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

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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 contemporaneous Eoraptor as a basal saurapodomorph, and 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 paleontologic 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 emargined 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 (Fig. 1B). The skull is relatively low and lightly built with a relatively spacious antorbital fenestra, which is emargined 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 (Fig. 1B). The snout is elongate and slender, and the retroarticular process of the squamosal is well developed posteriorly (Fig. 1B). The elongate tail, which is composed of ~45 sacral vertebrae, is relatively uniform in size, and the first tooth is located at the anterior tip of the dentary, unlike the condition in Eoraptor (Fig. 1A 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 hyposphene-hypapophyseal articulations (Fig. 2D). There appear to be three sacral vertebrae—a dorsosacral followed by two prymordial sacrats with robust ribs—which is 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 cylinndrical 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.

<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>
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<tr>
<td>Skull*</td>
<td>(120)</td>
<td>282†</td>
<td>114</td>
<td>115</td>
</tr>
<tr>
<td>Humerus</td>
<td>85</td>
<td>(175)</td>
<td>85</td>
<td>83</td>
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<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>
</tr>
<tr>
<td>Radius/forelimb</td>
<td>36%</td>
<td>39%</td>
<td>37%</td>
<td>36%</td>
</tr>
<tr>
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<td>16%</td>
<td>12%</td>
<td>14%</td>
</tr>
<tr>
<td>Tibia/femur</td>
<td>106%¶</td>
<td>91%</td>
<td>103%</td>
<td>130%</td>
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<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>
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<td>20%</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>
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<tr>
<td>Forelimb/hind limb</td>
<td>42%</td>
<td>47%</td>
<td>43%</td>
<td>50%</td>
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</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 the 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 comparatively 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.
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 coracoid 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 Eodromaeus and Eoraptor at the base of Theropoda and Sauropodomorpha, respectively (Fig. 3). Basal theropod status for Eodromaeus is supported by a suite of derived attributes in the skull (promaxillary fenestra, basiphenoid 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
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 astragulus 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 skeletal plan—a bipedal cursor (tibia longer than femur) with body length less than 2 m. (Fig. 2A 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).

If heterodontosaurs 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
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). Eodromaeus 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 boundary coincident with mass extinction of rhynchosaurs, traversodontid cynodonts, and dicynodonts and later of (noncrocodileiform) euroraptorid 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 dinocephalians, making it some 15 million years younger 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
7. Etymology: eos, dawn (Greek); dromaeus, runner (Greek); murchii; in allusion to its early, slender axis and appendicular proportions, and the Earthwatch volunteer who discovered the holotypic specimen (J. M. 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 catalogued in the collection of the Instituto y Museo de Ciencias Naturales de San Juan, Argentina. Type locality: 30°04′35.5″, 67°56′11.4″; Valle de la Luna, Ischigualasto Provincial Park, San Juan, Argentina. Horizon: Ischigualasto 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).

2. Ages range from ~232 to 229 Ma (Fig. 4) (6, 20).
3. 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 sinusus lateral margin, and pubic foot with squared posterior margin.

4. 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 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 Osmå 1924; Sauropsida, 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; Sauropterygia, the least inclusive clade containing Mosaurus patagonicus Bonaparte and Vinci 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 Coelophysis bauri (Cope 1889) and Passer domesticus (Linnaeus 1758); Coelophysoidea, the most inclusive clade containing Coelophysis bauri (Cope 1889) but not Carnotaurus sastrei Bonaparte 1985, Ceratosaurus nasicornis Marsh 1884, Passer domesticus (Linnaeus 1758).


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Materials and Methods
Fig. S1
Tables S1 to S6
References
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