
This copy is for your personal, non-commercial use only.

If you wish to distribute this article to others, you can order high-quality copies for your colleagues, clients, or customers by [clicking here](#).

Permission to republish or repurpose articles or portions of articles can be obtained by following the guidelines [here](#).

The following resources related to this article are available online at www.sciencemag.org (this information is current as of January 21, 2011):

Updated information and services, including high-resolution figures, can be found in the online version of this article at:

<http://www.sciencemag.org/content/331/6014/206.full.html>

Supporting Online Material can be found at:

<http://www.sciencemag.org/content/suppl/2011/01/11/331.6014.206.DC1.html>

A list of selected additional articles on the Science Web sites **related to this article** can be found at:

<http://www.sciencemag.org/content/331/6014/206.full.html#related>

This article **cites 24 articles**, 3 of which can be accessed free:

<http://www.sciencemag.org/content/331/6014/206.full.html#ref-list-1>

This article appears in the following **subject collections**:

Paleontology

<http://www.sciencemag.org/cgi/collection/paleo>

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

Ricardo N. Martinez,¹ Paul C. Sereno,^{2*} Oscar A. Alcober,¹ Carina E. Colombi,^{1,3} Paul R. Renne,^{4,5} 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.

An 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 paleoclimatic 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 (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 sidewall and ventral aspects of the braincase are marked by well-defined tympanic and basisphenoid recesses, respectively, and the basiptyergoid 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 interdental plates. All crowns are laterally compressed, recurved, 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 rela-

tively 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 preatlantal 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 low ventral keel and projecting epiphysal 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 hyposphene-hypantrum articulations (Fig. 2D). There appear to be three sacral vertebrae—a dorsosacral followed by two primordial sacra 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 murphi*, *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.

Measure or ratio	<i>Eodromaeus</i> PVSJ 562	<i>Herrerasaurus</i> PVSJ 373	<i>Eoraptor</i> PVSJ 512	<i>Heterodontosaurus</i> SAM-PK-K337
Skull*	(120)	282	114	115
Humerus	85	(175)	85	83
Radius	64	153	63	58
Metacarpal 3	28	62	21	22
Femur	160	345	152	112
Tibia	165	315	156	145
Metatarsal 3	(100)§	165	81	68
Humerus/forelimb†	48%	45%	50%	51%
Radius/forelimb	36%	39%	37%	36%
Metacarpal 3/forelimb	16%	16%	12%	14%
Tibia/femur	106%¶	91%	103%	130%
Femur/hind limb‡	38%	42%	39%	35%
Tibia/hind limb	39%	38%	40%	45%
Metatarsal 3/hind limb	24%	20%	21%	21%
Humerus/femur	53%	51%	56%	74%
Forelimb/hind limb	42%	47%	43%	50%

*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 109%, based on PVSJ 560 and 562, respectively.

¹Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan 5400, Argentina. ²Department of Organismal Biology and Anatomy and Committee of Evolutionary Biology, University of Chicago, Chicago, IL 60637, USA. ³Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina. ⁴Berkeley Geochronology Center, 2455 Ridge Road, Berkeley, CA 94709, USA. ⁵Department of Earth and Planetary Science, University of California, Berkeley, CA 94720, USA. ⁶Department of Geology, University of California, Davis, CA 95616, USA. ⁷Department of Geology, Miami University, Oxford, OH 45056, USA.

*To whom correspondence should be addressed. E-mail: dinosaur@uchicago.edu

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 carpus 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). The

pubic blades taper distally, where a small parasagittal pubic foot is located (Fig. 2H). Proximally, the femur has a dorsally projecting anterior trochanter and trochanteric shelf (Fig. 2, K and L). Distally, the end of the femur is marked by a broad rugose depression for femoral extensor musculature (Fig. 2M). The tibia is slightly longer than the femur, which, like other intra- and interlimb proportions, is similar to that in *Eoraptor* (Table 1). The fibula has a raised scar proximally for strong ligamentous attachment to the tibia (Fig. 2I). The astragalus has a rectangular medial margin and a wedge-shaped ascending process, and the calcaneum retains a prong-shaped posterior heel (Fig. 2J).

Phylogenetic analysis of basal dinosaurs positions the contemporaneous and similar-sized *Eodromaeus* and *Eoraptor* at the base of Theropoda and Sauropodomorpha, respectively (Fig. 3) (8). Basal theropod status for *Eodromaeus* is supported by a suite of derived attributes in the

skull (promaxillary fenestra, basisphenoid fossa), axial skeleton (cervical pleurocoels, elongate caudal prezygapophyses), forelimb (radioulnar shaft apposition, elongate penultimate phalanges), pelvic girdle (distally tapering pubic blade, pubic foot), and hind limb (femoral extensor depression, tibial crest for fibula) (8). Whereas herrerasaurids appear to be more basal in position among theropods (Fig. 3), *Eodromaeus* 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 *Eodromaeus*, but it also exhibits features previously seen only among basal sauropodomorphs. In the skull, these features include an enlarged narial opening, a

Fig. 1. Skull, carpus, and manus of the basal dinosaurs *Eoraptor lunensis* and *Eodromaeus 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 ventrolateral 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 561, 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: I to V, manual digits I to V; a, angular; antfo, antorbital fenestra; ar, articular; asaf, anterior surangular foramen; bo, basioccipital; bpt, basipterygoid process; bsf, basisphenoid fossa; bt, basal tubera; ce, centrale; d, dentary; d1, d12, and d16, dentary teeth 1, 12, and 16; dc1 to dc5, 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; mcot, medial cotylus; mdc, medial distal condyle; n, 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; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qf, quadrate foramen; qj, 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 (C) (for braincase); 3 mm in (D) and (E); 5 mm in (F) and (G) (enlarged views).

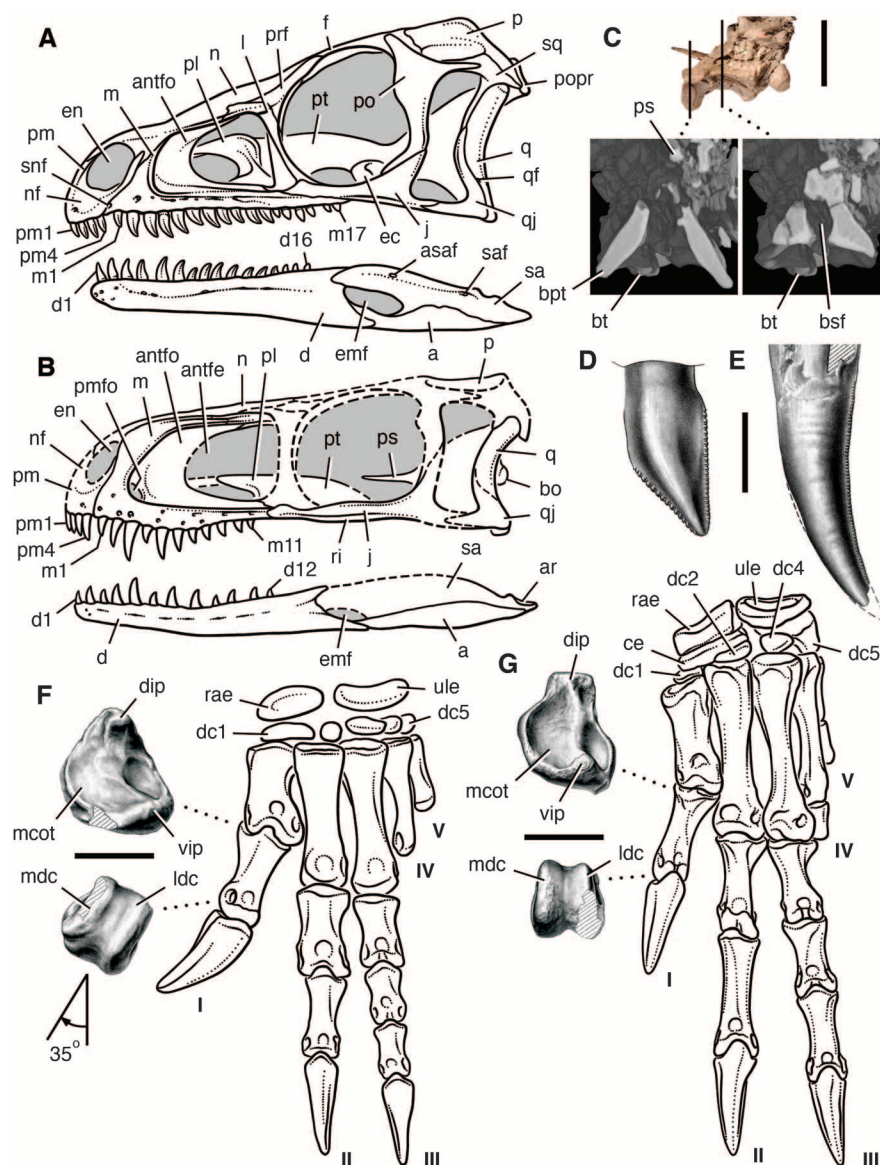
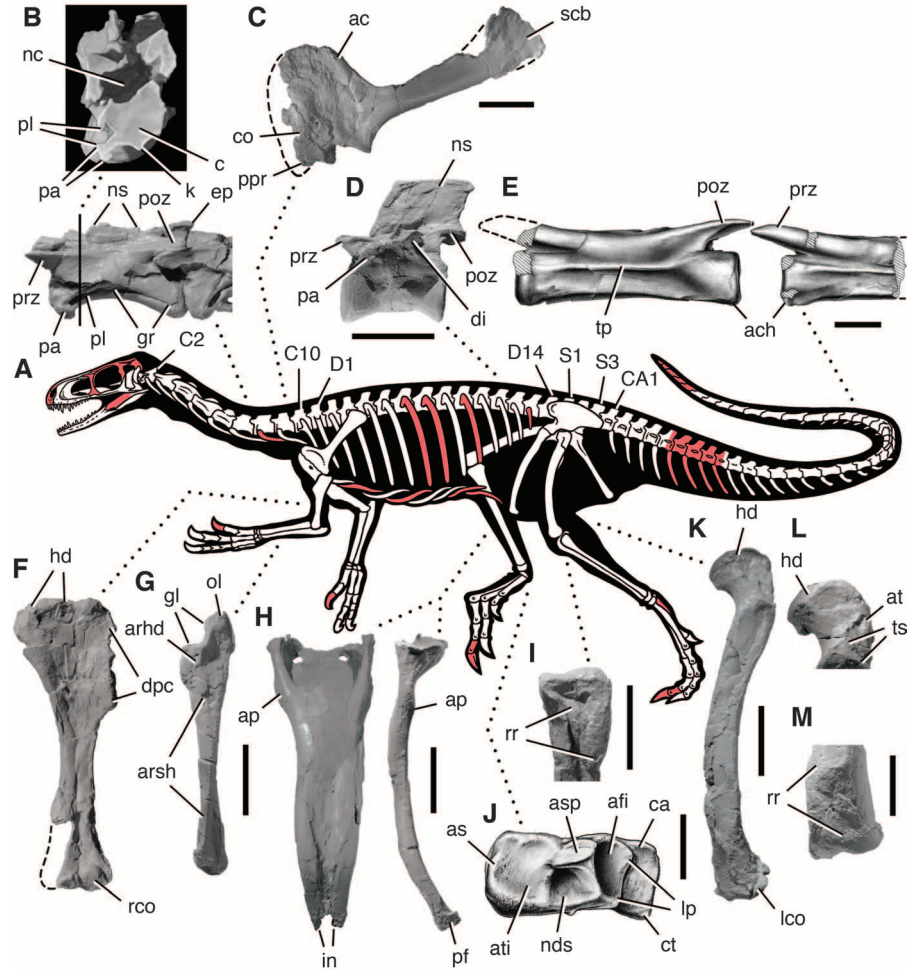


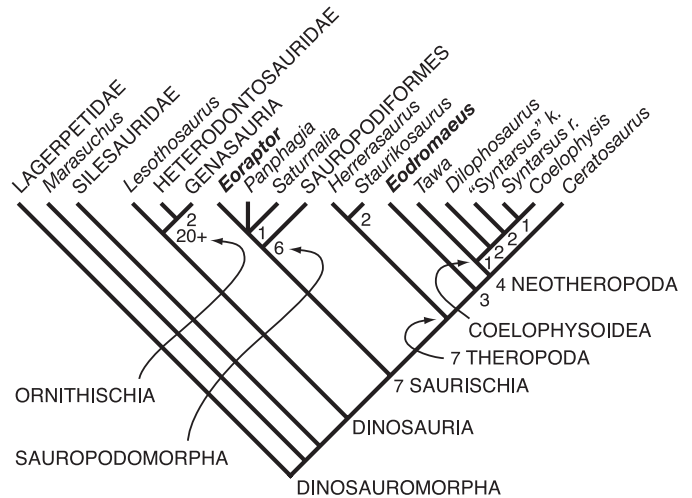
Fig. 2. Postcranial features of the Late Triassic basal theropod *Eodromaeus murphi*. Skeletal silhouette based on PVSJ 534, 560, and 562; postcranial bones are from PVSJ 562, except where indicated; bone casts and pencil drawings were used to eliminate color distraction and reversed as needed to left 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; afi, articular surface for the fibula; ap, ambiens process; arhd, articular surface for the radial head; arsh, articular surface for the radial shaft; as, astragalus; asp, ascending process; at, anterior trochanter; ati, articular surface for the tibia; c, centrum; C2 and C10, cervical vertebrae 2 and 10; ca, calcaneum; CA1, caudal vertebra 1; co, coracoid; ct, calcaneal tuber; D1 and D14, dorsal vertebrae 1 and 14; di, diapophysis; dpc, deltopectoral crest; ep, epiphysis; gl, glenoid; gr, goove; 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; ppr, posterior process; prz, prezygapophysis; rco, 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).



slender ventral process of the squamosal, and the inset position of the first dentary tooth (Fig. 1B). The toothless anterior end of the dentary, which is flanked by a conspicuous pair of vascular foramina, may have supported a small lower bill as in 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) (13) 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, thermo-

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).



pod) now appear to be converging on an ancestral skeletal plan—a 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

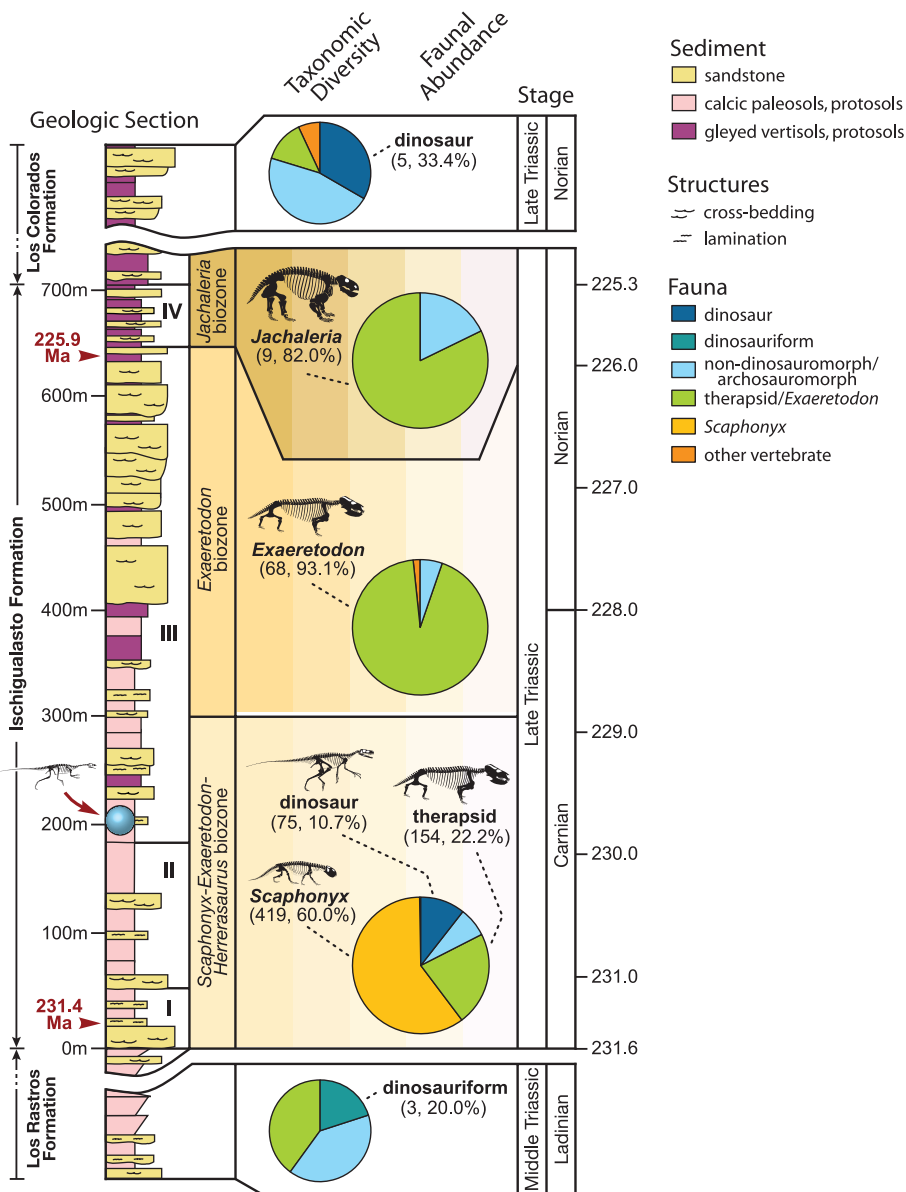


Fig. 4. Calibrated stratigraphic profile across the Ischigualasto Formation (northwest Argentina) showing tetrapod diversity and abundance. **(Left)** The chart shows a simplified stratigraphic section divided into four formational members (Roman numerals I to IV) as well as the stratigraphic positions 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 showing taxonomic diversity 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). *Eodromaesus* 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 Ischigualasto 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 (*Zupaysaurus*) and herbivores (*Lessemisaurus*). Increased body size probably enhanced the preservation potential of late Norian dinosaurs, which are also recorded from many more sites than late Carnian dinosaurs (6, 27). We cannot evaluate whether the increase in body size was gradual or rapid, as there are no dinosaurs in the section between late Carnian and late Norian faunas. Furthermore, increasing body size among dinosaurs was not limited to the Triassic but continued throughout the Jurassic (23, 28) long after the extinction of Triassic synapsids and (noncrocodyliform) crurotarsal archosaurs.

The earliest dinosaurs are currently restricted to late Carnian sites in southern Pangaea (Argentina, Brazil). The earliest dinosaur from northern Pangaea (*Tawa*, western North America) has recently been dated to the mid Norian (~214 Ma)

(11), making it some 15 million years younger in age. This has led to the view that the major dinosaurian clades (Ornithischia, Sauropodomorpha, Theropoda) may have originated in southern Pangaea (14, 16). The paleogeographic importance of this distribution, however, is compromised by the absence of well-preserved skeletal remains of Carnian age from northern locales (northern Africa, Europe, North America) (14, 21, 29). Discerning global patterns of replacement or areas of paleogeographic origin for particular groups in terrestrial ecosystems in the Triassic requires greater temporal and geographic control than is currently available.

References and Notes

- P. C. Sereno, C. A. Forster, R. R. Rogers, A. M. Monetta, *Nature* **361**, 64 (1993).
- P. C. Sereno, F. E. Novas, *Science* **258**, 1137 (1992).
- R. N. Martinez, O. A. Alcober, *PLoS ONE* **4**, e4397 (2009).
- O. A. Alcober, R. N. Martinez, *ZooKeys* **63**, 55 (2010).
- M. D. Ezcurrea, *J. Syst. Palaeontology* **8**, 371 (2010).
- B. S. Currie, C. E. Colombi, N. J. Tabor, T. C. Shipman, I. P. Montañez, *J. S. Am. Earth Sci.* **27**, 74 (2009).
- Etymology:** *eos*, dawn (Greek); *dromaesus*, runner (Greek); *murphy*; in allusion to its early age, slender axial and appendicular proportions, and the Earthwatch volunteer who discovered the holotypic specimen (J. Murphy). **Holotype:** PVSJ 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 Instituto y Museo de Ciencias Naturales (San Juan, Argentina). **Type locality:** 30°04'3.5"S, 67°56'11.4"W; Valle de la Luna, Ischigualasto Provincial Park, San Juan, Argentina. **Horizon:** Ischigualasto Formation, Valle de la Luna Member (PVSJ 560 to 563), ~200 m from base of the formation. Two referred specimens (PVSJ 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) (8, 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, centrale 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.
- See supporting material on Science Online.
- Higher taxa cited in the text are defined as follows (www.taxonsearch.org): **Dinosauria**, the least inclusive clade containing *Tyrannosaurus rex* Osborn 1905 and *Passer domesticus* (Linnaeus 1758); **Ornithischia**, the most inclusive clade containing *Tyrannosaurus rex* Osborn 1905 but not *Ornithomimus edmontonicus* Sternberg 1933, *Troodon formosus* Leidy 1856, *Velociraptor mongoliensis* Osborn 1924; **Saurischia**, the least inclusive clade containing *Tyrannosaurus 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* (Linnaeus 1758), *Triceratops horridus* Marsh 1889; **Sauropodiformes**, the least inclusive clade containing *Mussaurus patagonicus* Bonaparte and Vince 1979 and *Saltasaurus loricatus* Bonaparte and Powell 1980; **Theropoda**, the most inclusive clade containing *Passer domesticus* (Linnaeus 1758) but not *Saltasaurus loricatus*

- Bonaparte and Powell 1980; **Neotheropoda**, the least inclusive clade containing *Coelophysus bauri* (Cope 1889) and *Passer domesticus* (Linnaeus 1758); **Coelophysoidea**, the most inclusive clade containing *Coelophysus bauri* (Cope 1889) but not *Camotaurus sastrei* Bonaparte 1985, *Ceratosaurus nasicornis* Marsh 1884, *Passer domesticus* (Linnaeus 1758).
- P. C. Sereno, *Hist. Biol.* **19**, 145 (2007).
 - S. J. Nesbitt *et al.*, *Science* **326**, 1530 (2009).
 - R. S. Tykoski, thesis, University of Texas at Austin, Austin, TX (2005).
 - P. C. Sereno, in *Evolution and Paleobiology of Sauropodomorph Dinosaurs*, P. M. Upchurch, D. J. Batten, Eds. (Palaeontological Association, London, 2007), pp. 261–289.
 - M. C. Langer, M. D. Ezcurrea, J. S. Bittencourt, F. E. Novas, *Biol. Rev. Camb. Philos. Soc.* **85**, 55 (2010).
 - M. C. Langer, in *The Dinosauria*, D. B. Weishampel, P. Dodson, H. Osmólska, Eds. (Univ. of California Press, Berkeley, CA, 2004), pp. 25–46.
 - S. L. Brusatte *et al.*, *Earth Sci. Rev.* **101**, 68 (2010).
 - P. C. Sereno, *Science* **284**, 2137 (1999).
 - R. J. Butler, P. Upchurch, D. B. Norman, *J. Syst. Palaeontology* **6**, 1 (2008).
 - J. F. Bonaparte, *J. Vert. Paleol.* **2**, 362 (1982).
 - R. R. Rogers *et al.*, *Science* **260**, 794 (1993).
 - M. C. Langer, *J. S. Am. Earth Sci.* **19**, 219 (2005).
 - M. C. Langer, A. M. Ribeiro, C. L. Schultz, J. Ferigolo, in *The Global Triassic*, S. G. Lucas, J. A. Spielmann, Eds. (New Mexico Museum of Natural History, Albuquerque, NM, 2007).
 - P. C. Sereno, *Annu. Rev. Earth Planet. Sci.* **25**, 435 (1997).
 - A. J. Charig, *Zool. Soc. London Symp.* **57**, 597 (1984).
 - M. J. Benton, in *In the Shadow of the Dinosaurs*, N. C. Fraser, H.-D. Sues, Eds. (Cambridge Univ. Press, Cambridge, 1994), pp. 366–397.
 - M. J. Benton, "The origin of the dinosaurs," in *Actas de las III Jornadas sobre Dinosaurios y su Entorno* (Colectivo Arqueológico-Paleontológico Salense, Burgos, Spain, 2006), pp. 11–19.
 - P. D. Mannion, P. Upchurch, M. T. Carrano, P. M. Barrett, *Biol. Rev. Camb. Philos. Soc.*, published online 16 April 2010 (10.1111/j.1469-185X.2010.00139.x).
 - D. W. E. Hone, T. M. Keesey, D. Pisani, A. Purvis, *J. Evol. Biol.* **18**, 587 (2005).
 - S. J. Nesbitt, R. B. Irmis, W. G. Parker, *J. Syst. Palaeontology* **5**, 209 (2007).
 - P. R. Renne, R. Mundil, G. Balco, K. Min, K. R. Ludwig, *Geochim. Cosmochim. Acta* **74**, 5349 (2010).
 - J. D. Walker, J. W. Geissman, *GSA Today* **19**, 60 (2009).
 - F. E. Novas, *J. Vert. Paleol.* **13**, 400 (1994).
 - A. P. Santa Luca, *Ann. S. Afr. Mus.* **79**, 159 (1980).
 - We thank C. Abraczinskas for final drafts of all figures, personnel of the Fossil Lab at the Univ. of Chicago for preparation of fossil material, personnel of the High-Resolution X-ray Computed Tomography Facility at the Univ. of Texas at Austin for assistance with computed tomography imaging, and S. Nesbitt and R. Irmis for examination of fossil material in their care. This work was supported by the Whitten-Newman Foundation, the Island Fund of the New York Community Trust, Earthwatch Institute, Consejo Nacional de Investigaciones Científicas y Técnicas, the Ann and Gordon Getty Foundation, and the National Geographic Society.

Supporting Online Material

www.sciencemag.org/cgi/content/full/331/6014/206/DC1
Materials and Methods

Fig. S1
Tables S1 to S6
References

29 September 2010; accepted 8 December 2010
10.1126/science.1198467