

mocline shoals. Thus, the increase in the zonal SST difference after  $\sim 1.7$  Ma could indicate that tropical air-sea feedbacks (34) amplified the SST response to a changing thermocline once critical thermocline conditions were reached.

Mean tropical thermocline conditions can influence air-sea feedbacks that affect high-frequency climate variability (4, 15); the amplitude of ENSO variability is dampened when the thermocline is deeper or warmer in the EEP (5, 10). This effect applied to longer time scales may explain why permanent El Niño conditions during the Pliocene were accompanied by reduced-amplitude glacial-interglacial cycles; a deeper or warmer thermocline may have preconditioned the tropical system such that air-sea feedbacks needed to amplify small perturbations in solar forcing were weak. The establishment of Walker circulation at  $\sim 1.7$  Ma coincides with the Pliocene-Pleistocene epoch boundary, after which the sensitivity of climate to solar forcing peaked (16).

Our study indicates that today's zonally asymmetric SST pattern and thermocline structure of the tropical Pacific are not stable over long time scales. Given the importance of tropical Pacific processes in modulating meridional heat transport, these results indicate that in a warmer world, the ocean may accomplish redistribution of heat in a fundamentally different way. Thus, the Pliocene warm period provides a target and a test to climate models and theory and is an indication that climate feedbacks do not work to maintain the presently strong asymmetry across the Pacific under some circumstances. It may indicate that warming cannot continue indefinitely without substantial changes in the Walker circulation (10) and that changes in the subtropics, communicated through the thermocline, might cause a fundamental reorganization of the tropical Pacific ocean-atmosphere system (4, 10). Depending on one's interpretation of the instrumental data from the tropical Pacific, a shift in the baseline tropical Pacific pattern may already be occurring (2, 4, 5, 8).

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#### Supporting Online Material

[www.sciencemag.org/cgi/content/full/1112596/DC1](http://www.sciencemag.org/cgi/content/full/1112596/DC1)

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## Embryos of an Early Jurassic Prosauropod Dinosaur and Their Evolutionary Significance

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Articulated embryos from the Lower Jurassic Elliot Formation of South Africa are referable to the prosauropod *Massospondylus carinatus* and, together with other material, provide substantial insights into the ontogenetic development in this early dinosaur. The large forelimbs and head and the horizontally held neck indicate that the hatchlings were obligate quadrupeds. In contrast, adult *Massospondylus* were at least facultatively bipedal. This suggests that the quadrupedal gait of giant sauropods may have evolved by retardation of post-natal negative allometry of the forelimbs. Embryonic body proportions and an absence of well-developed teeth suggest that hatchlings of this dinosaur may have required parental care.

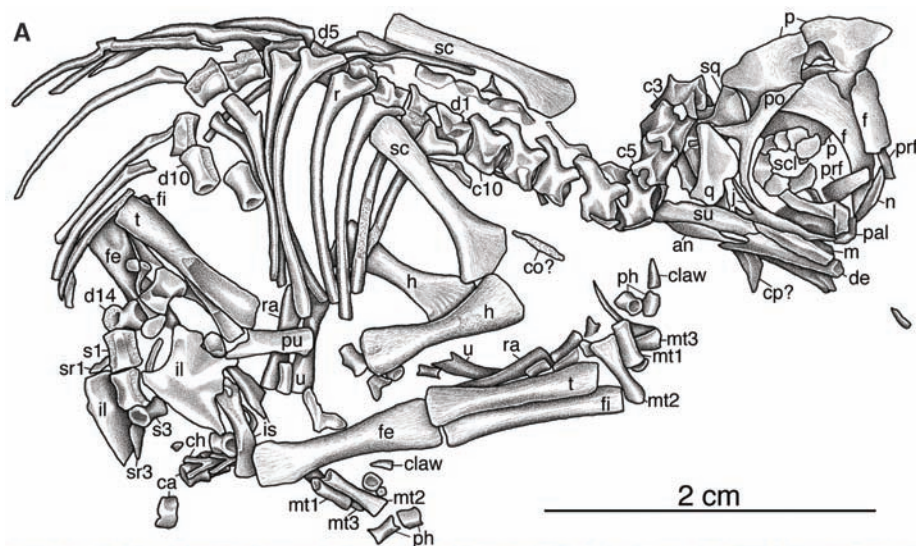
Prosauropod dinosaurs appeared during the early Late Triassic (1, 2) and became the dominant large herbivores in Late Triassic and Early Jurassic continental ecosystems (3) [220 to 183 million years ago (Ma)]. The prosauropod *Massospondylus carinatus* Owen, 1854 is known from numerous well-preserved speci-

mens from many localities in the Lower Jurassic Elliot and Clarens formations of South Africa and Lesotho (4, 5). It is represented by many articulated skeletons that form an extensive growth series. Here we describe articulated embryonic skeletons referable to *Massospondylus* and provide evidence that the quadrupedal gait in sauropods may have evolved through pedomorphosis.

A cluster of six subspherical eggs (6 cm in maximum diameter) was collected from the *Massospondylus* Range Zone of the upper Elliot Formation in Golden Gate Highlands National Park in South Africa (6, 7). During preparation, we identified embryonic skeletal material in the bottom halves of five of the eggs; the sixth egg seems to have hatched.

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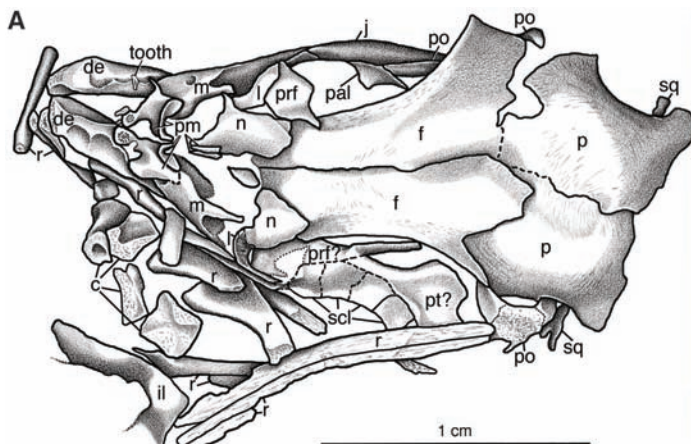
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**Fig. 1.** (A and B) An articulated embryonic skeleton of *Massospondylus* (BP/1/5347A). an, angular; c3 to c10, cervical vertebrae; ca, caudal vertebra; ch, hemal arch; co, coracoid; cp?, cultriform process?; de, dentary; d1 to d14, dorsal vertebrae; f, frontal; fe, femur; fi, fibula; h, humerus; il, ilium; is, ischium; l, lacrimal; m, maxilla; mc, metacarpals; mt1 to 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 to s3, sacral vertebrae; sc, scapula; scl, scleral ring; sr1 to sr3, sacral ribs; sq, squamosal; su, surangular; t, tibia; u, ulna.

Other known fossil dinosaur eggs containing articulated embryonic skeletons are Late Cretaceous in age. Although the precise developmental stage of the embryos could not be determined, the articulated skeleton completely fills the egg and together with the advanced level of ossification (as indicated by the presence of the ossified stapes and fourth trochanter on the femur) suggests that the animals were close to hatching (8, 9). Numerous skeletal features indicate that these embryos represent a prosauropod dinosaur: The first dentary tooth (alveolus) is set back from the anterior end of the bone; a lateral ridge is present on the dentary; the infratemporal fenestra extends below the orbit; the neck is horizontal rather than S-curved; the posterior dorsal centra are longer than they are tall; and humeral length exceeds 55% of that of the femur (3). We refer the embryos to *Massospondylus* based on a cranial autapomorphy, the maximum transverse width of the skull exceeding its height by at least 10% (10). *Massospondylus* is the most common sauropodomorph in this stratigraphic interval; two uncollected adult skeletons of this taxon have been found at the egg-producing locality, and several other skeletons are exposed within 500 m (11).

The embryonic contents of two of the six eggs have been completely prepared. One skeleton is preserved curled up and in articulation (Fig. 1). The skull has been slightly telescoped in the snout region before fossilization, with the anterior part of the mandible, the premaxilla, and the anterior end of the maxilla having been lost. The skull is virtually complete in the second embryo, and the position of various postcranial elements suggests that this skeleton was also articulated and curled up (Fig. 2). This skull is exposed in dorsal view, and the lower jaws have been shifted slightly forward, exposing their alveolar regions and symphysis. One fragment that may represent a partially erupted tooth is preserved in the dentary; all other alveoli are empty.



**Fig. 2.** (A and B) Embryonic skull and postcranial elements of *Massospondylus* (BP/1/5347A). The embryonic membrane is preserved inside the egg immediately to the right of the skull. Abbreviations are the same as in Fig. 1.

Embryonic skull structure (Fig. 3B) is consistent with referral to *Massospondylus*. The posterior part of the maxilla forms a distinct, slender process that underlies the jugal. The tall lacrimal is visible in dorsal view. A long posterodorsal process of the prefrontal is identical to that seen in other skulls of *Massospondylus*. The antorbital fenestra is tall and almost triangular in outline. The external naris is large in the embryo but not as tall as the antorbital fenestra. The nasal is small, the frontal is long, and the large, dome-like parietals are feebly emarginated for the upper temporal fenestra. In contrast, the largest known skull of *Massospondylus* (specimen BP/1/4934) has an elongate nasal, a relatively short frontal, and the parietals are strongly emarginated and form a median crest. Other smaller specimens show intermediate stages

between the two extremes (10). The embryonic skulls preserve a nearly complete ring of scleral ossicles in the proportionately enormous orbit (the diameter is 39% of the reconstructed skull length). In addition, a stapes is still in its original position in one of the embryonic skulls; its distal end is slightly expanded, as in adults.

The embryonic postcranial skeleton generally conforms to that in *Massospondylus* but differs markedly in its proportions. The atlas-axis complex could not be exposed. The remaining eight cervical vertebrae are short with delicate ribs, in contrast to the elongate cervicals and cervical ribs in adults. Juvenile skeletons show intermediate stages in cervical development. Thirteen dorsals are preserved with most ribs still in their original positions. Damage in the posterior region of the series

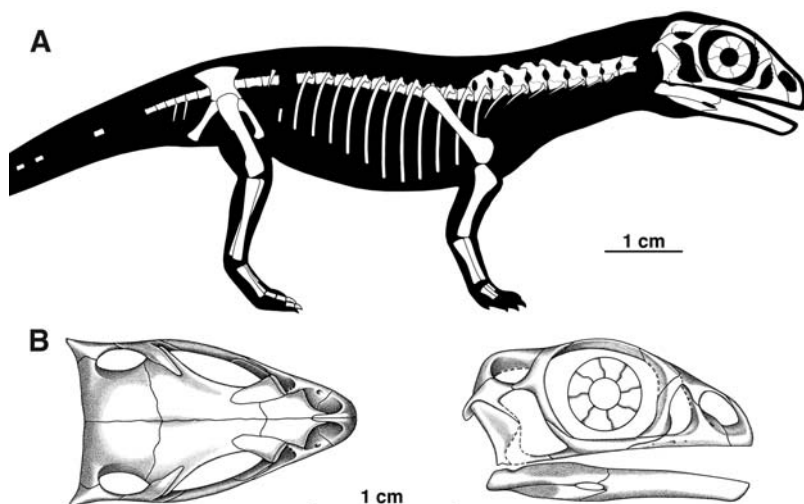
has disrupted the arrangement of ribs, but a tiny posterior left dorsal rib is preserved just anterior to the pelvis. The rod-like first sacral rib extends to the anterior edge of the iliac blade; its proportions support the hypothesis that the first sacral vertebra was a modified dorsal (5). The anterior caudals are substantially shorter than the dorsals, and their hemal spines form short, V-shaped chevrons.

Both pectoral and pelvic girdles are exposed. The scapula is tall and slender. Most of the right coracoid was lost during fossilization. There appear to be no ossified sternals. The iliac blade is well preserved; its preacetabular process is poorly developed and the supraacetabular crest is absent (i.e., not ossified). The ischium and pubis are slender and short, about one-half the length of the femur.

The limb bones are well preserved, but the texture of their external surfaces indicates the presence of substantial cartilaginous "epiphyseal" caps. All forelimb elements are relatively longer than those in the adults, including the metacarpals and proximal phalanges, but this is consistent with their ontogenetic trajectories. The right femur has a slightly inturned proximal head and a greatly expanded distal end. The left femur shows the presence of an ossified fourth trochanter. The posterior surface of the distal end of the left femur has an intercondylar fossa. The proximal head of the tibia is not as wide as the distal end of the femur, whereas the fibula is relatively broad, consistent with the generally columnar appearance of the hindlimb. In the manus, metacarpals I to III and at least two phalanges are ossified, as are metatarsals I to III and some phalanges of the pes, including a complete second digit.

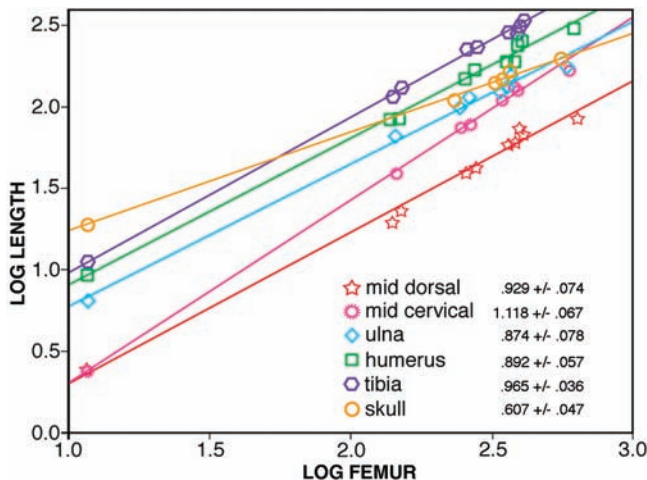
*Massospondylus* reached a total body length of up to 5 m (5). The large number of complete skeletons permits analysis of relative growth in the skull, vertebrae, and limbs (12). We made six bivariate comparisons using femur length as the standard variable (Fig. 4), which correlates well with overall body size in terrestrial vertebrates (13). Regression analyses show that the tibia and dorsal vertebrae in *Massospondylus* grew isometrically with reference to the femur. Both the humerus and the ulna show negatively allometric growth during ontogeny. The strongest negative allometry is observed in the skull, and the strongest positive allometry is seen in the length of the cervical vertebrae.

Relative incremental growth also accounts for proportional differences between the embryonic skulls and those of the adult. In embryonic skulls, the nasal is shorter than either the frontal or parietal, and the maxilla and premaxilla are also quite small relative to the rest of the skull. The known series of skulls of *Massospondylus* shows gradual elongation of the nasal, an increase in the relative length and height of the maxilla and premaxilla, and an increase in the size of the narial and antorbital



**Fig. 3.** Reconstructions of *Massospondylus* embryos. (A) An articulated skeleton in lateral view; the horizontally held neck is shown at maximum dorsiflexion. The total length of the tail could not be determined; the estimated minimum length is shown. Estimated snout-vent length of the embryo is 8.1 cm. (B) An embryonic skull in dorsal and lateral views.

**Fig. 4.** Relative growth in the skeleton of *Massospondylus*. Regression analysis shows growth trajectories of various parts of the skeleton relative to the length of the femur. Eight skeletons, including the embryo, were sufficiently complete for this analysis, their femora showing a 47-fold increase in length in the series. Several otherwise superbly preserved specimens could not be used because they lacked a femur. One of the specimens (BP/1/4934) used in this analysis had an incomplete femur, and we estimated its total length by using the fourth trochanter as a landmark for comparisons with complete isolated femora at a similar level of development. Allometric coefficient values that are significantly less than 1.0 indicate negative allometry, as seen in the skull and forelimb, whereas values that are significantly greater than 1.0 denote positive allometry, as seen in the neck.



openings as the antorbital region of the skull becomes increasingly longer (10). Associated with this change is the gradual emargination of the frontals and parietals along the edges of the upper temporal fenestrae for the increase in the attachment areas for the adductor jaw musculature. The quadrate also shows a gradual relative increase in height, possibly related to the increase in the adductor jaw muscles. Finally, as in other vertebrates, the relative size of the orbit decreases throughout ontogeny. Despite these changes, the embryo maintains the diagnostic skull width-to-height ratio of *Massospondylus*.

The proportionately enormous skull; the long, horizontally held neck; the proportionately long forelimbs; and the small caudals with weakly developed transverse processes and hemal spines all indicate that the hatchlings of *Massospondylus* were obligate quadrupeds (Fig. 3). This is in contrast to the body proportions of adult *Massospondylus*, which are characterized by a small head, short forelimbs, and robust caudals with large transverse processes and hemal arches. As in most prosauropods, these adult proportions indicate at least facultatively bipedal locomotion (14, 15). The changes from a sauropodlike condition with long forelimbs (16) and quadrupedal posture in early ontogenetic stages of *Massospondylus* to the plesiomorphic condition of short forelimbs and bipedal posture in the adult suggest that the quadrupedal posture of sauropods (17) may have evolved through paedomorphosis, the retention of early ontogenetic features in the adult, as first suggested by Bonaparte and Vince (18).

Modification of the sauropodomorph neck may have been correlated with the evolution of quadrupedality in this clade. The reconstructed quadrupedal posture for the embryo is at least in part related to the structure of the neck. As in most sauropodomorphs (19), the neck of *Massospondylus* was held more or less horizontally. This condition represents an autapomorphy for Sauropodomorpha and differs from the plesiomorphic condition of an S-curved neck in other dinosaurs and their immediate outgroups among Ornithomiridae (20). The S-curved neck is associated with their bipedal posture and the need for bringing the head closer to the center of gravity of the body. The presence of a horizontally held neck in the pre-hatching stages of basal sauropodomorphs like *Massospondylus* may have constrained them to a quadrupedal posture, one that required long forelimbs.

The combination of the body proportions and poorly developed dentition suggest that the hatchlings may have required parental care (21). The diminutive ventral elements of the pelvic girdle, small caudal vertebrae, and relatively enormous head of the *Massospondylus* embryos suggest it would have been difficult for the hatchlings to move around efficiently.

The virtual absence of teeth in these embryos is another indicator of altricial behavior. Only a single possible tooth fragment is preserved in the two skulls, whereas other delicate, loosely attached elements were preserved largely undisturbed. Even if most of the teeth were poorly mineralized or lost postmortem, they were not well suited for feeding. If this interpretation is correct, these embryos provide early evidence of altricial behavior in a non-avian dinosaur.

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#### Supporting Online Material

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## Pesticide Resistance via Transposition-Mediated Adaptive Gene Truncation in *Drosophila*

Yael T. Aminetzach, J. Michael Macpherson, Dmitri A. Petrov\*

To study adaptation, it is essential to identify multiple adaptive mutations and to characterize their molecular, phenotypic, selective, and ecological consequences. Here we describe a genomic screen for adaptive insertions of transposable elements in *Drosophila*. Using a pilot application of this screen, we have identified an adaptive transposable element insertion, which truncates a gene and apparently generates a functional protein in the process. The insertion of this transposable element confers increased resistance to an organophosphate pesticide and has spread in *D. melanogaster* recently.

The *Drosophila* genome contains a large number of active transposable element (TE) families that generate new TE insertions (1, 2). Many such TEs are deleterious at least partly because ectopic recombination among them scrambles chromosomes (3, 4). Thus, many new TE insertions cannot reach high population frequencies unless they either recombine infrequently (4) or they lead to a sufficiently beneficial change to overcome the disadvantage of ectopic recombination.

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To search for unusually frequent and therefore putatively adaptive TE insertions, we conducted a population survey of all of the 16 identified insertions of long interspersed element (LINE)-like *Doc* TEs (5) located in regions of high recombination in the sequenced *D. melanogaster* genome (4). All *Doc* elements except one (*Doc1420*) appeared to be subject to strong purifying selection. *Doc1420* occurred unusually frequently (4) despite being neither unusually short nor unusually divergent, which suggests that it either generates or is closely linked to an adaptive mutation.

*Doc1420* is very frequent worldwide (~80%) and is much more rare (*G* test; *P* = 0.0001) in putatively ancestral African pop-