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

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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 crocodilelike teeth were discovered in the Baharîya 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 *Spinosaurus*-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 skeleton (*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, invertebrate, 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 ramus 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 pneumatocoel 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, incipiently developed in *Baryonyx* (*13*), is distinct

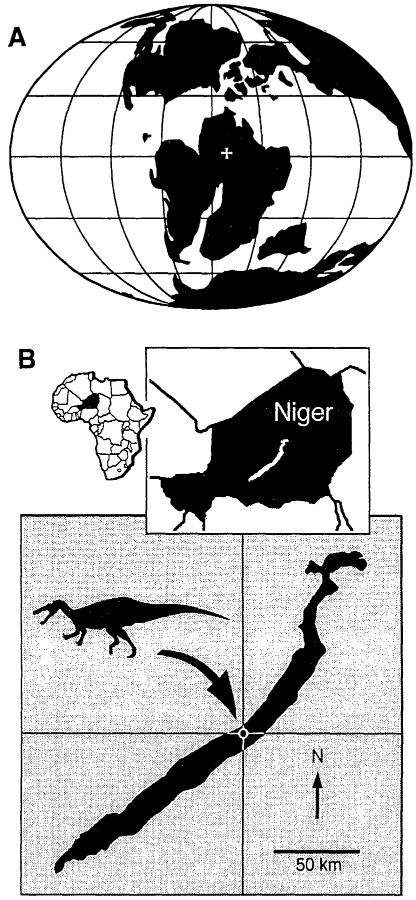

Fig. 1. Mid-Cretaceous paleogeography and principal exposures of fossiliferous beds in the region of Gadoufaoua, Niger. (**A**) Mid-Cretaceous (Aptian, 120 million years ago) paleogeographic map (Mollweide projection) with latitude and longitude lines spaced at 30° intervals (longitude greater than 120° is not shown) (*31*). White cross, fossil locality. (**B**) Maps showing Niger, the exposures of the GAD 5 beds (*12*) (white, above; black, below), and the location of the holotypic skeleton of *Suchomimus tenerensis* (16°25′N, 9°7′E).

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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 *Suchominus*, *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

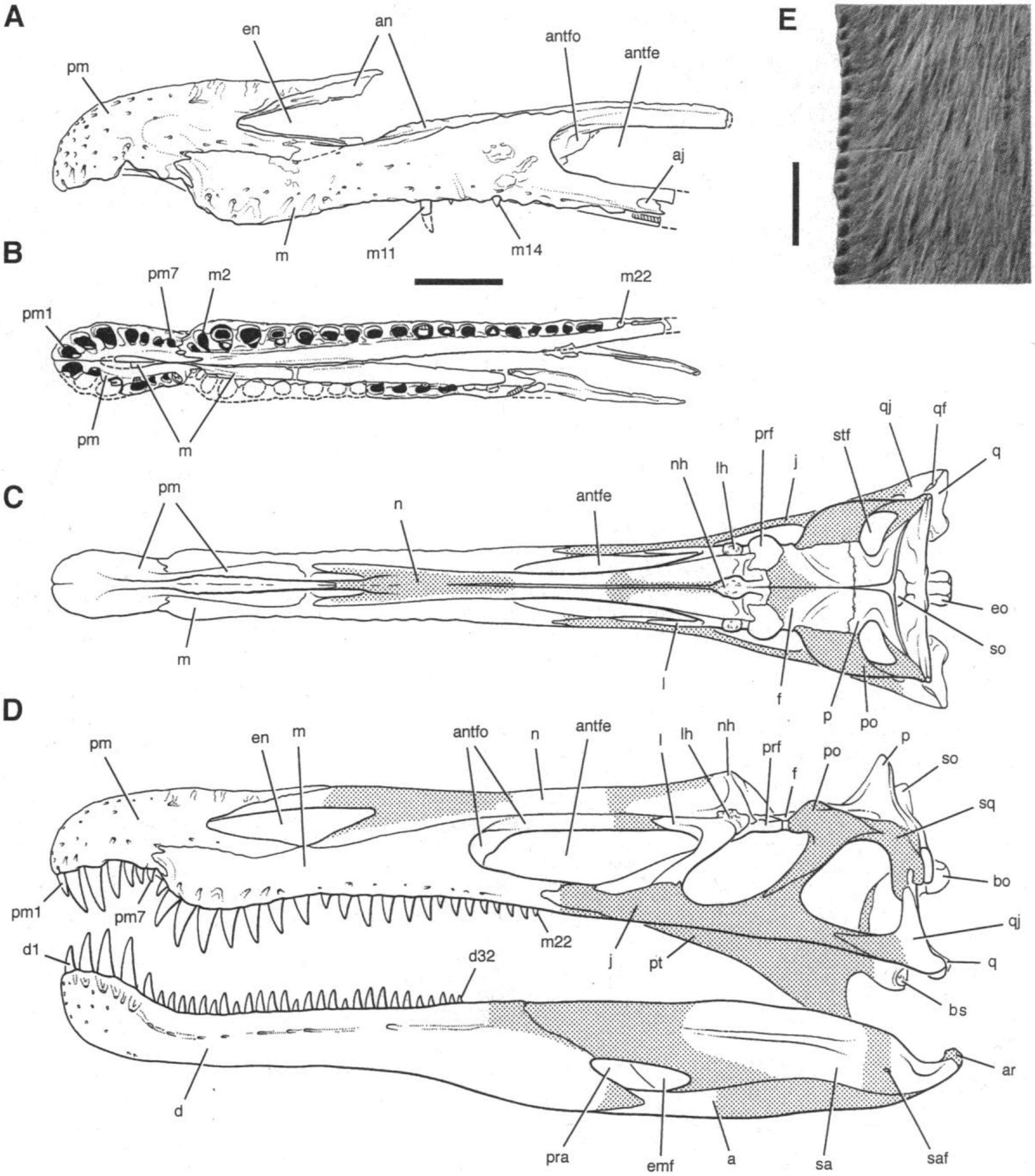

Fig. 2. Skull of the spinosaurid *Suchomimus tenerensis*. Articulated premaxillae and maxillae (MNN GDF501) in left (**A**) lateral (reversed from right) and (**B**) ventral views. Skull reconstruction of *S. tenerensis* based on remains from Niger and *Baryonyx walkeri* in (**C**) dorsal and (**D**) lateral views. Shaded portions are not currently known in any spinosaurid. (**E**) Scanning electron micrograph of the crown margin of an isolated tooth of *S. tenerensis* showing the small marginal serrations and textured enamel. Scale bar in (A) through (D), 10 cm; in (E), 1 mm. Abbreviations: a, angular; aj, articular surface for jugal; an, articular surface for nasal; antfe, antorbital fenestra; antfo, antorbital fossa; ar, articular; bo, basioccipital; bs, basisphenoid; d, dentary; emf, external mandibular fenestra; en, external naris; eo, exoccipital; f, frontal; j, jugal; l, lacrimal; lh, lacrimal horn; m, maxilla; n, nasal; nh, nasal horn; p, parietal; pm, premaxilla; po, postorbital; popr, paroccipital process; pra, prearticular; prf, prefrontal; pt, pterygoid; q, quadrate; qf, quadrate foramen; qj, quadratojugal; sa, surangular; saf, surangular foramen; so, supraoccipital; sq, squamosal; stf, supratemporial fossa; and 1 through 17, tooth positions.

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.

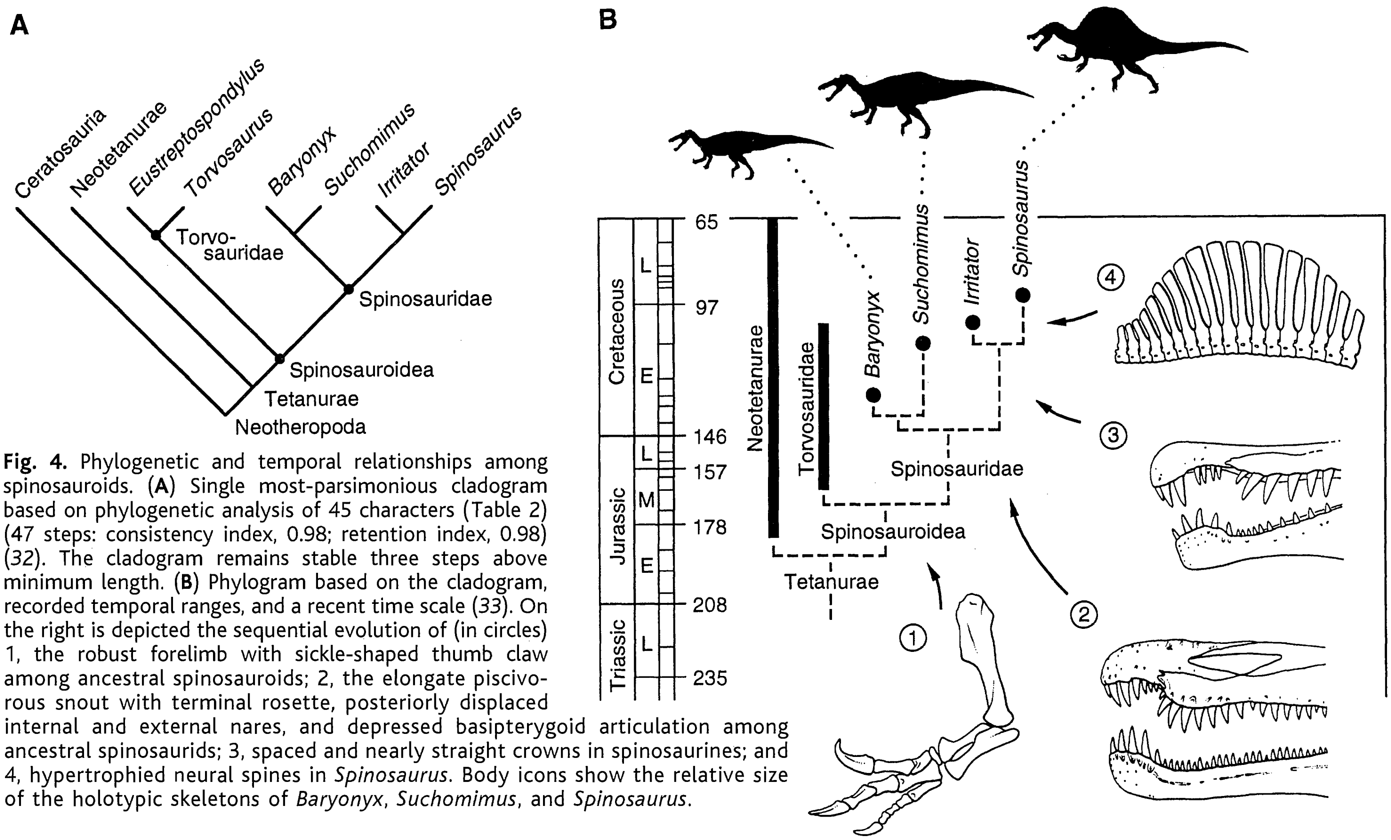

Fig. 4. Phylogenetic and temporal relationships among spinosauroids. (**A**) Single most-parsimonious cladogram based on phylogenetic analysis of 45 characters (Table 2) (47 steps: consistency index, 0.98; retention index, 0.98) (*32*). The cladogram remains stable three steps above minimum length. (**B**) Phylogram based on the cladogram, recorded temporal ranges, and a recent time scale (*33*). On the right is depicted the sequential evolution of (in circles) 1, the robust forelimb with sickle-shaped thumb claw among ancestral spinosauroids; 2, the elongate piscivorous snout with terminal rosette, posteriorly displaced internal and external nares, and depressed basipterygoid articulation among ancestral spinosaurids; 3, spaced and nearly straight crowns in spinosaurines; and 4, hypertrophied neural spines in *Spinosaurus*. Body icons show the relative size of the holotypic skeletons of *Baryonyx*, *Suchomimus*, and *Spinosaurus*.

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.

Bone	*Suchomimus*	*Baryonyx*	*Allosaurus*
	Lengths		
Humerus	560	483*	310
Radius	255	225	222
Metacarpal III	130	?	101
I	190	173*	102
II	165	?	92
III	120	120*	54
Femur	1075	?	850
Tibia	945	?	690
	Ratios		
Radius/humerus	0.46	0.47	0.72
I/radius	0.75	0.77	0.46
II/I	0.87	?	0.90
III/I	0.63	0.69	0.53
Tibia/femur	0.88	?	0.81

*This measurement was taken by the authors and differs slightly from that reported previously (*13*).

and the Spinosaurinae (*26*), which diverged before the Barremian (Fig. 4B). The baryonychines *Suchominus* and *Baryonyx* are distinct (*16, 27*) but closely related, as evidenced by several derived features that include the small size and increased number of dentary teeth posterior to the terminal rosette and the deeply keeled anterior dorsal vertebrae (*22*). Many other similarities between these two taxa are ambiguous because they are not preserved in other spinosaurids. The spinosaurines *Irritator* and *Spinosaurus* are united on the basis of the straight unserrated crowns, the small first premaxillary tooth (*4, 8*), and the increased spacing of the teeth in the upper and lower jaws (*8, 13, 22*) (Fig. 4B). The posterior displacement of the external nares in *Irritator* (*9*) and the deep sail in *Spinosaurus* (Fig. 4B) may eventually characterize the Spinosaurinae, but these features are currently known in only one member.

Table 2. Character-state matrix for two outgroups (Ceratosauria and Neotetanurae), six ingroups, and 45 characters (*22*) used in a phylogenetic analysis of spinosauroids (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	Characters								
		10		20		30		40	
Ceratosauria	00000	00000	00000	00000	00000	00010	00000	000X0	00000
Neotetanurae	00000	00000	00000	00000	00000	00011	00000	000X0	00000
Eustreptospondylus	111??	00000	00000	?0000	00000	0000?	00?00	000X1	11111
Torvosaurus	11111	00000	00000	?0000	00000	00000	00000	000X1	11111
Baryonyx	11111	11111	11111	11111	11111	11121	11110	0000?	?0??0
Suchomimus	11111	11111	1111?	?1111	11111	11121	11110	0000X	0??00
Irritator	11???	11111	111?1	?1?X1	1????	0????	????1	1111X	0????
Spinosaurus	1????	1????	???1?	111X?	?1000	0????	????1	1111?	?????

Before the discovery of *Suchomimus*, the geographic distribution and relationships of spinosaurids 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 Pangaea that was split by the opening of the Tethys; baryonychines evolved to the north (Europe, or Laurasia), and spinosaurines evolved on the southern landmass (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*).

References and Notes

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5. The holotypic skeleton of *Spinosaurus aegyptiacus* includes subconical teeth, dentaries with a squared distal end, and high-spined dorsal vertebrae (*1*); the association of these features is confirmed by additional remains from Morocco (*3*) and Algeria (*4*). Although the Moroccan and Algerian materials have been referred to a different species (*S. maroccanus*), its distinction from *S. aegyptiacus* (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. aegyptiacus*. Stromer (*30*) described other postcranial remains from the Baharîya oasis as "*Spinosaurus* B," but these can be shown to overlap with a partial skeleton of the allosauroid *Carcharodontosaurus saharicus* from the same locality (*21*). Recently a new genus and species, *Sigilmassasaurus brevicollis*, was erected on the basis of isolated vertebrae from Cenomanian-age rocks in Morocco (*3*). We question its distinction from *C. saharicus* (by proportions of the centrum of an isolated cervical vertebra). We regard *Sigilmassasaurus brevicollis* as a subjective junior synonym of *C. saharicus*, to which we provisionally refer all carcharodontosaurid material from Albian- and Cenomanian-age rocks in northern Africa.
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10. Shortly after *Irritator challengeri* was described (*9*), the anterior end of a spinosaurid snout was described from the same deposit as *Angaturama limai* (*8*), which may well pertain to the same taxon or possibly to the same specimen (*13*).
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14. The Tegama Group is composed of terrestrial rocks of middle to late Cretaceous age. Three formations (Tazolé, Elrhaz, and Echkar) have been recognized [H. Faure, *Mem. B.R.G.M. Paris* **47**, 1 (1966); J. Greigert and R. Pougnet, *ibid.* **48**, 1 (1967)]. In the region southeast of the Aïr highlands, the Tegama Group was divided into eight Gadoufaoua (GAD) levels by the Center for Atomic Energy [E. Molinas, *Rapp. C.E.A. Marseille* **1965**, 1 (1965)]. Horizons corresponding to GAD 5 have yielded all of the fossils in the present report and those described previously (*6*) (Fig. 1). GAD 5 appears to include the upper part of the Elrhaz Formation and the lower part of the Echkar Formation (*6*).
15. Theropods include the spinosaurid described here, an indeterminate tetanuran known primarily from teeth, and a small basal coelurosaur. Currently, there is no evidence to support the previous referral of small theropod remains from Gadoufaoua to *Elaphrosaurus iguidensis* (*6*) [A. F. de Lapparent, *Mem. Soc. Geol. Fr.* **88A**, 1 (1960)]. Sauropods include a common, high-spined basal diplodocoid [formerly referred to as a dicraeosaurine (*6*)] and a rare titanosaur. Ornithopods include the dryosaurid *Valdosaurus nigeriensis* [P. M. Galton and P. Taquet, *Geobios* **15**, 147 (1982)], the common "*Iguanodon* trapu" [S. Chablis, thesis, Université de Paris (1988)], and the high-spined *Ouranosaurus nigeriensis* (*6*). Nondinosaurian vertebrates that were not previously recorded include a long-snouted basal crocodyloid and an azhdarchid pterosaur.
16. **Etymology**: *Souchos*, crocodile (Greek); *mimos*, mimic (Greek); *tenere*, Ténéré 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 (MNN GDF500) cataloged in the collections of the Musée National du Niger (MNN), Niamey, Republic of Niger. **Referred material**: Articulated premaxillae and maxillae (MNN GDF501), right quadrate (MNN GDF502), partial dentaries (MNN GDF503, GDF504, and GDF505), axis (MNN GDF506), posterior cervical vertebra (MNN GDF507), posterior dorsal vertebra (MNN GDF508), two caudal vertebrae (MNN GDF510 and GDF511), and many additional bones and teeth. **Diagnosis**: Spinosaurid characterized by an elongate posterolateral premaxillary process that nearly excludes the maxilla from the external naris; broadened and heightened posterior dorsal, sacral, and anterior caudal neural spines; robust humeral tuberosities; hypertrophied ulnar olecranon process that is offset from the humeral articulation; and hook-shaped radial ectepicondyle.
17. 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 lapparenti*, 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. lapparenti* as a nomen dubium.
18. 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 neural arch, and left angular (*13*) as the posterior portion of the right surangular, right prearticular, central body of the left pterygoid, and right angular, respectively. These are repositioned accordingly in our cranial reconstruction (Fig. 2, C and D). The plate-shaped anteromedial process of the maxilla was formerly identified as the vomer (*13*). We regard the deeper proportions of the occiput as reconstructed in *B. walkeri* (*13*) as an artifact of unnatural ventral displacement of the quadrate. The cranium in *Baryonyx* was probably as low, long, and narrow as in

Suchomimus. The cervical series in both *Baryonyx* and *Suchomimus* shows a dorsal offset of the anterior articular surfaces.

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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. **Spinosauridae**: **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**, external nares positioned entirely posterior to the premaxillary tooth row; **9**, antorbital fossa, size: larger (0) or smaller (1) than the orbit; **10**, interpremaxillary suture, form: open (0); fused (1) at maturity; **11**, premaxillary-maxillary articulation, form: scarf or butt joint (0); interlocking (1); **12**, maxillary anteromedial process, shape: fluted prong (0); plate (1); **13**, maxillary anteromedial process, anterior extension: as far as (0) or far anterior to (1) the anterior margin of the maxilla; **14**, paradental 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**, midcrown cross section: elliptical (0); circular (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 (1); **21**, distal root shape: 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 webbing: absent (0); present (1); **25**, posterior dorsal neural spines, accessory centrodiapophyseal lamina: absent (0); present (1); **26**, dentary tooth count: ~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: low and rounded (0); crescentic (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: low and rounded (0); hypertrophied (1); **33**, radial external tuberosity and ulnar internal tuberosity, size: low and rounded (0); hypertrophied (1); **34**, pubic foot, size: moderate to large (0); reduced to a small flange (1). **Spinosaurinae (*Irritator* and *Spinosaurus*)**: **35**, crown recurvature: present (0); very reduced or absent (1); **36**, crown serrations: present (0); absent (1). **37**, dentary crowns, spacing: adjacent (0); with intervening space (1); **38**, premaxillary tooth 1, size: slightly smaller (0) or much smaller (1) than crowns 2 and 3; **39**, diastemata within the premaxillary rosette: narrow (0); broad (1). **Torvosauridae: 40**, antorbital fossa, width of ventral margin: more (0) or less (1) than 30% of the maximum depth of the posterior (principal) ramus; **41**, subcircular depression in the anterior corner of the antorbital fossa: absent (0); present (1); **42**, lacrimal foramen, position: near the base (0) or at midheight (1) on the ventral process; **43**, jugal posterior ramus, depth: less (0) or more (1) than that of the orbital ramus; **44**, postorbital ventral process, cross section of distal half: subcircular (0); U-shaped (1); **45**, puboischial fenestra: broadly open (0); closed or nearly closed (1).
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24. A previous cladistic analysis placed spinosaurids as the sister taxon to Neotetanurae (*13*). Notably, synapomorphies linking spinosaurids and torvosaurids were simply ignored in that analysis, and spinosaurids and neotetanurans were joined by one character with an ambiguous optimization (a hook-shaped coracoid).
25. The expanded terminal rosette has a very specific structure in spinosaurids that is probably related to the manner in which its teeth articulate. Seven premaxillary teeth are opposed by five dentary teeth. Three diastemata are present in the upper rosette (between teeth 3 and 4, between teeth 5 and 6, and between tooth 7 and the maxillary teeth).
26. Baryonychinae (*11*) is defined here as all spinosaurids that are more closely related to *Baryonyx* than to *Spinosaurus*; this clade currently includes *Baryonyx* and *Suchomimus*. Spinosaurinae (*1*) is defined here as all spinosaurids that are more closely related to *Spinosaurus* than to *Baryonyx*; this clade currently includes *Spinosaurus* and *Irritator* (= *Angaturama*).
27. Revised diagnosis for *Baryonyx walkeri*: Spinosaurid characterized by fused nasals with a median crest terminating posteriorly in a cruciate process, a solid subrectangular lacrimal horn, a marked transverse constriction of the sacral or anterior caudal centra, a well-formed peg-and-notch articulation between the scapula and coracoid, an everted distal margin of the pubic blade, and a very shallow fibular fossa.
28. Biogeographic hypotheses were optimized with dispersal-vicariance analysis [F. Ronquist, *Syst. Biol.* **46**, 195 (1997)], which counts the minimum number of dispersal or extinction events that is required to account for the observed distributions. There is no cost associated with vicariance. In our example, there is only one hypothesis that requires a single event (dispersal from Europe to Africa during the Early Cretaceous), if one accepts the general pattern of continental breakup as described in the text.
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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. Boldizar, J. Bradshaw, J.-P. Cavigelli, J. Ogradnick, and F. Stroik for participation in field excavation; C. Abraczinskas for drawing from the original specimens and executing the final 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. Lando, R. Molnar, and H.-D. Sues for reviewing an earlier draft of the paper. We gratefully acknowledge the assistance of I. Kouada of the Ministère de L'Enseignement Supérieur de la Recherche et de la Technologie (Niger). For permission to conduct fieldwork, we are indebted to the Republic of Niger.

31 August 1998; accepted 2 October 1998

Ultrastable Mesostructured Silica Vesicles

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A family of mesoporous molecular sieves (denoted MSU-G) with vesiclelike hierarchical structures and unprecedented thermal (1000°C) and hydrothermal stabilities (more than 150 hours at 100°C) associated with high SiO_4 cross-linking was prepared through a supramolecular assembly pathway that relies on hydrogen bonding between electrically neutral gemini surfactants of the type $C_nH_{2n+1}NH(CH_2)_2NH_2$ 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(IV) 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 framework structures to include hierarchical forms with a variety of particle shapes (*1–3*). Mesoporous metal oxide molecular sieves with vesiclelike morphologies are of interest as potential catalysts and sorbents, in part because the mesostructured shells and intrinsic textural pores of the vesicles should efficiently transport guest species to framework binding sites. However, all vesiclelike 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* spacing and surface patterns that mimicked diatom and radiolarian skeletons collapsed to $AlPO_4$-cristobalite with a complete loss of the hierarchical patterns at 300°C (*4*). Also, vesiclelike silicic acid polymers that were structured by a didodecyldimethylammonium 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

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