PALEONTOLOGY

Scimitar-crested *Spinosaurus* species from the Sahara caps stepwise spinosaurid radiation

Paul C. Sereno *et al.*

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https://doi.org/10.1126/science.adx5486

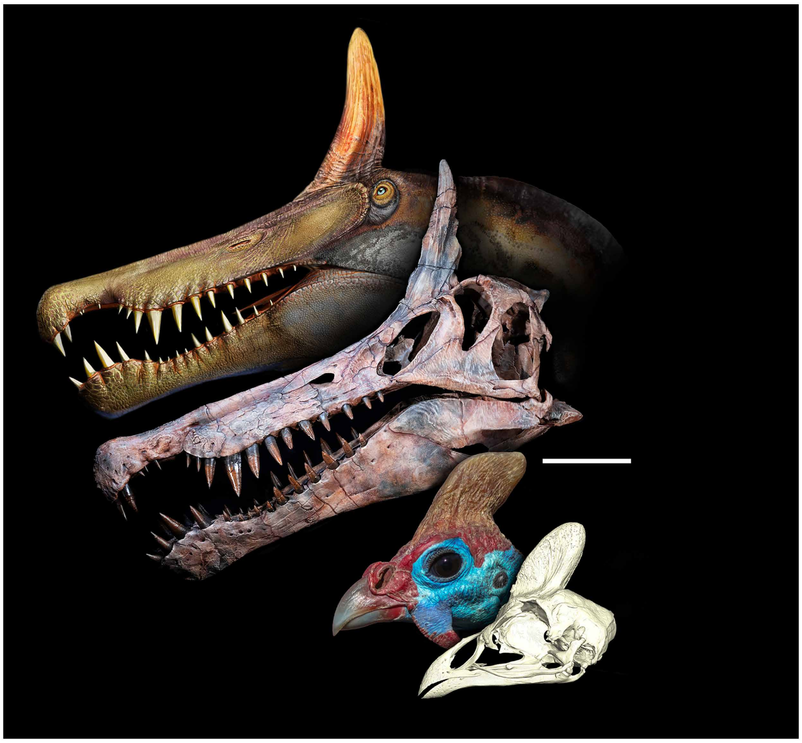
INTRODUCTION: The fossils of *Spinosaurus aegyptiacus*, a giant sail-backed, fish-eating theropod dinosaur from northern Africa, have inspired competing lifestyle interpretations, either as a semiaquatic ambush predator stalking shorelines and shallows or a fully aquatic predator in pursuit of prey underwater. Its bones and teeth have been found only in coastal deposits near marine margins, a locale potentially consistent with either lifestyle interpretation.

RATIONALE: In the central Sahara, a new fossiliferous area (Jenguebi) was discovered in beds equivalent in age [Farak Formation; Cenomanian ~95 million years ago (Mya)] to those yielding fossil remains of *S. aegyptiacus*. We describe from this area a new species, *Spinosaurus mirabilis* sp. nov., which is very similar to *S. aegyptiacus* in skeletal form but with a much taller, scimitar-shaped cranial crest. Two new sauropods were found in close association with the new spinosaurid buried in fluvial sediments indicative of an inland riparian habitat.

RESULTS: *S. mirabilis* sp. nov. is distinguished by the low profile of its snout, a hypertrophied nasal-prefrontal crest, greater spacing of posterior maxillary teeth, and other features. Its features highlight the extraordinary specializations of both species of the genus *Spinosaurus*, including interdigitating upper and lower teeth. Principal component analysis of body proportions places spinosaurids between semiaquatic waders (e.g., herons) and aquatic divers (e.g., darters) distant from all other predatory dinosaurs. A time-calibrated phylogenetic analysis resolves three evolutionary phases: an initial Jurassic radiation when their distinctive elongate fish-snaring skull evolved and split into two distinctive designs, baryonychine and spinosaurine; an Early Cretaceous circum-Tethyan diversification when both reigned as dominant predators; and a final early Late Cretaceous phase when spinosaurines attained maximum body size as shallow water ambush specialists limited geographically to northern Africa and South America.

CONCLUSION: The discovery of the tall-crested *S. mirabilis* sp. nov. in a riparian setting within an inland basin supports a lifestyle interpretation of a wading, shoreline predator with visual display an important aspect of its biology. At the end of the Cenomanian about 95 million years ago, an abrupt eustatic rise in sea level and the attendant climate change brought the spinosaurid radiation to an end. □

Corresponding authors: dinosaur@uchicago.edu (Paul C. Sereno); eoalulavis@gmail.com (Daniel Vidal) Cite this article as P. C. Sereno *et al.*, *Science* **391**, eadx5486 (2026). DOI: 10.1126/science.adx5486



Sheathed bony head crests in extinct and living dinosaurs. *S. mirabilis* sp. nov., evolved the tallest head crest of any theropod dinosaur, drawing attention to the midline ornamentation that characterizes the cranium and axial skeleton of all spinosaurids. In life, the crest would have been extended to some degree by a keratinous sheath, as in the living helmeted guinea fowl (*Numida meleagris*). Visual signaling, as is the case in guinea fowl and other crested avians, was likely the function of spinosaurid cranial crests and trunk and tail sails. Scale bar, 20 cm for *S. mirabilis* and 3 cm for *N. meleagris*.

FLESH RENDERING AND LAYOUT BY DANI NAVARRO; ADULT SKULL CAST BY THE FOSSIL LAB; HELMETED GUINEA FOWL IMAGES BY TODD GREEN

PALEONTOLOGY

Scimitar-crested *Spinosaurus* species from the Sahara caps stepwise spinosaurid radiation

Paul C. Sereno[1,2]*, Daniel Vidal[1,3]*, Nathan P. Myhrvold[4], Evan Johnson-Ransom[1], María Ciudad Real[3], Stephanie L. Baumgart[5], Noelia Sánchez Fontela[6], Todd L. Green[7], Evan T. Saitta[1], Boubé Adamou[8], Lauren L. Bop[1], Tyler M. Keillor[1], Erin C. Fitzgerald[1], Didier B. Dutheil[9], Robert A. S. Laroche[10], Alexandre V. Demers-Potvin[11], Álvaro Simarro[3], Francesc Gascó-Lluna[12], Ana Lázaro[13], Arturo Gamonal[3], Charles V. Beightol[14], Vincent Reneleau[9], Rachel Vautrin[9], Filippo Bertozzo[15], Alejandro Granados[16], Grace Kinney-Broderick[17], Jordan C. Mallon[18], Rafael M. Lindoso[19], Jahandar Ramezani[20]

We describe a close relative of *Spinosaurus aegyptiacus*, the sail-backed, fish-eating giant from nearshore deposits of northern Africa. *Spinosaurus mirabilis* sp. nov., discovered in the central Sahara alongside long-necked dinosaurs in a riparian habitat, is distinguished by a scimitar-shaped bony crest projecting far above its skull roof. We discern three discrete phases in spinosaurid evolution. During the first phase with roots in the Jurassic, an elongate fish-snaring skull emerged that soon was modified along divergent paths. During a second Early Cretaceous phase, spinosaurids became the dominant predators in circum-Tethyan habitats. The final phase began just before the Late Cretaceous during the opening of the Atlantic Ocean, when spinosaurines attained maximum body size as shallow water ambush specialists limited geographically to northern Africa and South America.

Spinosaurus aegyptiacus, a sail-backed fish-eating giant from nearshore deposits of northern Africa, has attracted renewed attention over its skeletal form and lifestyle interpretations (*1*–*3*). Secondarily aquatic vertebrates arose multiple times among reptiles, including ichthyosaurs, plesiosaurs, mosasaurs, fluked sea-faring crocodylomorphs, and diving penguins (*4*), but apparently never among nonavian dinosaurs that inhabited all major continental areas for nearly 150 million years. That is, unless *S. aegyptiacus* and some of its forebears were more than semiaquatic shoreline ambush predators wading into shallow waters (*2*, *3*, *5*, *6*) and instead were aquatic divers pursuing prey underwater with severely reduced functional capacity on land (*7*–*9*).

To date, *Spinosaurus* fossils are known only from nearshore deposits along Africa's margin of the Tethys Sea (*1*–*3*, *10*, *11*). Finding ~7-tonne *Spinosaurus* (*3*) within a terrestrial basin at distance from a marine shoreline could provide key evidence for a semiaquatic lifestyle, because all large-bodied (>1 tonne) secondarily aquatic tetrapods, living and extinct, are marine (*4*). Here, we describe a new *Spinosaurus* species with a scimitar-shaped cranial crest that otherwise is close in size and skeletal form to *S. aegyptiacus* (Figs. 1 to 3). Its remains were discovered in an inland basin in the central Sahara at the end of the final phase of spinosaurid evolution.

Results

Systematic paleontology

Dinosauria Owen, 1842
Theropoda Marsh, 1884
Spinosauridae Stromer, 1915
Spinosaurinae Stromer, 1915
Spinosaurini Stromer, 1915
Spinosaurus Stromer, 1915

Revised generic diagnosis

Large-bodied spinosaurine (skeletal length ~10 to 14 m) characterized by relatively small external naris and narial fossa (maximum diameter less than half that of the orbit) that are retracted to a position closer to the orbit than the anterior end of the snout, exclusion of the premaxilla from the border of the external naris*, blade-shaped, fused nasal crest lapped laterally along its base by a subtriangular prefrontal process*, "mushroom-shaped" snout where the anterior end of premaxillae is wider than long with a constriction after pm3*, interdigitating mid and posterior maxillary and dentary teeth with festooned alveolar external margins*, notch for dentary tooth 1 in the premaxillae at the height of the second alveoli*, diastema in maxillary and dentary tooth rows with paired tooth pairs*, anterior edge of dentary protruding, with a chin-like process more anterior than dentary tooth 1 that is directed anterodorsally*, midcervical neural spines (~C5) anteroposteriorly broadened (equal to centrum length without the condyle), anterior dorsal neural spines strap shaped (parallel sided); mid and posterior dorsal neural spines with an expanded spine base*, anterior caudal neural spines with cruciate cross section*, tibial medial malleolar edge not covered by astragalus. Asterisks indicate unambiguous generic synapomorphies.

Holotype

The holotype of *S. mirabilis* (MNBH JEN1, where MNBH is Musée National Boubou Hama, Niamey, Niger) is an associated right premaxilla, both maxillae, the base and the bottom half of the fused nasal crest with portions of both prefrontals, the alveolar edge of the right dentary, and five maxillary teeth found in association with the maxillae.

Referred specimens

Referred specimens come from Jenguebi (MNBH JEN2–9) and Iguidi (MNBH IGU11, IGU25, and IGU38) (Fig. 1A, "Fossil materials" section in the supplementary materials, and table S1).

Etymology

The species name *mirabilis*, meaning "astonishing" in Latin, is in reference to the hypertrophied nasal-prefrontal crest.

Type locality and horizon

The holotype was found in Sirig Taghat (meaning "no water, no goat" in Tamasheq), Jenguebi area, Agadez Region, Republic of the Niger, Farak Formation (*12*).

The arc of Mesozoic sediments to the south of the Aïr Massif infilling the Iullemeden Basin (*13*), initially informally described as "Continentale intercalaire" (*14*), includes four successive terrestrial formations of

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[1]Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL, USA. [2]Committee on Evolutionary Biology, University of Chicago, Chicago, IL, USA. [3]Grupo de Biología Evolutiva, UNED, Madrid, Spain. [4]Intellectual Ventures, Bellevue, WA, USA. [5]Department of Physiological Sciences, University of Florida, College of Veterinary Medicine, Gainesville, FL, USA. [6]Independent researcher, Navalcarnero, Madrid, Spain. [7]Department of Biomedical and Anatomical Sciences, New York Institute of Technology College of Osteopathic Medicine at Arkansas State University, Jonesboro, AR, USA. [8]Institute for Research in the Humanities, Abdou Moumouni University, Niamey, République du Niger. [9]Centre de Recherche en Paléontologie – Paris, Muséum National d'Histoire Naturelle, Paris, France. [10]Department of BioSciences, Rice University, Houston, TX, USA. [11]Department of Bioengineering, McGill University, Montreal, Canada. [12]Museo de Benagéber, Benagéber, Valencia, Spain. [13]Universidad de Valencia, Valencia, Spain. [14]Vicksburg National Military Park, Vicksburg, MS, USA. [15]Operational Directorate Earth and History of Life, Royal Belgian Institute of Natural Sciences, Brussels, Belgium. [16]Departamento de Ecología y Geología, University of Málaga, Málaga, Spain. [17]Department of Earth Sciences, University of Cambridge, Cambridge, UK. [18]Beaty Centre for Species Discovery and Palaeobiology Section, Canadian Museum of Nature, Ottawa, Canada. [19]Instituto Federal de Educação, Ciência e Tecnologia do Maranhão, Departamento Acadêmico de Biologia, Campus Monte Castelo, São Luís-MA, Brasil. [20]Department of Earth, Atmospheric and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, MA, USA. ***Corresponding author. Email: dinosaur@uchicago.edu (P.C.S.); eoalulavis@gmail.com (D.V.)**

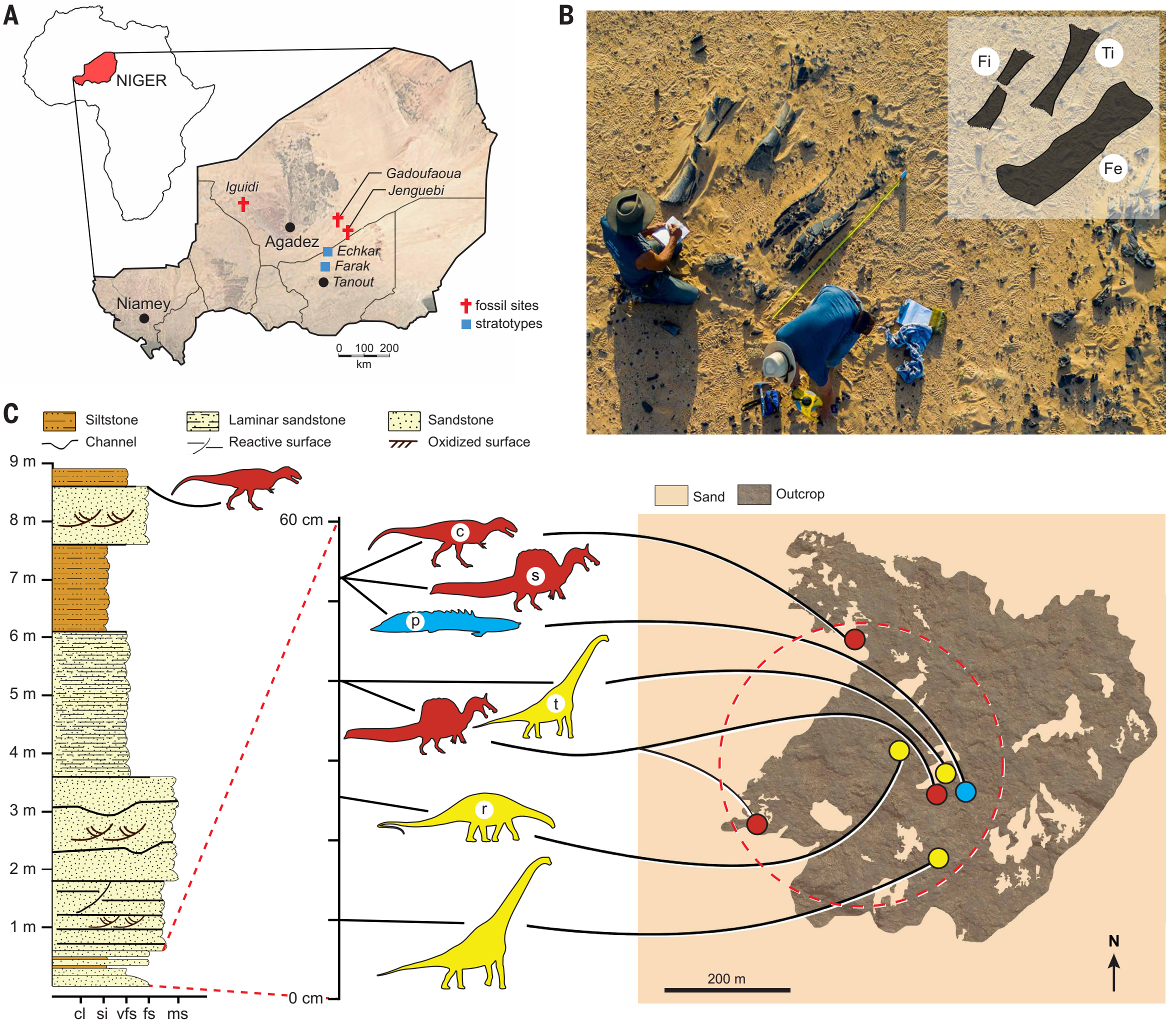

Fig. 1. Locality of *S. mirabilis* sp. nov. in Niger. (**A**) Location of the fossil areas Jenguebi, Gadoufaoua, and Iguidi (In Abangharit) and the stratotype sections of the Echkar and Farak Formations. (**B**) Drone photograph of the Sirig Taghat locality in the Jenguebi area showing the associated hind leg of a partial skeleton of a large unnamed titanosaurian. (**C**) Stratigraphic section (left) of the Farak Formation in the vicinity of the type locality for *S. mirabilis* with a map of key specimens from the lowermost 60 cm. Also shown in an ~8- to 9-m upsection is an associated carcharodontosaurid skeleton collected nearby. A map (right) of the central exposure at Sirig Taghat shows the proximity of the large-bodied fauna (dashed circle, 450 m diameter). c, *Carcharodontosaurus* sp.; cl, clay; Fe, femur; Fi, fibula; fs, fine sand; ms, medium sand; p, unnamed polypterid; r, unnamed rebbachisaurid; s, *S. mirabilis*; si, silt; t, unnamed titanosaurian; Ti, tibia; vfs, very fine sand.

Cretaceous age, Tazolé, Elrhaz, Echkar, and Farak (15), the last underlying the well-dated Cenomanian-Turonian limestone (16). We revisited the name-bearing sections for both the Echkar and Farak Formations and exposures of the overlying Cenomanian-Turonian limestone in terrain near Tanout (Fig. 1A). We conclude that both the Jenguebi and Iguidi (In Abangharit) fossil areas represent exposures of the Farak Formation (12). The collected vertebrate fauna at both locales compares closely with the Kem Kem Group of Morocco (10, 17) [Early to Middle Cenomanian, 100 to 95 million years ago (Mya); see the "Local stratigraphy and associated fauna" section in the supplementary materials].

Diagnosis

Spinosaurine with a low snout (parallel dorsal and ventral margins in profile)*, greater spacing of posterior maxillary (and presumably opposing dentary) teeth*, a scimitar-shaped nasal-prefrontal crest arching upward and backward with a lateral eminence offset toward the anterior margin*, postaxial cervical pleurocoels with greater anteroposterior diameter than adjacent parapophyseal articular facets, and a tibial articular depression for the ascending process of the astragalus reduced in area with the edge of the medial malleolus exposed in anterior view (Figs. 2, A and B and 3A and the "Fossil materials" section in the supplementary materials). Asterisks above indicate autapomorphies of *S. mirabilis* sp. nov.

Saharan fossil trove

In the 1950s, French uranium geologists discovered abundant vertebrate fossils on the western edge of a vast Saharan sand sea in Niger (18). Called Gadoufaoua (Fig. 1A), the area soon attracted return expeditions that have unearthed a landmark vertebrate fauna of mid-Cretaceous age (~110 Mya, Aptian-Albian), including the most completely known spinosaurid *Suchomimus tenerensis* (3, 19). Also in the 1950s, French geologist H. Faure (12, 20) discovered fossils in Cretaceous rocks of younger age (~95 Mya, Cenomanian). Akarazeras, his small, remote locale, yielded a few sabre-shaped teeth resembling those of the giant predator *Carcharodontosaurus saharicus* from similar-age rocks in the Western Desert of Egypt (17). Unlike Gadoufaoua, no one returned, and Faure's fossil teeth were lost.

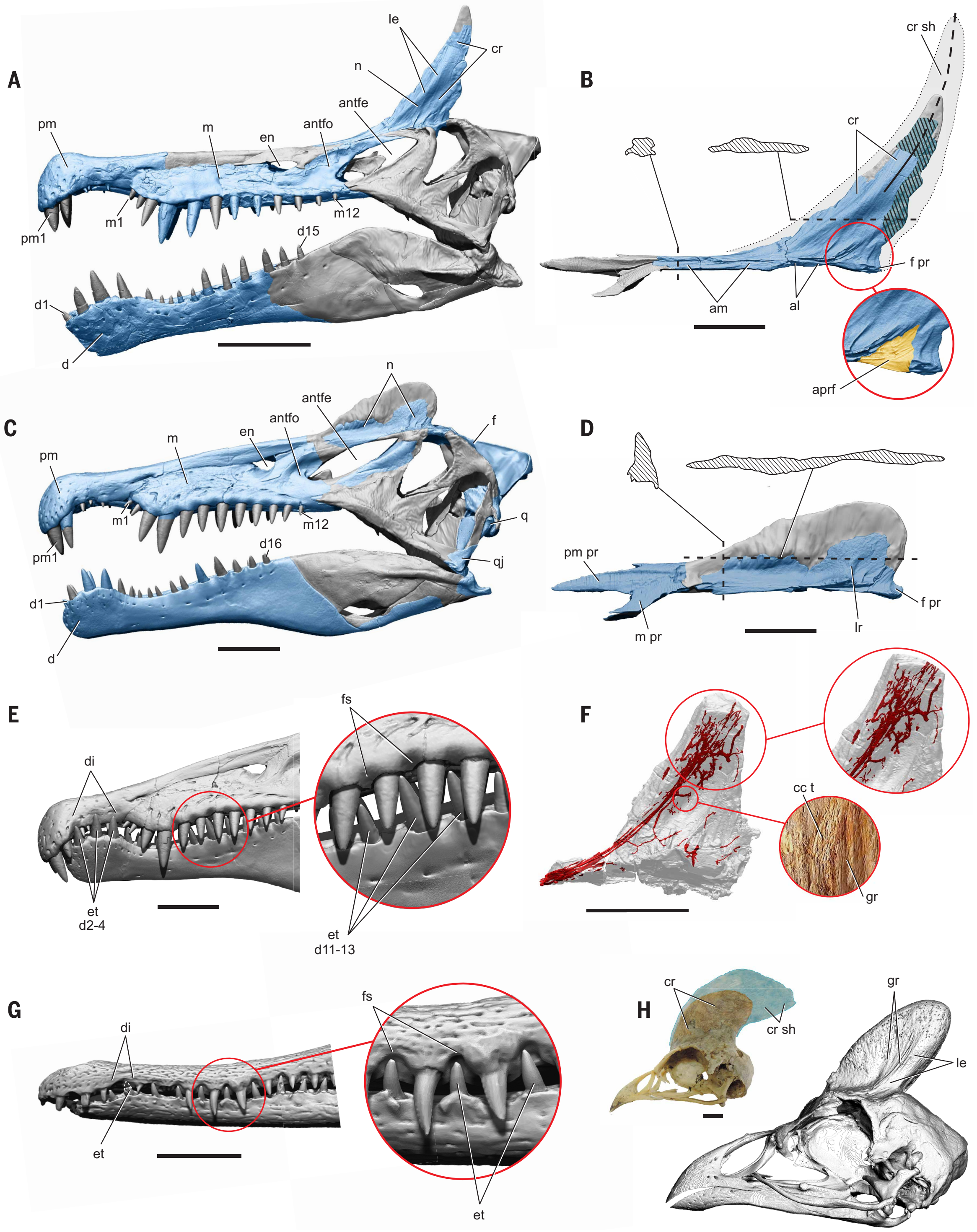

Fig. 2. Skull of *S. mirabilis* sp. nov. compared with *S. aegyptiacus* and modern analogs. (**A**) Composite skull reconstruction of *S. mirabilis* showing preserved bones (blue) with the occiput and posterior lower jaw based on *Irritator challengeri* (*43*,*48*). (**B**) Fused nasals of *S. mirabilis* (MNBH JEN3) are shown in left lateral view with transverse (anterior) and horizontal (posterior) cross sections of the anterior process and crest, respectively. Portions of the crest known in other specimens (MNBH JEN1, JEN2) are shown (cross-hatched blue) as well as reconstructed portions that are currently unknown (dark gray). The estimated extension of the crest as a keratinous sheath is shown (light gray). A magnified view of the articular surface for the prefrontal is shown (yellow). (**C**) Composite skull reconstruction of *S. aegyptiacus* showing preserved bones (blue) with most of the occiput and posterior lower jaw (dark gray) based on *I. challengeri* (*43*). (**D**) Fused nasals of *S. aegyptiacus* (UCRC PV14, 15, 192 scaled to match) with transverse (anterior) and horizontal (posterior) cross sections of the anterior process and crest, respectively, and the thin broken dorsal margin restored (dark gray). (**E**) Interdigitating teeth in *S. aegyptiacus* with magnified view showing alveolar festoons to accommodate everted dentary crowns (MSNM V4047, UCRC PV4). (**F**) CT-based digital rendering of neurovascular canals within the nasal crest of *S. mirabilis* in left lateral view with magnified views of vascularity at mid length and surface striations (MNBH JEN1). (**G**) Optical scan of the end of the snout of an African slender-snouted crocodile (*Mecistops cataphractus*, UF Herp 145926) in left lateral view showing a one-tooth upper diastema and festooned alveolar margins accommodating everted teeth. (**H**) Skull of the helmeted guineafowl (*Numida meleagris*, TLG NM007) in lateral view from a CT scan

([25]) and with lateral view of an adult male skull ([27]) showing the fused frontal crest and its extension by a keratinous crest sheath (green). MSNM, Museo Civico di Storia Naturale, Milan; TLG, T. L. Green Research Collection, Denver; UCRC, University of Chicago Research Collection, Chicago; UF, University of Florida, Gainesville. al, articular surface for the lacrimal; am, articular surface for the maxilla; antfe, antorbital fenestra; antfo, antorbital fossa; aprf, articular surface for the prefrontal; cc t, crisscross texture; cr, crest; cr sh, crest sheath; d, dentary; d1 to 4, 11 to 13, 15, and 16, dentary tooth 1 to 4, 11 to 13, 15, and 16; di, diastema; en, external naris; et, everted tooth; f, frontal; f pr, frontal process; fs, festoon; gr, groove; le, lateral eminence; lr, lateral ridge; m, maxilla; m1, 12, maxillary tooth 1, 12; m pr, maxillary process; n, nasal; pm, premaxilla; pm1, premaxillary tooth 1; pm pr, premaxillary process; q, quadrate; qj, quadratojugal. Scale bars, 20 cm in (A), (C), and (E); 10 cm in (B), (D), and (F); 5 cm in (G); and 1 cm in (H).

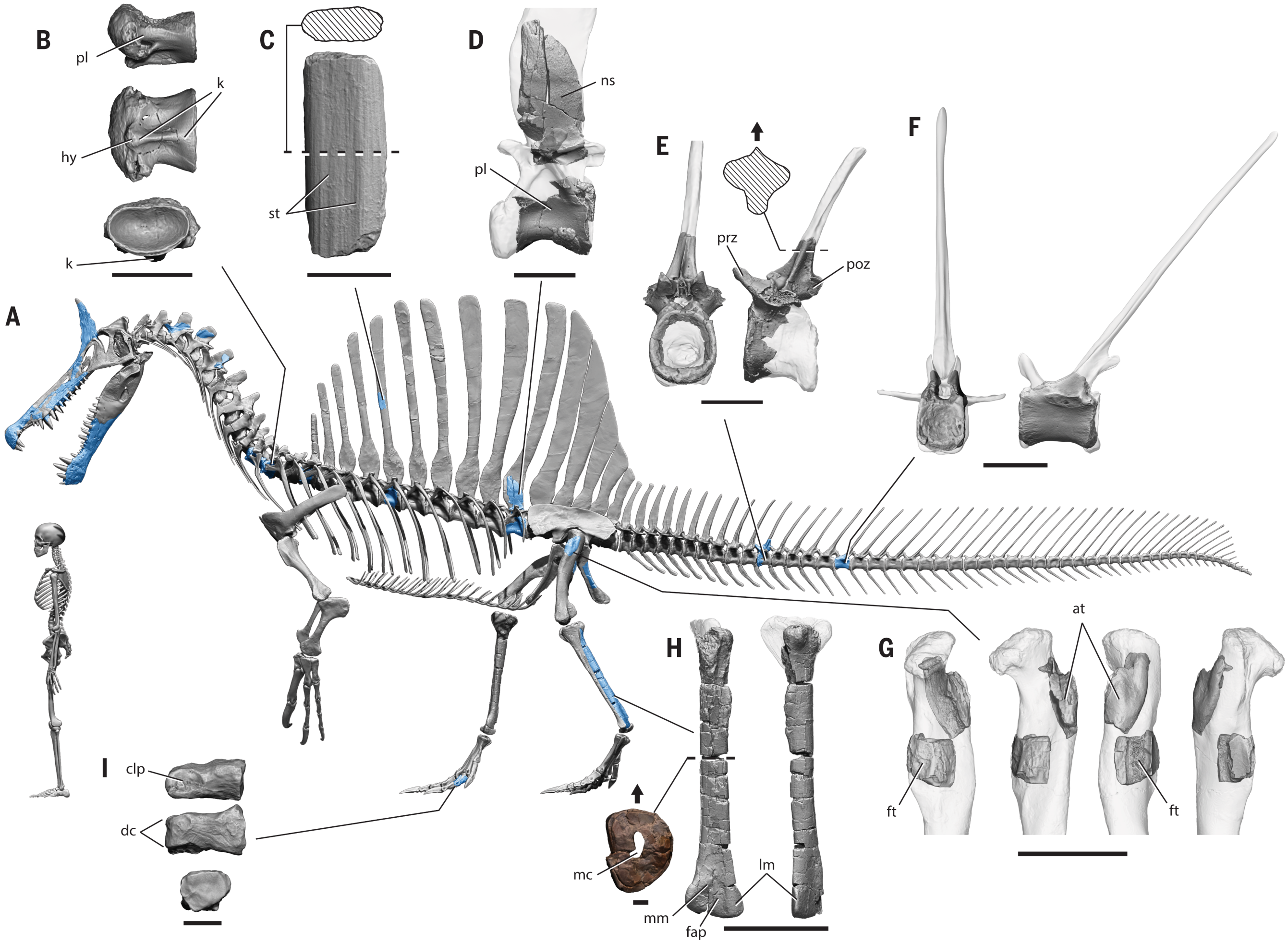

Fig. 3. Preserved postcranial bones of *S. mirabilis* sp. nov. (**A**) Composite skeletal silhouette showing preserved bones (blue) of *S. mirabilis* with skeletal length of ~8 m scaled to the size of the subadult holotype (MNBH JEN1). Missing bone is based on *S. aegyptiacus* ([3]). (**B**) First dorsal centrum in lateral, ventral, and posterior views (MNBH IGU11). (**C**) Dorsal neural spine section in lateral view with cross section (MNBH JEN2). (**D**) Partial posterior dorsal vertebra in left lateral view (MNBH JEN2). (**E**) Partial anterior caudal vertebra in anterior and left lateral views with cross section (MNBH JEN9). (**F**) Midcaudal centrum in anterior and left lateral views (MNBH IGU32). (**G**) Anterior and fourth trochanters of the left femur in lateral, medial, anterior, and posterior views (MNBH JEN2). (**H**) Left tibia in anterior, lateral, and midshaft cross-sectional views (arrow, anterior; MNBH JEN2). (**I**) Pedal digit II-1 phalanx in lateral, dorsal, and proximal views (MNBH IGU40). at, anterior trochanter; clp, collateral ligament pit; dc, distal condyle; fap, fossa for the ascending process of the astragalus; ft, fourth trochanter; hy, hypapophysis; k, keel; lm, lateral malleolus; mc, medullary cavity; mm, medial malleolus; ns, neural spine; pl, pleurocoel; poz, postzygapophysis; prz, prezygapophysis; st, striation. Human skeleton height, 170 cm. Scale bars, 5 cm in (B), (C), and (F); 10 cm in (D), (E), (G), and (H); and 3 cm in (I).

Nearly 70 years later, we rediscovered Akarazeras and, venturing farther into the sand sea, found a fossiliferous area called Jenguebi comparable in fossil preservation and faunal significance to Gadoufaoua (Fig. 1A). In addition to *S. mirabilis*, finds included a partial skull and skeleton of *Carcharodontosaurus* sp., new titanosaurian and rebbachisaurid sauropods, and the skull of a large polypterid fish (Fig. 1, B and C).

Riparian habitat

Multiple specimens of *S. mirabilis* were found in fluvial sediments near rebbachisaurid and titanosaurian sauropod skeletons indicative of a riparian habitat (Fig. 1, B and C). The proximity of the vertebrate fauna on site and within section and the degree of association and articulation of the skeletal remains leave no doubt about their coexistence in the same habitat (see the “Local stratigraphy and associated fauna” section in the supplementary materials). Specimens of *S. mirabilis* from the Jenguebi and Iguidi fossil areas (Fig. 1A) in the inland Iullemmeden Basin ([13]) were ~500 to 1000 km distant, respectively, from the closest marine margin in the Benue Trough during Early to Middle Cenomanian time [~100 to 95 Mya ([21])]. Later, toward the close of the Cenomanian and dawn of the Turonian (~ 94.5 Mya), the sea level rose abruptly, flooding low-lying continental areas to create the Trans-Saharan seaway (*16*, *22*). The inland setting during Early to Middle Cenomanian time suggests that *S. mirabilis* was a wading ambush piscivore (*3*, *5*). Given its detailed resemblance to contemporary *S. aegyptiacus* of northern Africa, it is unlikely the latter was a diving pursuit predator in marginal marine waters (*7*–*9*).

Discussion

Skull

The skull of *S. mirabilis* closely resembles that of its northern African relative *S. aegyptiacus* (Fig. 2, A and C). The diastema in the upper tooth row of *S. mirabilis* is broad with fossae accommodating three large dentary teeth, and the jaw margins are festooned to accommodate interdigitating crowns as in *S. aegyptiacus* and long-snouted crocodylians (Fig. 2, E and G). The snout end has a slightly different shape in profile, the premaxilla arching slightly above the rest of the snout and the expanded dentary end having more of a subquadrate than oval shape. The posterior half of the snout of *S. mirabilis* also has a lower profile toward the orbit with parallel rather than diverging dorsal and ventral margins (Fig. 2, A and C). Although the tooth count of *S. mirabilis* is similar to that of *S. aegyptiacus*, spacing between teeth in the posterior half of the snout is greater (see the "Skeletal reconstruction" section in the supplementary materials).

The scimitar-shaped nasal crest, the signature cranial feature of *S. mirabilis*, is gently upturned to an apex over the orbit and has a longitudinal thickening, or lateral eminence, along its length between thinning anterior and posterior margins (Fig. 2, A and B). It lacks the raised, vertical fluting present in the midsection of the nasal crest in *S. aegyptiacus* (Fig. 2D). The fused nasals that form the body of the crest are lapped laterally by a subtriangular process of the prefrontal (Fig. 2B, magnified view) as in *S. aegyptiacus*. The crest in *Spinosaurus*, thus, is accurately described as a nasal-prefrontal composite rather than fused nasals alone as occurs in baryonychine spinosaurids (*23*, *24*).

Paired vessels provide vascular supply to the dense bone of the crest in *S. mirabilis*, ramifying at midlength with very few canals opening externally (Fig. 2F). Unlike avian cranial casques, which are very porous and pneumatized (*25*, *26*), spinosaurid crests are composed of solid bone. Fine longitudinal, and in some areas crisscrossing, striations and deeper longitudinal grooves are present over sections of the crest (Fig. 2F). These surface details suggest that the bony crest in *S. mirabilis* was enveloped and likely extended by a keratinous sheath with its own vascular supply (Fig. 2B), based on extant avian analogs such as *Casuarius*, *Macrocephalon*, and *Numida* (Fig. 2H and supplementary materials) (*26*–*28*).

Asymmetry unrelated to taphonomic factors is present in all three crests of *S. mirabilis* and is most pronounced in the laterally deflected crest of the subadult holotype (MNBH JEN1; see the supplementary materials and fig. S7). Side-to-side asymmetry is also present in the crest flutings of *S. aegyptiacus* (Fig. 2D) and is common condition in cassowary casques [*Casuarius* (*28*)]. With only three examples from disparately aged individuals, it is not possible to assess crest dimorphism in *S. mirabilis*. The holotype and largest individual known has by far the most robust crest.

In nonavian theropods, the most common and sometimes flamboyant design of cranial ornamentation involves parasagittal, often pneumatized, crests along the dorsolateral edges of the snout (paired nasal, lacrimal, and prefrontal) as in *Dilophosaurus* (*29*) and *Cryolophosaurus* (*30*). A second design involves sagittal solid ornaments generated by fusion of paired bones as in the nasal crests in *Proceratosaurus* (*31*) and *Ceratosaurus* (*32*) or the cone-shaped frontal horn in *Majungasaurus* (*33*). This sagittal design characterizes spinosaurids (fused nasals) with minor contribution to each side by the prefrontal in *Spinosaurus* (Fig. 2B). Rarely in nonavian theropods has cranial ornamentation involved a combination of parasagittal and sagittal designs as in *Monolophosaurus* (*34*) and *Citipati* (*35*) or the elaboration of bilateral, cone-shaped horns on the skull roof (frontals) as in *Carnotaurus* (*36*).

The many examples of cranial ornamentation cited above in predatory (or omnivorous) nonavian theropods characterize individual species or select genera rather than all members of their more inclusive clades. A fused nasal or nasal-prefrontal crest, by contrast, is present in all spinosaurids in which that portion of the skull is known. The crest in *S. mirabilis* is relatively taller than in any other nonavian dinosaur, exceeding the height of the rest of the cranium at the orbits (Fig. 2A). If *S. mirabilis* grew to the size of *S. aegyptiacus*, then the bony cranial crest scaled isometrically would measure ~40 cm in length and perhaps >50 cm in life with a keratinous sheath.

Equally widespread among spinosaurids are heightened trunk and caudal sails, the primary function of which was likely visual display. Visual signaling (*3*, *5*, *37*, *38*) thus seems to have been enhanced in spinosaurids, possibly a consequence of their habitual presence in narrow shoreline habitats with less obstructed sightlines (*39*). The prominent sagittal cranial crest in *S. mirabilis* adds to the evidence that visual display, rather than aquatic propulsion (*6*), was the primary function of the heightened trunk and caudal sails (*3*, *5*).

Skeleton

Several vertebrae of *S. mirabilis* bear derived hallmarks of the axial column of *S. aegyptiacus*, including the advanced cervicalization and broad proportions of the first dorsal centrum, the presence of a trunk sail of unknown shape with striated neural spines, anterior caudal neural spines with a cruciate cross section, and short midcaudal centra with subquadrate articular faces (Fig. 3, A to F). Portions of the proximal end of the femur, including the narrow anterior and hypertrophied fourth trochanters, and a pedal phalanx with a low profile and reduced distal condyles are also similar to those in *S. aegyptiacus* (Fig. 3, G and I). Differences include relatively larger anterior dorsal pleurocoels and a proportionately longer tibia with an open, albeit reduced, medullary cavity (Fig. 3, A, B, and H, and supplementary materials).

We estimate the subadult skeletal length of the holotype at ~8 m, with adult length in *S. mirabilis* uncertain given the immaturity of all known individuals (Fig. 3A and supplementary materials). As in *S. aegyptiacus*, the holotype and most referred specimens are also immature. Cranial crest fusion occurs early in growth in spinosaurids (an unfused nasal has never been found), with later closure of other cranial and axial sutures (e.g., interpremaxillary and neural arch–centrum) with maturity. The holotype of *S. mirabilis* is ~15% smaller than the neotype subadult skeleton of *S. aegyptiacus*, or ~61% the size of the largest known specimen of *S. aegyptiacus* (see the supplementary materials and table S2).

Predatory mode

Long-snouted shoreline piscivores such as gharials among crocodylians and herons among waterbirds have been cited as modern analogs for spinosaurids (*1*–*3*, *5*, *40*), although these have starkly different postures (quadrupedal versus bipedal) and feeding modes (toothed lateral versus toothless vertical strike). Likewise, parallels have been drawn to the toothy snout end (terminal rosette and tooth-filled diastema) of the pike conger eel [*Muraenesox* (*41*)], although its body design (no head-neck mobility) and feeding setting (submerged bottom feeding in darkness) could not be more different. However, measurements of skull form with no other consideration (*5*, *42*) have not been able to clearly distinguish spinosaurids from other carnivorous archosaurs or to link them decisively with heron-like shoreline predators.

Although drawing attention by functional analogy to aspects of spinosaurid cranial anatomy (e.g., snout length, terminal rosette, and crest) can be informative, their presumed wading predatory mode (long snout, neck, and hind legs) should ally them with extant bipedal wading predators such as herons in a quantitative analysis. To test for the existence of such a predatory mode, we conducted a principal component analysis (PCA) of seven measures that capture cranial dimensions and neck and hind limb length in the two best known spinosaurids, *S. tenerensis* and *S. aegyptiacus*, and 41 additional extinct and extant carnivorous archosaurs (Fig. 4, fig. S18, and table S6).

Five predatory modes cluster discretely using minimum convex hulls in a plot of PC2 and PC3 (Fig. 4). PC1 captures overall size variation and accounts for most of the variance (91%) given body size range in sampled taxa across four orders of magnitude (see the supplementary materials and fig. S18). Spinosaurids plot far from short-necked, short-limbed crocodylians and all other nonavian terrestrial and aerial avian predators and between semiaquatic long-necked, long-limbed birds such as herons (Fig. 4, number 28), which capture prey while wading in shallow water (*43*, *44*), and the least modified of aquatic divers such as darters (Fig. 4, number 38). These two subgroups, waders and divers, hunt for prey in distinctive, nonoverlapping modes, although both avian subgroups share a relatively long neck with spinosaurids (Fig. 4, variable 1).

Divers have proportionately longer skulls than either avian waders or spinosaurids (Fig. 4, variable 3). These three aquaphilic groups differ in relative hind limb length, which is shortest in divers and longest in waders (Fig. 4, variable 2). For avian waders, long hind limbs allow prey capture in water depths up to ~50 cm (*43*, *44*), which is slightly less than the hip height (~60 cm) of a wading adult blue heron (Fig. 4, number 28). Spinosaurids are positioned just outside of the wading bird polygon, with proportionately shorter hind limbs due to their much greater body mass. Spinosaurid hind limbs, of course, have much greater absolute length than any avian wader, facilitating fish capture in water more than three times as deep (>150 cm) (*3*). Spinosaurid skeletal form is therefore the most consistent with predation of fish through wading in shallow waters.

Spinosaurid evolution

We augment a previous spinosauroid dataset (*3*) by one-third, incorporating new and recently introduced character data (*24*, *45*–*47*). In a maximum parsimony analysis, a basal baryonychine-spinosaurine split is resolved, the latter clade increasingly diversified by recent finds including a new Brazilian spinosaurine (Fig. 5B, Materials and methods, and supplementary materials). We recognize three distinct phases in spinosaurid evolution (Fig. 5B, phases I to III).

The first 35-million-year (Myr) phase (Fig. 5B, phase I and node 1), comprising approximately half of the spinosaurid fossil record, is currently known only from isolated teeth in Jurassic and lowermost Cretaceous

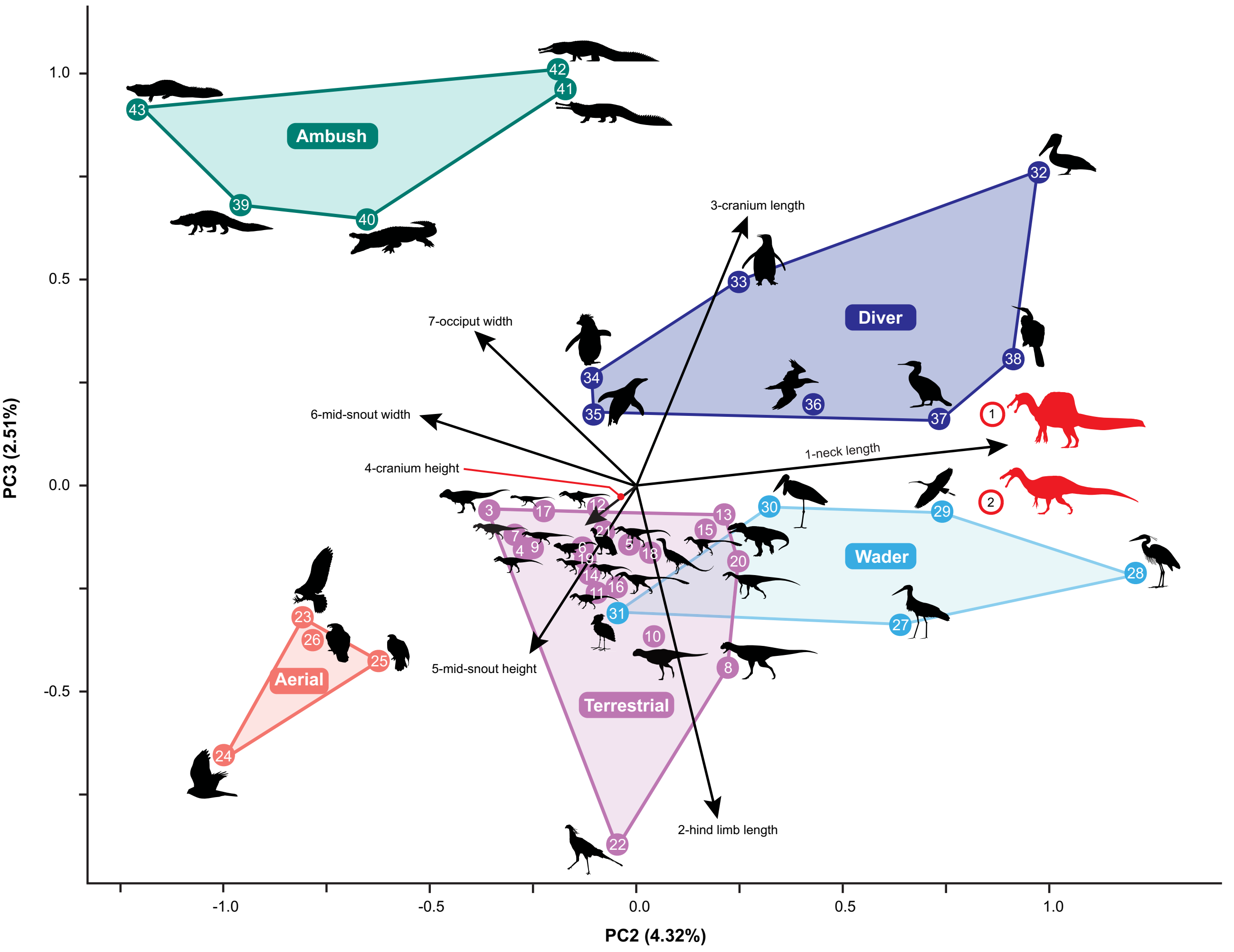

Fig. 4. Plot of predatory modes among archosaurs distinguishes spinosaurids. PCA (PC2 and PC3) of snout, neck, and hind limb dimensions (seven variables) with minimum convex hulls identifying five predatory modes (ambush, aerial, terrestrial, wader, and diver) in 43 extant and extinct carnivorous archosaurs including two spinosaurids (1 and 2), 18 other nonavian dinosaurs (3 to 20), two ground-based avian scavengers (21 and 22), four aerial birds of prey (23 to 26), six semiaquatic wading birds (27 to 32), six aquatic diving birds (33 to 38), and five crocodylians (39 to 43). Spinosaurids (*Suchomimus* and *Spinosaurus*) plot between avian waders and divers far from other nonavian dinosaurs and crocodylians. Arrows identify vectors for the loadings of seven variables: 1, cranium length; 2, cranium height; 3, occiput width; 4, midsnout height; 5, midsnout width; 6, neck length; and 7, hind limb length (for species and measurements, see the Materials and methods and the supplementary materials).

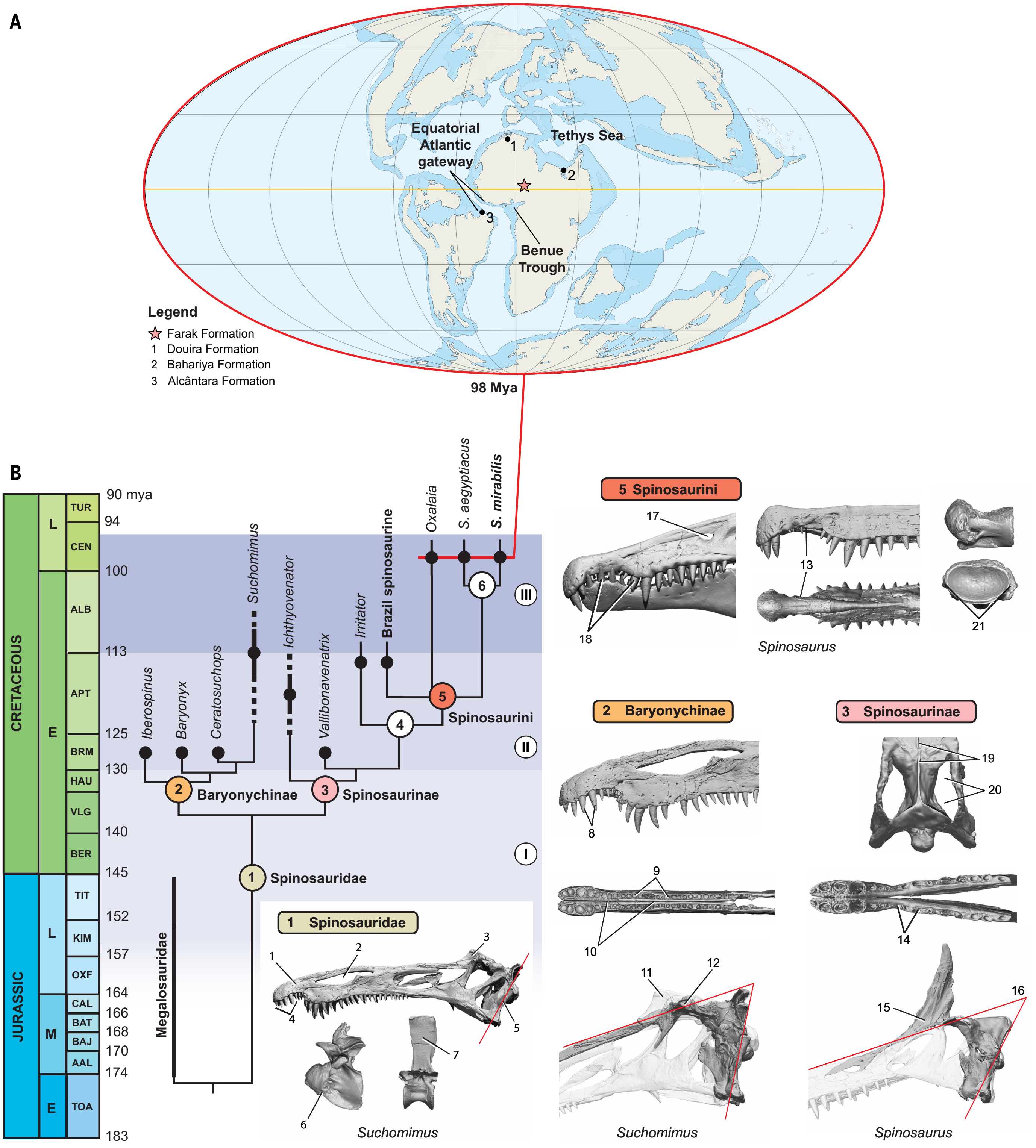

Fig. 5. Three-phase model for spinosaurid evolution. (**A**) Early-Middle Cenomanian paleobiogeographic map (~98 Mya) showing the formations and localities yielding the last known spinosaurines. (**B**) Time-calibrated phylogeny of spinosaurids highlighting 21 key features that arose during three successive evolutionary phases (I, II, and III). Dots sometimes extended by thick lines indicate estimated temporal age. 1, elongate snout; 2, partial retraction of external naris; 3, fused median nasal crest; 4, terminal rosette; 5, occiput-basipterygoid in a single plane; 6, cervical-like anterior dorsal vertebrae (D2 shown); 7, elevated dorsal-sacral-caudal neural spines; 8, elevated premaxillary dentition; 9, smaller, more numerous dentary teeth; 10, long dentary symphysis; 11, stout, cruciate nasal crest; 12, swollen lacrimal-postorbital brow; 13, diastema lengthening and transverse constriction; 14, spaced teeth in maxillary and dentary; 15, elevated sagittal nasal crest; 16, snout-occiput angle decreased to ~40°; 17, external nares small, more retracted; 18, interdigitating teeth with festooned alveolar margins; 19, frontal sagittal crest; 20, supratemporal fossa lengthened, removed from frontal; and 21, cervicodorsal centra wider than deep. Paleogeographic map is based on (*71*) with modifications after recent local paleogeographic research (*16*,*72*). The Brazil spinosaurine (UFMA ITA1, where UFMA is Universidade Federal do Maranhão, São Luís, Brazil) is based on a partial skeleton under study.

horizons (48). Nonetheless, the array of shared piscivorous features of all later spinosaurids arose during this initial phase, when spinosaurids evidently remained relatively uncommon or in habitats less suitable to preservation. These features include an elongate snout with some narial retraction, a terminal rosette of premaxillary teeth, and a median nasal crest (Fig. 5B, features 1 to 4). Other distinctive features include a very large prefrontal that forms the anterior roof of the orbit; an extremely deep, short braincase; and a reduced fossa for the olfactory bulb. The vertebral column is distinctive in the lengthening of the neck; cervicalization of the anterior dorsal vertebrae for enhanced dorsoventral flexion; and at least moderate heightening of the dorsal, sacral, and caudal neural spines (Fig. 5B, features 6 and 7). Increased forelimb strength for prey manipulation is shown by the strong deltopectoral crest, hypertrophied olecranon, and flaring forearm epicondyles in all known spinosaurids (Fig. 3A).

This array of trophic, structural, and sociosexual adaptations have masked major differences in skull and dental form that arose between baryonychines and spinosaurines during this poorly documented phase. In baryonychines, the dentary teeth are smaller and more numerous than the maxillary teeth and are anchored in dentary rami that lie immediately adjacent to one another in the midline (Fig. 5B, node 2 and features 9 and 10). This very narrow, gharial-like jaw occludes within a very narrow snout composed of maxillae that are joined in rugose suture for half their length (19, 24), unlike spinosaurines or any other nonavian dinosaurs. In baryonychines, both the premaxillary rosette and the opposing large dentary teeth that insert within the rosette are set above the principal tooth rows (Fig. 5B, feature 8). In addition, the orbital margin is greatly thickened by swellings of the lacrimal and postorbital (Fig. 5B, feature 12) (3, 24), closely resembling the condition in carcharodontosaurids (17).

In spinosaurines, by contrast, the dentary symphysis is limited to the ramus underlying the premaxillary rosette. More posteriorly, the dentary rami diverge from the midline to engage a broader posterior snout with fewer spaced teeth (Fig. 5B, node 3 and feature 14). The frontal thickens medially toward the midline, not laterally toward a thickened orbit margin, and fuses with its opposite to form a sagittal crest, joining the midline crest formed by fused nasals anteriorly and parietals posteriorly (Fig. 5B, feature 19). The occiput is tilted backward, narrowing the angle to the snout and lengthening the parietal and supratemporal fossa, the latter no longer extending onto the frontal (Fig. 5B, features 16 and 20). The nasal crest is further developed in the sagittal plane with reduction of the prominent lateral ridge that in baryonychines rises to the apex of the crest (Fig. 5B, feature 15).

During a second 20-Myr phase in the Early Cretaceous (Fig. 5B, phase II), spinosaurids diversified in habitats bordering the Tethys Sea, where they were the largest and most common predators. This holds to the south on Gondwana for the African baryonychine *Suchomimus* (3, 19) and Brazilian spinosaurine *Irritator* (45, 49–51) and to the north on Laurasia, with increasingly diverse baryonychines in Europe (23, 24, 52–54) and the spinosaurine *Ichthyovenator* in southern Asia (55). Evidence for both baryonychines and spinosaurines in the same fauna has also come to light in Iberia (56, 57) and possibly also in Thailand (58).

With less head weight than most large-bodied bipedal theropods, spinosaurids emphasized the reach and power of the forelimb for prey capture and manipulation beyond that seen in any other theropod group. The 1.4-m-long forelimb in *Suchomimus* is characterized by exceptionally stout shafts, hypertrophied flexor and extensor processes, and unguals measuring up to 32 cm along the outer curve. Although specialized jaws and small-sized posterior teeth in baryonychines suggest piscivory, the remainder of the baryonychine skeleton is that of a “generalist predator” (59). *Suchomimus,* possibly the last surviving baryonychine (Fig. 5B), dominated the large predator niche on land in central Africa while competing for fish along riverways with the 11-m-long crocodyliform *Sarcosuchus* (60). The best known spinosaurine of this phase, *Irritator* (45, 49–51) from the adjacent Araripe Basin of Brazil (61), has further piscivorous adaptations, including teeth with increased spacing and a more retracted external naris, while remaining the largest predator of its day.

A final 15-Myr phase (Fig. 5B, phase III) began during the latest Aptian or early Albian with a subset of spinosaurines here recognized as Spinosaurini. They survived only on the southern margin of the Tethys Sea on South America and Africa, areas that by 110 Mya were separated by a deep water straight (>500 m depth) called the Equatorial Atlantic gateway [(62); Fig. 5A]. The earliest representative is a yet unnamed late Aptian or early Albian genus from the Parnaíba Basin of Brazil (Fig. 5B). By the Early to Middle Cenomanian (~98 Mya), spinosaurines reached maximum body size as specialized fish eaters with a hypertrophied trunk sail (Fig. 3C), ceding inland predation to equal-sized carcharodontosaurids (17). *Oxalaia*, discovered on a coastal island in Brazil, is known from a snout end and isolated teeth and bones (63, 64). Across northern Africa, a better fossil record includes abundant teeth and skeletal remains provisionally referred to *S. aegyptiacus* (1–3, 8, 65, 66).

Increased piscivorous specializations include a lengthened upper diastema that accommodates three large dentary teeth (67) and the interdigitation of more posterior upper and lower tooth rows (Fig. 2E), as in long-snouted crocodilians (Fig. 2F), fish-eating pterosaurs (68), and secondarily aquatic tetrapods such as ichthyosaurs and plesiosaurs (4). The neck appears to have a tighter “S” shape with enhanced ventroflexion at the neck-trunk junction, and the manus has gently recurved unguals for raking (Fig. 5B, features 13, 18, and 21). Also present are tall trunk neural spines indicative of a hypertrophied sail (Fig. 3C).

Just before the close of the Cenomanian, a fast-paced global transgression (~94.5 Mya) flooded low-lying continental areas, creating a shallow seaway spanning the Sahara north to south (16, 21). The abrupt sea-level change was synchronous with global temperature flux and marked marine biotic turnover (22) that on land appears to have resulted in the extinction of these large-bodied piscivores. This discovery of *S. mirabilis* in an inland basin in the Sahara establishes a still poorly known inland presence for spinosaurines near the end of their reign.

Materials and methods

Structure from motion photogrammetry

Photogrammetry was conducted on cranial and postcranial bones of *S. mirabilis* and other spinosaurid remains to obtain three-dimensional (3D) digital meshes using a Fujifilm XT-4 camera and AgiSoft Metashape to compose the cranial and postcranial skeletal reconstructions.

Computed tomographic scanning

Computed tomography (CT) scans were taken at the University of Chicago Hospital (RRID:SCR_018372; N. Gruszauskas) using a Philips Brilliance iCT 256-slice multidetector scanner and at the University of Chicago PaleoCT facility (RRID:SCR_024763) using a Waygate Phoenix V|tomex|s microCT scanner.

PCA

We took seven linear measurements (cranium length, cranium height, occiput width, midsnout height, midsnout width, neck length, and hind limb length, all in centimeters) that capture key aspects of head and body form critical to predatory mode in 43 extant and extinct carnivorous archosaurs (Fig. 4, supplementary materials, and table S3). We plotted the two spinosaurids (spinosaurine *S. aegyptiacus* and baryonychine *S. tenerensis*) as unknown for the purposes of the analysis and group taxa into five predatory modes: ambush (semiaquatic), terrestrial, aerial, wader (semiaquatic), and diver (aquatic).

The sampled taxa range in body mass across four orders of magnitude (*Accipiter nisus*, ~0.2 kg; *Tyrannosaurus rex*, ~8000 to 9000 kg). To address skewness when considering such profound scaling, we

$\log_{10}$-transformed the dataset to linearize the relationship between variables. Then, we normalized the measurements by standardizing each variable to unit variance (i.e., mean of zero, SD of 1) to ensure that individual morphometric variables did not dominate the others. We performed PCA using R version 4.4.1 [setting scale=TRUE in the command prcomp()].

The seven morphometric variables have a negative loading of –0.367 to –0.392 on the first principal component (see the "Principal component analysis" section in the supplementary materials and table S4). This consistent pattern across the morphometric variables means that PC1 represents size, as expected, and captures most of the variation in the dataset (91.06%). Most of the rest of the variation involves cranium, neck, and hind limb proportions.

Spinosaurids plot between long and narrow snouted, long-necked semiaquatic waders and aquatic divers well separated from other (terrestrial) nonavian dinosaurs and carrion-feeding birds; short-necked, short-limbed semiaquatic crocodylians; and aerial raptors (Fig. 4). The darter (*Anhinga melanogaster*), a shallow diving suliform, plots close to spinosaurids, given its similar proportions (Fig. 4, number 38). Also known as snakebirds for their elongate necks, darters hunt at the surface with head intermittently above the water, plunge diving with rapid neck extension to impale prey on their elongate, pointed beaks (*69*, *70*). Like cormorants and grebes, the darter is a volant, foot-propelled (webbed) diver that has retained a longer skull and hind limb and more symmetrical pes for perching than other more specialized nonvolant divers such as penguins. With their large body size, spinosaurids do not need the proportionately elongate hind limbs of avian waders to hunt effectively in shallow water, plotting just outside their minimum convex hull (Fig. 4).

The long-necked but broad-snouted semiaquatic shoe-billed stork (*Balaeniceps rex*) clustered with terrestrial theropods including *T. rex* (Fig. 4, number 31). Its broad snout of modest length is very unusual among extant avians that hunt as waders in shallow water environments. At prey capture, the shoe-billed stork often captures vegetation along with its prey, unlike the more targeted prey capture of longer-snouted waders.

Phylogenetic analysis and definitions

We performed maximum parsimony phylogenetic analysis (TNT v1.6) of a data matrix composed of 159 characters statements scored in six outgroup species and 16 spinosaurid taxa or described specimens. Forty-one new character statements were added to a previous spinosaurid matrix (*3*), representing ~25% of the data. A total data analysis resulted in 42 minimum-length trees with the new species nested among derived spinosaurines. After a posteriori pruning of four poorly known unstable taxa and specimens identified with the iterPCR subroutine, the analysis yielded a single minimum-length tree showing the divergence of spinosaurids into baryonychine and spinosaurine subclades with increasing resolution (Fig. 5B). Phylogenetic definitions of spinosauroid taxa are summarized with recognition of Spinosaurini Stromer 1915 for the final suite of transatlantic spinosaurids (for decay and Bayesian analyses, see the "Phylogenetic definitions and analysis" section in the supplementary materials).

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ACKNOWLEDGMENTS

We thank O. Zant for comments on the manuscript, MorphoSource for archiving CT scans, and the Niger Republic for access to the field and for loan of fossil material to the University of Chicago. This study represents the views of the authors; any opinions, findings, or conclusions are not those of the US Federal Government. **Funding:** This work was supported by an anonymous gift to the University of Chicago to P.C.S., Marie Sklodowska Curie Actions Grant EvoSaurAf 101068861 of the European Commission to D.V, and a Santander-UNED FPI predoctoral grant to M.C.R. **Author contributions:** Conceptualization: P.C.S, D.V., E.J.-R., E.T.S.; Data curation: D.V., P.C.S., E.J.-R.; Fossil curation: T.M.K. and E.C.F.; Funding proposals: P.C.S., D.V., M.C.R., L.L.B.; Investigation – field work: P.C.S., D.V., N.S.F., M.C.R., S.L.B., B.A., E.C.F., R.A.S.L., A.V.D.-P., A.S., F.G.-L., A.L., A.Ga., C.V.B., V.R., R.V., F.B., A.Gr., G.K.-B., J.R.; Investigation – fossils: P.C.S., D.V., T.M.K., J.C.M., R.M.L.; Investigation – recent specimens: S.L.B. and T.L.G.; PCA analysis: E.J.-R. P.C.S, E.T.S.; Phylogenetic analysis: D.V.; Visualization: P.C.S., D.V., L.L.B., M.C.R, T.M.K., E.C.F.; Writing – original draft: P.C.S.; Writing – review & editing: D.V., N.P.M., E.T.S, A.S.L.R., S.L.B., T.L.G., D.B.D., R.A.S.L., A.V.D.-P., V.R., C.V.B., R.M.L, J.C.M., J.R. **Competing interests:** The authors declare no competing interests. **Data, code, and materials availability:** All reconstructions and data supporting the findings in this study are available within the main text or the supplementary materials. CT scans and 3D models are available on MorphoSource under project ID 000749095 (https://www.morphosource.org/projects/000749095?locale=en).

SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.adx5486
Supplementary Text; Figs. S1 to S22; Tables S1 to S10; References (*73*–*100*); Data S1 to S3; MDAR Reproducibility Checklist

Submitted 18 March 2025; resubmitted 1 July 2025; accepted 21 January 2026
10.1126/science.adx5486

Scimitar-crested *Spinosaurus* species from the Sahara caps stepwise spinosaurid radiation

Paul C. Sereno, Daniel Vidal, Nathan P. Myhrvold, Evan Johnson-Ransom, María Ciudad Real, Stephanie L. Baumgart, Noelia Sánchez Fontela, Todd L. Green, Evan T. Saitta, Boubé Adamou, Lauren L. Bop, Tyler M. Keillor, Erin C. Fitzgerald, Didier B. Dutheil, Robert A. S. Laroche, Alexandre V. Demers-Potvin, Álvaro Simarro, Francesc Gascó-Lluna, Ana Lázaro, Arturo Gamonal, Charles V. Beightol, Vincent Reneleau, Rachel Vautrin, Filippo Bertozzo, Alejandro Granados, Grace Kinney-Broderick, Jordan C. Mallon, Rafael M. Lindoso, and Jahandar Ramezani

Science **391** (6787), eadx5486. DOI: 10.1126/science.adx5486

Editor’s summary

Recent descriptions of and debates about the massive, fish-eating dinosaur *Spinosaurus* have brought this striking predator to the forefront of the dinosaur pantheon. Its huge size and distinctive morphology have stimulated much debate about the degree to which it lived an aquatic lifestyle. Sereno *et al*. describe a crested fossil *Spinosaurus* found in northern Africa as a new species. The researchers argue that this group of dinosaurs underwent three phases of evolution with increasing aquatic adaptations and existence in habitats around the Tethys Sea. —Sacha Vignieri

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