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A Basal Dinosaur from the Dawn of the Dinosaur Era in Southwestern Pangaea

Ricardo N. Martínez,1 Paul C. Sereno,2* Oscar A. Alcober,1 Carina E. Colombi,1,3 Paul R. Renne,1,5 Isabel P. Montañez,6 Brian S. Currie7

Upper Triassic rocks in northwestern Argentina preserve the most complete record of dinosaurs before their rise to dominance in the Early Jurassic. Here, we describe a previously unidentified basal theropod, reassess its contemporary Eoraptor as a basal sauropodomorph, divide the faunal record of the Ischigualasto Formation with biozones, and bracket the formation with 40Ar/39Ar ages. Some 230 million years ago in the Late Triassic (mid Carnian), the earliest dinosaurs were the dominant terrestrial carnivores and small herbivores in southwestern Pangaea. The extinction of nondinosaurian herbivores is sequential and is not linked to an increase in dinosaurian diversity, which weakens the predominant scenario for dinosaurian ascendancy as opportunistic replacement.

A
n arid valley in northeastern Argentina called Ischigualasto contains a well-exposed fossiliferous Upper Triassic section from the dawn of the dinosaur era. Some 50 years of intensive collecting have yielded nearly complete skeletons of the basal dinosaurs, Eoraptor (Fig. 1A) and Herrerasaurus (1, 2), and hundreds of additional fossil vertebrates. Recent finds include several previously unidentified dinosaurs based on partial skeletons (3–5), and recent geologic work has detailed stratigraphic and paleoecologic variation across the formation (6).

We describe here a nearly complete basal dinosaur, Eodromaeus murphi nov. gen. nov. sp. (7, 8), which helps to reveal skeletal form and function at the root of Theropoda, a clade that includes all predatory dinosaurs (Fig. 2A) (9). The skull is relatively low and lightly built with a relatively spacious antorbital fenestra, which is emarginated anteriorly by a relatively broad antorbital fossa (Fig. 1B). On the snout, an accessory pneumatic opening, the promaxillary fenestra, is present near the anterior margin of the antorbital fossa, the promaxillary fenestra, is present near the anterior margin of the antorbital fossa (specimen number PVSJ 560) (Fig. 1B). The promaxillary fenestra is present in the basal theropod Herrerasaurus (10) and in most later theropods, although it is secondarily closed in the early North American theropod Tawa and some coelophysoids (11, 12). The premaxilla-maxilla suture is long and akinetic, and the jugal ramus under the orbit is shallow (Fig. 1B). The side walls and ventral aspects of the braincase are marked by well-defined tympanic and basi sphenoïd recesses, respectively, and the basipterygoid processes are transversely compressed (Fig. 1C). In the lower jaw, the dentary is slender, and the retroarticular process is well developed posteriorly (Fig. 1B).

There are 4 premaxillary and 11 maxillary teeth, which are separated medially by inter dental plates. All crowns are laterally compressed, curved, and very finely serrated mesially and distally (nine serrations per millimeter), unlike the more numerous maxillary teeth in Eoraptor, which have larger denticles, less recurvature, and a constriction at the base of the crown (Fig. 1, D and E). Anterior maxillary crowns are caniniform, their ventral reach increased by a ventrally convex alveolar margin (Fig. 1, B and E). Dentary teeth, on the other hand, are relatively uniform in size, and the first tooth is located at the anterior tip of the dentary, unlike the condition in Eoraptor (Fig. 1, A and B). A row of very small rudimentary teeth crosses the palatal ramus of the pterygoid in Eodromaeus (PVSJ 560), as in Eoraptor, the only dinosaurs known to retain palatal teeth.

The cervical column is composed of proatlantal neural arches followed by 10 cervical vertebrae. Cervical vertebrae have spool-shaped centra that are more elongate than in Eoraptor; many centra have lengths more than three times the centrum diameter (Fig. 2, A and B). Cervical vertebrae have a long ventral keel and projecting epipophyseal processes. Invaginated pleurocoels are present in posterior cervicals, indicative of the presence of pneumatic invasion by parasagittal cervical air sacs (Fig. 2B). The pleurocoels open posteriorly into a lateral groove, which is present in most other vertebrae in the axial column. Thus, the cervical air sac system may have extended into the trunk, unlike in extant avians. There are 14 dorsal vertebrae in the trunk, the posterior of which are stabilized by hypopheno-hypantrum articulations (Fig. 2D). There appear to be three sacral vertebrae—a dorsosacral followed by two primordial sacrals with robust ribs—although the dorsosacral rib is not preserved in articulation. The elongate tail, which is composed of ~45 caudal vertebrae, has long anterior chevrons (Fig. 2A). Mid and distal caudal centra are cylindrical and have elongate prezygapophyses (Fig. 2, A and E).

Table 1. Skull and long-bone lengths (in millimeters, upper portion of table) and proportions (in percent, lower portion of) Eodromaeus morphi, Eoraptor lunensis, and other basal dinosaurs (32, 33). Parentheses indicate estimate. Skull length is measured from the anterior tip of the premaxilla to the posterior extremity of the occipital condyle. Measurements average long-bone lengths when both sides are available.

<table>
<thead>
<tr>
<th>Measure or ratio</th>
<th>Eodromaeus PVSJ 562</th>
<th>Herrerasaurus PVSJ 373</th>
<th>Eoraptor PVSJ 512</th>
<th>Heterodontosaurus SAM-PK-K337</th>
</tr>
</thead>
<tbody>
<tr>
<td>Skull*</td>
<td>(120)</td>
<td>282</td>
<td>114</td>
<td>115</td>
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<tr>
<td>Humerus</td>
<td>85</td>
<td>(175)</td>
<td>85</td>
<td>83</td>
</tr>
<tr>
<td>Radius</td>
<td>64</td>
<td>153</td>
<td>63</td>
<td>58</td>
</tr>
<tr>
<td>Metacarpal 3</td>
<td>28</td>
<td>62</td>
<td>21</td>
<td>22</td>
</tr>
<tr>
<td>Femur</td>
<td>160</td>
<td>345</td>
<td>152</td>
<td>112</td>
</tr>
<tr>
<td>Tibia</td>
<td>165</td>
<td>315</td>
<td>156</td>
<td>145</td>
</tr>
<tr>
<td>Metatarsal 3</td>
<td>(100)</td>
<td>165</td>
<td>81</td>
<td>68</td>
</tr>
<tr>
<td>Humerus/forelimb†</td>
<td>48%</td>
<td>45%</td>
<td>50%</td>
<td>51%</td>
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<tr>
<td>Radius/forelimb†</td>
<td>36%</td>
<td>39%</td>
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<tr>
<td>Metacarpal 3/forelimb</td>
<td>16%</td>
<td>16%</td>
<td>12%</td>
<td>14%</td>
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<tr>
<td>Tibia/femur</td>
<td>106%‡</td>
<td>91%</td>
<td>103%</td>
<td>130%</td>
</tr>
<tr>
<td>Femur/hind limb‡</td>
<td>38%</td>
<td>42%</td>
<td>39%</td>
<td>35%</td>
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<td>45%</td>
</tr>
<tr>
<td>Metatarsal 3/hind</td>
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<td>21%</td>
<td>21%</td>
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<tr>
<td>Humerus/femur</td>
<td>53%</td>
<td>51%</td>
<td>56%</td>
<td>74%</td>
</tr>
<tr>
<td>Forelimb/hind limb</td>
<td>42%</td>
<td>47%</td>
<td>43%</td>
<td>50%</td>
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</tbody>
</table>

*Skull length was measured between the anterior tip of the premaxilla and posterior extremity of the occipital condyle. †Forelimb length equals the sum of the lengths of the humerus, radius, and metacarpal 3. ‡Hind-limb length equals sum of the femur, tibia, and metatarsal 3 lengths. ††Metatarsal 3 is not preserved in PVSJ 562. In PVSJ 560, the distal end is missing; the length estimate is based on a comparison to digit I (plus 10% to account for the size differential for the major long bones of the hind limb). ||Skull length is based on the comparably sized specimen PVSJ 407, because the skull is not preserved in PVSJ 373. ¶Average of 103 and 10%, based on PVSJ 560 and 562, respectively.

"R"o"l o"c"a"n"217, 6A

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In the pectoral girdle, the coracoid has deep proportions with a relatively short posterior process, and the scapula has a relatively narrow neck between a prominent acromial process and a distally expanded blade (Fig. 2C). The straight-shafted humerus has a broad proximal end, a subrectangular deltopectoral crest, and a distal end with a hemispherical radial condyle (Fig. 2F). The ulna and radius have shafts in close contact, the former with a prominent olecranon process unlike the condition in Eoraptor (Fig. 2G). The well-ossified corpus is composed of a radiale, ulnare, centrale, and four distal carpals (Fig. 1G). There are five manual digits with a phalangeal formula of 2-3-4-1-1 (Fig. 1G). The manus has a pronounced lateral metacarpal arch, distal extensor depressions on metacarpals 1 to 3, and elongate penultimate phalanges on digits I to III.

In the pelvic girdle, the preacetabular process is proportionately deep, and the postacetabular process has an arched brevis fossa (Fig. 1A).

Phylogenetic analysis of basal dinosaurs positions the contemporaneous and similar-sized Eochothomus and Eoraptor at the base of Theropoda and Sauropodomorpha, respectively (Fig. 3). Basal theropod status for Eochothomus is supported by a suite of derived attributes in the skull (promaxillary fenestra, basiphenoid fossa), axial skeleton (cervical pleurocoels, elongate caudal prezygapophyses), forelimb (radiusulnare shaft apposition, elongate penultimate phalanges), pelvic girdle (distally tapering pubic blade, pubic foot), and hind limb (femoral extensor depression, tibial crest for fibula). Whereas herrerasaurids appear to be more basal in position among theropods (Fig. 3), Eochothomus is only marginally more derived, has few specializations (autapomorphies) (8), and thus approximates the hypothetical ancestral theropod in body size and morphology. The North American basal theropod Tawa is allied with coelophysoids in our analysis but with a single added step can be repositioned outside Neotheropoda as originally proposed (11).

Not only does Eoraptor lack all of the aforementioned theropod attributes in Eochothomus, but it also exhibits features previously seen only among basal sauropodomorphs. In the skull, these features include an enlarged narial opening, a

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**Fig. 1.** Skull, carpus, and manus of the basal dinosaurs *Eoraptor lunensis* and *Eochothomus murphi*. Skull reconstruction in lateral view of (A) *E. lunensis* (based on PVSJ 512) and (B) *E. murphi* (based on PVSJ 560 to 562). (C) Braincase of *E. murphi* (PVSJ 562) in ventralateral view (reversed) and in two computed-tomographic (CT) cross sections (at vertical lines). Anterior left maxillary teeth are shown at the same scale in (D) *E. lunensis* (PVSJ 512, drawing of right maxillary tooth 2 in lateral view (reversed)) and (E) *E. murphi* (PVSJ 563, cast of left maxillary tooth 3 in medial view (reversed)). Reconstruction of the left carpus and manus in dorsal view with enlarged views of the proximal and distal ends of phalanx 1 of digit I in (F) *E. lunensis* (based on PVSJ 512) and (G) *E. murphi* (based on PVSJ 560 and 562). The distal condyles in *E. lunensis* show 35° clockwise rotation with the proximal dorsal extensor process positioned dorsally. Abbreviations: l to v, manual digits 1 to v; a, angular; anteo, antorbital fenestra; antfo, antorbital fossa; ar, articular; asaf, anterior surangular foramen; bo, basioccipital; bpt, pterygoid process; bsf, basisphenoid fossa; bt, basil tubera; ce, centrale; d, dentary; d1, d12, and d16, dentary teeth 1, 12, and 16; dcl to d5, distal carpals 1 to 5; dip, dorsal intercondylar process; ec, ectopterygoid; emf, external mandibular fenestra; en, external naris; f, frontal; j, jugal; l, lacrimal; ldc, lateral distal condyle; m, maxilla; m1, m11, and m17, maxillary teeth 1, 11, and 17; mcp, medial cotylus; mdc, medial distal condyle; m, nasal; nf, narial fossa; p, parietal; pl, palatine; pm, premaxilla; pm1 and pm4, premaxillary teeth 1 and 4; pmfo, promaxillary fossa; po, postorbital; popr, paroccipital process; prl, prefrontal; ps, parapharyngoid; pt, pterygoid; q, quadratojugal; rae, radiale; ri, ridge; sa, surangular; saf, surangular foramen; snf, subnarial foramen; sq, squamosal; ule, ulnare; vip, ventral intercondylar process. Dashed lines indicate a missing margin; hatching indicates a broken surface. Scale bars, 2 cm in (G) (for braincase); 3 mm in (D) and (E); 5 mm in (F) and (G) (enlarged views).
REPORTS

Fig. 2. Postcranial features of the Late Triassic basal theropod Eoraptor murphi. Skeletal silhouette based on PVSJ 534, 560, and 562; postcranial bones are from PVSJ 562, except where indicated; bone casts and pencil drawings were used to eliminate color distortion and reversed as needed to left lateral view. (A) Skeletal silhouette showing preserved bones (missing portions in red). (B) Posterior cervical vertebrae (C7 and C8 anterior part) in lateral view (reversed) with enlarged cross-sectional view across the pleurocoel from a CT scan (at vertical line). (C) Scapulocoracoid in lateral view. (D) Posterior dorsal vertebra (~D11) in lateral view. (E) Distal caudal vertebrae (CA27 and CA28) in lateral view (PVSJ 560). (F) Humerus in anterior view. (G) Ulna in lateral view. (H) Pubes in anterior and lateral (reversed) views. (I) Proximal fibula in medial view. (J) Astragalus and calcaneum (right) in dorsal view (PVSJ 534). (K to M) Femur in lateral view, proximal end in lateral view, and distal end in anterior view, respectively. Abbreviations: ac, acromion; ach, articular surface for the chevron; afit, articular surface for the fibula; ap, ambiens process; arhd, articular surface for the radial head; arsh, articular surface for the radial shaft; as, astragalus; asc, ascending process; at, anterior trochanter; att, articular surface for the tibia; c, centrum; C2 and C10, cervical vertebrae 2 and 10; ca, calcaneum; CA1, caudal vertebra 1; cc, coracoid; ct, calcaneal tuber; D1 and D14, dorsal vertebrae 1 and 14; df, diaphysis; dpc, deltoidal crest or epiphysis; gl, glenoid; gr, groove; hd, head; in, interpubic notch; k, keel; lco, lateral condyle; lp, lateral process; nc, neural canal; nds, nonarticular dorsal surface; ns, neural spine; ol, olecranon; pa, parapophysis; pf, pubic foot; pl, pleurocoel; poz, postzygapophysis; pr, posterior process; prz, prezygapophysis; roco, radial condyle; rr, raised rugosity for attachment; S1 and S3, sacral vertebrae 1 and 3; scb, scapular blade; tp, transverse process; ts, trochanteric shelf. Dashed lines indicate a missing margin; hatching indicates a broken surface. Scale bars, 2 cm in (B) and (D); 2 cm in (C); 5 mm in (E); 2 cm in (F) and (G); 3 cm in (H); 2 cm in (I); 1 cm in (J); 3 cm in (K); 2 cm in (L) and (M).

Fig. 3. Phylogenetic relationships among basal dinosaurs. Consensus cladogram summarizing three minimum-length trees based on maximum-parsimony analysis of 139 characters in successive outgroups (Lagerpetidae, Marasuchus, Silesauridae) and 16 basal dinosaur taxa (246 steps; consistency index = 0.618, retention index = 0.800). Outgroup taxa were constrained as shown; numbers at nodes indicate decay index. Suprageneric terminal taxa are scored on the basis of two or more included species. Suprageneric taxa that label the cladogram are positioned on the basis of phylogenetic definitions (8).

slender ventral process of the squamosal, and the inset position of the first dentary tooth (Fig. 1B). The toothless anterior end of the dentary (Fig. 2A) is quite similar to that of Panphagia (Fig. 1F) and other basal sauropodomorphs (13). In addition, the form of the crowns (basal constriction, lateral crest, larger inclined denticles) strongly suggests that Eoraptor had an omnivorous, if not wholly herbivorous, diet. In the postcranial skeleton, sauropodomorph features include substantial medial rotation in the shaft of the first phalanx of the thumb (digit I) that directs the tip of the ungual inward (Fig. 1F) and an astragalus with a characteristic shape (anteriorly projecting anteromedial corner) (3).

Reinterpretation of Eoraptor as a basal sauropodomorph closely related to Panphagia (Fig. 3) differs from previous phylogenetic assessments of this early dinosaur as a basal saurischian (3, 5, 14–16) or basal theropod (1, 11, 12, 17). The phylogenetic analysis is decisive in this regard, requiring nine additional steps to reposition Eoraptor at the base of Theropoda. With Eoraptor as a basal sauropodomorph, the three principal clades of dinosaurs (ornithischians, sauropodomorphs, theropods) now appear to be converging on an ancestral bipedal cursor (tibia longer than femur) with body length less than 2 m. (Fig. 2A and Table 1). In our analysis, heterodontosaurids remain nested among basal ornithischians (Fig. 3).

If heterodontosaurids are repositioned as basal-most ornithischians (18), which is only slightly less parsimonious, the ancestral body plan for dinosaurs would have included a proportionately long forelimb (~45% hind-limb length) and sharp
clawed manus with pits to accommodate digital hyperextension.

The Ischigualasto Formation, a richly fossiliferous fluvial succession within a Triassic continental rift basin (6, 19), provides a window to faunal dynamics at the dawn of the dinosaur era. To quantify and temporally calibrate faunal abundance in the Ischigualasto Formation, we logged nearly 800 vertebrate specimens and obtained radioisotopic ages that bracket the formation between 231.4 and 225.9 million years ago (Ma) (Fig. 4) (8, 20).

All of the early dinosaurs from the Ischigualasto Formation thrived during what we identify here as the Scaphonyx-Exaeretodon-Herrerasaurus biozone, a narrow temporal interval from 231.5 to 229 Ma in the latter half of the Carnian stage (Fig. 4). During this interval, dinosaurs account for 11% of recorded vertebrate specimens, which is about twice that previously estimated (20). This biozone is dominated by mid-sized non-dinosaurian herbivores (rhynchosaurs, traversodontid cynodonts) (Fig. 4). Herrerasaurids and Eodromaeus, however, represent ~70% of all nonaquatic carnivores in the faunal assemblage. Similarly, all small-bodied omnivores or herbivores (<2 m in body length and/or <15 kg) are dinosaurs (Pisanosaurus, Eoraptor, Panphagia, Chromogisaurus). Dinosaurs are also taxonomically diverse within this biozone, making up 33% of recorded genera, a percentage equaling that in the overlying Los Colorados Formation near the close of the Late Triassic (late Norian) (Fig. 4, top pie chart).

A major faunal change seems to have occurred near the Carnian-Norian boundary ~229 Ma, when humidity increased as inferred from sedimentological (argillic paleosols) and paleofloral (palynomorph-cuticle-trunk) evidence (8). The rhynchosaur Scaphonyx, most therapsids, and all dinosaurs disappeared, leaving a depauperate fauna dominated by the traversodontid cynodont Exaeretodon (Exaeretodon biozone). A less constrained but consistent faunal record from southern Brazil (21, 22) suggests that this may have been a regional extinction event across southwestern Pangaea. Higher in the section, Exaeretodon is not present, and the mid-sized dicynodont Jachaleria is the dominant vertebrate (Jachaleria biozone). Although taphonomic bias against preservation of smaller vertebrates may play some role in the upper biozone, Exaeretodon is clearly not the dominant large vertebrate herbivore.

The discovery of Eodromaeus, the reinterpretation of Eoraptor as a sauropodomorph, and the faunal record of the Ischigualasto Formation provide additional evidence that, by mid Carnian time (~232 Ma), the earliest dinosaurs had already evolved the most functionally important trophic and locomotor features characterizing ornithischians, sauropodomorphs, and theropods (17, 23). These attributes are thus unlikely to have functioned as the competitive

Fig. 4. Calibrated stratigraphic profile across the Ischigualasto Formation (northwest Argentina) showing tetrapod diversity and abundance. (Left) The chart shows a simplified stratigraphic section divided into four formational members (Roman numerals I to IV) as well as the stratigraphic positions of the holotype of Eodromaeus murphi and a bracketing pair of radiometric dates using recently revised radioisotopic decay constants (30). (Middle) Three biozones, three large pie charts summarizing faunal abundance for each biozone, and two smaller pie charts pie showing taxonomically diverse before (Los Chañares Fm.) and after (Los Colorados Fm.) the Ischigualasto Formation. (Right) A current geologic time scale (31), which assumes an average rate of sedimentation between radioisotopically dated horizons.
advantage to account for the dominance of dinosaurs in abundance and diversity in terrestrial habitats some 30 million years later in the earliest Jurassic (~202 Ma). Eodraeaus increases the range of salient theropod features present in the earliest dinosaurs, and Eoraptor shows that the enlarged naris, basally constricted crowns, and a twisted pollex were present in the earliest sauropodomorphs.

One explanation for the rise of dinosaurs has been that a few key features led gradually to the competitive dominance of dinosaurs (20, 24). This view has been overtaken by a hypothesis of noncompetitive replacement, in which their rise is split into two successive episodes of extinction and noncompetitive infilling of vacant ecospace (25, 26). In the replacement hypothesis, the earliest dinosaurs are regarded as particularly rare (1 to 3% of terrestrial vertebrates), their abundance and diversity increasing successively at the Carnian-Norian and Triassic-Jurassic boundaries coincident with mass extinction of rhynchosaurs, traversodontid cynodonts, and dicynodonts and later of (noncrocodyliform) crurotarsal archosaurs.

In contrast, the fossil record from Ichiguialasto indicates that early dinosaurs in the latter half of the Carnian (231 to 228 Ma) were more common and diverse than previously thought, equaling the percentage of dinosaurian genera in the late Norian fauna from the overlying Los Colorados Formation (Fig. 4). Thus, in terms of taxonomic diversity, dinosaurs did not increase their percentage among terrestrial vertebrates toward the end of the Triassic in southwestern Pangaea.

The record also shows that extinction of rhynchosaurs and other large-bodied herbivores was not synchronous but rather spread out across 4 to 5 million years (Fig. 4). The disappearance of rhynchosaurs at the Carnian-Norian boundary was not linked to an increase in dinosaur diversity but rather coincided with the local extinction of dinosaurs. The most substantial change between the earliest dinosaurs in the Carnian and those in the late Norian is that the latter have expanded into the upper register of body size as both carnivores (Murphy). Holotype: PVS 560, articulated skeleton lacking only the scapulocoracoids, most of the right forelimb, some cervical and dorsal ribs, gastralia, four anterior caudal vertebrae, and most chevrons. Fusion of all neurocentral sutures suggests that the holotype has reached adult size. This specimen is cataloged in the collection of the Museo de Ciencias Naturales (San Juan, Argentina). Type locality: 30°04’3.5”S, 67°56’11.4”W; Valle de la Luna, Ichiguialasto Provincial Park, San Juan, Argentina. Horizon: Ichiguialasto Formation, Valle de la Luna Member (PVS 560 to 563), ~200 m from base of the formation. Two referred specimens (PVS 534, 877) were found in the underlying La Peña and Cancha de Bochas Members, overlapping the range of several other dinosaurs (Fig. 3).

Age: Ages range from ~232 to 229 Ma (Fig. 4) [6, 20]. Diagnosis: Basal theropod with no more than 11 maxillary teeth, caniniform maxillary crowns more than three times the basal mesiodistal width near the anterior end of the tooth row, fine serrations (~nine per millimeter) on mesial and distal margins, ventrally convex maxillary alveolar margin, very shallow jugal suborbital ramus, centrales in carpus between the radiale and distal carpal 1, large distal carpal 5 overlapping distal carpal 4 with a posteroventral heel; pubic apron with sinuous lateral margin, and pubic foot with squared posterior margin.

8. See supporting material on Science Online.

9. Higher taxa cited in the text are defined as follows (www.taxonsearch.org): Dinosauria, the least inclusive clade containing Tyrosaurus rex Osborn 1905 and Parcer domesticus (Luna 1758); Ornithischia, the most inclusive clade containing Tyrosaurus rex Osborn 1905 but not Ornithomimus edmontonicus Sternberg 1933, Troodon formosus Leidy 1856, Velociraptor mongoliensis Osborn 2192; Sauropsida, the least inclusive clade containing Tyrosaurus rex Osborn 1905 and Gorgosaurus libratus Lambe 1914, Albertosaurus sarcophagus Osborn 1905; Sauropodomorpha, the most inclusive clade containing Saltasaurus loricatus Bonaparte and Powell 1980 but not Passer domesticus (Luna 1758), Triceratops horridus Marsh 1889; Sauropofidiformes, the least inclusive clade containing Megasaurus patagonicus Bonaparte and Vince 1979 and Saltasaurus loricatus Bonaparte and Powell 1980; Theropoda, the most inclusive clade containing Passer domesticus (Luna 1758) but not Saltasaurus loricatus Bonaparte and Powell 1980; Neotheropoda, the least inclusive clade containing Coelophysis bauri (Cope 1889) and Passer domesticus (Luna 1758); Coelophysoidea, the most inclusive clade containing Coelophysis bauri (Cope 1889) but not Carnotaurus sacristi Bonaparte 1985, Ceratosaurus nasicornis Marsh 1884, Passer domesticus (Luna 1758).


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Supporting Online Material www.sciencemag.org/cgi/content/full/331/6014/206/DC1 Materials and Methods: Fig. 51 Tables 51 to 56 References 29 September 2010; accepted 8 December 2010 10.1126/science.1198467