A Long-Snouted Predatory Dinosaur from Africa and the Evolution of Spinosaurids


Fossils discovered in Lower Cretaceous (Aptian) rocks in the Ténéré Desert of central Niger provide new information about spinosaurids, a peculiar group of piscivorous theropod dinosaurs. The remains, which represent a new genus and species, reveal the extreme elongation and transverse compression of the spinosaurid snout. The postcranial bones include blade-shaped vertebral spines that form a low sail over the hips. Phylogenetic analysis suggests that the enlarged thumb claw and robust forelimb evolved during the Jurassic, before the elongated snout and other fish-eating adaptations in the skull. The close phylogenetic relationship between the new African spinosaurid and Baryonyx from Europe provides evidence of dispersal across the Tethys seaway during the Early Cretaceous.

In 1912, a series of extremely high-spined vertebrae and a peculiar lower jaw with subconical crocodilike teeth were discovered in the Baharıˆya oasis in central Egypt (1). These fossils provided evidence that a large, piscivorous, sail-backed predator roamed the northern shores of Africa during the Late Cretaceous (Cenomanian). This partial skeleton, *Spinosaurus aegyptiacus*, was destroyed during World War II, and few remains that are attributable to this taxon have since been recovered in these horizons (2–5).

Additional bones of *Spinosauridae*-like predators have been discovered in Lower Cretaceous (Aptian or Albian) deposits in Niger and Brazil and in somewhat older (Barremian) rocks in Europe. The Nigerien fossils include peculiar arched snout tips and enormous manual unguals (6–8); the Brazilian remains consist of a single partial skull, *Irritator* (9, 10); and the European fossils, *Baryonyx*, include the first relatively complete spinosaurid skull (11–13).

Fossils were recovered recently from the Elrhaz Formation in Niger (Fig. 1). These Aptian-age rocks consist predominantly of fluvial channel deposits and are exposed in low outcrops amid dune fields in the Ténéré Desert (6, 14). The fossils found here include plant, vertebrate, and vertebrate remains; the vertebrate remains consist mainly of disarticulated bones and teeth in basal channel lag deposits. Dinosaurs are represented by at least three theropods, two sauropods, and three ornithopods (15).

The newly discovered fossils include a partial skull and skeleton of a new spinosaurid, *Suchomimus tenerensis* gen. nov. sp. nov. (16), which can be distinguished from other spinosaurids (17). An articulated snout (Fig. 2A and B) reveals its remarkably long, low, and narrow proportions. The elongation of the snout is the result of the hypertrophy of both the premaxilla and the anterior rami of the maxilla. The premaxillae, which fuse early in growth, each contain alveoli for seven teeth. The subconical crowns are slightly recurved and have fine marginal serrations and textured enamel surfaces (Fig. 2E). The external nares are retracted posterior to the premaxillary teeth (Fig. 2, A and D), as in *Baryonyx* (14). The unusually long, plate-shaped anteromedial processes of the maxillae (18) are firmly held by the premaxillae (Fig. 2B). The medial wall of the antorbital fossa is confined to the anterior end of the antorbital fenestra, and a simple conical pneumatocoele extends anteriorly into the body of the maxilla. As in *Baryonyx*, the quadrate foramen is very large, and the distal condyles are very broad.

The new cranial bones indicate that the spinosaurid skull is considerably lower, narrower, and longer (Fig. 2D) than previously reconstructed (13, 19). In dorsal view, the snout is extremely narrow (Fig. 2C). In ventral view, the maxillae meet along the midline, displacing the internal nares and palatal complex (pterygoid, palatine, and ectopterygoid) toward the rear of the skull.

In the postcranial skeleton, the cervical series arches upward (18) and has prominent epipophyses for muscle attachments. The neural spines increase in height rapidly in the middorsal vertebrae, forming a low median sail that is deepest over the sacral vertebrae (Fig. 3). This vertebral morphology, incidently developed in *Baryonyx* (13), is distinct.
from that in *Spinosaurus* (1), in which the much deeper sail arches to an apex over the middorsal vertebrae (Fig. 4B).

Complete pectoral and pelvic bones show a deep subrectangular acromion on the scapula and a low obturator flange on the ischium. The distal end of the pubis is distinctive. Although there is a short, sagittal, symphyseal flange that may correspond with the pubic foot in other theropods, the flattened, subrectangular distal end of the pubis faces anteriorly, perpendicular to the sagittal plane (Fig. 3). The forearm is remarkably stout, and manual digit III is robust, as seen in the size of metacarpal III and the third ungual (Fig. 3 and Table 1). The femur has a blade-shaped anterior trochanter, and the ascending process of the astragalus is taller than that in *Allosaurus* (20).

Phylogenetic analysis (21, 22) links spinosaurids with torvosaurids (23) and places this clade (Spinosauroidea) as the sister group to Neotetanurae (Fig. 4A and Table 2). The derived features that are shared between spinosaurids and torvosaurids, including the short forearm and the enlarged manual digit I ungual (22), appear to have evolved by the Middle Jurassic (Fig. 4B). A hook-shaped coracoid characterizes *Suchomimus*, *Baryonyx*, and neotetanurans but not torvosaurids (24). Thus, the hook-shaped coracoid either evolved convergently in neotetanurans and spinosaurids or originated as a tetanuran synapomorphy that was subsequently lost in torvosaurids (21, 22).

Spinosaurids are characterized by numerous derived features, many of which are related to piscivory [including an unusually long snout with a long secondary palate; a terminal rosette of teeth in the upper and lower jaws (25); subcylindrical, spaced crowns; posteriorly displaced external nares; ventrally positioned basipterygoid articulation; and other features (8, 13, 22)]. Our analysis suggests that spinosaurids can be divided into two clades, the Baryonychinae
Fig. 3. Skeletal reconstruction of the spinosaurid *Suchomimus tenerensis* showing preserved bones (total length is ~11 m). Height of human silhouette, 1.68 m (5 feet 6 inches); scale bar, 1 m.

Table 1. Length measurements (millimeters) and ratios in *Suchomimus tenerensis* (MNN GDF500), *Baryonyx walkeri* (13), and *Allosaurus fragilis* (20). Unguals are measured perpendicular to the articular end. Question mark indicates lack of preservation; I, II, and III are unguals of manual digits I, II, and III, respectively.

<table>
<thead>
<tr>
<th>Bone</th>
<th>Suchomimus</th>
<th>Baryonyx</th>
<th>Allosaurus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Humerus</td>
<td>560</td>
<td>483*</td>
<td>310</td>
</tr>
<tr>
<td>Radius</td>
<td>255</td>
<td>225</td>
<td>222</td>
</tr>
<tr>
<td>Metacarpal III</td>
<td>130</td>
<td>?</td>
<td>101</td>
</tr>
<tr>
<td>I</td>
<td>190</td>
<td>173*</td>
<td>102</td>
</tr>
<tr>
<td>II</td>
<td>165</td>
<td>?</td>
<td>92</td>
</tr>
<tr>
<td>III</td>
<td>120</td>
<td>120*</td>
<td>54</td>
</tr>
<tr>
<td>Femur</td>
<td>1075</td>
<td>?</td>
<td>850</td>
</tr>
<tr>
<td>Tibia</td>
<td>945</td>
<td>?</td>
<td>690</td>
</tr>
</tbody>
</table>

Lengths

<table>
<thead>
<tr>
<th>Ratios</th>
<th>Suchomimus</th>
<th>Baryonyx</th>
<th>Allosaurus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Radius/humerus</td>
<td>0.46</td>
<td>0.47</td>
<td>0.72</td>
</tr>
<tr>
<td>I/radius</td>
<td>0.75</td>
<td>0.77</td>
<td>0.46</td>
</tr>
<tr>
<td>II/II</td>
<td>0.87</td>
<td>?</td>
<td>0.90</td>
</tr>
<tr>
<td>III/III</td>
<td>0.63</td>
<td>0.69</td>
<td>0.53</td>
</tr>
<tr>
<td>Tibia/femur</td>
<td>0.88</td>
<td>?</td>
<td>0.81</td>
</tr>
</tbody>
</table>

*This measurement was taken by the authors and differs slightly from that reported previously (13).
Before the discovery of Suchomimus, the geographic distribution and relationships of spinosauroids matched the general pattern of continental fragmentation during the latter half of the Mesozoic and thus could be explained by large-scale vicariance. The split between the northern Baryonyx and the southern spinosaurines, in this hypothesis, could be attributed to the opening of the Tethyan seaway between Laurasia and Gondwanaland, and the divergence among spinosaurines could be the result of the subsequent opening of the Atlantic Ocean between South America and Africa. The discovery of Suchomimus on Africa in the mid-Cretaceous, however, complicates this scenario. Its closest relative is the European Baryonyx rather than the African Spinosaurus—a pattern of relationships that is inconsistent with the large-scale sequence of continental rifting described above.

One biogeographic hypothesis accounts most parsimoniously for the distribution of the four spinosaurids (28), assuming that we have correctly ascertained their phylogenetic relationships and accept the rifting sequence between the continental areas outlined above. Initially, spinosaurids may have had a distribution across Pangea that was split by the opening of the Tethys; baryonychines evolved to the north (Europe, or Laurasia), and spinosaurines evolved on the southern landsmass (South America and Africa, or Gondwanaland). A single dispersal event from Europe to Africa during the Early Cretaceous would account for the presence of Suchomimus in Africa. Alternative scenarios involve additional dispersal or extinction events to account for recorded distributions. The phylogenetic and biogeographic relationships of Suchomimus and other spinosaurids provide further evidence of dispersal across the Tethyan seaway during the Early Cretaceous (21, 29).

Table 2. Character-state matrix for two outgroups (Ceratosauria and Neotetanurae), six ingroups, and 45 characters (22) used in a phylogenetic analysis of spinosaurids (Fig. 4A). The holotypic specimens of Angaturama and Irritator were scored as one taxon (Irritator). X, unknown as a result of transformation; ?, not preserved.

### Taxa

<table>
<thead>
<tr>
<th></th>
<th>Characters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ceratosaurus</td>
<td>00000</td>
</tr>
<tr>
<td>Neotetanurae</td>
<td>00000</td>
</tr>
<tr>
<td>Eustreptospondylus</td>
<td>1111?</td>
</tr>
<tr>
<td>Torvosaurus</td>
<td>11111</td>
</tr>
<tr>
<td>Baryonyx</td>
<td>11111</td>
</tr>
<tr>
<td>Suchomimus</td>
<td>11111</td>
</tr>
<tr>
<td>Irritator</td>
<td>1111?</td>
</tr>
<tr>
<td>Spinosaurus</td>
<td>1111?</td>
</tr>
</tbody>
</table>

References and Notes

5. The holostylic skeleton of Spinosauroidea agutiicus includes subconical teeth, dentaries with a squared distal end, and high-spired dorsal vertebrae (7); the association of these features is confirmed by additional new remains from Morocco (3) and Algeria (4). Although the Moroccan and Algerian material have been referred to a different species (S. maroccanus), its distinction from S. aguticus (by the proportions of the centrum of an isolated cervical vertebra) and the basis for the referral of additional material are questionable. We regard S. maroccanus as a nomen dubium and provisionally refer all spinosaur material from Albian- and Cenomanian-age rocks in northern Africa to S. aguticus. Storzer (30) described other postcranial remains from the Ba-harilertas as “Spinosauroidea B.,” but these can be shown to overlap with a partial skeleton of the allisaudroid Carcosharodontosaurus saharicus from the same locality (21). Recently a new genus and species, Sigilmassauroides brevicollis, was erected on the basis of isolated vertebrae from Cenomanian-age rocks in Morocco (4). We question its distinction from C. saharicus (by proportions of the centrum of an isolated cervical vertebra). We regard Sigilmassauroides brevicollis as a subjective junior synonym of C. saharicus, to which we provisionally refer all carcosharodontosaurid material from Albian- and Cenomanian-age rocks in northern Africa.
10. Shortly after Irritator challengeri was described (9), the anterior end of a spinosaurid snout was described from the same deposit as Angaturama limai (10), which may well pertain to the same taxon or possibly to the same spinosaurid, as the referred to an indeterminate species of C. saharicus (13).
14. The Tetanga Group is composed of terrestrial rocks of middle to late Cretaceous age. Three formations (T. meli, Elrhaz, and Echkar) have been recognized (J. Ha. Feure. Mem. B.R.G.M. Paris 47, 1 [1966]; G. Creighton and R. Pounget, ibid. 48, 1 [1967]). In the region southeast of the Air highlands, the Tetanga Group was divided into eight Gadoufaoua (GAD) levels by the Center for Atomic Energy [E. Molinas, ibid (Tazole, Elrhaz, and Echkar) have been recognized [H. K. Chablis, thesis, Universite de Paris-6 (1988)], and the high-spined Ouranosaurus nigeriensis (6). Nodosaurid vertebrae that were not previously recorded include a long-snouted basal crocodyliform and an azhdarchid pterosaur.
15. Etymology: Souchous, crocodyl (Greek); mimos, mimic (Greek); tenere, Tenere Desert; ensis, from (Latin). Named for the low elongate snout and piscivorous adaptations of the jaws and for the region of the Sahara in which it was discovered. Holotype: Partial disarticulated skeleton (MNHN GDF500) cataloged in the collections of the Musée National du Niger (MNHN), Niamey, Republic of Niger. Referenced material: Articulated premaxillae and mandible (MNHN GDF501), right mandible (MNHN GDF502), partial dentaries (MNHN GDF503, GDF504, and GDF505), axis (MNHN GDF506), posterior cervical vertebra (MNHN GDF507), posterior dorsal vertebra (MNHN GDF508), two caudal vertebrae (MNHN GDF510 and GDF511), and many additional bones and teeth. Diagnosis: Spinosaurid characterized by an elongate posteroventral premaxilla process that nearly excludes the maxilla from the external nares; broadened and heightened posteriorly, hypotrophied urostyle; ischium oriented posteriorly; and hooked-rod articular articulation.
16. In contrast to the specimens described here, previously known spinosaurid material from Niger has been limited to fragmentary disarticulated bones that are attributable to an as yet indeterminate spinosaurid (6–8). Recently, however, a new spinosaurid, Cristatusaurus lapponnai, was named on the basis of material from Gadoufaoua (4). The holotypic specimen consists of portions of the premaxillae, maxilla, and dentary, the association of which was not established. The authors state that the material differs from Baryonyx walkeri by the "brevirostrine condition of premaxilla." However, no distinguishing features or proportions are apparent to us or to previous authors (13), who attributed the premaxillae to an indeterminate species of Baryonyx. We therefore regard C. lapponnai as a nomen dubium.
17. We offer alternative identifications for several cranial elements in the holotypic specimen of Baryonyx walkeri. We regard the bones that were identified as the left postorbital, left jugal, right atlantal arch, and left angular (13) as the posterior portion of the right surangular, right præarticular, central body of the left pterygoid, and right angular, respectively. These are reposi-
Suchomimus. The cervical series in both Baryonyx and Suchomimus shows a dorsal offset of the anterior articulations.


22. The following 45 synapomorphies (optimized with delayed transformation) correspond with the scored character states [0] or [1] (Table 2) that were used in the analysis of the spinosaurid relationships presented in Fig. 4A. Synapomorphies 27 through 34 uniting Baryonyx and Suchomimus cannot be observed in other spinosaurids because of incomplete preservation. Spinosauroidea 1, anterior ramus of maxilla, length: 70% (0) or 100% or more (1) of maximum depth; 2, lacrimal anterior ramus, length: more (0) or less (1) than 65% of the ventral ramus; 3, humeral deltopectoral crest, length: less (0) or more (1) than 45% of humeral length; 4, radial (forearm) length: more (0) or less (1) than 50% of humeral length; 5, manual digit I—ungual, length: 2.5 (0) or 3 (1) times the depth of the proximal end. Spinosauroidea 6, anterior end of upper and lower jaws, form: convergent (0); expanded into a premaxillary/dentary rosette (1); 7, snout length: less (0) or more (1) than three times the length of the antorbital fenestra; 8, exterior of the maxillary tooth row: 9, antorbital fossa, size: larger (0) or smaller (1) than the orbit; 10, intermaxillary suture, form: open (0); fused (1) at maturity; 11, premaxillary maxillary anteromedial process, shape: ßuted prong (0); plate (1); 12, maxillary anteromedial process, anterior extension: as far as (0) or far (1) beyond the ventral ramus; 13, maxillary anteromedial process, anterior extension: as far as (0) or far (1) beyond the ventral ramus; 14, paradelphal laminae: present (0); absent (1); 15, lacrimal anterior and ventral rami, angle of divergence: 75° to 90° (0); 30° to 45° (1); 16, splenial foramen, size: small (0); large (1); 17, middle coracoid, shape: subcircular (0); elliptical (1); 18, crown striations: absent (0); present (1); 19, premaxillary tooth count: 3 to 4 (0); 6 to 7 (1); 20, maxillary crowns, spacing: adjacent (0); with intervening space; 21, distal end of roof shelf: broad (0); strongly tapered (1). Baryonychinae (Suchomimus and Baryonyx): 22, anterior dorsal centra, depth of ventral keel: weak (0); blade-shaped (1); 23, maximum height of dorsal neural spines: less (0) or more (1) than 2.5 times the centrum height; 24, posterior dorsal neural spines, basal webbling: absent (0); present (1); 25, posterior dorsal neural spines, accessory centrodiasaphal laminae: absent (0); present (1); 26, dentary tooth row: ~15 (0); ~30 (1); 27, quadrate head, shape: oval (0); subquadrate (1); 28, quadrate foramen, size: foramen (0); broad fenestra (1); 29, coracoid posterior process, shape: broad and rounded (0); crecentic (1); 30, humeral trochanters, size: low and rounded (0); hypertrophied (1); 31, humeral deltopectoral crest, orientation of apex: anterior (0); lateral (1); 32, humeral internal tuberosity, size: broad and rounded (0); hypertrophied (1); 33, neotetanurans were joined by one character with an ambiguous optimization (a hook-shaped coracoid).


34. Supported by the David and Lucile Packard Foundation, National Geographic Society, Pritzker Foundation, and the Women’s Board of the University of Chicago. We thank K. Bainbridge, A. Boldizsar, J. Bradshaw, J.-P. Cavugelli, J. Ogradnick, and F. Stroik for participation in field excavation; C. Abraczinskas for drawing from the original specimens and executing the ßnal drafts of Figs. 1A and 2 through 4; B. Strack (Field Museum) for assistance with microphotography; Q. Cao and E. Dong for directing fossil preparation and casting; and J. Hopson, F. Landou, B. Molnar, and H.-D. Sues for reviewing an earlier draft of the paper. We gratefully acknowledge the assistance of I. Kouada of the Minist e ’re de L’Enseignement Supérieur et de la Technologie (Niger). For permission to conduct ßeldwork, we are indebted to the Republic of Niger.

31 August 1998; accepted 2 October 1998

Ultrastable Mesostructured Silica Vesicles
Seong Su Kim, Wenzhong Zhang, Thomas J. Pinnavaia*

A family of mesoporous molecular sieves (denoted MSU-G) with vesicle-like hierarchical structures and unprecedented thermal (100°C) and hydrothermal stabilities (more than 150 hours at 100°C) associated with high SiO2, cross-linking was prepared through a supramolecular assembly pathway that relies on hydrogen bonding between electrically neutral gemini surfactants of the type CTnH2n−1,1,N(CH2)n,NH2 and silica precursors derived from tetraethylorthosilicate. The vesicle shells are constructed of one or more undulated silica sheets that are about 3 nanometers thick with mesopores (average diameters from 2.7 to 4.0 nanometers) running both parallel and orthogonal to the silica sheets, which makes the framework structure bicontinuous and highly accessible. Catalytic metal ion centers [for example, Ti(V ) and Al(III)] have been incorporated into the framework with the retention of hierarchical structure.

Substantial progress has been made recently in extending the supramolecular assembly of mesostructured inorganic frameworks to include hierarchical forms with a variety of particle shapes (J–3). Mesoporous metal oxide molecular sieves with vesicle-like morphologies are of interest as potential catalysts and sorbents, in part because the mesosstructured shells and intrinsic textural pores of the vesicles should efﬁciently transport guest species to framework binding sites. However, all vesicle-like mesostructures reported to date had shells of undesirable thickness. More important, like many mesoporous molecular sieves with conventional particle morphologies, the framework structures deﬁning the vesicle shells were lacking in structural stability. For instance, a vesicular aluminophosphate with mesoscale d spacings and surface patterns that mimicked diatom and radiolarian skeletons collapsed to AlPO4-5 cristobalite with a complete loss of the hierarchical character at 300°C (4). Also, vesicle-like silicic acid polymers that were structured by a didodecyl(dimethylammonium) bromide template lost their hierarchical structures when washed with alcohols (5). Macroscopic hollow spheres of mesoporous MCM-41 (2, 6) have been prepared from oil-in-water emulsions, but

*To whom correspondence should be addressed. E-mail: Pinnavaia@cmu.edu

Downloaded from http://science.sciencemag.org/ on May 26, 2017
A Long-Snouted Predatory Dinosaur from Africa and the Evolution of Spinosaurids
Science 282 (5392), 1298-1302, [doi: 10.1126/science.282.5392.1298]

Editor's Summary

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

Article Tools
Visit the online version of this article to access the personalization and article tools:
http://science.sciencemag.org/content/282/5392/1298

Permissions
Obtain information about reproducing this article:
http://www.sciencemag.org/about/permissions.dtl