Cretaceous Sauropods from the Sahara and the Uneven Rate of Skeletal Evolution Among Dinosaurs
Paul C. Sereno et al.
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These results demonstrate the ability of present-day ultrashort-laser–driven x-ray sources to study transiently generated extreme states of matter. Although further studies of important outstanding problems related to the structure of superheated solids and transient liquid phases (1, 2) are natural extensions of this work, foreseeable improvements already in development in tabletop laser-driven plasma sources should expand the scope of ultrafast x-ray diffraction to the dynamic study of many other ultrafast processes in physics, chemistry, and biology, including the ultrafast atomic and molecular dynamics by which other solid-state processes and chemical and biochemical reactions take place.

References and Notes


22. Our experimental setup, discussed previously in (7), consisted of a visible-pump x-ray probe apparatus, with which the 1.03-Å x-ray pulses were generated by 1.07-μJ laser pulses, which generated soft x-rays by circularly polarized laser pulses. The x-rays were focused to a diameter of 100 μm.


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25. Postmortem examination with interference micro-
adult skull of *Jobaria*, for example, is comparable to that of a subadult *Camarasaurus*, which has substantially shorter limb bones (Table 1). The external naris is particularly large, and the snout is abbreviate anteriorly (Fig. 2, A and B), unlike macronarians such as *Brachiosaurus*. There are at least 20 teeth in the upper and lower jaws, and the spatulate crowns have a variable number of marginal denticles (3). *Jobaria* has a relatively short neck composed of only 12 cervical vertebrae. The centra are only moderately elongate and show a distinct elevation of the anterior face (Fig. 3, A and B). One articulated neck was preserved in a fully dorsiflexed, C-shaped posture, suggesting that the cervical column had considerably more latitude in the sagittal plane than suggested recently for some other sauropods (7). Pleurocoels are divided in the cervical vertebrae but extend posteriorly only as far as the anterior dorsal vertebrae. All neural spines are simple (undivided) (Fig. 3, B and C), and all caudal centra are amphiplatyan (Fig. 3D). The first chevron has a unique inverted U shape. Middle chevrons are distinguished by a ridge crossing the blade; more distal chevrons become anteroposteriorly elongate (Fig. 3, G to I). Clavicles and gastralia, rarely preserved in sauropods (8), are present (Fig. 3, A and E). The proportions of the limbs are primitive; the forelimb is not as elongate relative to the hind limb as in *Brachiosaurus*, and the manus (relative to the forearm) is not as elongate as in *Camarasaurus* or other macronarians (9) (Table 1; metacarpal II/radius ratio < 0.40).

Despite its Cretaceous age, *Jobaria* is strikingly primitive. Primitive features include the abbreviate snout, terminally positioned nares, low number of cervical vertebrae, simple neural spines, and many other features and suggest that *Jobaria* lies outside the neosauropod radiation, which encompasses all other known *Camarasaurus* sauropods (diplolecodoids, *Camarasaurus*, brachiosaurids, and titanosaurs) (Fig. 4A) (10). *Jobaria* represents an unknown lineage of broad-toothed sauropods that had diverged by the Middle Jurassic some 30 to 40 million years earlier. During this substantial interval, relatively few skeletal changes accrued, as shown by the small number of diagnostic features for the species (5, 10).

The sauropod from the Tegama Group, *Nigersaurus* *taqueti* gen. nov. sp. nov. (11), is a new basal diplodocoid represented by several partial skeletons. *Nigersaurus* is one of the most common vertebrates in the Gadoufaoua exposures. It is also one of the smallest sauropods on record, reaching a maximum body length of about 15 m. The fossiliferous exposures of the Tegama Group in the Gadoufaoua region consist almost entirely of cross-bedded fluviatile sands and silts that are from MNN TIG3 except metatarsal III, which comes from an equal-sized individual (MNN TIG4). Length estimates for the radius and manual ungual I in *Camarasaurus* are based on *C. lentus* (37). Abbreviations: f, femur; h, humerus; mcII, metacarpal II; mtIII, metatarsal III; r, radius; and t, tibia. Parentheses indicate estimated measurements.

**Table 1.** Length measurements (centimeters) and ratios in *Jobaria* *tiguidensis*, *Shunosaurus* *lii* (36), and *Camarasaurus* *grandis* (36). All measurements for *J. tiguidensis* are from MNN TIG3 except metatarsal III, which comes from an equal-sized individual (MNN TIG4). Length estimates for the radius and manual ungual I in *Camarasaurus* are based on *C. lentus* (37). Abbreviations: f, femur; h, humerus; mcII, metacarpal II; mtIII, metatarsal III; r, radius; and t, tibia. Parentheses indicate estimated measurements.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Shunosaurus</th>
<th>Jobaria</th>
<th>Camarasaurus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Skull</td>
<td>37</td>
<td>(73)</td>
<td>(75)</td>
</tr>
<tr>
<td>Cervical number, total length</td>
<td>13, (130)</td>
<td>12, (403)</td>
<td>12, (299)</td>
</tr>
<tr>
<td>Humerus</td>
<td>67</td>
<td>136</td>
<td>113</td>
</tr>
<tr>
<td>Radius</td>
<td>48</td>
<td>104</td>
<td>(75)</td>
</tr>
<tr>
<td>Metacarpal II</td>
<td>16</td>
<td>39</td>
<td>32</td>
</tr>
<tr>
<td>Manual I ungual</td>
<td>23</td>
<td>18</td>
<td>(15)</td>
</tr>
<tr>
<td>Femur</td>
<td>120</td>
<td>180</td>
<td>149</td>
</tr>
<tr>
<td>Tibia</td>
<td>68</td>
<td>108</td>
<td>93</td>
</tr>
<tr>
<td>Metatarsal III</td>
<td>18</td>
<td>30</td>
<td>22</td>
</tr>
<tr>
<td>r/h</td>
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<td>0.77</td>
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<tr>
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<tr>
<td>t/f</td>
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<td>0.60</td>
<td>0.62</td>
</tr>
<tr>
<td>mtIII/t</td>
<td>0.27</td>
<td>0.28</td>
<td>0.24</td>
</tr>
</tbody>
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**Fig. 1.** Early Cretaceous paleogeography and principal fossiliferous exposures in central Niger. (A) Maps showing Niger and the location of the fossiliferous exposures in the Tiourarén Formation (localities: 1, Tiourarén and In Kaf; 2, Tamerat; 3, Fako and In Abaka; and 4, Tawachi) and middle horizons of the Tegama Group (Gadoufaoua); latitude in degrees north, longitude in degrees east. (B) Hauterivian-Barremian (−130 Ma) and (C) Alban (−110 Ma) Early Cretaceous paleogeographic maps (Molleweide projection) with latitude and longitude lines spaced at 30° intervals (longitude greater than 60° not shown) (34). White crosses indicate the fossiliferous exposures discussed in this report. (D) Geologic subdivision of Lower Cretaceous rocks in central Niger with fossiliferous levels in gray (12). Fm, formation.
sandstones (12), and the diverse associated dinosaursia fauna includes a rare titanosaurian sauropod (13), the large-bodied ornithischians Ouranosaurus (14) and Lurdosaurus (15), and the spinosaurid Suchomimus (16).

In the skull, the external nares are retracted, as in more advanced diplodocoids (dicraeosaurs and diplodocids) (Fig. 2D). The shape of the snout is unique among sauropods, as best shown by the dentary (Fig. 2C). The tooth rows are oriented strictly transversely and extend lateral to the plane of the lower jaw, features unknown in any other sauropod. The symphysis for the opposing dentary is broad and circular, another unique feature. The extreme width of the symphysial ramus most closely resembles that of a dentary attributed to Antarctosaurus (17), from rocks of Campanian age in Argentina.

In Nigersaurus, the teeth have gently curved slender crowns that are oval in cross section and distinguished by highly asymmetric enamel (Fig. 2D). The enamel is many times thicker on the lateral than on the medial side of the crown, a condition that has been reported previously among dinosaurs only in advanced ornithischians. There are 34 teeth in the dentary and at least 20 in the maxilla, three times as many as are present in Diplocodocus. Replacement teeth are stacked inside the dentary and maxilla, with seven replacement teeth in the first maxillary alveolus (Fig. 2D). More than 600 teeth would have been present in the jaws of Nigersaurus.

Presacral vertebrae have large, sharp-rimmed pleurocoels and simple (undivided) neural spines. The broad, paddle-shaped form of the scapular blade with a broad U-shaped notch at the base of the acromial process (Fig. 2E) is similar to that in Rayososaurus, from Albian-Cenomanian rocks in Argentina (9, 18), and Rebbachisaurus, a fragmentary sauropod from Cenomanian rocks in Morocco (19). Nigersaurus and the dentary referred to Antarctosaurus appear to be the earliest and latest known representatives, respectively, of this basal clade of diplodocoids, the Rebbachisauridae (10) (Fig. 4A).

The new fossils provide a framework for understanding the history of African sauropods during the Cretaceous. At least three
lineages of sauropods survived into the Cretaceous on Africa: a primitive, broad-toothed lineage, represented by *Jobaria*, which flourished during the Neocomian but has not been recorded in younger rocks; rebbachisaurid diplodocoids, represented by *Nigersaurus*, which now are recorded from the Aptian-Albian through the Cenomanian, although unknown in post-Cenomanian rocks; and basal titanosaurids, such as *Malawisaurus* (20), which were present during the Early Cretaceous but appear to have been relatively rare at least through the Cenomanian (21).

A slow rate of evolutionary change seems to characterize the lineage that gave rise to *Jobaria*. To more adequately gauge the qualitative difference among dinosaurs generally, we plotted (i) the order of the first occurrence of 70 nonavian dinosaurian taxa (age rank) (21) against their predicted order of divergence based on phylogenetic analysis (clade rank) (23) (Fig. 4B) and (ii) the number of skeletal changes per node (total synapomorphies) in dinosaurian phylogeny (24) against the minimum elapsed time during which those changes must have arisen (minimum missing ancestral lineage) (25) (Fig. 4C).

The dinosaurian fossil record, like that of basal synapsids and several nonvertebrate groups (26–28), shows significant positive correlation between age and clade rank (Fig. 4B). This is apparent in sauropods, despite the presence of missing ancestral lineages of significant duration (29) (Fig. 4A). Stratigraphic data thus carry some phylogenetic signal among dinosaurs (1, 30).

Skeletal change between these same taxa, in contrast, shows little discernible correlation with estimates of elapsed time (Fig. 4C). The number of synapomorphies between nodes in higher level dinosaurian phylogeny, unlike that for basal nodes within synapads (28), shows little or no correlation with estimates of the duration of missing ancestral lineages. Sauropods, for example, exhibit slow rates of skeletal change in the Early and Middle Jurassic, when the relevant missing ancestral lineages are relatively long (31) (Fig. 4A). Nor can this result be understood as particular to the phylogenetic survey used in the correlations (4); a similar lack of correlation between skeletal change and elapsed time exists in alternative phylogenetic analyses (32).

These data provide the first quantitative assessment of rates of skeletal change among dinosaurs, the best documented terrestrial radiation of the Mesozoic. Some lineages, such as that leading to *Jobaria*, remained relatively static for tens of millions of years, whereas others changed rapidly. Considerable variation in the rate of skeletal change appears to have been the norm in dinosaur evolution.

References and Notes
5. Fragmentary sauropod remains from the Tsiouraren Formation were initially described as a new species, *Rebbachisaurus tamesnensis* [A. F. de Lapparent, Mem. Soc. Geol. France B8A, 1 (1960)]. Type material, however, was not designated, and no diagnostic features were mentioned (3). Lapparent considered the Tsiouraren sauropod to be a camarasaureid; elsewhere it has been referred to the Diplodocidae (1). S. McIntosh, in *The Dinosauria* (Univ. of California Press, Berkeley, CA, 1990), pp. 345–401. Etymology: *Jobar*, *Jobar* (Tamacheck); ia, pertaining to (*Greek*; *tiguid*: *Tiguidi* (Tamacheck); essis, from (*Latin*). Named after the mythical creature "Jobar," to whom local Touregs had attributed the exposed bones, and after the Falaise de Tiguidi, a cliff near the base of which lie the horizons yielding all of its remains. Holotype: Partial articulated skeleton including the axis, forelimbs and hind limbs, pubes, and most of the tail, from the locality Tamiaret, cataloged in the collections of the Musée National du Niger (MNN TIG3).

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Fig. 3. Skeletal reconstruction of the sauropod *Jobaria tiguidensis* showing (A) preserved bones (about 95% of skeleton), (B) cervical 7 and associated rib in left lateral view, (C) dorsal 9 in left lateral view, with spine in posterior view, (D) caudal 35 in left lateral view, (E) right clavicle in anterior view (ventral end toward top) and medial view, (F) right metacarpus in proximal view (anterior side toward top), (G) chevron 1 in anterior view, (H) chevron 16 in left lateral view, and (I) chevron 24 in left lateral view. Scale bar in (A), 1 m (human silhouette, 1.68 m or 5 feet 6 inches tall; skeleton 18 m long with maximum adult length about 21 m); in (B) and (C), 20 cm; in (F), 15 cm; in (D), (E), and (G) to (I), 10 cm. Abbreviations: i, V, metacarpals I and V; aap, accessory anterior process; aCA2, articular surface for second caudal vertebra; C, cervical; CA, caudal; D, dorsal; di, diaphysis; ep, epiphysis; g, gastralia; hc, hemal canal; ns, neural spine; pa, parapophysis; pl, pleurocoel; poz, postzygapophyses; prz, prezygapophysis; r, ridge; S, sacral vertebrae 1 to 5; sp, spine; and tu, tuberculum.
Fig. 4. (A) Calibrated phylogeny of sauropods (9, 10) showing the phylogenetic position of Jobaria tiguidensis and Nigersaurus taqueti. The phylogenetic position of Jobaria is stable in trees two steps longer than the minimum-length tree. Solid dots and bars indicate recorded occurrence, shaded bars estimate missing range, and error bars indicate age uncertainty. Temporal values for stage boundaries are based on a recent time scale (33). Numbers indicate age in millions of years ago. (B) Plot of age rank versus clade rank (scaled from 0 to 1) for 72 genera of suprageneric taxa of dinosaurs based on recent phylogenetic analyses (4, 9) and temporal estimates calculated from a recent time scale (33). Spearman rank correlation (corrected for ties) is positive and significant ($S = 0.709$, $P < 0.0001$). (C) Plot of unambiguous synapomorphies versus the minimum duration of missing ancestral lineage [millions of years (My)] for the same set of taxa. Spearman rank correlation (corrected for ties) is negative and not significant ($S = -0.151$, $P = 0.4256$). Except for two outlier nodes (Paraves and Ommithorhachia) that show more than 45 skeletal changes over less than 10 million years, the majority of nodes in dinosaurian phylogeny show 30 or fewer changes accumulating over durations ranging from 3 to 40 million years. Cladograms, age and clade rank data, synapomorphy counts, and estimates of the minimum durations for missing ancestral lineages are available at www.sciencemag.org/feature/data/1045224.shl.
Intracellular calcium stores are important in the function of excitable cells (1, 2). For example, mitochondrial calcium uptake followed by rapid re-release from the mitochondrial matrix shapes the time course of calcium transients during synaptic activity and prolongs the elevated levels of intracellular calcium (also called “residual calcium”) that underlie post-tetanic potentiation (PTP) (3).

Mitochondria take up calcium in response to depolarization (4), but account for less than 2% of the internal calcium. High levels of intramitochondrial calcium interact with matrix enzymes and then exit rapidly, which allows the mitochondria to regain their electrochemical gradient across the inner mitochondrial membrane (4). Calcium can therefore flow readily along its electrochemical gradient into the mitochondrial matrix (5). Calcium signals can be detected only after a high-resistance seal was obtained (5).

Mitochondria and neurofilaments (Fig. 1) are the only internal organelles that are compatible with seal formation by the patch pipettes. Although large conductances (0.5 to 2.5 nanosiemens) could be detected occasionally. During a train of action potentials, the conductance of the mitochondrial membrane increased up to 60-fold. The conductance increased after a delay of several hundred milliseconds and continued to increase after stimulation had stopped. Recovery occurred over tens of seconds.

High levels of intramitochondrial calcium discharge mitochondrial calcium stores that underlie post-tetanic potentiation (PTP) (3).

Prolonged Activation of Mitochondrial Conductances During Synaptic Transmission

Elizabeth A. Jonas,1 JoAnn Buchanan,2 Leonard K. Kaczmarek 1,2

Although ion channels have been detected in mitochondria, scientists have not been able to record ion transport in mitochondria of intact cells. A variation of the patch clamp technique was used to record ion channel activity from intracellular organelles in the presynaptic terminal of the squid. Electron microscopy indicated that mitochondria are numerous in this terminal and are the only organelles compatible with the tips of the pipettes. Before synaptic stimulation, channel activity was infrequent and its conductance was small. After formation of a gigohm seal, the potential difference increased 500-fold, and the conductance increased an order of magnitude (1). Calcium can therefore flow on a current scale into the mitochondrial matrix (5).

During Synaptic Transmission

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Intracellular calcium stores are important in the function of excitable cells (1, 2). For example, mitochondrial calcium uptake followed by rapid re-release from the mitochondrial matrix shapes the time course of calcium transients during synaptic activity and prolongs the elevated levels of intracellular calcium (also called “residual calcium”) that underlie post-tetanic potentiation (PTP) (3).

Mitochondria take up calcium in response to depolarization (4), but account for less than 2% of the internal calcium. High levels of intramitochondrial calcium interact with matrix enzymes and then exit rapidly, which allows the mitochondria to regain their pre-stimulation levels within 5 min of a cytosolic load (2, 8).

Studies on isolated mitochondria or artificial lipid bilayer preparations have revealed several types of ion channels on both inner and outer mitochondrial membranes (9–13). However, no technique was available to record ion channel activity from intracellular membranes in intact cells. We have recently described the use of such a technique (14), and we have applied it here to the giant presynaptic terminal of the squid.

With electron microscopy, we determined that the dominant structures in the central region of the presynaptic terminal are mitochondria and neurofilaments (Fig. 1) (15). Clusters of synaptic vesicles occur at active zones and, occasionally, in more central regions. Vesicle size (50 nm) is too small, however, to allow seal formation across the tips of the pipettes. Thin strips of membranes, possibly from endoplasmic reticula, could also be detected sometimes but accounted for less than ~2% of the internal membranes. Thus the mitochondria (Fig. 1), whose cross-sectional diameters range from ~300 to 1200 nm [mean = 575 ± 181 (SD) nm, n = 15] are the only internal organelles that are compatible with seal formation by the patch pipettes, which have tip diameters of ~180 to 200 nm (16).

Seals (0.5 to 6.0 gigohm) were obtained in 94 experiments using the technique in (17); 71 of the 94 seals were greater than 1.5 gigohm. The successful recordings represented approximately 40% of attempts. When a fluorescent lipophilic dye was included in the patch pipette, a fluorescent signal could be detected only after a high-resistance seal was obtained (n = 7). The fluorescent signals in all the dye experiments were located within the large terminal finger of the presynaptic terminal (18).

After formation of a gigohm seal, the potential of the patch was set between −100 and +100 mV to record the spontaneous and voltage-dependent activity in the membranes. We observed spontaneous channel activity in 50% of the seals (n = 47 out of 94) and the amplitude of such activity was usually low. In many