the glenoid surface. In

dorsal view, the articular tapers caudally to form the short retroarticular process, which has a sub-triangular transverse cross-section. The dorsal surface of the retroarticular process is transversely concave, forming a groove that becomes confluent with the more rounded glenoid cavity rostrally.

COMPARISONS AND DISCUSSION

In most respects, the palate and lower jaw of *Massospondylus* are similar to those of other basal sauropodomorphs, such as *Thecodontosaurus*, *Lufengosaurus*, *Plateosaurus* and *Anchisaurus* (Young 1951; Galton 1976, 1984, 1985; Yates 2003; Galton & Upchurch 2004; Barrett *et al.* 2005). Unfortunately, prosauropod palates are very poorly known, so the following comparative comments are far from comprehensive and more detailed investigation must await the description or further preparation of other specimens. However, a number of useful comparisons can be made. For example, *Massospondylus* lacks both the palatine peg (Sues *et al.* 2004), which is considered to be an autapomorphy of *Plateosaurus* (Galton 1984), and the ventrally (?pneumatically) excavated ectopterygoid seen in *Thecodontosaurus* (a possible autapomorphy of the latter: Yates 2003), allowing clear distinctions to be made between the palates of these taxa.

Several other differences are also apparent. In both *Lufengosaurus* (Young 1951; Barrett *et al.* 2005) and *Plateosaurus* (Galton 1984; Galton & Upchurch 2004) the vomers are elongate, parallel-sided elements in ventral view; in *Plateosaurus* vomer length is approximately 27% of total skull length (based on the reconstruction in Galton & Upchurch 2004). By contrast, the central portions of the vomers of *Massospondylus* are mediolaterally expanded relative to their rostral and caudal terminations, giving them a convex lateral outline in ventral view (see above and BP/1/4779). Additionally, the vomers are relatively shorter reaching only 20% of total skull length (based on SAM-PK-K1314). Sues *et al.* (2004) note that the pterygoid of *Massospondylus* lacks the hook-like process that contacts the basiptyergoid process in *Plateosaurus*: however, a broad, flattened medial process of the pterygoid, which is separated from the main body of the pterygoid by a deep notch, is present in SAM-PK-1314. In SAM-PK-1314, at least one *Plateosaurus* specimen (HMN XXIV), the skull of '*Massospondylus*' from the Kayenta Formation (A.M.Y., pers. obs. of MCZ 8893), *Lufengosaurus* (Barrett *et al.* 2005) and a basal sauropodomorph skull from the lower Elliot Formation (Welman 1999), the basiptyergoid process sits in this notch. The palate of another *Plateosaurus* specimen (SMNS 13200) appears to show a different condition where the hook-like medial process of the pterygoid wraps around the basiptyergoid process (Galton 1985). This is reproduced in most reconstructions of the skull of *Plateosaurus* (e.g. Galton & Upchurch 2004), but we suggest that the basiptyergoid processes of this specimen are in an unnatural position due to lateral compression and that the condition in SAM-PK-1314 is typical for Prosauropoda.

SAM-PK-K1314 possesses a prominent caudomedial process on the premaxilla, a feature absent in *Plateosaurus*

(Galton 1984; Galton & Upchurch 2004). This feature is not determinable in the *Massospondylus* skulls described by Sues *et al.* (2004), but is clearly much reduced in at least one South African specimen referred to *Massospondylus* (SAM-PK-K388). It is possible that this character may, therefore, be subject to intraspecific variation. Alternatively, this feature may prove to have taxonomic relevance, as it has been suggested that two basal sauropodomorph taxa are present in the upper Elliot Formation dinosaur fauna that can be differentiated on the basis of tooth crown, braincase and skull roof morphology (Barrett 2004). The presence/absence of a caudomedial process may help to further distinguish *Massospondylus* from this second, unnamed, taxon. Interestingly, a skull referred to *Massospondylus* from the Lower Jurassic Kayenta Formation of Arizona, U.S.A. possesses a long caudomedial process (Attridge *et al.* 1985), though a full description and systematic evaluation of this specimen has yet to be published. Similarly, the relative contribution of the ectopterygoid to the pterygoid flange also varies. In SAM-PK-K1314 and *Thecodontosaurus* (Yates 2003), the ectopterygoid comprises most of the lateral portion of the flange, while in *Lufengosaurus* (Barrett *et al.* 2005) and *Plateosaurus* (Galton 1984) the ectopterygoid is restricted to a small portion of the rostralateral part of the flange. Other specimens of *Massospondylus* (BP/1/4779 and BP/1/4934; Sues *et al.* 2004) show an intermediate condition. Again, it is possible that this feature may either vary within *Massospondylus* or be taxonomically significant. Additional comparative data on prosauropod palates are needed in order to test these suggestions.

We thank Sheena Kaal and Roger Smith of the South African Museum for permission to borrow the specimen and access to comparative material in the collections of the SAM. Access to comparative specimens was granted by M.A. Raath (BP), David Unwin (HMN), Rupert Wild and Rainer Schoch (SMNS) and Charles Schaff (MCZ). We are grateful to Phil Crabb (NHM Photographic Unit) for his wonderful images of the skull and to Robert Laws for his expert preparation of the line-drawings. P.M. Galton, R.R. Reisz and M.C. Langer provided useful reviews of the manuscript. John Attridge is thanked for many useful discussions relating to the discovery and initial study of SAM-PK-K1314. Hans-Dieter Sues shared unpublished information on the BP *Massospondylus* skulls. P.M.B.'s trips to South Africa were funded by grants from The Royal Society of London and the Palaeontological Research Fund of the Natural History Museum.

LIST OF ABBREVIATIONS

Institutional

BP	Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg.
HMN	Museum für Naturkunde der Humboldt Universität, Berlin.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A.
SAM	South African Museum (Iziko Museums of Cape Town), Cape Town.
SMNS	Staatliches Museum für Naturkunde, Stuttgart.

Anatomical

ang	angular	la	lachrymal
art	articular	j	jugal
bocc	basioccipital condyle	lsp	laterosphenoid
co	coronoid	mg	Meckelian groove
d	dentary	mx	maxilla
ect	ectopterygoid	n	nasal
f	frontal	nc	neurocranium
ic	intercoronoid	pa	parietal

pal	palatine	q	quadrate
palr	palatine rugosity	qj	quadratojugal
part	prearticular	sa	surangular
pf	prefrontal	so	supraoccipital
pmx	premaxilla	spl	splénial
po	postorbital	sq	squamosal
par	paroccipital process	sym	symphysis
ps	parasphenoid rostrum	v	vomer
pt	pterygoid		

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