

ON THE SKULL OF *MASSOSPONDYLUS CARINATUS* OWEN, 1854
(DINOSAURIA: SAUROPODOMORPHA) FROM THE ELLIOT AND CLARENS FORMATIONS
(LOWER JURASSIC) OF SOUTH AFRICA

HANS-DIETER SUES

Research Associate, Section of Vertebrate Paleontology
National Museum of Natural History, Smithsonian Institution
NHB MRC 106, PO Box 37012, Washington, DC 20013-7012 (suesh@si.edu)

ROBERT R. REISZ

Research Associate, Section of Vertebrate Paleontology
Dept. of Biology, University of Toronto at Mississauga, Mississauga, ON L5L 1C6, Canada

SANJA HINIC

Department of Geology, University of California, One Shields Avenue, Davis, CA 95616

MICHAEL A. RAATH

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand
Private Bag 3, Wits 2050, South Africa

ABSTRACT

This paper presents a comprehensive description of the cranial structure of the sauropodomorph dinosaur *Massospondylus carinatus*, based on four well-preserved skulls (including one of a juvenile individual) from the Lower Jurassic Elliot and Clarens formations of South Africa. *Massospondylus* can be distinguished from other basal sauropodomorph dinosaurs by the following combination of primitive and derived cranial character-states: The greatest transverse width of the skull exceeds its dorsoventral height by at least 10 percent. Even in adult specimens, the orbit is proportionately large and the antorbital region proportionately short. The maxilla has a tall, nearly vertical dorsal process, and its medial sheet is narrow anteroposteriorly. A long posterior process of the prefrontal extends along the dorsal margin of the orbit, but the frontal still participates significantly in the formation of the orbital margin. There is a distinct ridge on the dorsolateral aspect of the lacrimal and a knob on the lateral surface of the prefrontal. A partial skull from the Lower Jurassic Kayenta Formation of Arizona previously attributed to *Massospondylus* differs from the South African material in several cranial and dental features and is not referable to this taxon.

KEY WORDS: Dinosauria, Saurischia, Sauropodomorpha, Lower Jurassic, Elliot Formation, Clarens Formation, South Africa

INTRODUCTION

Sauropodomorph dinosaurs first appear in the fossil record during the early Late Triassic (Carnian) (Langer et al. 1999; Yates 2003A; Yates and Kitching 2003). Basal taxa of this clade, which are traditionally grouped together as Prosauropoda Huene, 1920, became the principal large herbivores in Late Triassic and Early Jurassic continental ecosystems worldwide (Galton 1984; Wing and Sues 1992). Skeletal remains of these dinosaurs have been known to science since the first half of the nineteenth century. First named 150 years ago (Owen 1854), *Massospondylus carinatus* is now known from scores of well-preserved specimens from the Lower Jurassic Elliot and Clarens formations (commonly informally grouped together with the Molteno Formation as the "Stormberg Group") in South Africa and Lesotho, and from the correlative Forest Sandstone Formation in Zimbabwe (Cooper 1981). Cooper (1981) presented a detailed description of its postcranial skeleton. Haughton (1924) and Huene (1932) described (under the specific designation *Massospondylus harriesi*) fragments of a skull that had been destroyed by the blow of a pick during excavation. Later authors (Cooper 1981; Attridge et al. 1985; Crompton and Attridge 1986; Galton 1990; Gow et al. 1990) reported on cranial features of *Massospondylus carinatus* and even attempted reconstructions of the skull, but the cranial structure of this dinosaur, with the exception

of the braincase (Gow 1990), has never been documented in detail.

The present account is based on four well-preserved skulls, which formed part of a suite of specimens briefly reviewed by Gow et al. (1990) and are housed in the collection of the Bernard Price Institute for Palaeontological Research at the University of the Witwatersrand in Johannesburg. They are of particular interest because they represent different growth stages. We did not have access to cranial material referable to *Massospondylus carinatus* housed in the collections of the South African Museum in Cape Town. Gow et al. (1990) deemed it unnecessary to provide a detailed account of the skull of *Massospondylus* in view of its overall similarity to that of *Plateosaurus* from the Upper Triassic (Norian) of France, Germany, and Switzerland. As Huene (1932) noted, there exist a number of cranial differences between these taxa, and, in view of their different phylogenetic relationships (Yates 2003B), a comprehensive description of the skull of *Massospondylus* is clearly warranted. Throughout the following description, comparisons are made with the skull of *Plateosaurus*, which is currently the best known basal sauropodomorph dinosaur. These comparisons draw on the detailed, profusely illustrated descriptions by Huene (1926) and Galton (1984, 1985) and on our examination of

an excellently preserved, disarticulated skull referable to *P. longiceps* (AMNH 6810).

In this paper, we employ the standard directional terminology of comparative anatomy rather than that of veterinary anatomy now used by some students of dinosaurian anatomy. Furthermore, for teeth, "mesial" denotes toward the mandibular symphysis and "distal" toward the jaw joint.

INSTITUTIONAL ABBREVIATIONS

AMNH—American Museum of Natural History, New York

BP—Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa

MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, MA

SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842

Saurischia Seeley, 1887

Sauropodomorpha Huene, 1932

Massospondylidae Huene, 1914 *sensu* Yates, 2003B

Massospondylus carinatus Owen, 1854

Holotype.—The holotype of *Massospondylus carinatus* formed part of a suite of postcranial skeletal remains, representing at least two individuals, discovered by Dr. R.J.N. Orpen and Mr. J.M. Orpen on the farm Beauchef (frequently incorrectly given as "Beaucherf") Abbey in the Harrismith District of South Africa (28° 31' S 29° 10' E; straddling the boundary between 1:50000 map sheets 2829CA Harrismith and 2829CA Oliviershoek). This material was subsequently sent to the famous Museum of the Royal College of Surgeons in London (Seeley 1895; Cooper 1981). Owen (1854:97–100) briefly described (without illustration) this material, which comprised some 55 catalogued bones and fragments of bone, and somewhat arbitrarily assigned these remains to three separate taxa, *Massospondylus carinatus*, *Pachyspondylus orpeni*, and *Leptospondylus capensis*. He considered the three forms to have lacertilian affinities. Seeley (1895) argued that Owen's specimens represented but a single taxon, *Massospondylus carinatus*, which he explicitly compared to *Zanclodon*, which was the common generic designation for most Late Triassic sauropodomorphs from Germany at that time. Huene (1906) concurred with Seeley's assessment and described a number of bones in more detail. Owen's material of *Massospondylus carinatus* was derived from strata of the upper Elliot Formation (Kitching and Raath

1984: table 1). It was destroyed during a German air raid on London during World War II, but plaster casts of at least some of Owen's specimens had previously been distributed to and are still preserved in other museums (Huene 1906; Cooper 1981). In view of the fragmentary nature of Owen's (now lost) original material, we consider it advisable to designate a neotype for *Massospondylus carinatus*, but this step must await a comprehensive revision of all basal sauropodomorph dinosaurs from the "Stormberg Group" of South Africa. Specimen BP/1/4934, comprising a well-preserved skull and much of the postcranial skeleton of a large individual, would be an excellent candidate for a neotype.

Distribution.—The known stratigraphic range of *Massospondylus carinatus* extends from the middle Elliot to the lower Clarens formations (*Massospondylus* Range Zone) of the "Stormberg Group" (Kitching and Raath 1984). These units are considered Early Jurassic in age (Olsen and Galton 1984).

Attridge et al. (1985) referred a badly crushed but otherwise well-preserved partial cranium and mandible (MCZ 8893) from the Lower Jurassic Kayenta Formation of Arizona to *Massospondylus*. Our examination of this specimen, however, revealed several differences in cranial and dental features from the South African material that cast doubt on the validity of the original generic assignment. A reassessment of MCZ 8893 will be presented elsewhere.

The alleged occurrence of *Massospondylus* in the Lower Jurassic McCoy Brook Formation of Nova Scotia, Canada (Russell 1989), cannot be confirmed. Although the sauropodomorph material from that unit has yet to be studied in detail there is nothing to suggest its referral to *Massospondylus* (H.-D.S., pers. obs.).

Referred Specimens in this Study.—BP/1/4376 represents the smallest skull used in this study (Gow et al. 1990: fig. 3; Figs. 1 and 2). Cooper (1981:fig. 3) first presented a slightly diagrammatic drawing of this skull. It is associated with a considerable quantity of postcranial bones (Gow et al. 1990). Only the right side of the skull, including most of the right mandibular ramus and first ceratobranchial, is completely preserved. Many cranial bones on the left side are incomplete, displaced, or missing. The skull has been strongly compressed laterally during fossilization. Based on its small size (skull length: 94 mm) as well as its proportionately very large orbits and short snout, we consider BP/1/4376 a juvenile specimen of *Massospondylus carinatus*.

As a result of obliquely dorsoventral crushing during fossilization, the skull of BP/1/4779 (Gow et al. 1990:fig. 4; Figs. 3 and 4) appears wider transversely than the other specimens. It has also been compressed anteroposteriorly, especially in the antorbital region. Otherwise, the skull is complete. Its occipital surface

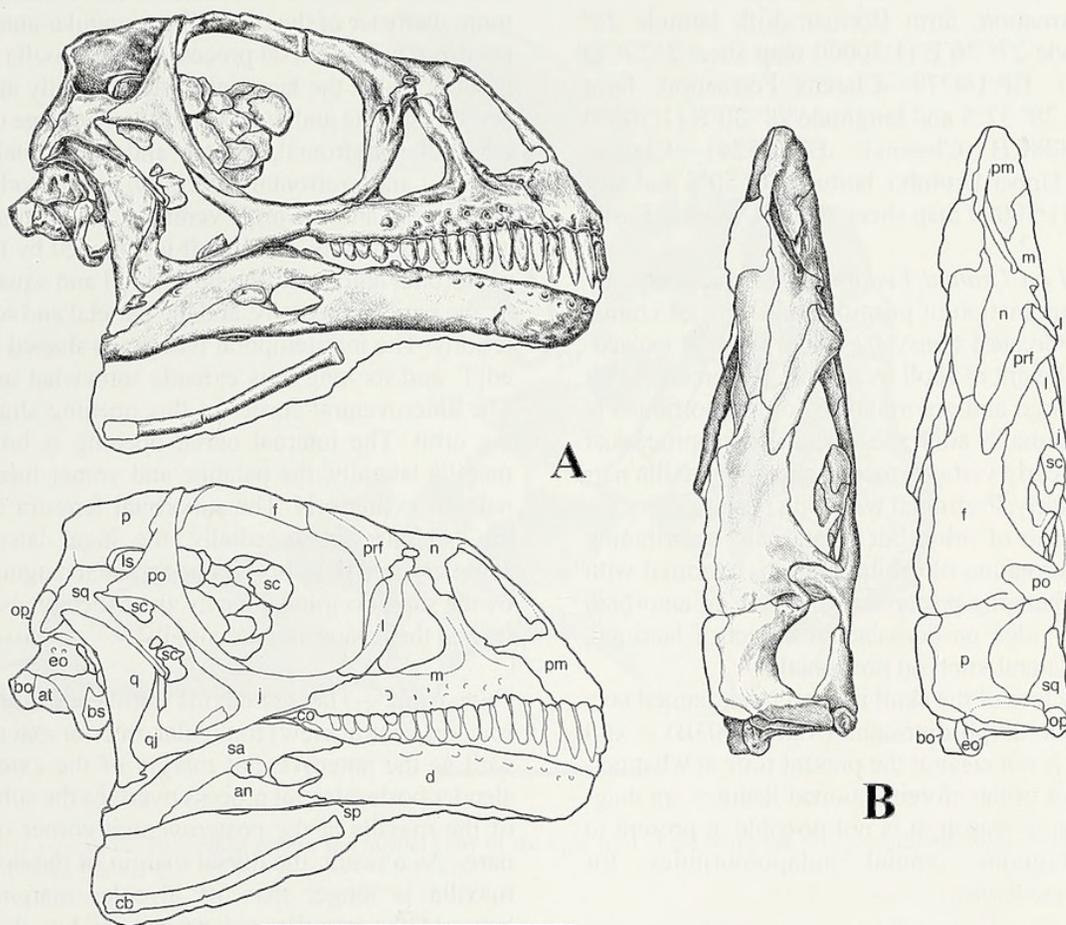


Fig. 1.—Skull of a juvenile specimen of *Massospondylus carinatus* (BP/1/4376) in (A) right lateral and (B) dorsal views, with explanatory diagrams. Scale bar = 5 cm. Abbreviations used in Figures 1–7: **an**, angular; **ar**, articular; **at**, atlantal intercentrum; **atn**, atlantal neural arch; **ax**, axis centrum; **bo**, basioccipital; **bs**, basisphenoid; **c.p.**, cultriform process of parasphenoid; **cb**, ceratobranchial I; **co**, coronoid; **d**, dentary; **ec**, ectopterygoid; **eo**, exoccipital; **ep**, epipterygoid; **f**, frontal; **fm**, metotic foramen; **fo**, fenestra ovalis; **i.c.**, foramen for passage of A. carotis interna; **j**, jugal; **l**, lacrimal; **ls**, laterosphenoid; **m**, maxilla; **n**, nasal; **o.c.**, occipital condyle; **op**, opisthotic; **os**, orbitosphenoid; **p**, parietal; **pa**, proatlas; **pl**, palatine; **pm**, premaxilla; **po**, postorbital; **pr**, prootic; **prf**, prefrontal; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **sc**, scleral ossicle; **so**, supraoccipital; **sp**, splenial; **sq**, squamosal; **st**, stapes; **t**, tooth; **v**, vomer. Roman numerals denote exits for cranial nerves.

is partially concealed by the still attached atlas-axis complex.

The skull of BP/1/4934 (Gow et al. 1990:fig. 1; Figs. 5 and 6) is the largest in the sample used in this study (reconstructed skull length: 210 mm) and is associated with much of a skeleton, which lacks only the tail and hind-limbs. In addition to considerable lateral compression, the skull was distorted along the sagittal plane during fossilization. Otherwise, it is well preserved and includes the complete right side of the cranium as well as the braincase. Much of the left side of the snout and skull roof was destroyed, exposing the left wall of the braincase and much of the palate in lateral view. The incomplete left side of the snout was displaced forward relative to the complete right side, and the two mandibular rami became separated at the symphysis.

BP/1/5241 (Gow et al. 1990:fig 2—listed incorrectly as “5247” in the figure legend; Fig. 7), the second largest individual used in this study, comprises a well-

preserved skull (skull length: 175 mm) associated with much of an articulated postcranial skeleton. The skull was strongly crushed laterally during fossilization. Only the more posterior portion of the palate could be exposed during preparation. The occipital region of the skull is, for the most part, concealed by the articulated cervical vertebrae. The mandible is not preserved.

Preservation of the skulls, especially those of BP/1/4934 and BP/1/5241, is generally good. In addition to the preservational deficiencies enumerated above, however, there is considerable small-scale fracturing and displacement of bone due to crushing of individual cranial elements.

Horizon and Locality Data for Referred Specimens.—

Gow et al. (1990) provided the following provenance information for the specimens used in this study: BP/1/4376—middle Elliot Formation, Blikana Mountain, Herschel District, latitude 30° 36'S and longitude 27°

37°E (1:50000 map sheet 3027AD Blikana); BP/1/4934—upper Elliot Formation, farm Bormansdrift, latitude 28° 57'S and longitude 27° 26'E (1:50000 map sheet 2827CD Mekoatlengnek); BP/1/4779—Clarens Formation, farm Tevrede, latitude 28° 32'S and longitude 28° 30'E (1:50000 map sheet 2828CB Clarens); BP/1/5241—Clarens Formation, farm Upper Drumbo, latitude 30° 50'S and longitude 27° 45'E (1:50000 map sheet 3027DC Barkly East).

Diagnosis Based on Cranial Features.—Characterized by the following combination of primitive and derived cranial character-states: Greatest transverse width of skull exceeding dorsoventral height of skull by at least 10 percent. Orbit proportionately large and antorbital region proportionately short even in presumably adult specimens. Dorsal process of maxilla tall and nearly vertical; medial sheet of maxilla narrow anteroposteriorly. Prefrontal with long posterior process along dorsal margin of orbit, but frontal still contributing significantly to formation of orbital margin. Lacrimal with lateral sheet overhanging posterodorsal corner of antorbital fenestra. Distinct ridge on dorsolateral aspect of lacrimal, continuous with lateral knob on prefrontal.

As the structure of the skull in most other named taxa of basal sauropodomorph dinosaurs (Yates 2003B) is still poorly known, it is not clear at the present time at what taxonomic level most of the aforementioned features are diagnostic. For the same reason, it is not possible at present to identify unambiguous cranial autapomorphies for *Massospondylus carinatus*.

DESCRIPTION

The following description is based on examination of all four skulls. The external surfaces of the cranial bones can be readily documented in detail, but most of the interior of three of the skulls could not be examined because it is still filled with matrix. Therefore, the description of the elements comprising the braincase is based primarily on BP/1/4376, which shows the medial surface of the right wall of the braincase and the basicranial region (Figs. 1 and 2), and BP/1/4934 (Figs. 5 and 6), which exposes much of the left lateral wall and occipital surface of the braincase. Additional information on the structure of the braincase is available in Gow's (1990) account, which was based on disarticulated material. Observations of palatal features are based on BP/1/4779 (Fig. 3) and BP/1/4934 (Fig. 5). Individual and ontogenetic variation in structural details is noted where appropriate. Few reliable measurements can be made on the skulls due to often extensive deformation and crushing of these specimens during fossilization (Gow et al. 1990).

Skull

The greatest transverse width of the skull is at the level of the sutural contact between the frontals and parietals. The large external naris is bounded by the premaxilla, maxilla,

and nasal. Its greatest diameter is more than half the maximum diameter of the orbit. The triangular antorbital fossa is bordered by the dorsal process of the maxilla anteriorly, the nasal dorsally, the lacrimal posterodorsally and posteriorly, and the maxilla and jugal ventrally. The large orbit is bounded by the prefrontal, frontal, and postorbital dorsally, the lacrimal and prefrontal anteriorly, the postorbital and jugal posteriorly, and the jugal ventrally. The supratemporal fenestra faces mainly dorsally. It is bounded by the frontal and postorbital anteriorly, the postorbital and squamosal laterally, the parietal medially, and the parietal and squamosal posteriorly. The infratemporal fenestra is shaped like an inverted T, and its long axis extends somewhat anteroventrally. The anteroventral corner of this opening slightly underlies the orbit. The internal narial opening is bordered by the maxilla laterally, the palatine and vomer medially, and the palatine posteriorly. The suborbital fenestra is bounded by the palatine anteromedially, the jugal laterally, and the ectopterygoid posteriorly. The foramen magnum is bordered by the supraoccipital dorsally, the exoccipitals ventrolaterally, and the basioccipital ventrally.

Premaxilla.—The premaxilla forms the transversely narrow, (in ventral view) triangular anterior end of the snout as well as the anteroventral margin of the external naris. Its slender posterolateral process overlaps the subnarial process of the maxilla at the posteroventral corner of the external naris. As a result, the dorsal margin of the body of the premaxilla is longer than its alveolar margin. The suture between the maxilla and premaxilla has the shape of an inverted L and intersects the alveolar margin just behind the fourth premaxillary tooth. A large, elliptical subnarial foramen is situated on the descending segment of this suture well above the tooth row. The transversely flattened dorsal (internarial) processes of the premaxillae taper as they curve posterodorsally and are overlapped by the anterior ends of the nasals posterolaterally. A row of small foramina extends above the alveolar margin, and additional openings are scattered on the anterolateral surface of the rather deep body of the premaxilla. These foramina presumably served as exits for terminal branches of subnarial branches of A. maxillaris and N. ethmoidalis medialis (Oelrich 1956). The narrow palatal surface of the premaxilla is not fully exposed in any of the available specimens. We concur with Yates (2003B) that the premaxilla exhibits no features that would indicate the presence of a rhamphotheca in life. Unlike in the dentary, the alveolus for the first tooth is situated close to the anterior end of the premaxilla, leaving no room for a rhamphotheca.

Maxilla.—The maxilla is triradiate, with a distinct anterior (subnarial) ramus, a long, nearly straight posterior ramus, and a tall, slightly recurved dorsal process, which separates the antorbital fossa from the external naris and is set back from the anterior end of the maxilla. The subnarial ramus of the maxilla forms a shallow fossa at the pos-

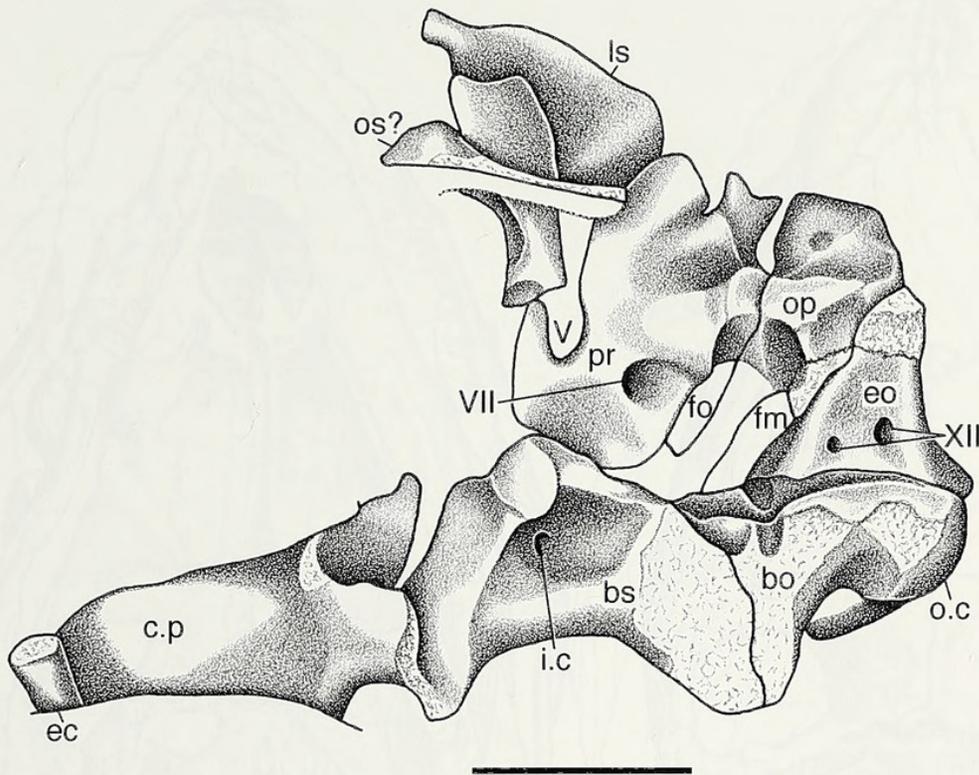


Fig. 2.—Left lateral view of the basicranial region and medial view of the right wall of the braincase of a juvenile specimen of *Massospondylus carinatus* (BP/1/4376). Scale bar = 1 cm.

teroverventral corner of the external naris and at the anteroventral corner of the antorbital fossa. The medial sheet of the maxilla forms the medial wall of the fossa anterior to the antorbital fenestra (internal antorbital fenestra sensu Witmer 1997). The sheet is narrow and distinctly embayed from behind, unlike the broad medial sheet with an almost straight posterior margin present in *Plateosaurus*. The posterior margin of the medial sheet extends more or less parallel to the anterior margin of the antorbital fossa. The nasal overlaps the dorsal process of the maxilla anterolaterally, but the maxilla contacts the lacrimal above the antorbital fenestra. The jugal overlaps the maxilla posterodorsally; the suture between these two bones extends obliquely from the posteroventral corner of the antorbital fenestra back to the level of the posterior part of the orbit. The posterior ramus of the maxilla is low dorsoventrally and, in lateral view, tapers to a point below the posterior half of the orbit. A row of six or seven supralabial foramina extends dorsal and parallel to the alveolar margin of the maxilla. These openings probably served as exits for cutaneous branches of *A. maxillaris* and *N. alveolaris superior* (Oelrich 1956). The posterior-most supralabial foramen is the largest and opens posteriorly. The right maxilla of BP/1/4934 has three minute foramina behind this large posterior foramen. In addition to the row of supralabial foramina, one or two additional openings are situated just anterior to the base of the dor-

sal (ascending) process of the maxilla. The medial contact of the maxilla with the vomer is short (BP/1/4779).

Nasal.—Dorsally, the nasals are gently arched above the external nares. The nasal is long, equivalent to about half the total length of the largest skulls. Anteriorly, the nasals are separated by the dorsal processes of the premaxillae, and, more posteriorly, by the intervening frontals. Each nasal is convex transversely, resulting in a longitudinal depression along their median sutural contact. Laterally, the nasal contributes to the lateral edge of the antorbital fossa dorsally and overhangs the dorsal apex of the fossa, forming a deep recess similar to that in *Plateosaurus* (Witmer 1997). The nasal does not have a posterolateral process, unlike in *Plateosaurus* (Yates 2003A:fig. 10B, cl.p). It forms the posterodorsal margin of the external naris and overhangs this opening dorsally. The triangular ventral process of the nasal does not contact the posterior process of the premaxilla, and the maxilla forms the posteroventral margin of the external naris. The right nasal of BP/1/4934 bears two small openings, possibly for passage of cutaneous branches of *N. ethmoidalis lateralis*, on its dorsolateral aspect; these features are absent on the other skulls used in this study. The anterior foramen opens into an anteriorly extending groove whereas the posterior one has a posteriorly extending groove.

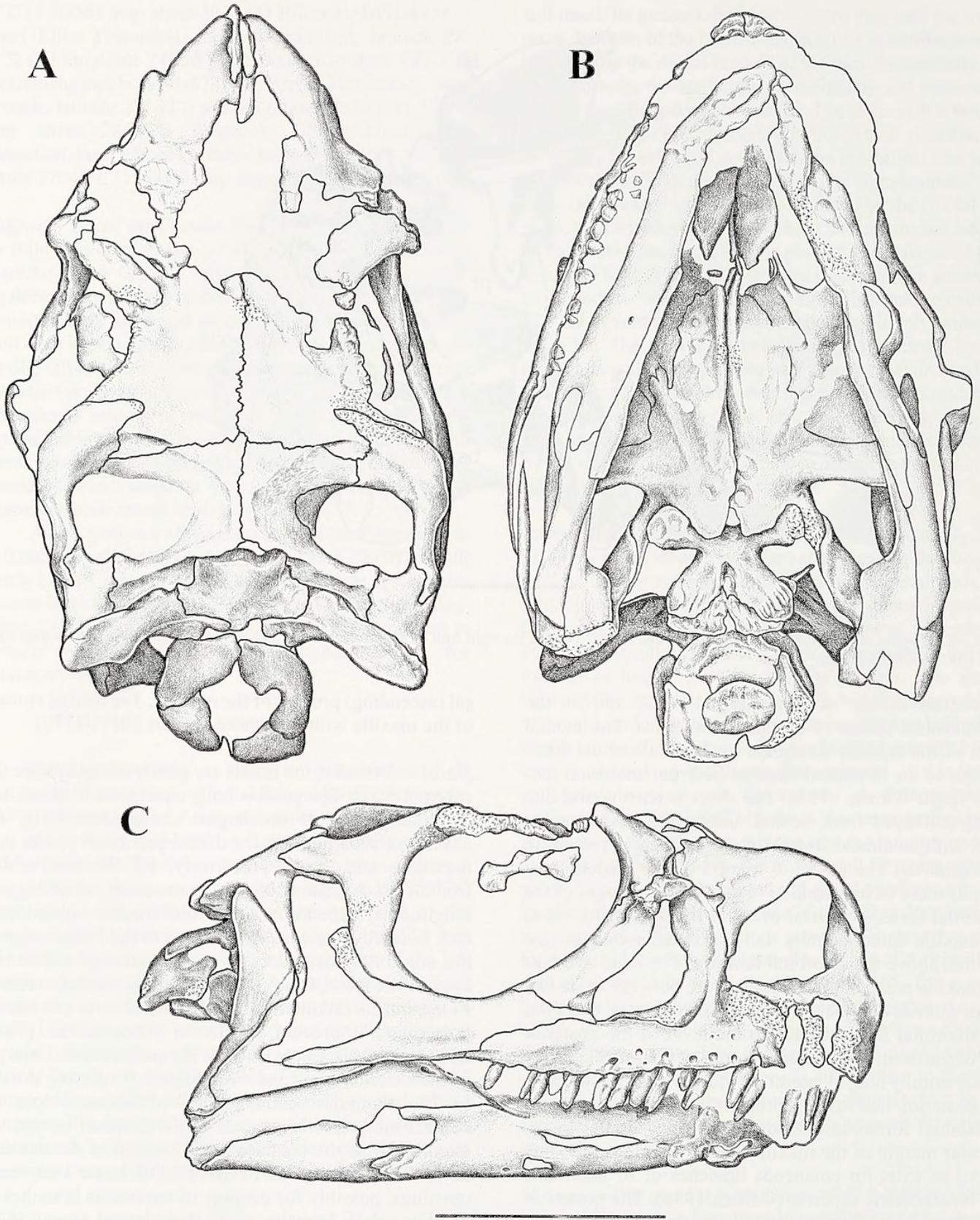
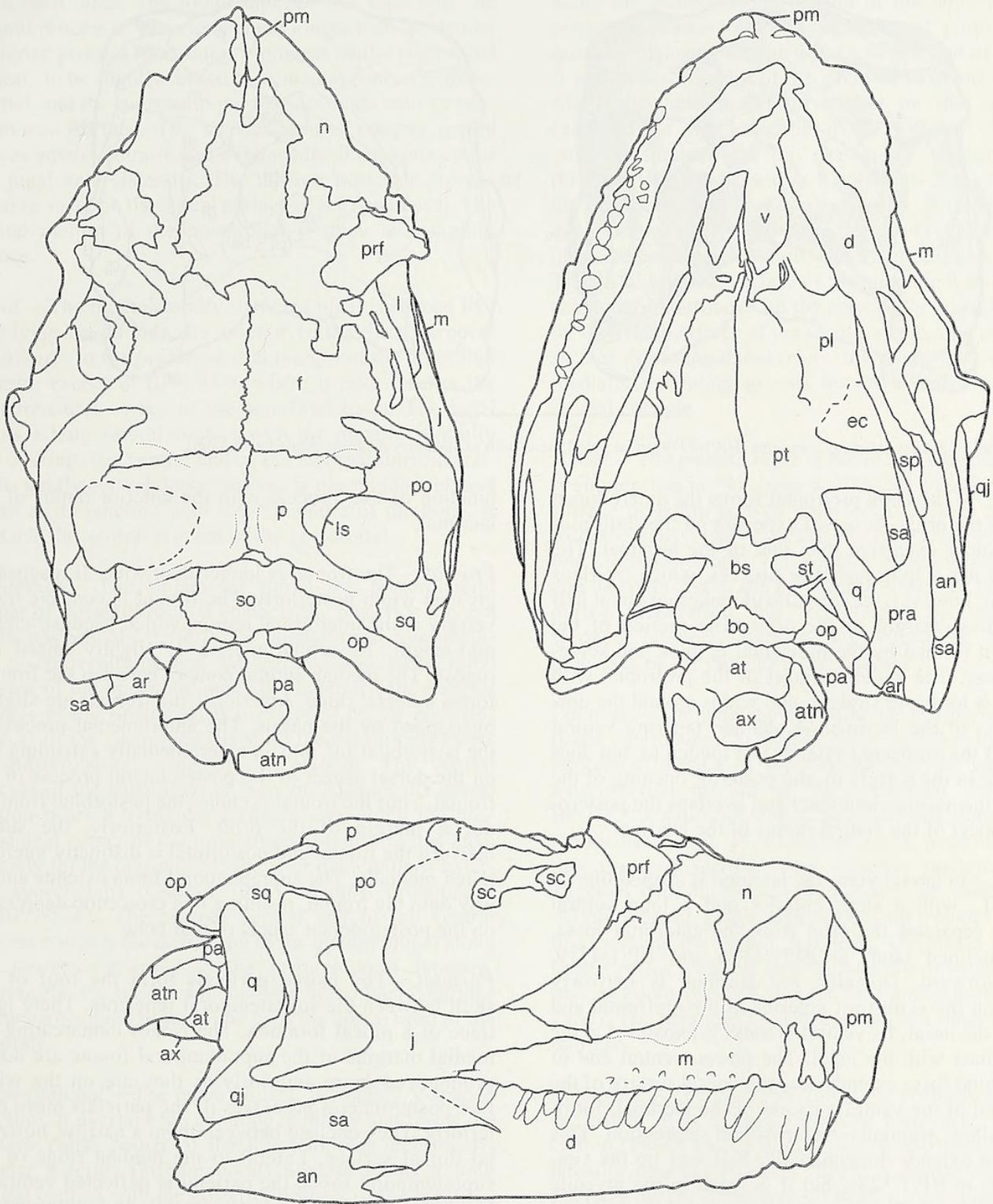


Fig. 3.—Skull of *Massospondylus carinatus* (BP/1/4779) in (A) dorsal, (B) ventral, and (C) right lateral views, with explanatory diagrams. Scale bar = 5 cm.



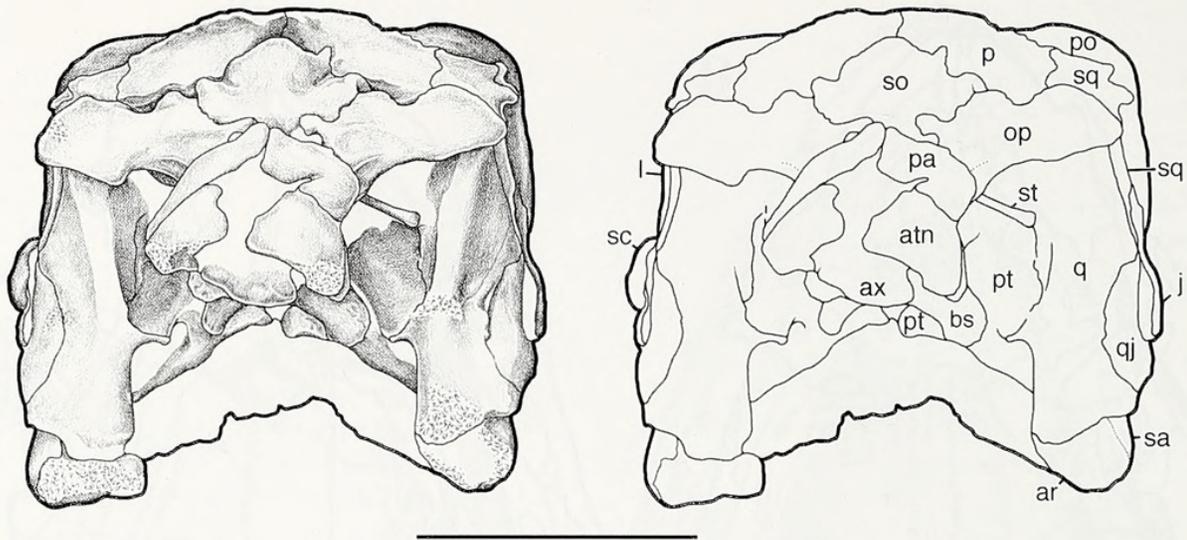


Fig. 4.—Skull of *Massospondylus carinatus* (BP/1/4779) in occipital view, with explanatory diagram. Scale bar = 5 cm.

Prefrontal.—The large prefrontal forms the anterodorsal margin of the orbit. Its dorsal exposure on the skull roof is much more extensive than that of the lacrimal. The prefrontal has a long posterior process, which overlaps the frontal; however, the frontal still makes up about half of the dorsal margin of the orbit. The section of the orbital rim formed by the prefrontal is thick and somewhat rugose. The sutural contact of the prefrontal with the nasal is long and straight, and wraps around the dorsal portion of the lacrimal. A slender, tapering ventral process of the prefrontal extends just medial to, but does not participate in the margin of, the posterior opening of the canal for the nasolacrimal duct and overlaps the posteromedial aspect of the ventral ramus of the lacrimal.

Lacrimal.—In lateral view, the lacrimal is shaped like an inverted L, with a short anterior and a long ventral ramus. It separates the orbit from the antorbital fossa, and is inclined (and, in BP/1/4376 and BP/1/4779, bowed) forward. Dorsally, the lacrimal is narrowly exposed on the skull roof anterior to the prefrontal and lateral to the nasal. Its ventral process is expanded at the distal contact with the jugal. The posteroventral end of the antorbital fossa extends onto the lateral surface of the ventral end of the ventral process of the lacrimal, forming a shallow, triangular ventrolateral depression. This depression extends dorsomedially half way up the ventral ramus in BP/1/5241, but it is small in the juvenile specimen BP/1/4376. The anterior ramus of the lacrimal forms a subtriangular lateral lamina that overhangs the posterodorsal portion of the antorbital fossa. The dorso-lateral surface of the lacrimal bears a ridge, which is most pronounced in BP/1/4934. This ridge is associated with a knob on the lateral aspect of the prefrontal on all four specimens. The posterior opening of the canal for the nasolacrimal duct is situated on the posteromedial aspect of the ventral ramus of the lacrimal below the

junction of that process with the anterior ramus of the lacrimal.

Frontal.—The frontal is longer than wide. It reaches its greatest width posteriorly. The frontal is concave transversely in the interorbital region, which is constricted at mid-length. Its orbital margin is slightly raised and rugose. The median sutural contact between the frontals forms a dorsal ridge. Anteriorly, the frontals are slightly overlapped by the nasals. The anteromedial process of the postorbital fits into an anteromedially extending slot on the dorsal aspect of the posterolateral process of the frontal. Thus the frontal excludes the postorbital from the dorsal margin of the orbit. Posteriorly, the suture between the frontal and postorbital is distinctly interdigitated medially. The supratemporal fossa extends anteriorly onto the frontal, resulting in a crescentic depression on the posterodorsal aspect of that bone.

Parietal.—The paired parietals form the roof of the skull between the supratemporal fenestrae. There is no trace of a pineal foramen. The ridges demarcating the medial margins of the supratemporal fossae are not as pronounced more anteriorly as they are on the wing-like posterolateral processes of the parietals more posteriorly. They enclose between them a narrow, horizontal dorsal surface. Lateral to the median ridge of the supratemporal fossa, the parietal is deflected ventrally. In dorsal view, the posterolateral and anterolateral processes of the parietal separated by a median constriction. The posterolateral process is deflected ventrolaterally and contacts the medial process of the squamosal slightly below the level of the dorsal surface of the skull roof.

Postorbital.—The triradiate postorbital separates the orbit, infratemporal fenestra, and supratemporal fenestra

from each other. The robust anterior and especially the ventral process of this element are longer than its slender posterior process. The anterior process of the postorbital appears to be slightly forked at its medial contact with the frontal, and the supratemporal fossa extends onto its posterodorsal surface. The slender ventral process gently curves anteroventrally and overlaps the dorsal process of the jugal anterolaterally. The tapered posterior process fits into a slot on the lateral surface of the squamosal. The orbital margin of the postorbital is thick and slightly rugose.

Jugal.—The mediolaterally flattened jugal is shaped like a Y lying on its side. Its anterior (infraorbital) process contributes to the posteroventral margin of the antorbital fenestra except in BP/1/4376 where it only reaches the posteroventral corner of the antorbital fossa. The jugal forms a long sutural contact with the maxilla ventrally and overlaps the ventral end of the lacrimal dorsolaterally. Its gently curved dorsal process is placed far back and broad at its junction with the remainder of the bone. It contacts the ventral process of the postorbital.

Squamosal.—The squamosal forms the posterolateral corner of the skull roof. It contacts the posterior process of the postorbital anteriorly, the quadrate and quadratojugal posteroventrally, and the parietal and paroccipital process of the opisthotic medially. Laterally, the anterior process of the squamosal is overlapped by the posterior process of the postorbital. Its short medial process meets the posterolateral wing of the parietal. The ventral process of the squamosal is long and slender. Its dorsal portion bears a triangular recessed area along the posterodorsal corner of the infratemporal fenestra; this area, possibly for the origin of *M. adductor mandibularis externus superficialis* (Ostrom 1961), is most pronounced in BP/1/5241. The tapered ventral end of the ventral process contacts the dorsal end of the quadratojugal along the posterior margin of the infratemporal fenestra. Posteriorly, the squamosal abuts the anterolateral surface of the paroccipital process and caps the dorsal head of the quadrate.

Quadratojugal.—The quadratojugal is roughly V-shaped and thin. It overlaps the quadrate medially and forms the posteroventral corner of the infratemporal fenestra. Its slender anterior (infratemporal) process forms a long sutural contact with the posterior process of the jugal.

Quadrate.—The tall quadrate is gently sigmoidal in lateral view and divided into two parts that extend at nearly right angles to each other. A large, anteromedially directed flange overlaps the pterygoid; the base of this flange is not as deep dorsoventrally as in *Thecodontosaurus* (in which it equals more than 70 percent of the total height of the quadrate; Yates 2003B). A thickened ridge extends

along the posteromedial margin of the bone where the pterygoid flange joins the anterolateral portion of the quadrate that supports the distal articular end of the bone. It terminates dorsally in the small head of the quadrate, which fits into a ventral socket on the squamosal (exposed on the left side in BP/1/4934). A narrow quadrate foramen for the passage of *V. mandibularis* (Oelrich 1956) is incised as a notch into the lateral margin of the quadrate medially and is bounded by the quadratojugal laterally. The posterior surface of the quadrate bears a depression with a central pit or foramen. The distal articular surface of the quadrate is more or less triangular in outline, with the apex of the triangle formed by the lateral corner of the facet and the long axis of the surface extending transversely. It is divided by an antero-medially extending groove into a lateral and a larger medial condyle.

Vomer.—The paired vomer is broad and relatively slightly shorter than in *Plateosaurus* (AMNH 6810). Its ventral surface is gently convex transversely, which sets it off from the transversely concave ventral surface of the palatine more posteriorly. The anterior extent of the element and its contact with the premaxilla could not be exposed during preparation, but, posteriorly, the vomers are wedged between slender, dorsoventrally expanded processes of the pterygoid and palatine.

Palatine.—The palatine forms the central portion of the palate anterolateral to the pterygoid. It makes up the posteromedial margin of the internal naris as well as the anteromedial margin of the suborbital fenestra. In BP/1/4779, a distinct ventral ridge extends along the posteromedial margin of the internal naris; posteromedial to this crest, a second ridge extends posterolaterally. Together with the median pterygoid ridge, these features delimit a broad, gently concave palatal trough. The palatine contacts the vomer anteriorly, and has a relatively short contact with the maxilla laterally. It lacks the ventral, peg-like process present in *Plateosaurus* (Galton 1984). The palatines do not contact each other along the midline.

Pterygoid.—The pterygoid forms the posterior portion of the palate. It is a large, complex bone that, following Galton (1984), can be divided into a posterodorsally and laterally directed quadrate flange, a central region with the facet for the basiptyergoid joint, a transverse process, and an anterodorsally extending palatal ramus. Posteriorly, the quadrate flange forms a deep vertical lamina of bone, which rises just lateral to the basiptyergoid joint and is separated from the central region of the bone by a constriction. The basiptyergoid joint is situated between the palatal and quadrate rami of the pterygoid; a dorsomedially facing facet on the pterygoid receives the distal end of the basiptyergoid process of the basisphe-

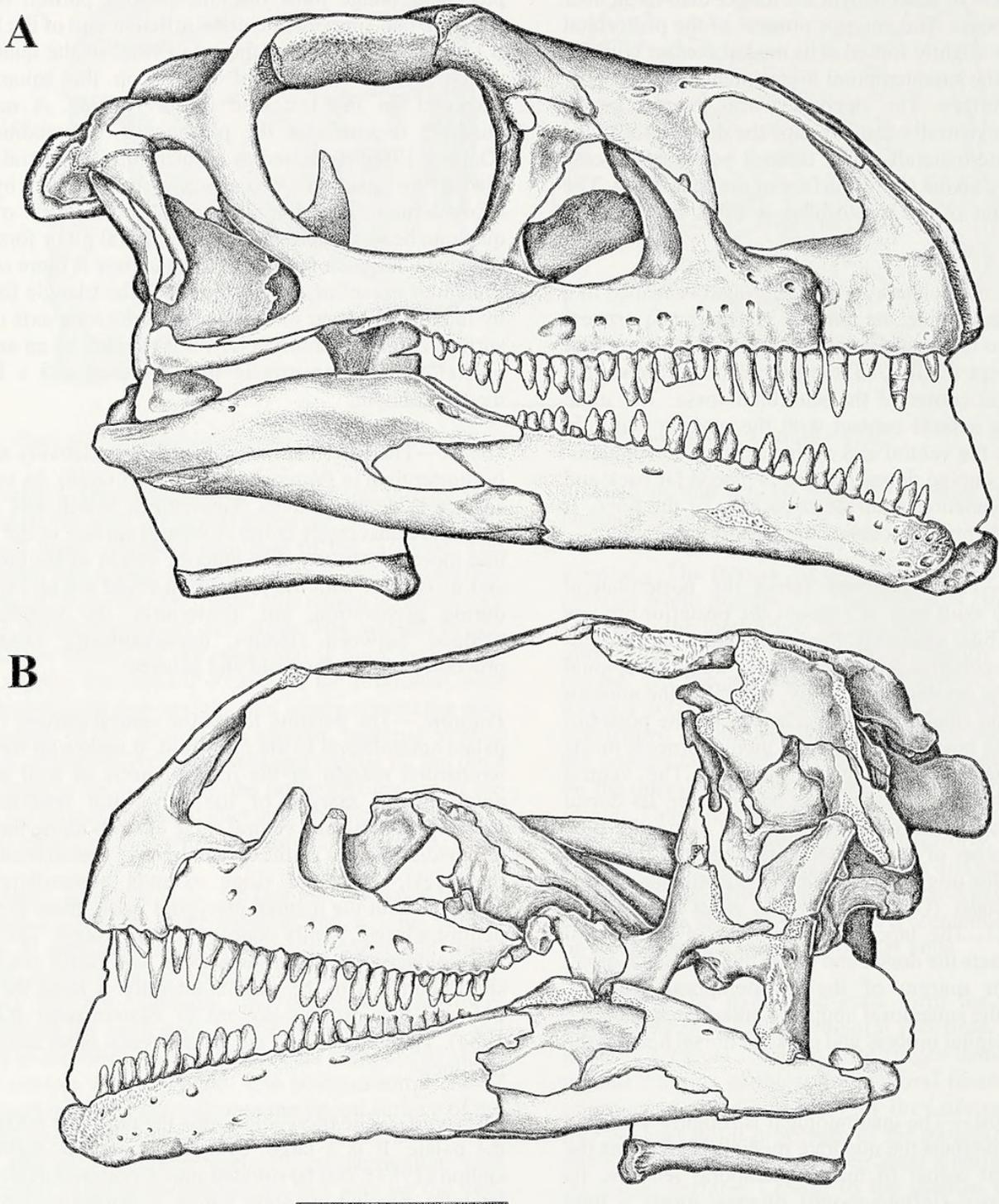
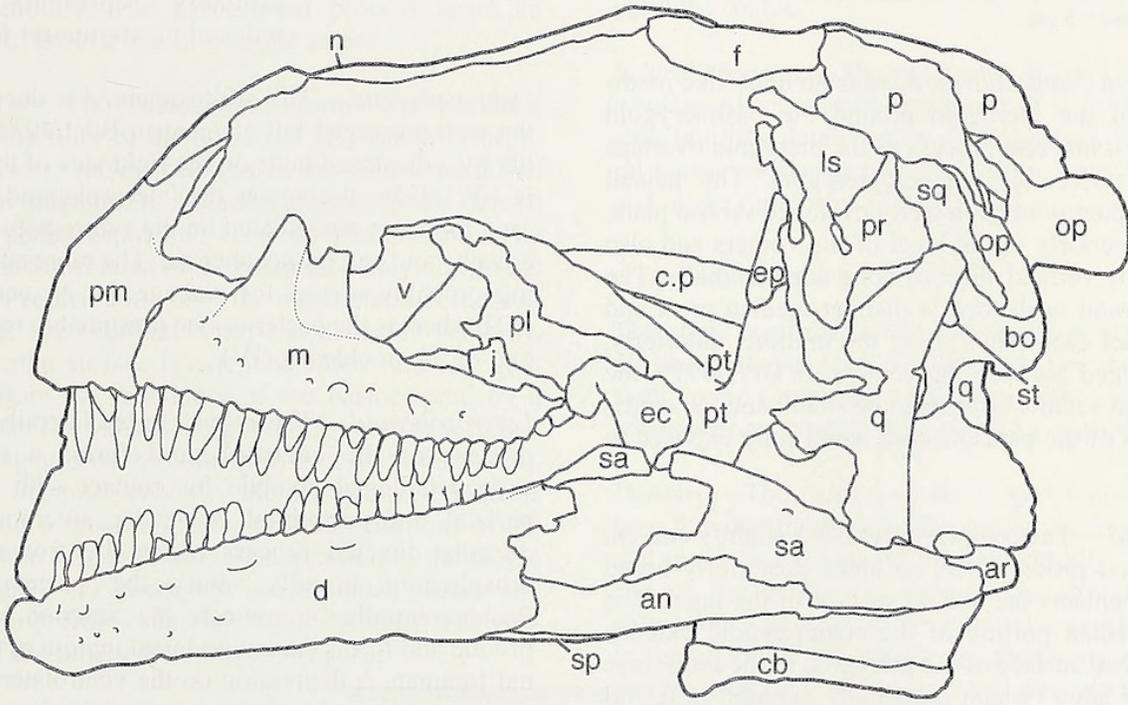
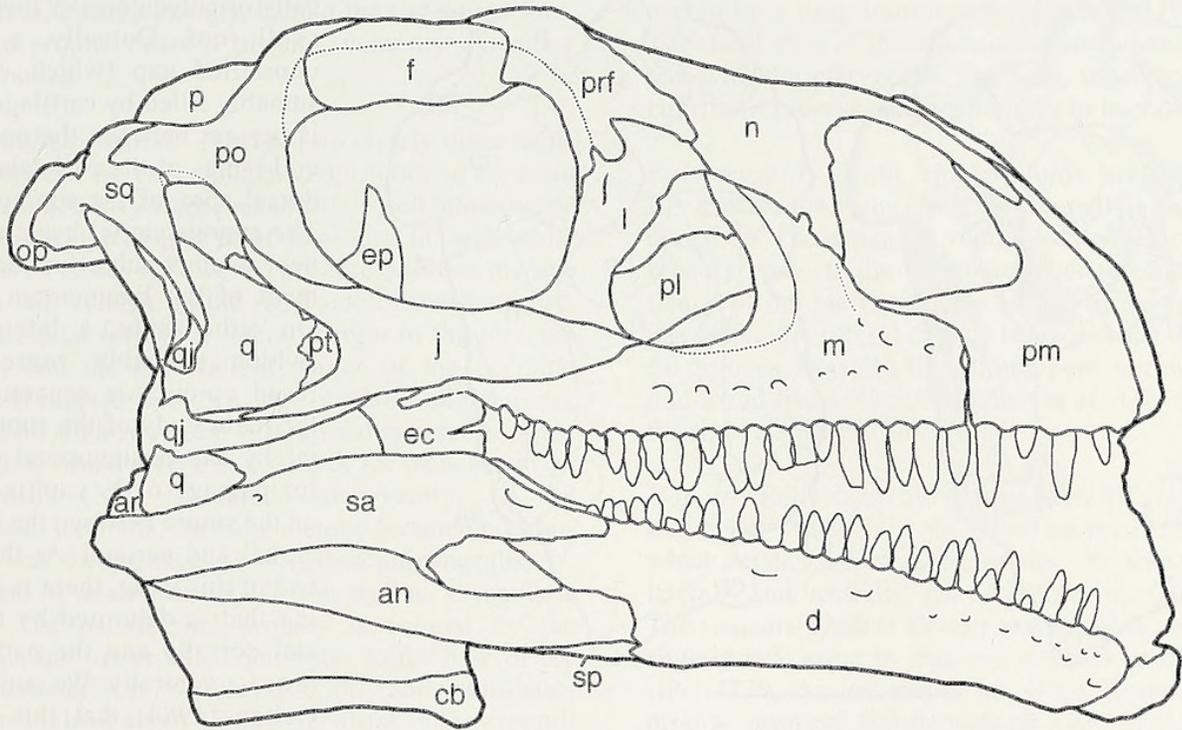


Fig. 5.—Skull of *Massospondylus carinatus* (BP/1/4934) in (A) right and (B) left lateral views with explanatory diagrams. Scale bar = 5 cm.



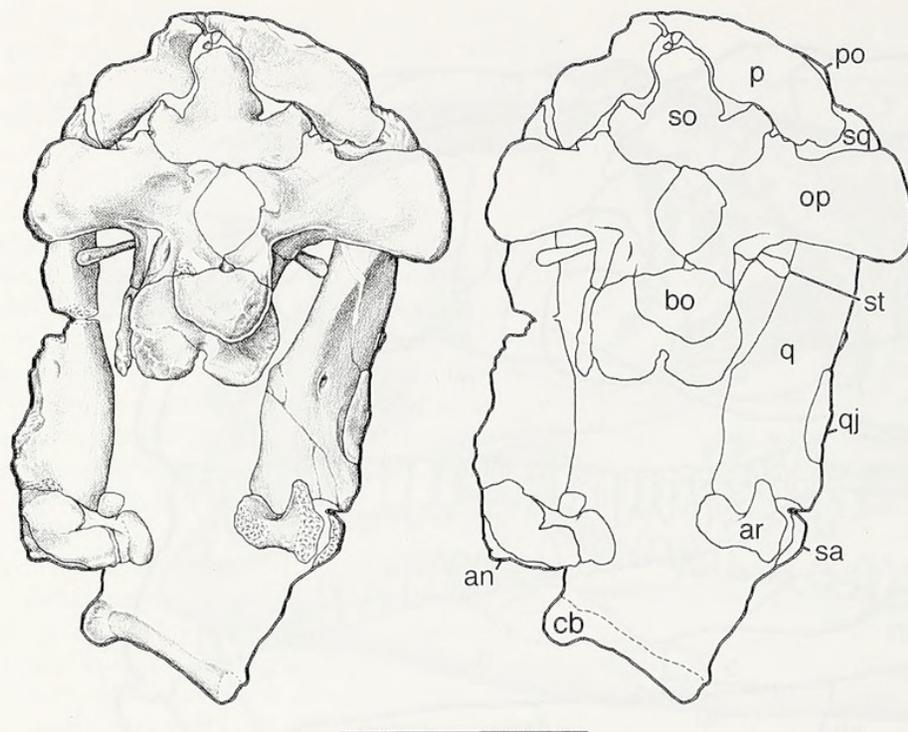


Fig. 6.—Skull of *Massospondylus carinatus* (BP/1/4934) in occipital view, with explanatory diagram. Scale bar = 5 cm.

noid. Unlike in *Plateosaurus*, there is no hook-like medial process of the pterygoid around the basiptyergoid process. The transverse process of the pterygoid overlaps the medial surface of the ectopterygoid. The palatal ramus of the pterygoid has a well-developed ventral plate, but tapers anteriorly to the level of the vomers and also forms a nearly vertical sheet of bone dorsomedially. The two palatal rami each form a distinct median crest and almost contact each other along the midline; anteriorly, they are wedged between the vomers. In BP/1/4779, the interptyergoid vacuity appears to be small, and the cultriform process of the parasphenoid is not fully exposed in ventral view.

Ectopterygoid.—The ectopterygoid has a slightly curved, rod-like lateral process with an anteroposteriorly broad end, which contacts the medial surface of the jugal. The expanded median portion of the ectopterygoid extends along the dorsal surface of the pterygoid to the transverse flange of the latter (which is partially exposed in lateral view on the left side of BP/1/4934), and meets the palatine dorsomedially.

Supraoccipital.—The supraoccipital makes up the dorsal margin of the foramen magnum and slopes anterodorsally, projecting slightly above the opening posteriorly. It contacts the occipital flanges of the parietals dorsally and laterally and the exoccipitals-opisthotics ventrolaterally. The supraoccipital is slightly wider transversely than tall dorsoventrally, being widest in its ventral portion, and

becomes narrower and more vertically oriented dorsally towards the skull roof. Dorsally, a median unossified gap (which was presumably filled by cartilage in life) is present between the posterolateral wings of the parietals and the dorsal apex of the supraoccipital. The supraoccipital bears a prominent median ridge for the attachment of the ligamentum nuchae. On either side, a lateral wing (which probably represents a fused epiotic) is separated from the main body of the supraoccipital by the posttemporal foramen for passage of V. capitis dorsalis on the suture between the supraoccipital and parietal. At the lateral end of this wing, there is an opening that is delimited by the parietal dorsally and the paroccipital process ventrally. We concur with Galton (1984) that this opening probably represents a much reduced posttemporal fenestra.

Orbitosphenoid.—The orbitosphenoid is documented by the well-preserved left element in BP/1/4934 and possibly by a displaced bone on the right side of the braincase in BP/1/4376. It contacts the laterosphenoid posteriorly. Two foramina are situated on the suture between the laterosphenoid and orbitosphenoid. The more anterior opening probably served for passage for N. oculomotorius (III), whereas the posterior one presumably represents the exit for N. trochlearis (IV).

Laterosphenoid.—The robust, anterolaterally projecting process of the laterosphenoid forms a transversely expanded dorsal condyle for contact with the frontal, parietal, and postorbital. A slender, anteromedially and dorsally directed process meets the frontal. The laterosphenoid broadly abuts the parietal dorsally. Posteroventrally, it contacts the anterior edge of the prootic and forms the anterodorsal margin of the trigeminal foramen. A depression on the ventrolateral aspect of the laterosphenoid probably received the dorsal end of the columella of the epipterygoid.

Prootic.—The prootic forms much of the lateral wall of the braincase, and broadly contacts the parietal dorsally. Its lateral surface is perforated by a large foramen for N. trigeminus (V), which is bounded posteriorly by a depression. A groove for ramus ophthalmicus of N. trigeminus (V_1) extends anterodorsally along the ventrolateral aspect of the laterosphenoid. Posteriorly, the prootic overlaps the

lateral aspect of the opisthotic at the base of the paroccipital process. Posterolaterally, behind the trigeminal foramen, the prootic bears a distinct, ventrally extending crista prootica.

Exoccipital-Opisthotic.—There is no clearly discernable suture between the exoccipital and opisthotic in the adult specimens, and they were presumably fused into a single element (otoccipital) as in most dinosaurs. In the juvenile specimen BP/1/4376, however, a suture between the two bones is still evident on the right side of the braincase. The exoccipital forms the lateral margin of the foramen magnum and the dorsolateral corner of the occipital condyle. It is perforated by a large posterior foramen and, anterior and slightly ventral to it, a smaller anterior opening, both of which served as passages for branches of *N. hypoglossus* (XII). Situated anteroventral to the hypoglossal foramina, the large metotic foramen presumably served for passage of *N. glossopharyngealis*, *N. vagus*, and *N. accessorius* (IX-XI) as well as *V. jugularis interna*. The paroccipital process is formed by the opisthotic, but the prootic contributes to the base of the process anteriorly. It projects posteriorly and ventrolaterally at an angle of about 45°, and its distal end is expanded dorsoventrally. The paroccipital process bears an anteroventral groove that houses the stapes.

Basioccipital.—The basioccipital forms the posterior portion of the floor of the braincase and narrowly separates the bases of the exoccipitals on the ventral margin of the foramen magnum. It contacts the exoccipitals dorsally and the parabasisphenoid ventrally and laterally. The basioccipital forms most of the occipital condyle, with the exoccipitals contributing only the dorsolateral corners of the condyle. The occipital condyle is deflected ventrally, and its articular surface is extended anteroventrally. It is separated from the remainder of the basioccipital by a distinct neck. The ventral margin of the condyle is in line with the long axis of the cultriform process (BP/1/4934). Below the occipital condyle, the basioccipital extends ventrally and forms the greater posterior portions of the stout and short basal tubera. In occipital view, the tubera are separated by a small but deep median recess and slightly diverge from each other ventrolaterally. The ventral ends of the tubera are distinctly rugose.

Basisphenoid-Parasphenoid.—As in most dinosaurs, the basisphenoid and parasphenoid are indistinguishably fused into a single element (parabasisphenoid), which forms the anterior portion of the floor of the braincase as well as the cultriform process, and contributes the small anterior portions of the basal tubera. The body of the compound bone bears an elliptical lateral depression; a small foramen at the anterior end of this depression represents the posterior opening of the canal for passage of *A. carotis interna*. The basiptyergoid processes sharply

diverge from each other ventrolaterally, and are not connected by a deep transverse septum as in *Plateosaurus*. The distal ends of these processes are expanded for contact with the pterygoids. The long, transversely narrow cultriform process tapers anteriorly in lateral view.

Epipterygoid.—Both epipterygoids are preserved in BP/1/4934; the right element is complete except for its dorsal tip. The expanded ventral base of the epipterygoid broadly contacts the anterodorsal edge of the quadrate flange of the pterygoid. The lateral surface of the bone just above the sutural contact bears a series of fine vertical grooves. Dorsally, the epipterygoid narrows gradually into a rod-like columella, which is slightly recurved on the right element in BP/1/4934.

Stapes.—Both stapes are preserved in BP/1/4779 (Fig. 4) and in BP/1/4934 (Fig. 6). Based on the latter specimen, which retains the elements in situ, the stapes projected laterally and ventrally, as in *Plateosaurus* (Huene 1926). The stapedial shaft is slender and round in cross-section, slightly increasing in diameter towards its distal end. In BP/1/4779, the left stapes has been displaced from its original position, and its expanded proximal footplate is partially visible.

Scleral Ossicles.—The right orbit of BP/1/4376 contains a collapsed scleral ring composed of thin, plate-like ossicles, but little detail can be distinguished. Scattered scleral plates are also preserved in both orbits of BP/1/4779 and in the right orbit of BP/1/5241.

Mandible

This study confirms the statement by Gow et al. (1990) that the mandible of *Massospondylus* is not shorter than the skull, *contra* Crompton and Attridge (1986), who based their assessment on strongly dorsoventrally crushed specimens.

Dentary.—The dentary is the largest bone of the lower jaw. It is overlapped by the surangular posterodorsally, and overlaps the angular posteroventrally. The posterior end of the dentary is forked. The dentary forms the anterodorsal margin of the external mandibular fenestra. In the region of the symphysis, the lateral surface of the dentary bears numerous scattered neurovascular foramina. The splenial apparently covers much of the medial surface of the dentary. The first dentary tooth is set back from the anterior end of the bone by a distance equivalent to about one alveolar diameter, as in *Plateosaurus* and other basal sauropodomorph dinosaurs. A row of infralabial foramina (for passage of cutaneous branches of *N. alveolaris inferior* and associated vessels) extends parallel and just ventral to the alveolar margin of the dentary; the more posterior openings are slit-like and spaced further apart. A ridge extends obliquely anteroposteriorly

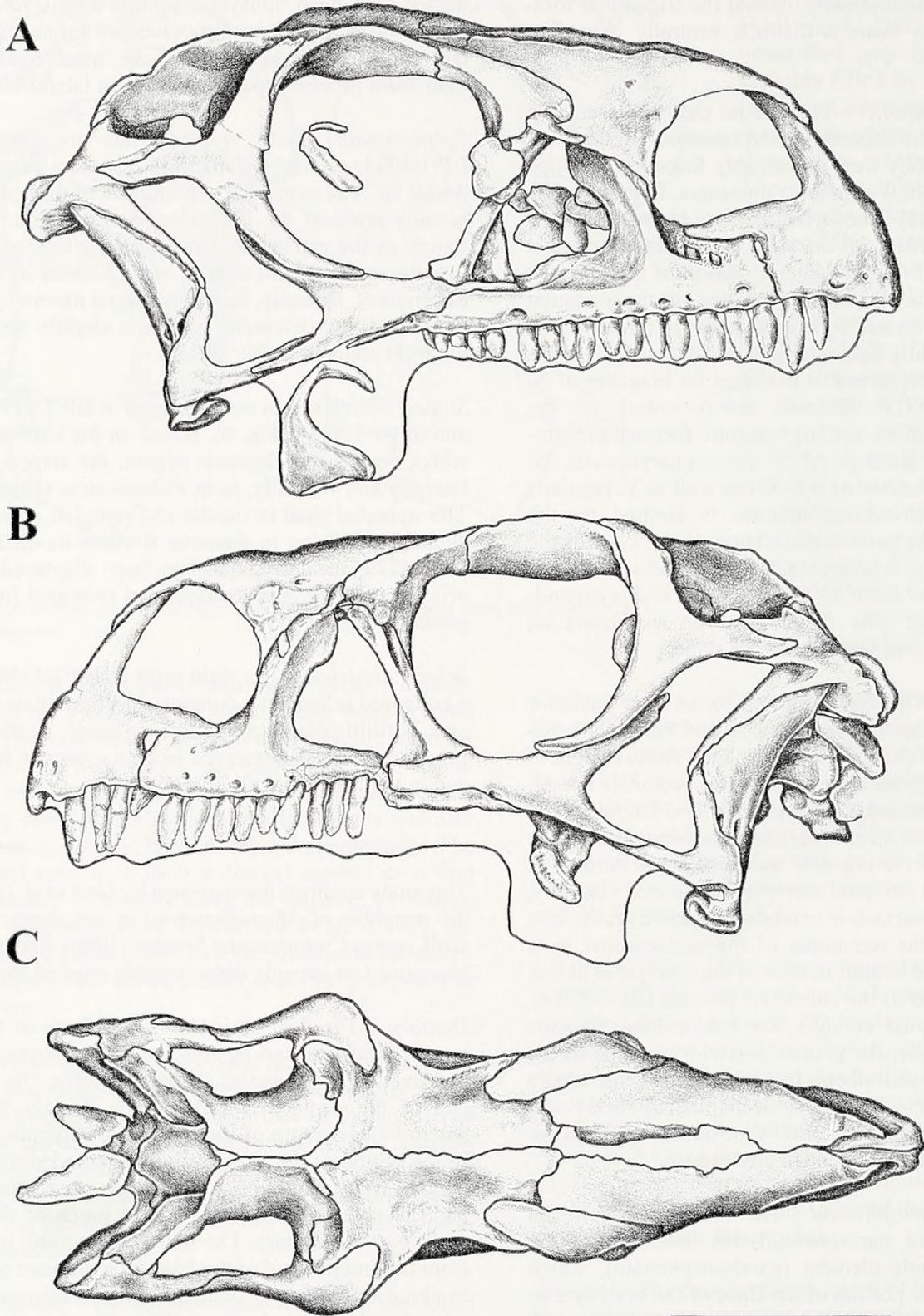
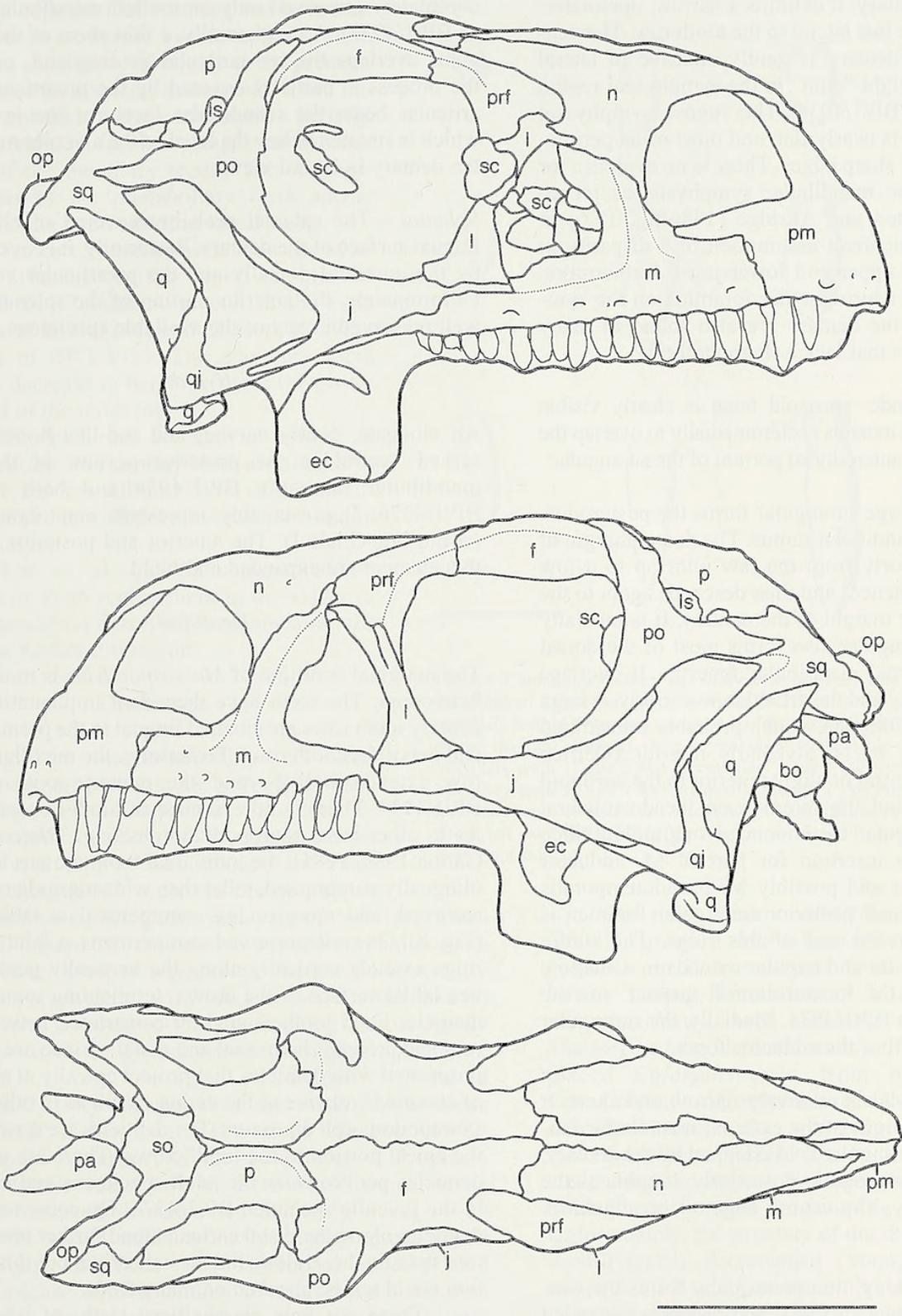


Fig. 7.—Skull (without mandible) of *Massospondylus carinatus* (BP/1/5241) in (A) right lateral, (B) left lateral, and (C) dorsal views, with explanatory diagrams. Scale bar = 5 cm.



below the posterior portion of the tooth row on the lateral surface of the dentary. It delimits a narrow, dorsolaterally inclined surface just lateral to the tooth row. The ventral margin of the dentary is gently concave in lateral view and forms a slight "chin" in the symphyseal region in BP/1/4376 and BP/1/4934. The rugose symphyseal facet of the dentary is nearly flat, and most of its perimeter is demarcated by sharp edges. There is no evidence for a beak covering the mandibular symphysis, as reconstructed by Crompton and Attridge (1986:fig. 17.6) in part based on the incorrect assumption of a disparity in length between the upper and lower jaws; furthermore, numerous scattered neurovascular foramina on the symphyseal portion of the dentary are also found in many archosaurian reptiles that lack a rhamphotheca.

Coronoid.—The slender coronoid bone is clearly visible only in BP/1/4376. It extends posteromedially to overlap the medial aspect of the anterodorsal portion of the surangular.

Surangular.—The large surangular forms the posterodorsal portion of the mandibular ramus. The dorsal margin of the jaw rises anteriorly from the jaw joint up to a low peak (coronoid eminence) and then descends again to the level of the alveolar margin of the dentary. It is medially thickened. The surangular also forms most of the dorsal margin of the external mandibular fenestra. It overlaps the dentary anteriorly and the articular posteriorly. A large anterior surangular foramen, which probably transmitted cutaneous branches of N. alveolaris inferior (Oelrich 1956), is situated ventral or slight anterior to the coronoid eminence. Just behind the foramen on the dorsolateral surface of the surangular, a pronounced longitudinal ridge probably marks the insertion for part of M. adductor mandibulae externus and possibly M. pseudotemporalis (Galton 1985). A small posterior surangular foramen is situated at the posterior end of this ridge. The suture between the surangular and angular extends in a shallow depression along the posterolateral aspect of the mandibular ramus in BP/1/4934. Medially, the surangular forms the lateral wall of the adductor fossa.

Angular.—The angular is relatively narrow and short. It forms the ventral margin of the external mandibular fenestra. Anteriorly, the angular is overlapped by the dentary, and it overlaps the surangular posteriorly. It contacts the prearticular medially. The ventral edge of the angular is rounded.

Prearticular.—The long, thin prearticular forms the ventral margin of the adductor fossa, and becomes expanded toward its anterior end. Its posterior contact with the articular cannot be identified on the available specimens.

Articular.—The articular projects medially from the medial surface of the mandibular ramus. Posteriorly, it

forms a long, slender retroarticular process (which is completely preserved only on the left mandibular ramus of BP/1/4934). Anterolaterally, a thin sheet of the surangular overlaps the retroarticular process and, medially, the process is partially covered by the prearticular. The articular bears the mandibular facet for the jaw joint, which is situated below the level of the alveolar margin of the dentary in lateral view.

Splénial.—The splénial probably covered much of the lingual surface of the dentary. Posteriorly, it is overlapped by the coronoid dorsally and the prearticular ventrally. Unfortunately, the anterior portion of the splénial is not well preserved in any of the available specimens.

Hyoid

An elongate, gently curved, and rod-like bone is preserved ventral to the posterior portion of the right mandibular ramus in BP/1/4934 and both rami in BP/1/4376. It presumably represents ceratobranchial I (cornu branchiale I). The anterior and posterior ends of this element are expanded and blunt.

Dentition

The marginal dentition of *Massospondylus* is moderately heterodont. The teeth have thecodont implantation. The dentary tooth rows are situated lingual to the premaxillary and maxillary tooth rows. Posteriorly, the maxillary tooth row extends well beyond the dentary tooth row in BP/1/4934. There is no evidence of tooth-to-tooth wear. As in other basal sauropodomorphs (e.g., *Plateosaurus*; Galton 1984, 1985), the individual tooth crowns are labiolingually compressed, taller than wide mesiodistally, not recurved, and more or less symmetrical in labial view (Fig. 8). On well-preserved tooth crowns, a faint median ridge extends vertically along the vertically gently convex labial surface of the crown, terminating in an apical denticle. Each tooth is slightly constricted between the root and crown. The mesial and distal carinae are coarsely serrated with denticles that project apically at an angle of about 45° relative to the carina, much as in other basal sauropodomorph dinosaurs. The denticles are restricted to the apical portion of the tooth crown. There are up to 11 denticles per crown in the adult specimens and up to 13 in the juvenile specimen BP/1/4376. On some teeth, the denticles along the distal carina extend further toward the root than do those along the mesial carina, but this condition could not be checked on many teeth.

There are four premaxillary teeth, of which the fourth typically has the tallest crown. They are the tallest teeth in the upper jaw; the disparity in size between the premaxillary and maxillary teeth is particularly evident in BP/1/4376. The premaxillary teeth also differ from the maxillary ones in being slightly further separated from

each other so that there is less overlap between adjacent tooth crowns and both carinae of each crown are visible in labial view. They are set slightly obliquely in the premaxilla so that their mesial carinae face more lingually and their distal carinae more labially. (This condition is also present on at least some of the maxillary teeth.) This arrangement makes the premaxillary teeth appear more slender and conical in labial view.

There are 14 teeth plus at least one additional alveolus in the right maxilla of BP/1/4376, 17 teeth or alveoli in the right maxilla of BP/1/5241, and 22 teeth in either maxilla of BP/1/4934. The maxillary tooth crowns decrease in height towards the posterior end of the tooth row.

BP/1/4934 has 26 teeth or alveoli in each dentary. The dentary teeth are similar in shape to but less tall than those of the maxilla; their crowns slightly decrease in height posteriorly.

Gow et al. (1990) commented on aspects of tooth replacement in the skulls of *Massospondylus* described here, obviating the need for further discussion.

DISCUSSION

Although the interrelationships of basal sauropodomorph dinosaurs have long been the subject of discussion in the literature (Huene 1932; Galton 1990; Sereno 1999; Benton et al. 2000), Yates (2003B) and Yates and Kitching (2003) were the first to publish comprehensive phylogenetic analyses of these taxa. Yates (2003B) argued that the basal sauropodomorph dinosaurs traditionally grouped together as Prosauropoda actually form a paraphyletic array of successive sister-taxa to Sauropoda. He showed that constraining the parsimony analysis to retain Prosauropoda (including *Saturnalia*; Langer et al. 1999) resulted in trees 24 steps longer than the most parsimonious trees with a length of 309 steps. Sereno (1999) had argued in support of the monophyly of Prosauropoda. Yates's reanalysis of Sereno's character-taxon matrix, however, demonstrated that only 3 out of 19 characters would unambiguously support prosauropod monophyly, and Yates raised additional issues related to the exclusion of a number of sauropodomorph taxa from that dataset. Later, Yates and Kitching (2003) restricted Prosauropoda to *Riojasaurus*(*Plateosaurus* (*Coloradisaurus*(*Massospondylus* + *Lufengosaurus*))), excluding *Saturnalia*, *Thecodontosaurus*, and *Efraasia* from that grouping, and reinterpreted *Anchisaurus* as the most basal member of Sauropoda.

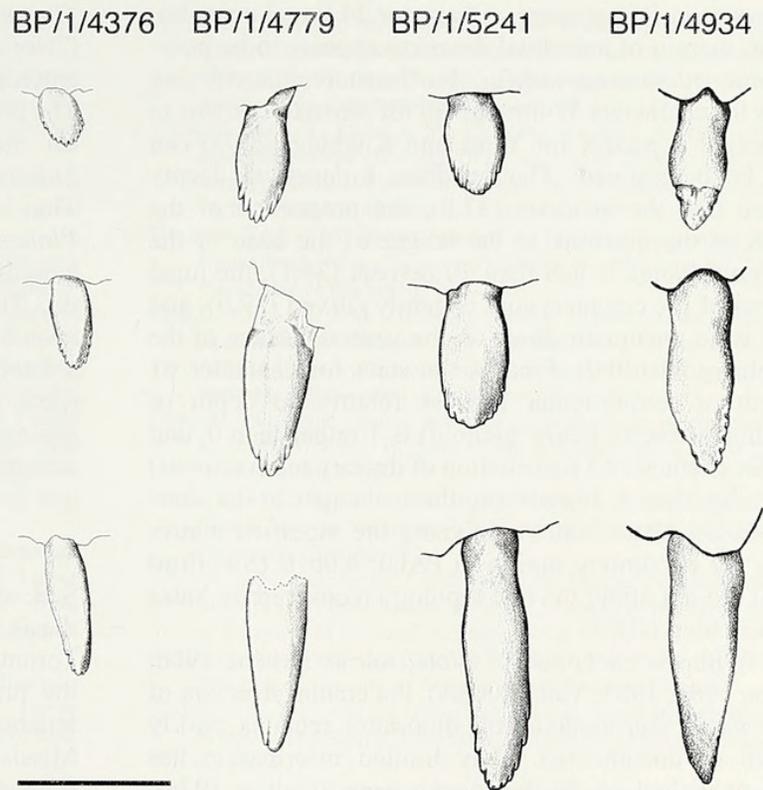


Fig. 8.—Camera-lucida drawings of the crowns of selected teeth in labial view from the skulls of *Massospondylus carinatus* described in this study. **Top row:** posterior maxillary teeth. **Center row:** anterior maxillary teeth (at the level of the dorsal process of the maxilla). **Bottom row:** premaxillary teeth. Scale bar = 1 cm. **BP/1/4376:** Maxillary teeth 11 and 5 and premaxillary tooth 3 (all from right side); **BP/1/4779:** Maxillary teeth 10 and 7 and premaxillary tooth 2 (all from right side); **BP/1/4934:** Maxillary teeth 17 (from left side) and 4 (from right side) and premaxillary tooth 4 (from left side); **BP/1/5241:** Maxillary teeth 13 and 6 and premaxillary tooth 4 (all from right side).

The most parsimonious trees recovered by Yates (2003B) grouped *Massospondylus* with either *Lufengosaurus* or *Yunnanosaurus* from the Lower Jurassic Lower Lufeng Formation of Yunnan, China. More recently, Yates and Kitching (2003) considered *Massospondylus* the sister-taxon of *Lufengosaurus* and placed *Coloradisaurus*, from the Upper Triassic Los Colorados Formation of Argentina (originally described under the preoccupied generic nomen *Coloradia*; Bonaparte 1978), as the sister-taxon to the clade *Massospondylus* + *Lufengosaurus*. They united these three taxa in a grouping Massospondylidae. Unfortunately, the structure of the skull in *Lufengosaurus* is still poorly documented (Young 1941), preventing more detailed comparison with *Massospondylus*. Two character-states for *Massospondylus* in the online appendix for Yates and Kitching (2003) must be revised based on the present study. The state for character 19 (pointed posterolateral process of nasal overlapping lacrimal) is 0 rather than 1; although the nasal overlaps the lacrimal posterolaterally it does not form a distinct posterolateral

process as in *Plateosaurus*. Character 24 (jugal contribution to margin of antorbital fenestra) appears to be polymorphic in *Massospondylus*. Furthermore, the missing states for characters 37 through 40 for *Massospondylus* in the online appendix for Yates and Kitching (2003) can now be determined: The quadrate foramen is deeply incised into the quadrate (37.0), the proportion of the length of the quadrate to the length of the base of the pterygoid flange is less than 70 percent (38.1), the jugal process of the ectopterygoid is gently curved (39.0), and there is no pneumatic fossa on the ventral surface of the ectopterygoid (40.0). Finally, the state for character 61 (length of retroarticular process relative to depth of mandibular ramus below glenoid) is 1 rather than 0, and that for character 63 (orientation of dentary tooth crowns) is 0 rather than 1. Introducing these changes in the character-taxon matrix and reanalyzing the modified matrix using the parsimony option in PAUP 4.0b10 (Swofford 1998) did not affect the tree topology recovered by Yates and Kitching (2003).

With the exception of *Plateosaurus* (Huene 1926; Galton 1984, 1985; Yates 2003A), the cranial structure of most basal sauropodomorph dinosaurs remains poorly known or documented. Only limited information has been published so far for *Anchisaurus* (Galton 1976), *Coloradisaurus* (Bonaparte 1978), *Efraasia* (Galton and Bakker 1985; Yates 2003A), *Lufengosaurus* (Young 1941), *Mussaurus* (Bonaparte and Vince 1979), *Riojasaurus* (Bonaparte and Pumares 1995), and *Thecodontosaurus* (Benton et al. 2000; Yates 2003B). This dearth of comparative data makes it difficult to identify autapomorphic cranial features for *Massospondylus*. One feature cited by Sereno (1999) is the proportionately greater width of the skull compared to that in other basal sauropodomorph taxa such as *Plateosaurus*. The greatest transverse width of the skull of *Massospondylus* exceeds its dorsoventral height by at least 10 percent. *Massospondylus* further differs from *Plateosaurus* and at least some other basal sauropodomorph taxa in the proportionately large size of the orbit and shorter antorbital region of the skull even in adult specimens (Gow et al. 1990). Galton (1990:339) cited the "centrally situated and almost vertical" dorsal process of the maxilla as a derived feature of Massospondylidae, which only comprised *Massospondylus* in his usage. Although the dorsal process is not centrally situated at least in the specimens of *Massospondylus* described here, it is tall and nearly vertical. The maxilla of *Mussaurus* from the Upper Triassic (Norian) El Tranquilo Formation of Santa Cruz, Argentina, also has a tall, nearly vertical dorsal process and an anteroposteriorly narrow medial sheet (Bonaparte and Vince 1979). The anteroposteriorly narrow medial sheet of the maxilla in *Massospondylus* is similar to that in more basal sauropodomorph taxa such as *Efraasia* (Yates 2003A) from the Upper Triassic (Norian) Löwenstein Formation of southern Germany and

Thecodontosaurus (Yates 2003B) from the Upper Triassic (?Norian) of southwest England but differs from the anteroposteriorly broad medial sheet in *Plateosaurus*. The prefrontal has a long posterior process along the dorsal margin of the orbit, similar to the condition in *Lufengosaurus* (Young 1941) and in *Plateosaurus*. The lacrimal of *Massospondylus* resembles that of *Plateosaurus* in the development of a lateral sheet overhanging the posterodorsal corner of the antorbital fenestra. The dorsolateral aspect of the lacrimal in *Massospondylus* bears a distinct ridge, which is continuous with a knob on the lateral surface of the prefrontal. Barrett (pers. comm. 2004) observed similar features in *Lufengosaurus*, but they are not evident in Young's (1941) account.

ACKNOWLEDGMENTS

S.H. studied the specimens described here for an M.Sc. thesis in the Department of Zoology at the University of Toronto, and produced a preliminary account from which the present paper has been developed. We are greatly indebted to Kevin Dupuis (University of Toronto at Mississauga) who made the drawings and to Diane Scott (University of Toronto at Mississauga) who provided technical assistance throughout this project and produced the final layout of the figures. Bruce S. Rubidge (BP) and the South African Heritage Resources Agency (SAHRA) authorized the loan of the specimens used in this study. Mark A. Norell (AMNH) and Farish A. Jenkins, Jr. (MCZ) granted access to comparative material in their care. Adam M. Yates (BP) provided electronic copies of the character-taxon matrices for Yates (2003B) and Yates and Kitching (2003), respectively. We thank Paul M. Barrett (Natural History Museum, London), Peter M. Galton (University of Bridgeport), and an anonymous reviewer for helpful comments on the manuscript. H.-D.S. and R.R.R. gratefully acknowledge financial support from their respective operating grants from the Natural Sciences and Engineering Research Council of Canada (NSERC). We dedicate this paper to the memory of our colleague James W. Kitching, who collected three of the specimens described here as well as the bulk of the fossil vertebrate material now housed in the Bernard Price Institute for Palaeontological Research.

LITERATURE CITED

- ATTRIDGE, J., A.W. CROMPTON, AND F.A. JENKINS, JR. 1985. The southern African Liassic prosauropod *Massospondylus* discovered in North America. *Journal of Vertebrate Paleontology*, 5:128–132.
- BENTON, M.J., L. JUUL, G.W. STORRS, AND P.M. GALTON. 2000. Anatomy and systematics of the prosauropod dinosaur *Thecodontosaurus* from the Upper Triassic of southwest England. *Journal of Vertebrate Paleontology*, 20:77–108.
- BONAPARTE, J.F. 1978. *Coloradia brevis* n. g. et n. sp. (Saurischia, Prosauropoda), dinosaurio Plateosauridae de la Formación Los

- Colorados, Triásico superior de La Rioja, Argentina. *Ameghiniana*, 15:327–332.
- BONAPARTE, J.F., AND J.A. PUMARES. 1995. Notas sobre el primer cráneo de *Riojasaurus incertus* (Dinosauria, Prosauropoda, Melanosauridae) del Triásico superior de La Rioja, Argentina. *Ameghiniana*, 32:341–349.
- BONAPARTE, J.F., AND M. VINCE. 1979. El hallazgo del primer nido de dinosaurios Triásicos (Saurischia, Prosauropoda), Triásico superior de Patagonia, Argentina. *Ameghiniana*, 16:173–182.
- COOPER, M.R. 1981. The prosauropod dinosaur *Massospondylus carinatus* Owen from Zimbabwe: its biology, mode of life and phylogenetic significance. *Occasional Papers of the National Museums and Monuments (Rhodesia)*, B, 6(10):689–840.
- CROMPTON, A.W., AND J. ATTRIDGE. 1986. Masticatory apparatus of the larger herbivores during Late Triassic and Early Jurassic times. Pp. 223–236, in *The Beginning of the Age of Dinosaurs: Faunal Change across the Triassic-Jurassic Boundary* (K. Padian, ed.). Cambridge University Press, Cambridge and New York.
- GALTON, P.M. 1976. Prosauropod dinosaurs (Reptilia: Saurischia) from North America. *Postilla*, 169:1–98.
- . 1984. Cranial anatomy of the prosauropod dinosaur *Plateosaurus* from the Knollenmergel (Middle Keuper, Upper Triassic) of Germany. I. Two complete skulls from Trossingen/Württ. with comments on the diet. *Geologica et Palaeontologica*, 18:139–171.
- . 1985. Cranial anatomy of the prosauropod dinosaur *Plateosaurus* from the Knollenmergel (Middle Keuper, Upper Triassic) of Germany. II. All the cranial material and details of soft-part anatomy. *Geologica et Palaeontologica*, 19:119–159.
- . 1990. Basal Sauropodomorpha—Prosauropoda. Pp. 320–344, in *The Dinosauria* (D.B. Weishampel, P. Dodson, and H. Osmólska, eds.). University of California Press, Berkeley.
- GALTON, P.M., AND R.T. BAKKER. 1985. The cranial anatomy of “*Efraasia diagnostica*,” a juvenile individual of *Sellosaurus gracilis* from the Upper Triassic of Nordwürttemberg, West Germany. *Stuttgarter Beiträge zur Naturkunde, Serie B*, 117:1–15.
- GOW, C.E. 1990. Morphology and growth of the *Massospondylus* braincase (Dinosauria, Prosauropoda). *Palaeontologia africana*, 27:59–75.
- GOW, C.E., J.W. KITCHING, AND M.A. RAATH. 1990. Skulls of the prosauropod dinosaur *Massospondylus carinatus* Owen in the collections of the Bernard Price Institute for Palaeontological Research. *Palaeontologia africana*, 27:45–58.
- HAUGHTON, S.H. 1924. The fauna and stratigraphy of the Stormberg Series. *Annals of the South African Museum*, 12:323–497.
- HUENE, F.V. 1906. Ueber die Dinosaurier der aussereuropäischen Trias. *Geologische und Palaeontologische Abhandlungen, Neue Folge*, 8(2):97–156.
- . 1914. Saurischia et Ornithischia triadica (“Dinosauria” triadica). *Fossilium Catalogus I: Animalia* (F. Frech, ed.), Pars 4. W. Junk, Berlin.
- . 1920. Bemerkungen zur Systematik und Stammesgeschichte einiger Reptilien. *Zeitschrift für induktive Abstammungs- und Vererbungslehre*, 24:162–166.
- . 1926. Vollständige Osteologie eines Plateosauriden aus dem schwäbischen Keuper. *Geologische und Palaeontologische Abhandlungen, Neue Folge*, 15(2):139–179.
- . 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monographien zur Geologie und Palaeontologie*, 1(4):1–361 plus atlas.
- KITCHING, J.W., AND M.A. RAATH. 1984. Fossils from the Elliot and Clarens formations (Karoo sequence) of the Northeastern Cape, Orange Free State and Lesotho, and a suggested biozonation based on tetrapods. *Palaeontologia africana*, 25:111–125.
- LANGER, M.C., F. ABDALA, M. RICHTER, AND M.J. BENTON. 1999. A sauropodomorph dinosaur from the Upper Triassic (Carnian) of southern Brazil. *Comptes Rendus de l’Académie des Sciences Paris, Science de la terre et des planètes*, 329:511–517.
- OELRICH, T.M. 1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). *Miscellaneous Publications, Museum of Zoology, University of Michigan*, 94:1–122.
- OLSEN, P.E., AND P.M. GALTON. 1984. A review of the reptile and amphibian assemblages from the Stormberg Group of southern Africa, with special emphasis on the footprints and the age of the Stormberg. *Palaeontologia africana*, 25:87–110.
- OSTROM, J.H. 1961. Cranial morphology of the hadrosaurian dinosaurs of North America. *Bulletin of the American Museum of Natural History*, 122:33–186.
- OWEN, R. 1842. Report on British fossil reptiles. Part II. Reports of the British Association for the Advancement of Science, 11th Meeting, Plymouth, 1841:60–204.
- . 1854. *Descriptive Catalogue of the Fossil Organic Remains of Reptilia and Pisces Contained in the Museum of the Royal College of Surgeons of England*. London, 184 p.
- RUSSELL, D.A. 1989. *An Odyssey in Time: The Dinosaurs of North America*. University of Toronto Press, Toronto, 239 pp.
- SEELEY, H.G. 1887. On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London*, 43:165–171.
- . 1895. On the type of the genus *Massospondylus*, and on some vertebrae and limb bones of *M(?) Browni*. *Annals and Magazine of Natural History*, (6)15:102–125.
- SERENO, P.C. 1999. The evolution of dinosaurs. *Science*, 284:2137–2147.
- SWOFFORD, D.L. 1999. PAUP*. *Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Version 4. Sinauer Associates, Sunderland, Massachusetts.
- WING, S.L., AND H.-D. SUES (rapporteurs). 1992. Mesozoic and early Cenozoic terrestrial ecosystems. Pp. 326–416, in *Terrestrial Ecosystems through Time* (A.K. Behrensmeier, J.D. Damuth, W.A. DiMichele, R. Potts, H.-D. Sues, and S.L. Wing, eds.). University of Chicago Press, Chicago.
- WITMER, L.M. 1997. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Society of Vertebrate Paleontology Memoir* 3:1–73.
- YATES, A.M. 2003A. The species taxonomy of sauropodomorph dinosaurs from the Löwenstein Formation (Norian, Late Triassic) of Germany. *Palaeontology*, 46: 317–337.
- . 2003B. A new species of the primitive dinosaur *Thecodontosaurus* (Saurischia: Sauropodomorpha) and its implications for the systematics of early dinosaurs. *Journal of Systematic Palaeontology*, 1:1–42.
- YATES, A.M., AND J.W. KITCHING. 2003. The earliest known sauropod dinosaur and the first steps towards sauropod locomotion. *Proceedings of the Royal Society of London, Biological Sciences*, 270:1753–1758.
- YOUNG, C.-C. 1941. A complete osteology of *Lufengosaurus huenei* Young (gen. et sp. nov.) from Lufeng, Yunnan, China. *Palaeontologia Sinica, New Series C*, 7:1–53.



Sues, Hans-Dieter et al. 2004. "On the skull of *Massospondylus carinatus* Owen, 1854 (Dinosauria: Sauropodomorpha) from the Elliot and Clarens formations (Lower Jurassic) of South Africa." *Annals of the Carnegie Museum* 73(4), 239–257. <https://doi.org/10.5962/p.316084>.

View This Item Online: <https://www.biodiversitylibrary.org/item/216934>

DOI: <https://doi.org/10.5962/p.316084>

Permalink: <https://www.biodiversitylibrary.org/partpdf/316084>

Holding Institution

Smithsonian Libraries and Archives

Sponsored by

Biodiversity Heritage Library

Copyright & Reuse

Copyright Status: In Copyright. Digitized with the permission of the rights holder

Rights Holder: Carnegie Museum of Natural History

License: <https://creativecommons.org/licenses/by-nc-sa/4.0/>

Rights: <https://www.biodiversitylibrary.org/permissions/>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.