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Embryonic skeletal anatomy of the sauropodomorph dinosaur *Massospondylus* from the Lower Jurassic of South Africa

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EMBRYONIC SKELETAL ANATOMY OF THE SAUROPODOMORPH DINOSAUR *MASSOSPONDYLUS* FROM THE LOWER JURASSIC OF SOUTH AFRICA

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ABSTRACT—Two embryonic skeletons preserved inside thin-shelled eggs of a partially preserved clutch from the Upper Elliot Formation (Lower Jurassic) of South Africa have been attributed to the sauropodomorph dinosaur *Massospondylus carinatus*. A virtually complete skeleton is exposed in right lateral view, with the slightly telescoped skull and several cervical vertebrae extending beyond the eggshell. A second, partial skeleton has a skull preserved in dorsal view. The embryos have proportionately very large skulls, with the broad skull table formed by wide parietals and frontals. The wide posterolateral wing of the frontal separates the postorbital from contact with the parietal. The embryos have short rather than elongated cervical vertebrae, with tall rather than low neural arches. The large forelimbs are only slightly shorter than the hind limbs, which suggests an obligatory quadrupedal posture for the hatchlings. This pattern may represent an ontogenetic constraint related to the large size of the head and horizontally oriented neck. Similarities between the embryonic and post-hatchling specimens include the slenderness of the lower jaw and slight ventral curvature of the symphyseal portion of the dentary, the large supraorbital process of the prefrontal, and the tall antorbital and infratemporal fenestrae. There are 10 cervical, 14 dorsal, and three sacral vertebrae. The large distal claw-bearing phalanx of manual digit 1 is longer than any other phalangeal element of either manus or pes. The embryos of *Massospondylus carinatus* represent the oldest dinosaurian embryos known to date.

INTRODUCTION

Basal sauropodomorph dinosaurs ('prosauro pods') first appeared in the fossil record in the early Late Triassic (Sereno, 1999; Galton and Upchurch, 2004; Martínez and Alcober, 2009). They became the dominant large herbivores in Late Triassic and Early Jurassic continental ecosystems. Among them, *Massospondylus carinatus* Owen, 1854, is known from numerous well-preserved specimens from many localities (Fig. 1) in the Lower Jurassic Lower Elliot, Upper Elliot, and Clarens formations in South Africa and Lesotho (*Massospondylus* Range Zone; Kitching and Raath, 1984), as well as from the correlative Forest Sandstone in Zimbabwe (Cooper, 1981). It is represented by an extensive growth series of well-preserved, articulated skeletons, with femoral lengths ranging from 12.7 to 54 cm (specimens housed in the Bernard Price Institute for Palaeontological Research at the University of Witwatersrand, in Johannesburg, South Africa; BP/1/5253, BP/1/4934).

In 1976 the late James W. Kitching collected a block containing subspherical eggs from a layer of reddish-brown, muddy siltstone that is part of the Upper Elliot Formation (Lower Jurassic) in a roadcut at Rooidraai, in Golden Gate Highlands National Park, South Africa. The block, BP/1/5347, preserves 10 eggs (6 of which are complete) tightly clustered as part of a single clutch. All eggs are tilted slightly in one direction, possibly because of modest crushing, each egg extending into the sediment and noticeably beneath the neighboring egg. Kitching tentatively assigned these eggs to a dinosaur, probably a prosauropod, in a brief preliminary report on the embryos that were partially exposed (Kitching, 1979). This identification was subsequently questioned by Zelenitsky and Modesto (2002).

New preparation on this partial cluster of eggs has revealed the presence of articulated embryonic skeletons (Figs. 2–6) referable to a basal sauropodomorph, probably *Massospondylus carinatus* (Reisz et al., 2005). Partial preparation of all the eggs revealed that 5 of the 10 eggs contain embryonic remains (Reisz et al., 2005). Small sections of the eggshell were removed from each of the original six eggs, exposing skeletal elements near the surface of the bone-bearing eggs, but only two embryos were completely exposed during preparation. One of the eggs at the center of this clutch lacks embryonic remains. During preparation, numerous shell fragments were discovered around this egg, suggesting that the embryo may have hatched prior to fossilization of the clutch. The remaining four eggs are too incomplete to yield embryonic remains.

The exposed articulated skeletons essentially fill the two eggs. The size of the embryos, together with the advanced level of ossification indicated by the presence of the well-ossified stapes, vertebrae, the fourth trochanter on the femur, and metapodials, suggests that the animals within these eggs were close to hatching. This contrasts with embryos of Late Cretaceous titanosaurian sauropod from the Anacleto Formation in Neuquén Province (Argentina) that have well-developed skulls but poorly ossified limb elements and vertebrae, and were not close to hatching (Chiappe et al., 1998, 2001). Computed tomography scans of the eggs from Rooidraai failed to reveal the delicate bones of the embryos, but established the presence of a highly reflective envelope surrounding the skeletal remains inside the unprepared egg at the corner of the clutch, indicating that the organic content of the eggs had settled to the bottom half of the egg. A mineralized layer next to the bones is also present in the two fully prepared eggs. It possibly represents remnants of either the egg membrane or extra-embryonic membranes that enclosed the developing embryo.

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FIGURE 1. Map of South Africa and Lesotho showing main localities that have yielded skeletal remains of *Massospondylus*. The majority of these localities have sufficiently complete skeletons to allow for their identification as those of *M. carinatus*. The asterisk designates the Rooidraai locality, near the town of Clarens, in the Golden Gates Highlands National Park, South Africa.

These embryos represent the oldest dinosaurian embryos known to date. In view of the rarity of articulated dinosaurian embryos and their potential significance for understanding embryonic development and reproduction in early dinosaurs, this paper documents the anatomy of these specimens in detail for the first time.

DESCRIPTION

Two skeletons have been fully exposed by mechanical preparation for examination (Table 1) and description. They are referred

TABLE 1. Measurements for embryonic skeleton of *Massospondylus* (BP/1/5347A).

Element	Measurement
Skull, reconstructed length	19.5
Quadrate, height	5.2
Middle cervical centrum, length	2.3
Middle dorsal centrum, length	2.4
Sacral centrum 1, length	2.5
Scapula, height	11.3
Humerus, length	9.5
Ulna, length	6.5
Iliac blade, length	6.5
Femur, length	11.5
Tibia, length	11
Fibula, length	11.4
MT II, length	5.1

All measurements (in millimeters) taken from the right side of the specimen.

to as BP/1/5347A-1 and BP/1/5347A-2 on the larger block, and as BP/1/5347B-1 and BP/1/5347B-2 on the counterpart blocks. The most complete skeleton, BP/1/5347A-1, is preserved curled-up and still in articulation (Fig. 2); only the neural arches of its dorsal vertebrae and portions of some ribs were lost during fossilization. Most of the embryonic skeleton is preserved on BP/1/5347A, whereas only parts of the bones are present on the counterpart BP/1/5347B as a result of the splitting process that originally exposed the embryonic remains. Most of the embryonic skeleton is still contained within the egg on BP/1/5347A, but preparation revealed four cervical vertebrae protruding beyond the perimeter of the egg, and the skull is preserved at the end of the cervical series in an area covered with eggshell fragments (Figs. 2, 3). It is impossible to determine if this position of the skull was the result of an unsuccessful hatching or due to taphonomic changes, but we tend to favor the latter interpretation because of the sharp, unnatural angle formed between two successive cervical vertebrae and the telescoping of the snout. Some postmortem displacement of dorsal vertebrae is evident just anterior to the pelvis, but otherwise the skeleton has remained largely undisturbed. After the two skeletons had already been prepared, the counterpart BP/1/5347B of the original block finally became available for study. This allowed us to determine that little if any bone was lost because parts that were missing on the main block were preserved on the counterpart (BP/1/5347B-1), including dorsal vertebra 12.

The skull of the articulated skeleton (BP/1/5347A and BP/1/5347B-1) is partially exposed in right lateral view (Figs. 2–4). It has been slightly telescoped in the snout region, and the anterior part of the mandible, the premaxilla, and the anterior end of the maxilla were lost. We interpret this loss as at least partially due to preservation because a small bone fragment is present in the area where the end of the snout would have been. Elements of the skull roof and the right side of the orbital and temporal regions are exposed, with parts of the palate visible through the orbit, and parts of the braincase protruding through the temporal fenestrae and skull roof. Despite damage to the snout region, the rest of the skull is preserved in nearly perfect condition, with even the delicate stapes remaining in its original position medial to the quadrate.

In the second prepared egg (BP/1/5347A and BP/1/5347B-2), the embryo was preserved fairly evenly on the part and counterpart blocks. Most of its skull was split in two, exposing both the dorsal and ventral surfaces of the skull roof. We were able to prepare both part and counterpart (Fig. 5). The skeletal remains on BP/1/5347A were prepared shortly after the original discovery and illustrated in a brief preliminary report (Kitching, 1979). Unfortunately its counterpart on BP/1/5347B suffered extensive damage caused by past attempts to extract samples of embryonic bone using a circular sawblade. However, important elements of the skeleton were still buried sufficiently deeply in the siltstone matrix and thus escaped damage; they were subsequently exposed through careful preparation. Preparation of the skull and other regions of the egg's interior revealed excellent preservation of bone in the previously concealed or uncut portions of the egg. The skull is virtually complete on the part and counterpart blocks, with parts of the skull roof preserved as positive and negative impressions. The positions of various postcranial elements indicate that this skeleton was also preserved in a curled-up, partially articulated condition.

The skull is preserved in dorsal view, showing the skull roof, parts of the orbital region and right side of the palate, as well as portions of the snout. The mandibular rami have shifted slightly forward, exposing the alveolar region and symphysis. There is a small sliver between the second and third alveoli that might represent a partial tooth in the right dentary, but we reject this interpretation because it is not in the right position for a tooth; all other alveoli are empty. Two small, slender, elongate

structures on the dorsal process of the premaxilla resemble teeth, and may represent teeth that fell out after death. An alternative interpretation of these two tooth-like structures is that they were egg 'teeth,' possibly used to break the eggshell open during hatching. The dorsal processes of the premaxillae and nasals have been pushed slightly back relative to the rest of the premaxillae and maxillae.

Despite proportional differences between the embryos and adults, the structure of the embryonic skulls (Figs. 3–7) is entirely consistent with their referral to *Massospondylus*. The posterior part of the maxilla forms a distinct, slender process that underlies the jugal. As in juvenile and adult individuals of *Massospondylus*, this process lacks teeth (Sues et al., 2004). The tall lacrimal is visible in dorsal view. A long posterodorsal process of the prefrontal has been separated slightly from the frontal, but the shape of this part of the bone is identical to that seen in other skulls of *Massospondylus*. As in both juvenile and adult *Massospondylus* and other basal sauripodomorphs, the anterior end of the dentary is slightly deflected ventrally, although this deflection is less pronounced than in the adults, especially in the largest known individual (BP/1/4934). A noteworthy feature of the embryonic skulls is the preservation of nearly complete rings of scleral ossicles in the orbit. Although most of the known skulls of *Massospondylus* preserve some of these elements in the orbital region or nearby on the skull (Sues et al., 2004:fig.1), their presence in nearly perfect articulation in the embryos is surprising. In addition, the rod-like stapes is still in its original position on one of the embryonic skulls. It is well ossified, and its distal end is slightly expanded, as in the adults.

As in basal sauripodomorphs, the antorbital fenestra is tall and approximately triangular in outline (Galton and Upchurch, 2004). The external naris is large in the embryo, but not as tall as the antorbital fenestra. Other notable features of the embryonic skull include the wide, domed parietal with feeble emargination of the bone for the supratemporal fenestra, the small size of the nasal, and the large size of the frontal and its substantial contribution to the orbital margin. In contrast, the largest known skull of *Massospondylus* (BP/1/4934) has a relatively short frontal, the nasal is the longest paired element in the skull roof, and the parietals are strongly emarginated along the medial edge of the fenestra. However, other, smaller specimens show intermediate stages between the two extremes (Sues et al., 2004).

Comparisons in the following description focus on the post-hatchling cranial growth series of *Massospondylus* described by Sues et al. (2004) and will highlight changes during growth in addition to the unique features of the embryo. The antorbital fenestra is tall and approximately triangular in outline. The external naris is large in the embryo but not as tall as the antorbital fenestra. The supratemporal fenestra is longer than wide, unlike its shape in adult *Massospondylus* where this fenestra is approximately as wide as long (BP/1/4779). Unique to the embryo is the slight contribution of the frontal to the anterior margin of the fenestra, and the absence of a contact between the parietal and postorbital anteriorly. In the smallest known juvenile, BP/14376 (Sues et al., 2004:fig. 1), the frontal has a slight emargination for the edge of the fenestra, but there is a narrow contact between the postorbital and parietal. The infratemporal fenestra is hourglass-shaped, as in adults, and bounded by the same bones.

Skull Roof

The premaxilla, observable only in BP/1/5347A-2 (Fig. 6A), forms the anterior end of the snout and the anteroventral margin of the external naris. Its small size indicates that the anterior end of the snout was narrow in dorsal view. The posterolateral process, which overlaps the anterior ramus of the maxilla below the external naris, is not as well developed as in larger specimens of *Massospondylus* (e.g., BPI/1/5241, BPI/1/4934), but this may be

due to breakage. As a result, the suture between the premaxilla and maxilla is inclined posterodorsally, rather than being shaped like an inverted L in lateral view (Sues et al., 2004). The presence of a subnarial foramen on the suture between the premaxilla and maxilla in the embryos is uncertain, because the left premaxilla of BP/1/5347A-2 has been displaced and overlies the anterior end of the maxilla. The dorsal (internarial) processes curve posterodorsally, and appear in dorsal view as two thin straps that are appressed at the midline and separate the anterior ends of the nasals. At the anteroventral corner of the external naris there is a shallow fossa at the confluence of the dorsal process and lateral ramus. The body of the premaxilla and its tooth-bearing margin are poorly preserved, and the number of alveoli is unknown. Two small, slender, conical structures with a waxy patina on the dorsal process of the premaxilla may represent teeth, but their identity is uncertain. They are much smaller than the empty alveoli of the mandible, as is another tooth-like structure that was exposed in cross-sectional view as an isolated element on the counterpart block BP/1/5347B-2. However, in the latter case, the cross-sectional view exposes a tiny pulp cavity, a dense, dentine-like core, and a very thin outer layer that may be the enamel layer. If this interpretation is correct, these small teeth would have been at a very early stage of development, and nowhere near a size to approach eruption. Their postmortem displacement, while the rest of the skeleton has remained largely in place, also supports this interpretation.

The triradiate maxilla (Figs. 4, 6A) comprises a dorsoventrally tall anterior process, a dorsal process, and a straight posterior ramus. Below the external naris, the maxilla is tall and has a dorsoventrally convex lateral surface. The dorsal surface of the subnarial process and base of the dorsal process are transversely concave at the posteroventral corner of the external naris. Just anterior to the base of the dorsal process, a large neurovascular foramen, also present in this region on adult skulls of *Massospondylus* (Sues et al., 2004), pierces the lateral surface along the margin of the narial fossa. The posterodorsally directed dorsal process is set back approximately one-third from the anterior end of the bone. It forms the posteroventral margin of the external naris anteriorly and the anterior margin of the antorbital fenestra posteriorly. The surface of the maxilla is gently concave adjacent to the antorbital fenestra to form the antorbital fossa, which is particularly well demarcated at the base of the posterior ramus. The margin of the inset medial lamina that defines the edge of the antorbital fenestra is close and parallel to the rim of the antorbital fossa where preserved, as in *Massospondylus* and *Lufengosaurus* but unlike *Plateosaurus* (Galton and Upchurch, 2004) and *Aardonyx* (Yates et al., 2010), in which the flange is much broader. The posterior ramus of the maxilla forms a straight, slender process that tapers beneath the jugal in lateral view. This process, which terminates posteriorly just beyond the anterior margin of the orbit in the embryo, extends past the ventral midpoint of the orbit in larger specimens of *Massospondylus* (Sues et al., 2004) as well as *Lufengosaurus* (Barrett et al., 2005). The lateral surface of the body of the maxilla has several supralabial foramina. The long alveolar margin preserves no erupted teeth.

The right nasal of BP/1/5347A-2 is almost complete (Fig. 6). Its total length is less than 25% the length of the embryonic skull; its relatively smaller size than that of large individuals of *Massospondylus* (in which the nasal is approximately half the skull length; Sues et al., 2004) implies a positive allometry of the antorbital region of the skull during growth. This is confirmed by the size of the nasal in juvenile skulls. The anteromedial and anterolateral processes of the nasal diverge and form the posterodorsal margin of the external naris. The anteromedial process overlaps the dorsal processes of the premaxilla as it curves ventrally and tapers to a point anterior to the dorsal midpoint of the naris. The triangular anterolateral process does not reach the lateral process



FIGURE 2. Photograph of skeleton of the first embryo of *Massospondylus carinatus* (BP/1/5347A-1). White materials represent eggshell that remained around the embryonic skeleton after they had been exposed. Scale as indicated.

of the premaxilla. It is unclear whether the anterolateral process contributes to the margin of the antorbital fenestra. The posterior end of the nasal is flattened at its contact with the frontal on the skull roof. In dorsal view, the nasals are slightly separated posteriorly by an anteromedial projection of the frontals.

The prefrontal forms the anterodorsal margin of the orbit. It articulates with the lacrimal ventrally, and has a long posterodorsal process that extensively overlaps the frontal on the skull roof. Nevertheless, in dorsal view (Figs. 3, 6), the posterodorsal process is relatively shorter than in skulls of post-hatchling specimens of *Massospondylus* (BP/1/4376, BP/1/5241), suggesting this portion of the prefrontal increases in relative length through ontogeny, perhaps related to the increasing elongation of the snout. The anteromedial suture with the nasal anterior to the frontal contact is long and well developed.

The lacrimal (Figs. 3, 6A) is similar to that in adult *Massospondylus*, with a tall ventral ramus and a short anterodorsal ramus. The anteriorly bowed ventral ramus forms the anterior margin of the orbit and the posterior margin of the antorbital fenestra. Ventrally, the lacrimal articulates with the jugal. The presence of a medial lamina just above the contact with the jugal, which corresponds to the posteroventral region of the antorbital fossa, is uncertain; if indeed present, it was likely small. The relative size of the medial lamina increases in *Massospondylus* during growth (Sues et al., 2004). Dorsally, the lacrimal is expanded and extends towards the dorsal apex of the maxilla, but it is unclear whether they meet to exclude the nasal from the antorbital fenestra.

The lacrimal forms a small contribution to the skull roof lateral to the nasal in dorsal view. The lacrimal is identical to that seen in other, larger skulls of *Massospondylus* and appears to have changed little during ontogeny (Sues et al., 2004).

The frontal (Figs. 3, 6) is the largest bone of the embryonic skull. In dorsal and lateral views, the frontal makes a large contribution to the dorsal rim of the orbit. This feature is unchanged ontogenetically, as the degree of exposure of the frontal along the orbit is similar to that in juvenile and adult specimens of *Massospondylus* (Sues et al., 2004), but differs from the relatively small contribution to the orbital margin in *Lufengosaurus* (Barrett et al., 2005). The total length of the frontal is more than three times the transverse width of the bone at midlength of the orbit. In this respect, the embryo more closely resembles the smallest known juvenile *Massospondylus* (BP/1/4376) than larger specimens, in which the frontal is proportionately shorter. The nasal and prefrontal overlap the anterior end of the frontal adjacent to the anterior end of the orbit. Posteriorly, the anteromedial extension of the parietals results in a W-shaped frontal-parietal contact in dorsal view. In larger specimens of *Massospondylus* this suture is essentially straight, and, although the posterior margin of the frontal is slightly emarginated by the supratemporal fenestra, the anterior margin of the opening is formed mainly by the parietal and postorbital. The frontal is overlapped by the postorbital at the posterodorsal corner of the orbit.

The large, domed parietals (Figs. 3, 6) are emarginated laterally along the margin of the supratemporal fenestra. The

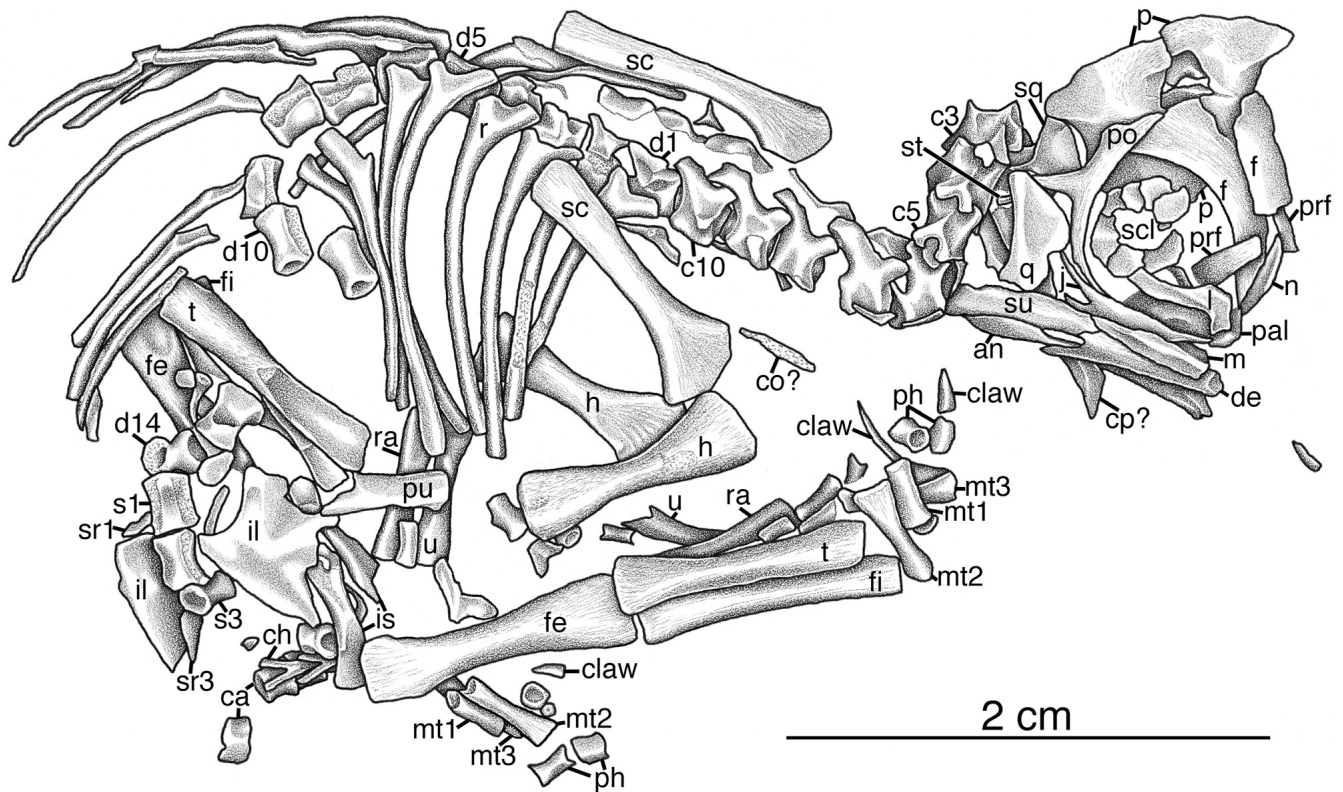


FIGURE 3. Illustration of the first embryo of *Massospondylus carinatus* (BP/1/5347A-1), showing details of the skull and skeleton in partial right lateral view. **Abbreviations:** an, angular; c, centra; c3–c10, cervical vertebrae; ca, caudal vertebra; ch, hemal arch; co, coracoid; cp?, cultriform process?; d1–d14, dorsal vertebrae; de, dentary; f, frontal; fe, femur; fi, fibula; h, humerus; il, ilium; is, ischium; j, jugal; l, lacrimal; m, maxilla; mc1–mc4, metacarpals; mt1–mt3, metatarsals; n, nasal; p, parietal; pal, palatine; ph, phalanges; pm, premaxilla; po, postorbital; prf, prefrontal; pt, pterygoid; pu, pubis; q, quadrate; r, rib; ra, radius; s1–s3, sacral vertebrae; sc, scapula; scl, scleral ring; sr1–sr3, sacral ribs; sq, squamosal; st, stapes; su, surangular; t, tibia; u, ulna. Scale as indicated.

lateral emargination in the embryo is substantially less developed than in larger specimens of *Massospondylus*, in which the parietals form a relatively narrow, stout bony separation between the two supratemporal fenestrae, best seen in BP/1/5241 (Sues et al., 2004:fig. 7). In addition, the attachment area for the adductor jaw musculature, which is extensively developed in adults, is also poorly demarcated in the embryo. Anteriorly, the parietal does not meet the postorbital to exclude the frontal from the margin of the supratemporal fenestra, as in larger specimens of *Massospondylus* (BP/1/5241, BP/1/4779). The parietals are depressed anteromedially adjacent to the frontals, but there is no pineal foramen. Short posterolateral processes contact the squamosals.

In lateral view, the postorbital is triradiate (Figs. 3, 6B). Its ventral process separates the orbit from the infratemporal fenestra. The ventral half of this process forms an extensive contact with the jugal. It curves distally and tapers to a point near the midpoint of the ventral margin of the orbit. The short posterior process of the postorbital articulates with the squamosal posteriorly and forms the bony bar separating the supra- and infratemporal fenestrae. Dorsally, the postorbital becomes a thin sheet that extends onto the skull roof where it extensively overlaps the frontal.

The jugal, excellently preserved in both embryos (Figs. 3, 6), is triradiate in lateral view and forms the ventral margin of the orbit and the anteroventral corner of the infratemporal fenestra. Its anterior process articulates with the lacrimal medially and forms a long ventral suture with the maxilla below the anterior third of the orbit. In lateral view, the anterior process tapers to a point

ventral to the lacrimal and reaches the antorbital fossa or fenestra but does not make a noticeable contribution to its margin. The dorsal process of the jugal extends posteriorly at an angle of about 45° to the maxillary ramus and forms the posteroventral half of the postorbital bar that separates the orbit from the infratemporal fenestra. The short posterior process articulates with the quadratojugal at the midpoint of the ventral margin of the infratemporal fenestra.

We interpret a small, slender piece of bone preserved close to the jugal and partially covered by the quadrate in BP/1/5347A-1 (Fig. 3) as the anteroventral part of the quadratojugal. The contact between the jugal and quadratojugal is relatively shorter and different in structure from that in adult *Massospondylus*, in which the quadratojugal tapers to a point below the posterior process of the jugal in lateral view.

The right quadrate is fully exposed in posterolateral view in BP/1/5347A-1 (Fig. 3), and the dorsal end of this bone is also preserved in BP/1/5347A and B-2 (Fig. 6). Its small dorsal head fits into a ventral cotylus on the squamosal. In lateral view, the large, anteriorly directed lateral wing progressively expands from the head to the point of the quadratojugal articulation. Dorsal to the quadratojugal, the lateral wing articulates with the elongate ventral process of the squamosal in all known specimens of *Massospondylus* (Sues et al., 2004), but the condition is unclear in the embryo because this portion of the squamosal is not preserved. Along the contact with the quadratojugal, the lateral wing becomes narrower toward the mandibular condyle. The mandibular condyle is expanded in both the transverse and parasagittal

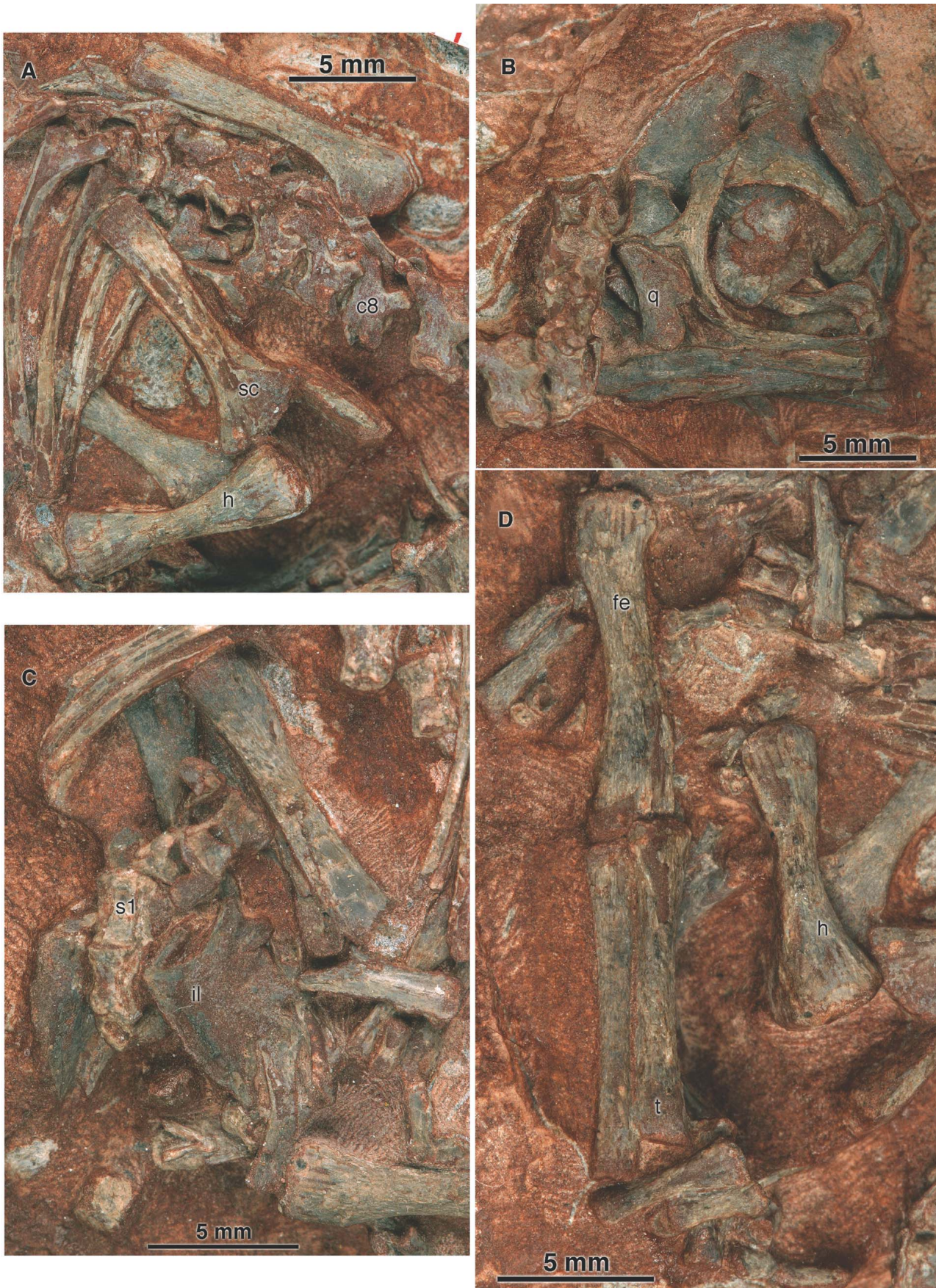


FIGURE 4. Close-up photographs of the first embryo of *Massospondylus carinatus* (BP/1/5347A-1), showing various parts of the articulated skeleton, including (A) shoulder region, (B) skull, (C) pelvic region, and (D) limbs. Abbreviations as in Figure 3. Scale as indicated.

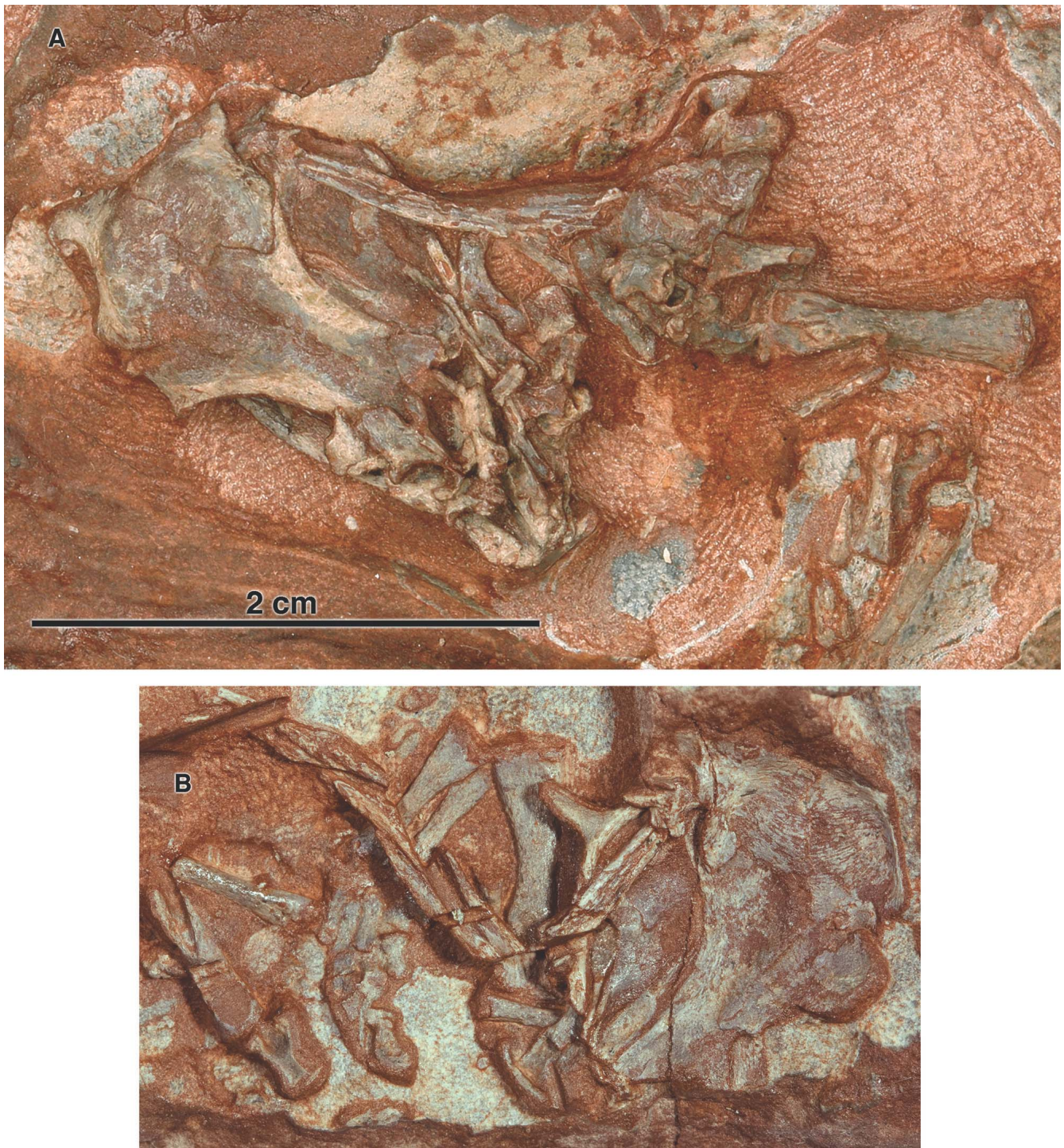


FIGURE 5. Photograph of the skull and nearby elements of the skeleton in the second embryo of *Massospondylus carinatus*, preserved on part and counterpart blocks, (A) BP/1/5347A and (B) BP/1/5347B. Scale as indicated.

planes. It is saddle-shaped and smoothly convex in lateral view. The medial (pterygoid) wing of the quadrate is not exposed.

The squamosal (Figs. 3, 6B) forms the posterodorsal corner of the skull in lateral aspect and contributes to the posterolateral and posterodorsal margins of the supra- and infratemporal fenestrae, respectively. The ventral process of the squamosal, which is typically well developed in prosauropods, is poorly exposed on both embryonic skulls.

Palate and Braincase

The palatine, exposed in dorsal view in both specimens, forms a large anterolateral portion of the palate medial to the maxilla. The anterior, medial, and posterior contacts of this bone cannot be identified in the embryonic skulls. The lateral (maxillary) ramus of the palatine is exposed in BP/1/5347A-2 (Fig. 6A). It is expanded anteroposteriorly where it contacts the medial surface of

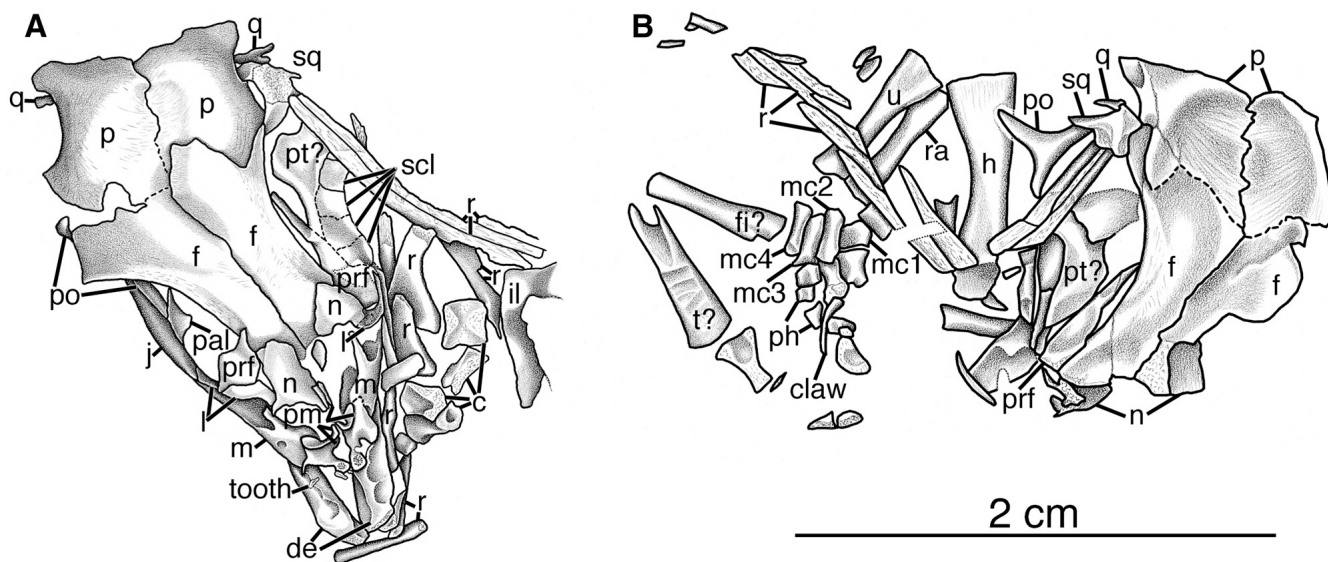


FIGURE 6. Illustrations of skull and associated skeletal elements of second embryo of *Massospondylus carinatus* preserved in part and counterpart blocks. (A) BP/1/5347A and (B) BP/1/5347B, showing details of the skull in dorsal view. Parts of the postcranial skeleton are also shown. Abbreviations as in Figure 3. Scale as indicated.

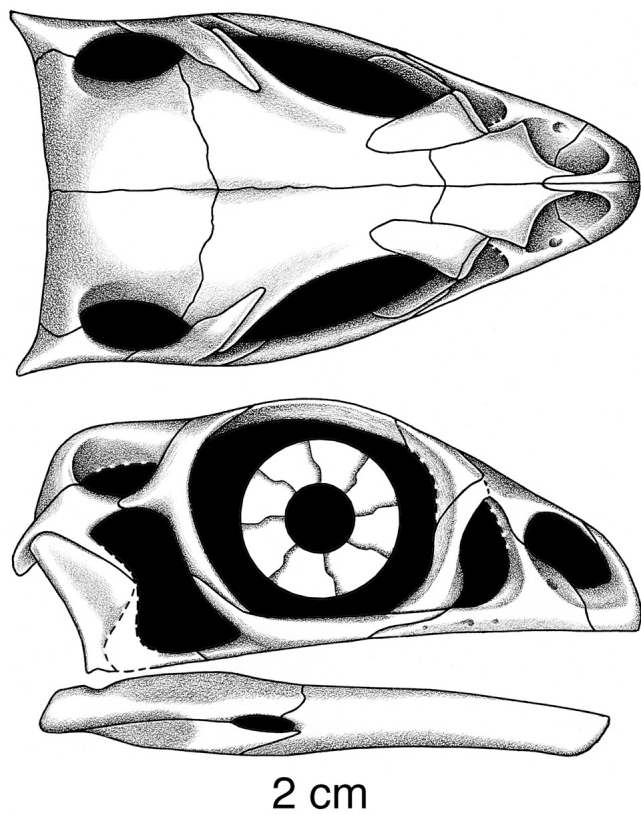


FIGURE 7. Reconstruction of embryonic skull of *Massospondylus carinatus* in dorsal and lateral views. The reconstructions do not show any teeth because there is no conclusive evidence for any teeth being associated with this embryonic stage. Scale as indicated.

the maxilla below the orbit. The bone is anteroposteriorly longer in adult specimens.

A large, irregularly shaped bone visible in dorsal view through the left orbit of the BP/1/5347A-2 (Fig. 6) probably represents the pterygoid. It consists of a large posterior plate and an elongate anterior palatal ramus for contact with the vomer and palatine as in other prosauropods (Sues et al., 2004). The medial margin of the bone is slightly bowed laterally as preserved. Posteriorly, the bases of the quadrate flange and the transverse process extend at approximately right angles to one another, but their articular relationships cannot be determined.

Other than for the bones of the skull roof, little information on the braincase is available. None of the endochondral bones that make up the braincase is exposed. What we tentatively identify as the cultriform process of the parabasisphenoid has been displaced ventrally and is exposed between the mandibular rami in BP/1/5347A-1 (Fig. 3).

A right stapes is preserved in its original position in the skull of BP/1/5347A-1 (Fig. 4). Its distal end is slightly expanded, as in the adults; its proximal end is not exposed. If correctly identified, the stapes appears to be more robust than that in larger skulls of *Massospondylus* (Sues et al., 2004:fig. 4). Ossified scleral plates are also present in both embryonic skulls (Figs. 3, 6A). BP/1/5347A-1 preserves a complete scleral ring comprised of approximately eight thin bony plates.

Hyoid ossifications have not been identified in the embryonic material.

Mandible

A nearly complete mandible is preserved exposed in lateral view in BP/1/5347A-1 (Fig. 3), whereas the lower jaws in the second skull, BP/1/5347A-2 (Fig. 6A) are almost completely covered by the skull. However, they have shifted forward sufficiently to expose the anterior portion of the alveolar rami in dorsal view. The prearticular, articular, splenial, and coronoid are not visible in any of the specimens under study. As in post-hatching individuals, the mandible is approximately the same length as the cranium. The anteroposteriorly elongate, oval external

mandibular fenestra is formed by the dentary, surangular, and angular. It is approximately 11% the length of the lower jaw in the embryo and appears somewhat more elongate than in post-hatchling individuals (BP/1/4376, BP/1/4779).

The dentary, the largest bone of the mandible, bears the distinct ridge on its posterolateral surface; this feature is characteristic of most basal sauropodomorphs (Galton and Upchurch, 2004) but is absent in *Aardonyx* (Yates et al., 2010). In lateral view, the tooth-bearing ramus is slightly bowed dorsally and has subparallel dorsal and ventral margins. A short edentulous region approximately equal to one alveolus in length occurs at the anterior end of the dentary, another feature diagnostic for basal sauropodomorphs (Galton and Upchurch, 2004). Posteriorly, the dentary bifurcates around the external mandibular fenestra. The dorsal and ventral branches articulate with the surangular and angular, respectively, and the region between them forms the anterior margin of the opening.

The anterior four alveoli as exposed in BP/1/5347A-2 (Fig. 6A) are notably large and long; each alveolus is approximately 1 mm in length, and the tooth-bearing ramus of the dentary is approximately 10 mm long. Therefore, there were approximately 10–12 tooth positions in the dentary of the embryos, which is a lower count than in juveniles and adults, but consistent with the progressively increasing number of dentary teeth seen in later growth stages of *Massospondylus* (Sues et al., 2004). A small fragment at the confluence of the second and third alveolus of BP/1/5347A-2 has a 'waxy' texture distinct from the dentary and may represent a partial dentary tooth, although there are no serrations or other morphological features that would confirm this identification. The remaining alveoli are empty.

The surangular is the second largest mandibular element and forms the dorsal region of the mandibular ramus posterior to the dentary. The lateral surface bears a horizontal ridge that is continuous with that on the dentary. Anteriorly, the surangular overlaps the dentary and forms the dorsal margin of the external mandibular fenestra. In lateral view, the dorsal margin of the surangular rises posteriorly from the anterior end of the bone to a slightly convex coronoid eminence anterior to jaw joint. Ventrally, the surangular contacts the angular along a subhorizontal suture that extends posteriorly from the external mandibular fenestra.

The angular is a long, strap-like bone ventral to the surangular on the posterolateral surface of the mandibular ramus. It forms the ventral margin of the external mandibular fenestra and is overlapped by the dentary anteriorly. In lateral view, the ven-

tral margin of the angular curves gently upwards from its contact with the dentary to the region below the jaw joint.

Postcranial Skeleton

The structure of the embryonic postcranial skeleton generally conforms to that in more mature individuals of *Massospondylus* (Cooper, 1981), but differs dramatically in its relative proportions, presumably in part related to constraints associated with accommodating the developing embryo in a small egg.

Vertebral Column—There are eight exposed cervical vertebrae; very slender, delicate, relatively short ribs are associated with all of them. The cervical vertebrae are preserved in articulation; the atlas-axis complex could not be exposed without inflicting damage to the skull. The cervical centra are not elongated relative to the dorsal centra, but there is already extensive zygapophyseal contact between the vertebrae. Little detailed information is available on the centra, except for basic measurements (Table 1). The centra are slender, spool-shaped, and slightly shorter than the dorsal centra; there is little variation in centrum length along the series. This is in marked contrast to the condition seen in the adults (Cooper, 1981), where the cervical centra are greatly elongated, with the mid-cervical centra being significantly longer than either the anterior and posterior cervical centra. Juveniles (e.g., BP/1/4376) show an intermediate condition between the embryos and the adults. The cervical neural arches are quite tall in the embryos, possibly associated with the presence of the proportionately very large head. As a result, the height of all cervical vertebrae is greater than their respective lengths. In addition, the neural arches vary in height along the cervical series, becoming tallest on the posterior cervical vertebrae, possibly even taller than in the dorsal vertebrae. This is in marked contrast to the adult condition, where the cervical vertebrae are greatly elongated, and the neural arches are low and anteroposteriorly long. The slender, well-ossified cervical ribs are relatively short and thus differ from those in adult *Massospondylus*, in which they extend for the length of at least two vertebrae (R.R.R., pers. observ.). The last embryonic cervical rib is significantly longer than the others, being more than twice as long the fourth cervical rib. The ribs are too delicate and small to preserve the distinctive, anteriorly directed process seen in adults. The shape of the cervical column indicates that the neck was held horizontally, as in adult *Massospondylus* and other basal sauropodomorphs (Galton and Upchurch, 2004). The skeletal reconstruction (Fig. 8) shows the

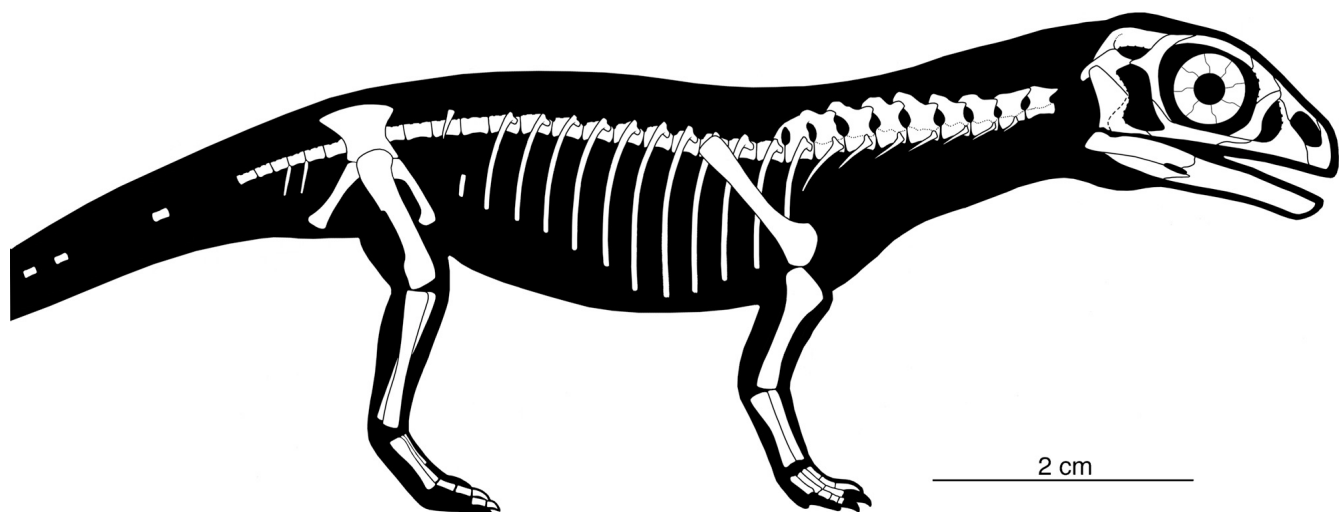


FIGURE 8. Skeletal reconstruction of the embryonic *Massospondylus carinatus* in right lateral view. Scale as indicated.

long neck in maximum dorsiflexion, with the skull held far anteriorly.

Thirteen dorsal vertebrae are preserved in BP/1/5347A-1 (Figs. 2, 3), with most of the ribs still in their original position. Damage in the posterior region of the series has somewhat disrupted the ribs, but a tiny posterior left dorsal rib is preserved just anterior to the pelvis. There is a gap within the dorsal series that corresponds to dorsal vertebra 12. The centrum of this vertebra is preserved, however, in BP/1/5347B-1, the result of the original split of the egg-containing block into part and counterpart. This counterpart piece was recently reexamined, once it has been returned from an extended loan, allowing for a more complete reconstruction of the skeleton (Fig. 8) than was previously possible (Reisz et al., 2005). As in juvenile and adult *Massospondylus*, there appears to be little if any variation in centrum length along the series (Table 1). No useful information is available about the shape and size of the dorsal neural spines. The first and third sacral ribs are preserved. The rod-like first sacral rib extends to the anterior edge of the iliac blade, and, as in adult *Massospondylus*, it is even narrower than the third rib. Its proportions suggest that the first sacral vertebra was a dorsosacral, as previously inferred in the adult (Cooper, 1981). Slight postmortem displacement occurred between the third sacral and first caudal vertebra in BP/1/5347A-1 (Figs. 2, 3). The caudal vertebrae are significantly shorter than the dorsal vertebrae, and the hemal arches form V-shaped chevrons (Fig. 3, 4C). The hemal spines are poorly developed in the embryos and extend only slightly beyond the base of the V-shaped arch, unlike the condition in the adults, which have greatly elongated hemal spines. Partially concealed by the right hind limb, some of the anterior caudal vertebrae are exposed behind the iliac blades in BP/1/5347A-1 and underneath the right metatarsals. It appears that the tail has not remained in articulation, because several caudal vertebrae are present close to and beneath the right hind limb. Too few caudal vertebrae are exposed to allow a reliable estimate of the length of the tail. Originally, the tail probably extended anteriorly beneath the right hind limb and the right forelimb. The simple, spool-shaped caudal vertebrae are difficult to distinguish from the phalanges of the right manus and pes.

Appendicular Skeleton—The pectoral and pelvic girdles are preserved in BP/1/5347A-1 (Figs. 2–4), and part of the pelvic girdle is preserved in BP/1/5347A-2 (Figs. 5, 6). The scapula is tall and slender. The scapular blade is expanded at its contact with the coracoid. It is not possible to separate its edge of contact with the coracoid from the area that would have formed the glenoid articular surface. The right scapula seems to be preserved in place, its distal end pushed up only slightly towards the vertebral column. The left scapula appears to have been flipped dorsally and rotated counterclockwise. It is now preserved slightly above the vertebral column. In contrast to the adult *Massospondylus* but similar to the condition in the small juveniles, the dorsal portion of the scapular blade is not expanded anteroposteriorly. Most of the right coracoid was lost, and it is difficult to determine how much of it was ossified at the time of death. There appear to be no ossified sternal elements, and there is no evidence of a clavicle. The pelvic girdle is partially exposed in BP/1/5347A-1, with both ilia and ischia but only the right pubis visible. The left iliac blade is also exposed in BP/1/5347A-2. Although the iliac blade is already ossified, its supra-acetabular crest is not preserved and possibly was not yet ossified. The iliac blade has a slender postacetabular process but a poorly developed preacetabular process. The ischium and pubis, exposed in BP/1/5347A-1, are short and slender, approximately one-half the length of the femur, and are much thinner and less well ossified than either the scapula or the ilium. These pelvic proportions are even more pronounced than in the holotype post-hatchling skeleton of *Mussaurus patagonicus*, a basal sauropodomorph from the Upper Triassic El Tranquilo Formation of Santa Cruz Province, Argentina (Bonaparte

and Vince, 1979). In contrast, the ischium and pubis are large and massive in the adults and exceed the ilium in size (Cooper, 1981).

The limbs are well preserved. All limb bones have thin bony walls and probably had large cartilaginous internal cones in the expanded proximal and distal portions. This is evident on the left tibia, where the internal surface of the shaft was exposed by post-mortem loss of bone along the distal half of the element. In addition, the external surfaces of all proximal limb bones are strongly fluted near their proximal and distal ends, indicating the presence of substantial cartilaginous ‘epiphyseal’ caps. Despite the thinness of the ossified portions of these elements, there is surprisingly little crushing.

The forelimbs are preserved in position on either side of the body. They comprise both humeri, radii, and ulnae, as well as some elements of the manus (Table 1). The proximal head of the humerus is larger than the distal end, probably due to the enormous size of the deltopectoral crest. This is evident on the left humerus of BP/1/5347A-1 (Figs. 2–4), which has a the proximal head exposed in anteromedial view, with a small, ossified crest projecting upwards, exposed right next to the edge of the shaft of the right humerus. The distal end of the left humerus is almost completely covered by three thoracic ribs in BP/1/5347A-1, but the distal end of the right humerus is exposed, showing a slight depression that probably represents the intercondylar groove. Part of the humerus is also exposed in BP/1/5347B-2, showing a well-ossified distal end of the bone (Figs. 5, 6B). The proximal head of the ulna is wider than that of the radius, as in the adults, and lacks an ossified olecranon, best seen in BP/1/5347B-2 (Fig. 6B). The radius and ulna are preserved in a pronated position on the right side of BP/1/5347A-1 (Figs. 2–4), with the slightly curved, slender radius crossing over the more massive, less curved ulna. They are located beneath the right tibia and fibula, and only partly visible as illustrated. The left radius and ulna are partly covered by ribs and the right pubis. Both radius and ulna are significantly shorter and more slender than the fibula or tibia (Table 1). Parts of both hands are preserved in BP/1/5347A-1 (Figs. 2–4). Only a single metacarpal of the left manus is exposed, whereas the right manus is more complete but concealed by the distal end of the tibia and right tarsus. No carpal elements are ossified in the embryos, and there is a wide gap between the distal ends of the radius and ulna and the proximal ends of the metacarpals in both skeletons. This lack of ossification is not unexpected because juvenile individuals of *Massospondylus* usually have unossified carpals; for example, BPI 4376 preserves a complete manus with fully ossified metacarpals and phalanges but lacks any carpals. In BP/1/5347A-1 (Figs. 2–4), the right manus, with two metacarpals, which are approximately equal in size, and three associated phalanges can be readily identified. The bones have flipped over at the level of the wrist, and have come to rest against the radius and ulna. A relatively robust, wide element, slightly displaced, may be the first metacarpal, but there are no phalangeal elements associated with it. If this identification is correct, then the other metacarpals belong to digits II and III, respectively. The latter two metacarpals are wider proximally than distally, and are closely appressed to each other. The slightly more robust metacarpal has two proximal phalanges preserved in articulation with it. The second, slightly more slender metacarpal has only one phalanx preserved in articulation, but it is slightly longer than the other proximal phalanx in the hand. All phalanges are shorter than the metacarpals. BP/1/5347B-2 (Figs. 5, 6B) preserves a nearly complete right manus, which is separated slightly from the radius and ulna by a gap that would have been occupied by cartilaginous carpal elements. Identification of the ossified elements of the manus is therefore easier than in BP/1/5347A-1. Four of the five metacarpals are ossified. The robust and short first metacarpal is in articulation with a particularly robust proximal phalanx. This condition is similar to that seen in juvenile and adult skeletons of *Massospondylus*. A very large, elongated, and

strongly curved ungual phalanx, the longest of the preserved phalanges, is interpreted as the distal phalanx of the first digit, but has shifted slightly laterally from its original articulated position. This ungual is also very large in all known post-hatchling skeletons. Metacarpals II and III are similar in size, whereas metacarpal IV is slightly shorter and more slender than the other two elements. They are all significantly longer and more slender than the first metacarpal, as in the juvenile and adult specimens of *Massospondylus*. Interestingly, whereas the preserved proximal phalanx of manual digit II is nearly as long as the metacarpal of this digit, the proximal phalanx and the other two phalanges of digit III are quite short. An additional, short, broad ossification distal to digit II may represent additional phalangeal elements of that digit, but their identity is uncertain.

The left hind limb is still preserved in articulation with the pelvis in BP/1/5347A-1 (Figs. 2–4), but its pes has been displaced to the other side of the right hind limb. The right hind limb is almost complete and articulated in this skeleton; the proximal head of its femur has been slightly dislocated from the acetabulum. Its femur has a slightly inturned proximal head and a much expanded distal end. The left element is exposed in posterior view, and has an ossified fourth trochanter, although the latter is partially concealed by a rib and by dorsal vertebra 13. A well-ossified fourth trochanter is also exposed on the left femur preserved in the other embryo, BP/1/5347A-2 (Fig. 5). The posterior surface of the distal end of the femur has an intercondylar fossa. Both tibiae and fibulae are well ossified in BP/1/5347A-1 (Figs. 2–4). The proximal head of the tibia is much more slender than the distal end of the femur, whereas the fibula is relatively broad, consistent with the overall columnar appearance of the hind limb. This is in strong contrast to the condition in the subadult and adult limbs of *Massospondylus*, where the proximal end of the tibia is massive, and nearly equal in size to the distal end of the femur (Cooper, 1981). There is no evidence of an ossified astragalus or any other tarsal element in BP/1/5347A-1. The absence of tarsal ossifications is unexpected, considering the robust astragalus in the adult, but may reflect the ontogenetic sequence of ossification of the pes. The hind limb of the smallest known juvenile of *Massospondylus carinatus* (BP/1/4376) has well-ossified limb bones, but the tarsus is surprisingly small. Only metatarsals I–III are present in both hind limbs in BP/1/5347A-1 (Figs. 2–4). A proximal phalanx articulates with metatarsal I but extends down into the matrix, and only part of its proximal articular surface is visible. Metatarsal II does not have any phalanges in articulation in BP/1/5347A-1, but metatarsal III is preserved with at least three phalanges in partial articulation, including a terminal phalanx.

The forelimb is proportionately much longer in the embryo (Table 1) than in the adult (Cooper, 1981), but this is consistent with the growth trajectory throughout ontogeny (Reisz et al., 2005). All elements of the forelimb, even the metacarpals and proximal phalanges of the manus, are proportionately longer than those in the adults.

DISCUSSION

Identity of the Embryos

The affinities of the eggs have been debated since the original report by Kitching (1979); even their dinosaurian origin has been questioned (e.g., Zelenitsky cited in Carpenter, 1999). Zelenitsky and Modesto (2002) argued that the peculiar microstructure of the eggshell was the result of diagenetic alteration and thus taxonomically uninformative. They noted that only the embryos themselves could provide secure identification of the eggs. Numerous skeletal features of the embryos now provide clear evidence that these individuals represent a sauropodomorph dinosaur (Reisz et al., 2005). These include the first dentary tooth (or its alveolus) being set back from the anterior end of the bone, presence of a lateral ridge on the dentary,

anteroventral extension of the infratemporal fenestra below the orbit, a horizontally extending rather than S-shaped neck, posterior dorsal centra that are longer than tall, and the length of the humerus exceeding 55% of that of the femur.

Taxonomic assignment of the embryo at a lower taxonomic level is more difficult due to the generalized anatomy of embryos, the morphological subtleties that differentiate some sauropodomorph taxa from the region, and the unstable nature of their taxonomy (Yates and Kitching, 2003; Barrett, 2004, 2009; Galton and Upchurch, 2004; Barrett et al., 2007). Reisz et al. (2005) assigned the embryos to *Massospondylus carinatus* based on a single autapomorphy for this taxon, greatest skull width exceeding skull height by at least 10% (Serenó, 1999; Sues et al., 2004). In addition, this taxonomic assignment was greatly strengthened by the tight fit of the embryonic materials with the growth trajectory of *Massospondylus carinatus* (Reisz et al., 2005). Nevertheless, recent assessments of sauropodomorphs from the Upper Elliot and Clarens formations reveal a much greater diversity during the latest Triassic and Early Jurassic in southern Africa than previously assumed (Yates, 2003; Yates and Kitching, 2003; Barrett, 2004, 2009; Galton and Upchurch, 2004). Since the publication of Reisz et al. (2005), a new species of *Massospondylus*, *M. kaalae*, has recently been named based on a single specimen with distinctive jaw proportions (Barrett, 2009). The presence of several basal sauropods or derived sauropodomorphs in the underlying Lower Elliot Formation (*Antetonitrus*, Yates and Kitching, 2003; *Melanorosaurus*, Yates, 2007) even raised the possibility that basal sauropods could be considered potential candidates for the identity of the embryos although we found no apomorphies in support of this. Yates et al. (2010) recently reported a new basal sauropodomorph, *Aardonyx celestae*, from the Upper Elliot Formation. *Aardonyx* can be ruled out as the taxon to which the embryos can be referred because the dentary lacks the lateral ridge, the premaxilla has a steeply ascending dorsal process, and the maxilla has an extensive medial lamina (Yates et al., 2010).

The identification of the embryos to either of the two currently recognized species of *Massospondylus* is difficult given the lack of ontogenetic data for the new species. However, the genus-level identification of the embryos as *Massospondylus* remains sound because one would expect the skull to be taller than wide in the embryos based on the proportionately enormous size of the eye in early ontogenetic stages of most tetrapods, yet their cranial proportions exhibit the diagnostic autapomorphy of *Massospondylus*. In addition, *Massospondylus* is by far the most commonly found sauropodomorph in the Upper Elliot Formation in southern Africa. Two as yet uncollected subadult skeletons of *Massospondylus* are currently eroding out of the matrix at the egg-producing locality, and several other skeletons have been identified within a radius of 500 m from the site in Golden Gate Highlands National Park. A morphometric analysis of skull growth in *Massospondylus*, currently in progress, may help resolve the specific identity of the embryonic remains, but until then, we prefer to retain our original identification of this material as *M. carinatus* (Reisz et al., 2005).

The Fossil Record of Dinosaur Embryos

The fossil record of non-avian dinosaurian embryos preserved within eggs is still very limited. The specimens of *Massospondylus* reported by Reisz et al. (2005) and described in detail in this paper represent the oldest example of dinosaurian embryos found to date. They are also the oldest known example of terrestrial vertebrate embryos in the fossil record. Remarkably, the small size of both the embryo and egg also set them apart from similar finds of other dinosaurian taxa. This is particularly interesting because the largest known adult specimen of *Massospondylus carinatus* had an estimated body length of more than five meters.

Dinosaurian embryos and hatchlings ('babies') have attracted a great deal of scientific and popular attention (Carpenter, 1999). A stratigraphically older example of dinosaurian hatchlings is a find of seven post-hatchling skeletons, all similar in size but in various degrees of completeness, of the sauropodomorph dinosaur *Mussaurus patagonicus* from the Upper Triassic (?Norian) El Tranquilo Formation of Santa Cruz Province, Argentina (Bonaparte and Vince, 1979; Pol and Powell, 2007). The skull of the holotype of *Mussaurus patagonicus* is about 30 mm long and the overall length of the skeleton is approximately 20–25 cm. None of these skeletons was apparently preserved inside an egg, and their size and level of ossification indicates that they are young, post-hatchling individuals (Pol and Powell, 2007). Bonaparte and Vince (1979) and Pol and Powell (2007) reported but did not describe or illustrate portions of two associated eggs and eggshell.

Two specimens of juvenile sauropodomorph dinosaurs have been described from the Lower Lufeng Formation of Yunnan Province, China. One is a small skull (less than 40 mm in length) with articulated mandible preserved in a nodule with an associated vertebra. Originally interpreted as an early squamate and named *Fulengia youngi* by Carroll and Galton (1977), Evans and Milner (1989) and Sereno (1991) demonstrated that it is, in fact, a juvenile sauropodomorph. The other is an incomplete, very small skull (23 mm in length) that Yang (1982) designated as the holotype of a new 'fabrosaurid' ornithischian, *Tawasaurus minor*. Sereno (1991) restudied this specimen and concluded that it probably represents a hatchling 'prosauropod.' He noted that neither '*Fulengia*' nor '*Tawasaurus*' displayed autapomorphies to support unequivocal referral to the common large sauropodomorph *Lufengosaurus huenei* from the Lower Lufeng Formation. Both specimens are much larger than we expect for basal sauropodomorph embryos based on the specimens described here, and we consider them small post-hatchling individuals.

The stratigraphically next oldest well-documented examples of dinosaurian embryonic remains in and associated with eggs are from the Upper Jurassic (Kimmeridgian-Tithonian) of Lourinhã, Portugal. Here, several well-preserved clutches of eggs referable to the form genus *Preprismatoolithus* were found with many fragmentary postcranial bones of embryos and/or hatchlings of an unidentified theropod preserved in the matrix surrounding the eggs or, in at least one instance, within an egg (Mateus et al., 1997:fig. 4). Based on the dimensions of the eggs, the total length of the embryos was about 40 cm. The bones within the egg are very fragmentary and suggest a relatively early stage of embryonic development.

From the more or less coeval Morrison Formation of the western United States, embryonic remains of several dinosaurian taxa have been reported although in no instance were these specimens found in eggs. Chure et al. (1994) described a partial postcranial skeleton of a tiny dinosaur from the Brushy Basin Member in the Utah portion of Dinosaur National Monument. They interpreted this specimen as an advanced embryonic individual of the ornithomorph *Camptosaurus* with an estimated overall length of 24 cm. They interpreted the fact that the articular ends of the limb bones are unossified as evidence for altricial behavior. Carpenter (1994) reported a partial skeleton including a complete skull of a very small individual ('baby') of the ornithomorph *Dryosaurus* from the same horizon and general region. He also mentioned other occurrences of presumed embryonic bones of this taxon. Again, the articular ends of the limb bones are poorly developed. Finally, Britt and Naylor (1994) described a minute premaxilla of the sauropod *Camarasaurus* from the Morrison Formation of the Dry Mesa Quarry in west-central Colorado. They interpreted this bone as representing an embryonic individual and noted the absence of erupted teeth.

Coombs (1982) described in detail two skulls and numerous postcranial bones of possible hatchlings of the basal ceratopsian dinosaur *Psittacosaurus* from the Lower Cretaceous Oshih For-

mation of Mongolia. He estimated the skull length of the smaller specimen as 28 mm and the total length as about 23–27 cm.

There are now numerous examples of dinosaurian remains in eggs from Late Cretaceous strata in Asia and in North and South America (see review by Carpenter, 1999). The best-known examples include the embryo of an oviraptorid theropod in an eroded egg of the *Elongatoolithus* type from the Djadokhta Formation (Campanian) of Mongolia (Norell et al., 1994), embryos of titanosaurian sauropods in numerous eggs of the form genus *Megaloolithus* from the Río Colorado Formation (Santonian) of Neuquén Province, Argentina (Chiappe et al., 1998, 2001), embryos of the lambeosaurine hadrosaurid *Hypacrosaurus stebingeri* in eggs of the form genus *Sphaeroolithus* from the upper part of the Two Medicine Formation (Campanian) of Montana and Alberta (Horner and Currie, 1994), extraordinarily preserved embryos of therizinosauroid theropods in eggs from the Nanchao Formation (?Santonian-Campanian) of Henan Province, China (Kundrát et al., 2008), and numerous embryonic bones referable to a variety of dinosaurian taxa from the Bissekty Formation (Turonian) of Uzbekistan (Sues and Averianov, in preparation).

In the absence of extensive comparative data for early development in non-avian dinosaurs, it is difficult to assess the exact developmental stage of the two embryos of *Massospondylus carinatus* described here. However, comparisons with remains from dinosaurian eggs from geologically much younger sediments does support our previous hypothesis that the level of ossification of these two embryos indicates that these individuals were close to hatching. The embryonic remains found inside eggs of Late Jurassic age and those of Late Cretaceous titanosaurian sauropods have well-developed skulls, with teeth already formed, but the postcranial skeletons of these embryos show a much earlier developmental stage than those of *Massospondylus*. The level of ossification seen in the two embryos described here, along with the preservation of well-ossified scleral plates and stapes, the preservation of much of the manus and pes, and the presence of a well-developed deltopectoral crest on the humerus and fourth trochanter on the femur all support the hypothesis that these embryos were close to hatching. The best examples of Late Cretaceous dinosaur embryos found inside eggs and similarly well ossified are those of *Hypacrosaurus stebingeri* (Horner and Currie, 1994). Although their skeletal structure indicates a comparable level of ossification, the embryos of *Hypacrosaurus stebingeri* are significantly larger than those of *Massospondylus carinatus*, with a skull length of about 60 mm, and well-developed dentition in the maxillae and dentaries. Moreover, a well-preserved embryonic skull of *H. stebingeri* already has two generations of teeth erupted from several tooth positions and has started to develop occlusal surfaces (Horner and Currie, 1994). Thus there is little doubt that these embryos were close to hatching. The similarities in the levels of ossification of the postcranial skeleton between these two taxa does support our hypothesis of the near-hatching condition of the two embryos of *Massospondylus carinatus*, although neither preserves definite teeth. Comparisons with sauropod and theropod embryos of clearly earlier developmental stages (Chiappe et al., 2001; Mateus et al., 1997) than those of *M. carinatus*, with well-developed teeth, militates against the use of the presence of teeth as an indicator of the developmental stage in this dinosaur. The slightly larger skulls of the two presumed hatchlings of sauropodomorph dinosaurs from the Lower Lufeng Formation (Lower Jurassic) already have marginal teeth (Evans and Milner, 1989; Sereno, 1991).

The temporal and phylogenetic distance between these basal sauropodomorph dinosaurs and their extant relatives, birds and crocodylians, makes direct comparisons with their embryos difficult. Additional embryonic stages of *Massospondylus carinatus* are required in order to gain a better understanding of the early ontogenetic development of this taxon. Continuing work at the Rooidraai locality has already resulted in the discovery of ad-

ditional egg clusters that remain to be collected, prepared, and studied.

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