

Tail-propelled aquatic locomotion in a theropod dinosaur

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Intensive research on non-avian dinosaurs in recent decades strongly suggests that these animals were restricted to terrestrial environments¹. Historical views proposing that some groups, such as sauropods and hadrosaurs, lived in aquatic environments^{2,3} were abandoned decades ago^{4,5,6}. Recently, however, it has been argued that at least some spinosaurids, an unusual group of large-bodied Cretaceous theropods, were semi-aquatic^{7,8}, but this idea has been challenged on anatomical, biomechanical, and taphonomic grounds and remains controversial^{9,10,11}. Here we present the first unambiguous evidence for an aquatic propulsive structure in a dinosaur, the giant theropod *Spinosaurus aegyptiacus*^{7,12}. This dinosaur has a tail with an unexpected and unique shape consisting of extremely tall neural spines and elongate chevrons forming a large, flexible, fin-like organ capable of extensive lateral excursion. Using a robotic flapping apparatus to measure undulatory forces in physical tail models, we show that the tail shape of *Spinosaurus* produces greater thrust and efficiency in water than the tail shapes of terrestrial dinosaurs, comparable to that of extant aquatic vertebrates that use vertically expanded tails to generate forward propulsion while swimming. This conclusion is consistent with a suite of adaptations for an aquatic lifestyle and a piscivorous diet in *Spinosaurus*^{7,13,14}. Although developed to a lesser degree, aquatic adaptations are also found in other spinosaurids^{15,16}, a clade with a near global distribution and a stratigraphic range of more than 50 million years¹⁴, documenting a significant invasion of aquatic environments by dinosaurs.

Detailed anatomical and functional studies, combined with abundant trackways, all point to a strictly terrestrial ecology for dinosaurs¹, with one clade, Maniraptora, taking to the air¹⁷. Dinosaurs are not currently thought to have invaded aquatic environments following the abandonment, several decades ago^{5,6}, of century-old ideas of semi-aquatic habits in sauropods and hadrosaurs^{2,3}. Recently, potential semi-aquatic lifestyles have been hypothesised for a small number of dinosaurs^{18,19}. However, the only group of dinosaurs for which multiple plausible lines of evidence indicate aquatic adaptations are the spinosaurids, large-bodied theropods interpreted as near shore waders that fed on fish along the margins of, rather than within, water bodies^{10,15,20}.

A recent reappraisal of the largest known spinosaurid, *Spinosaurus aegyptiacus*, identified a series of adaptations consistent with a semi-aquatic lifestyle, including reduced hindlimbs, wide feet with large, flat unguals, long bones with a highly reduced medullary cavity, and a suite of cranial features such as retracted nares, interlocking conical teeth, and a rostromandibular integumentary sensory system⁷. This interpretation has been challenged on the basis of taphonomy⁸, biomechanical modeling¹⁰, and anatomical concerns⁸. Locomotion in water is a major point of contention^{10,11}, because no unambiguous evidence for a plausible mode of propulsion has been presented. Furthermore, our understanding of the anatomy and ecology of this highly derived theropod has been hampered by the fact that only one associated *Spinosaurus* skeleton exists, with all other associated remains having been destroyed in World War II⁷. The posterior portion of the skeleton, in particular the caudal vertebral series, which has the potential to shed light on likely adaptations for aquatic locomotion, has, until recently, been poorly understood¹². Consequently, the tail anatomy and function of *Spinosaurus* has been reconstructed on the basis of highly incomplete remains and spurious comparisons with other similar-sized theropods.

Here we describe a nearly complete, partially articulated tail of a subadult individual of *Spinosaurus aegyptiacus* (FSAC-KK 11888) from the Cretaceous Kem Kem beds of south-eastern Morocco (Figs. 1, 2, Extended Data Figs. 1–4, Supplementary information Part 1, Supplementary Information Video 1). The skeleton represents the most complete dinosaur known from the Kem Kem^{21,22} and the most complete skeleton of a Cretaceous theropod from mainland Africa (Supplementary Information Part 2). As we show here, the tail forms part of the neotype of *S. aegyptiacus*⁷ and was found in direct juxtaposition to the remainder of the skeleton (Extended Data Fig. 3). Over 90% of the new material, which confirms that a single subadult individual is preserved at the site, was recovered during field excavations in late 2018 and digitally recorded (Extended Data Figs. 1–4, Supplementary Information Parts 2–5). Several elements compare closely to drawings of *Spinosaurus* fossils destroyed in World War II (Extended Data Fig. 6).

More than 30 near-sequential caudal vertebrae (located within caudal positions 1–41) of FSAC-KK 11888 are preserved, representing approximately 80% of original tail length (Extended Data Figs. 3, 4, Extended Data Table 1). Both proximal and distal elements of the tail are complete and preserved in three dimensions, indicating minimal taphonomic distortion (Fig. 2, Supplementary Information Video 2). At the level of the caudal transition point¹, the centra become proportionally more elongate. In addition, the prezygapophyses no longer overhang the preceding centrum and show a marked decrease in size compared to many theropod dinosaurs¹. The postzygapophyses also decrease in size, leading to a reduced contact with the prezygapophyses, and are completely absent in the distalmost caudal vertebrae (Fig. 2). This again is different from the condition seen in most theropods, where zygapophyses become more elongate and more prominent toward the tail tip¹, restricting flexibility in more distal intervertebral joints.

The neural arches are distinctive elements of the *Spinosaurus* tail. A remarkably complex array of vertebral laminae and fossae is present in the proximal caudal vertebrae, and partly persists in mid-caudal neural arches. The morphology of the neural spines shows considerable variation along the sequence (Figs. 1, 2, Extended Data Table 1): spines of proximal caudals are about three times taller than their centra and are cross-shaped in cross-section from base to mid-height, in mid-caudals the spines become much longer, and in the small distal caudals neural spine length reaches well over seven times the height of the centrum (contra ref.¹¹). The neural spines of mid-distal caudal vertebrae of *Spinosaurus* have a unique cross-section, whereby they are proximo-distally rather than transversely flattened. This is due to hyper-developed spinodiapophyseal laminae and the loss of pre- and postspinal laminae. The chevrons also differ from those of other theropods. Their morphology varies little throughout the caudal series, except for a slight gradual reduction of the haemal canal: distal chevrons are as elongate as the proximal chevrons, but they become slender, paralleling the gradual decrease in size of the centra. Taken together, the elongate neural and haemal arches result in a dramatically, vertically expanded tail shape with extensive lateral surface area (Fig. 1, Extended Data Figs. 3, 4).

The skeletal anatomy of *Spinosaurus* represents a major departure from that of other theropods including the clade within which it is located¹, Tetanurae, which comprises crown group birds and all other stem theropods more closely related to birds than to *Ceratosaurus*¹. A key feature of this group is a stiffened tail in which the degree of overlap in articulation between pre- and postzygapophyses increases along the caudal series, drastically diminishing the range of motion between individual vertebrae¹. This trend in mobility reduction is emphasised in paravians with the appearance of ossified ligaments and/or reduction and fusion of the caudals into a pygostyle¹⁷. By contrast, in *Spinosaurus*, the pre- and postzygapophyses are much further reduced than in other tetanurans and, in the middle and distal portions of the tail, not only do not overlap but almost

disappear (Fig. 2), allowing the caudal region considerable flexibility, especially with regard to lateral movements.

The highly specialised tail morphology in *Spinosaurus* is thus hypothesised to have functioned as a propulsive structure for aquatic locomotion. To test this idea, we evaluated the swimming potential of the *Spinosaurus* tail shape by comparing it to the tails of two terrestrial theropods (*Coelophysis bauri* and *Allosaurus fragilis*), two semi-aquatic tetrapods (the crocodile *Crocodylus niloticus* and the crested newt *Triturus dobrogicus*), and a rectangular control. Two-dimensional tail shapes were cut from 0.93 mm-thick plastic of flexural stiffness $5.8 * 10^{-5} \text{ Nm}^2$. The plastic tails were attached to a robotic controller and actuated in a water flume to provide tail tip amplitudes approximately 40% of tail length during swimming at 0.5 tail lengths/second. This swimming speed and amplitude of motion is similar to that of slow aquatic locomotion in modern tetrapods^{23,24,25}. Measurement of swimming performance was assessed by quantifying mean thrust and efficiency using a six-axis force-torque sensor attached to the shaft driving each tail shape²⁶ (Fig. 3, Methods, Supplementary Information Fig. 4, Supplementary Information Videos 3–5).

Our experimental results show that the *Spinosaurus* tail shape was capable of generating more than eight times the thrust of the other theropod tail shapes and achieved 2.6 times the efficiency (Fig. 3; Supplementary Data File 1). The greatest thrust was achieved by the crested newt tail shape (1.8 times *Spinosaurus*; 14.8 times *Coelophysis*), but the crocodile tail shape achieved greater propulsive efficiency (1.5 times *Spinosaurus*; 4.0 times *Coelophysis*), comparable to the rectangular control (Fig. 3). The lower efficiency recovered in this experiment for *Spinosaurus* (compared to the control with the same surface area) and the crested newt indicates an effect of tail shape on performance. Overall, the vertically expanded tail shape of *Spinosaurus* imparts a substantial positive benefit to aquatic propulsion relative to the long and narrow tails of

terrestrial theropods, supporting the inference that *Spinosaurus* utilised tail propelled swimming. This tail morphology may have also increased lateral stability of the body in the water, reducing the tendency to roll while floating¹⁰.

Contrary to recent suggestions¹⁰ that *Spinosaurus* was confined to wading and the apprehension of prey from around the edges of water bodies, the morphology and function of the tail along with other adaptations for life in water⁷ point to an active, highly specialised aquatic predator that pursued and caught its prey in the water column (Extended Data Fig. 7). The skeletal remains of *Spinosaurus* (Supplementary Information) from the Kem Kem beds – composed of sediments deposited in a major fluvio-deltaic system⁷ that have yielded a diverse vertebrate assemblage²⁷ – provide further insights into the ecology of this dinosaur. The Kem Kem assemblage is highly atypical, containing a rich freshwater fauna dominated by fishes, including lungfish and large to very large sawfish and coelacanths²⁷, a diverse range of crocodyliforms²⁸, and several giant predatory dinosaurs^{7,22}. The seemingly anomalous occurrence in the same deposits of several large-bodied predators, but few terrestrial herbivores, is partially explained by the largely aquatic, likely piscivorous, lifestyle of *Spinosaurus* that considerably expands the morphological and ecological disparity of Kem Kem tetrapods^{7,29}. At the same time, competition with several co-occurring large aquatic predators²⁸ may have driven the evolution of giant size in *Spinosaurus*.

While the unique postcranial adaptations of *Spinosaurus* point towards an entirely novel mode of locomotion in dinosaurs, other spinosaurids share a wide range of derived anatomical features consistent with a partially aquatic, piscivorous mode of life^{7,8,11,14,30}. The exact extent to which an aquatic lifestyle was adopted by these other taxa and how this varied across Spinosauridae remains to be established. However, the near global distribution of spinosaurids, now reported from all continents except North America and Antarctica³⁰, and their substantial temporal range, first

appearing, based on phylogenetic inference, in the Middle, or possibly even Early Jurassic, with a fossil record spanning more than 50 million years (Upper Jurassic-early Upper Cretaceous)¹⁴, all point to a persistent and widespread invasion of aquatic habitats by dinosaurs.

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Supplementary Information is available in the online version of the paper.

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Author Contributions

N.I. led the expeditions and the project. N.I., S.M., C.D.S., M.F., M.A., D.M.M., G.B., S.Z. D.M. and A.A. collected the specimens in the field. N.I., S.M., C.D.S., M.F., J.W., G.V.L. and S.E.P. designed the research. N.I., S.M., C.D.S., M.F., J.W., G.V.L. and S.E.P. designed and performed the experiments. N.I., S.M., C.D.S., M.F., M.A., D.M.M., J.W., G.B., S.Z. D.M., D.M.U., U.J., J.J., A.A., G.V.L., and S.E.P. analysed the data. G.B., M.A., C.D.S., S.E.P., D.M.M., S.M., and D.B. created the figures. D.B. sculpted the life reconstruction. N.I., S.M., C.D.S., M.F., J.W., D.M.U., G.V.L., and S.E.P. wrote the manuscript which was reviewed by all authors.

Conflicts of Interest Declaration

The authors declare no financial or non-financial competing interests. Correspondence and requests for materials should be addressed to N.I. (ibrahini@udmercy.edu).

Data Availability Statement

The authors declare that all data supporting the findings of this study are available within the paper and its Supplementary Information and source data. 3D data are available on SketchFab (flesh model [LINK](#); scanned caudal vertebrae and chevrons [LINK](#)).

Figures

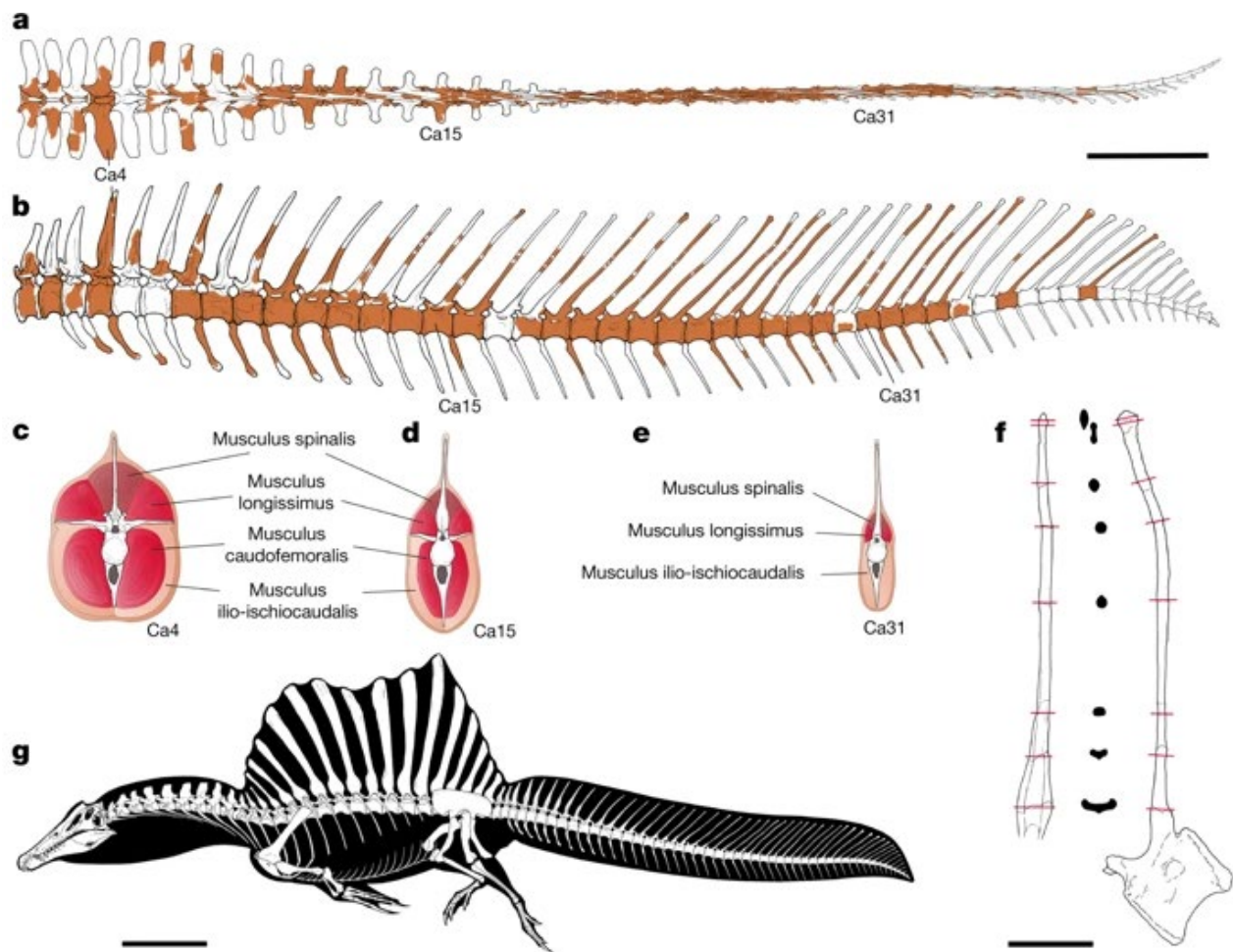


Figure 1 Reconstructed skeleton and caudal series of *Spinosaurus* FSAC-KK 11888. Caudal series (preserved parts in colour) in **a**, dorsal view; **b**, left lateral view; **c–e**, reconstructed sequential cross sections through the tail show proximal/distal changes in the arrangement of major muscles; **f**, sequential cross sections (proximal face pointing upwards) through the neural spine of vertebra Ca23 to show apicobasal changes (see text); **g**, skeletal reconstruction. Abbreviations: Ca, caudal vertebra. Scale bar = 50 cm (a–e), 10 cm (f), 1m (g).

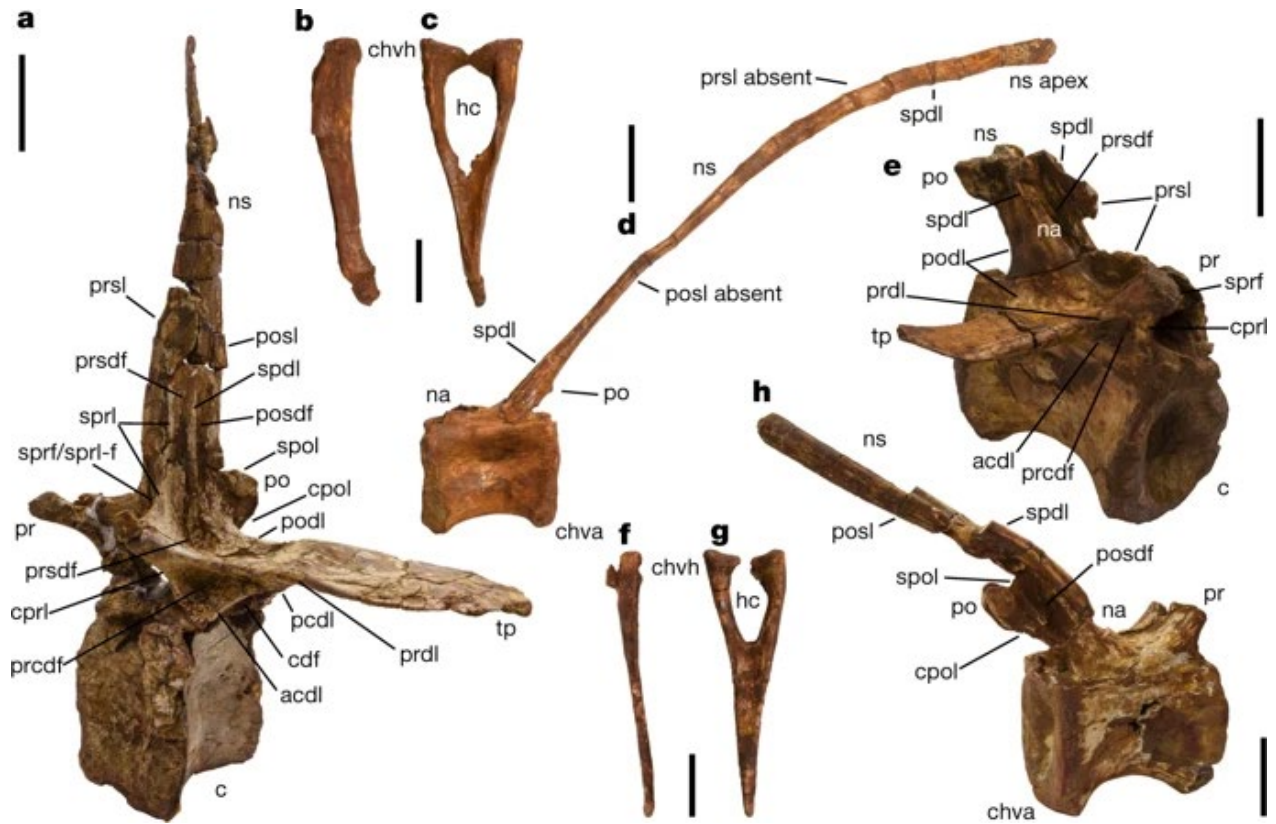


Figure 2 Selected caudal vertebrae and chevrons of *Spinosaurus aegyptiacus* FSAC-KK 11888. **a**, proximal caudal (Ca4) in left proximolateral view. **b–c**, proximal chevron (Chv7) in left lateral and proximal view. **d**, distal caudal (Ca31) in left lateral view. **e**, mid-caudal (Ca12) in right proximolateral view. **f–g**, distal chevron (Chv27) in left lateral and proximal views. **h**, mid-caudal (Ca16) in right distolateral view. Abbreviations: acdl, anterior centrodiapophyseal lamina; c, centrum; ca, caudal vertebra; cdf, centrodiapophyseal fossa; chva, chevron articulation; chvh, chevron head; cpol, centropostzygapophyseal lamina; cpri, centroprezygapophyseal lamina; hc, haemal canal; na, neural arch; ns, neural spine; pcdl, posterior centrodiapophyseal lamina; po, postzygapophysis; pocdf, postzygapophyseal centrodiapophyseal fossa; podl, postzygodiapophyseal lamina; posdf, postzygapophyseal spinodiapophyseal fossa; posl, postspinal lamina; pr, prezygapophysis; prcdf, prezygapophyseal centrodiapophyseal fossa; prdl, prezygodiapophyseal lamina; prsdf, prezygapophyseal spinodiapophyseal fossa; prsl, prespinal

lamina; spdl, spinodiapophyseal lamina; spol, spinopostzygapophyseal lamina; spof, spinopostzygapophyseal fossa; sprl, spinoprezygapophyseal lamina; sprl-f, spinoprezygapophyseal lamina fossa; tp, transverse process. Scale bars = 10 cm (a), 5 cm (b–h).

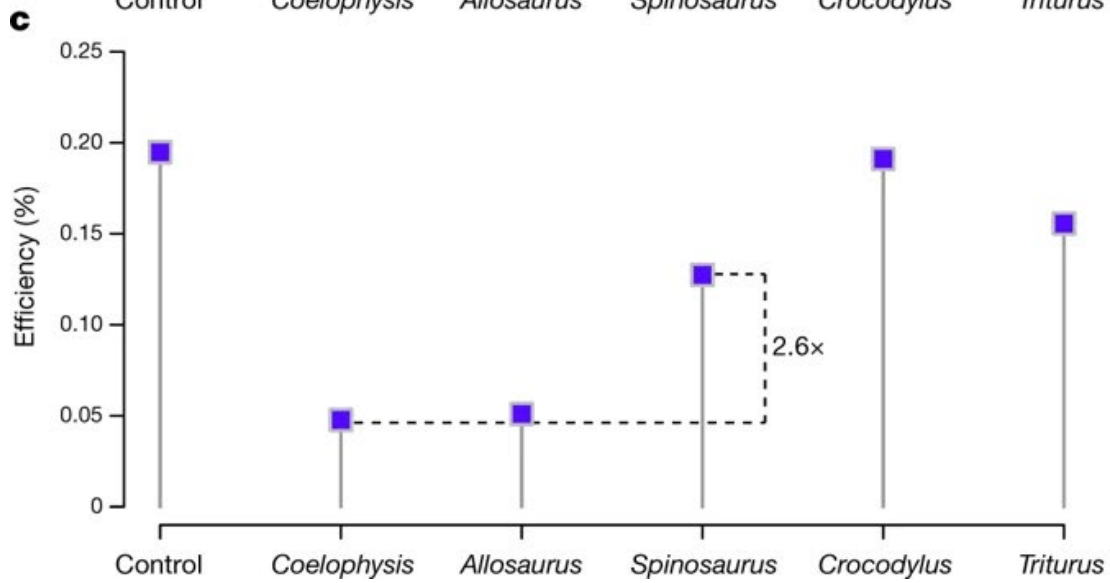
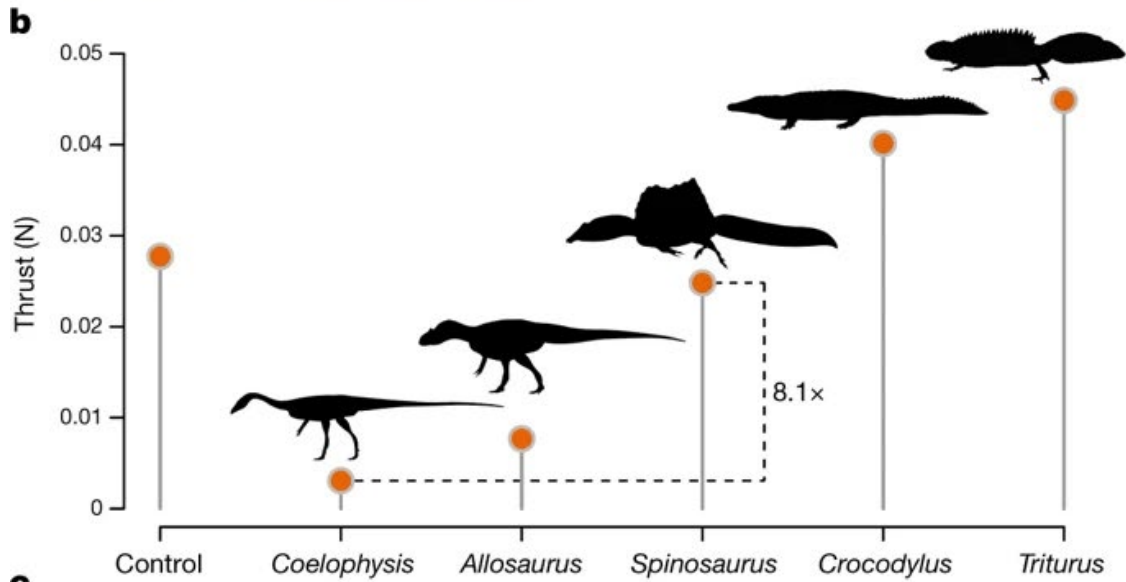
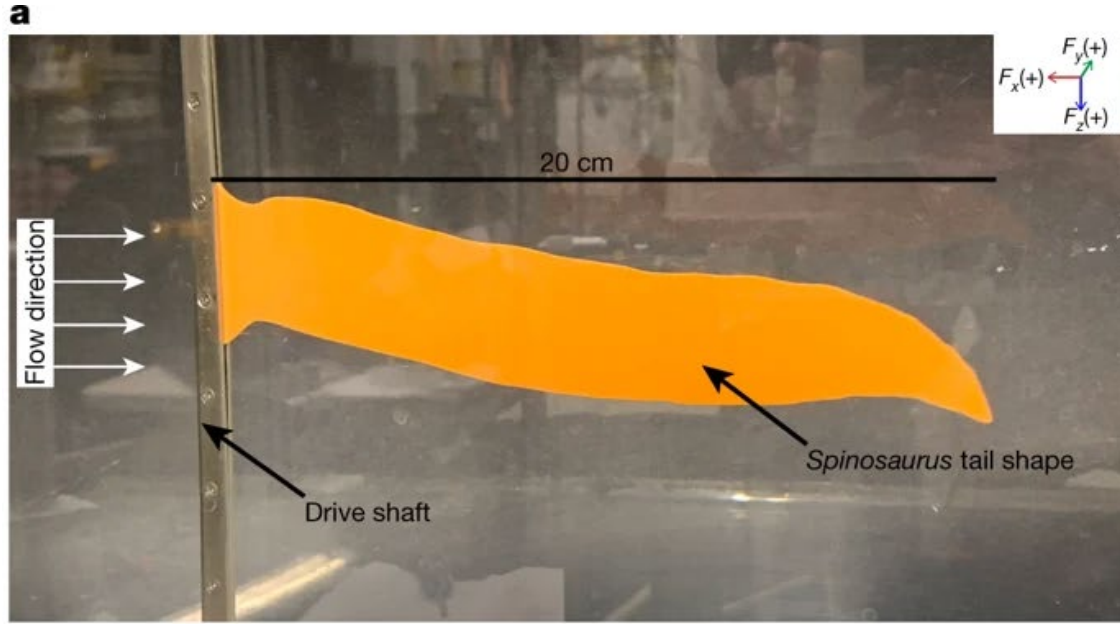


Figure 3: Comparative tail swimming performance. **a**, *Spinosaurus* plastic tail shape attached to robotic drive shaft in water flume with water flowing at 10 cm/s. With reference to the tail, positive x forces (F_x) are generated proximally (or upstream), positive y forces (F_y) in the right lateral direction, and positive z forces (F_z) in the ventral direction. **b**, Mean thrust and **c**, mean efficiency generated by tail shapes during robotically-controlled swimming. All tails scaled to 20 cm length (Supplementary Information Fig. 4). The control tail was rectangular in shape with the same surface area as the scaled *Spinosaurus* tail (63 cm²). See methods for experimental setup. Raw thrust and efficiency data, including mean and standard error, are provided in Supplementary Data File 1. Swimming motions of the *Spinosaurus* tail are visualized in Supplementary Videos 3–5.

Methods

Excavation

The Cretaceous Kem Kem beds of Morocco crop out along an extensive escarpment near the Moroccan-Algerian border region⁷. After the accidental discovery and partial excavation by a local collector in 2008, part of a single skeleton (FSAC-KK 11888), subsequently deposited at the Faculté des Sciences of Casablanca University (FSAC), was recovered, published, and designated as the neotype⁷. A multi-institutional collaborative project in the years 2015–2019, led by N.I., resulted in four joint expeditions to the neotype site. Detailed and careful exploration of the debris around the site, as well as a systematic and extended excavation of the unexposed portion of the fossiliferous layer of the Zrigat hill, led to the recovery of many additional elements of the neotype skeleton (Extended Data Figs. 1–5). A detailed description of the new material, as well as the geological context, is included in the Supplementary Information. The Supplementary Information also includes details on a full-body

flesh reconstruction of *Spinosaurus* based on FSAC-KK 11888, as well as estimates of whole-body mass, segment masses, segment centres of mass, and whole-body centre of mass (Supplementary Data File 2). Position of centre of mass in comparison to prior analyses can be found in Extended Data Figure 8.

Osteohistological analysis

The aim of the osteohistological analysis was to determine if the remains assigned to FSAC-KK 11888 belong to a single individual rather than a chimeric association of juvenile and adult individuals preserved in the same location and at the same horizon. The analysis was based on five skeletal elements. The primary assumption is that should histological details suggest that all five elements represent the same ontogenetic stage then they are more likely to represent one rather than multiple individuals. By contrast, should these elements exhibit two or more, distinct ontogenetic stages, this would point to the presence of multiple individuals of one, or perhaps several, taxa, all fortuitously preserved at a single location during a single depositional event^{31,32,33}. The following elements were sectioned: the right femur; the left fibula; one rib; one gastralia; and two neural spines. All specimens were sectioned prior to preparation in order to ensure that no outer layers of the compact cortex were accidentally removed. In the case of the neural spines the apical portion was sectioned.

Thin sectioning followed standard protocol³⁴. The thin sections have a thickness of 50–70 microns and were analysed with a petrographic microscope, Leica DM 2500 P. Digital images were captured using a ProgRes Cfscan camera. Only continuous lines were counted as lines of arrested growth (LAGs). Annuli were interpreted as a single year, following Lee and O'Connor³⁵. Retrocalculation, following the method proposed by Horner and Padian³⁶, was applied to determine the likely number of missing LAGs, eroded through remodelling of the bone. In the case of the

neural spines, only the width of the inner–most zone was used to retrocalculate the missing LAGs, because the shape of the section could not be approximated to a circular outline. The calculation of the major and minor axis used for the retrocalculation was performed in ImageJ³⁷. Results of the histological analysis are included the in Supplementary Information.

Experimental testing of tail shape swimming performance.

To test the aquatic locomotor potential of the newly reconstructed *Spinosaurus aegyptiacus* tail, we determined the swimming performance of its tail shape using a robotic controller developed for studies of propulsive hydrodynamics^{38,39,40,41,42}. The swimming performance of the *Spinosaurus* tail shape was compared to the performance of five other tail shapes from the following species: the small-bodied terrestrial theropod *Coelophysis bauri*, the large-bodied terrestrial theropod *Allosaurus fragilis*, the semi-aquatic crocodile *Crocodylus niloticus*, the semi-aquatic crested newt *Triturus dobrogicus*, and a rectangular control tail that was scaled to the same surface area as the *Spinosaurus* tail. Tail shapes (Supplementary Information Fig. 4) were all scaled to 20 cm proximodistal length (L), manufactured from 0.93 mm thick plastic of flexural stiffness $5.8 * 10^{-5}$ Nm² and cut using an Epilog Zing24 laser cutter.

The plastic tails were attached to a robotic controller that allowed us to impose specific motion programs on the rigid shaft to which each tail was affixed (Fig. 3 and Supplementary Information Videos 3–5). This shaft was moved in both heave (side-to-side) motion, as well as in pitch (angular rotation) to achieve undulatory tail motions. The imposed motion program was 1 Hz frequency, +/- 1 cm heave, and +/- 25° pitch which resulted in the tail tip undergoing peak-to-peak lateral excursions of approximately 40% L, comparable to that exhibited by swimming axolotls and alligators^{23,24,25}.

The shaft supporting each simulated tail at the leading edge was attached to an ATI Inc. (Apex, NC, USA) Nano-17 six-axis force/torque sensor located just above the water surface. Testing occurred in a recirculating water flume and a free-stream flow of 0.5 L (10 cm/s) was imposed for all tests. Custom LabVIEW programs (National Instruments Corp., Austin, TX, USA) were used to control flapping frequency, flow speed, heave, and pitch. A custom LabVIEW program also was used to acquire data from the ATI transducer at a sampling rate of 1000 hz. Each tail shape was tested N=5 times, except for the *Spinosaurus* tail which was tested N=5 times on two different days for a total of N=10 tests. Output data can be found in Supplementary Data File 1.

Thrust and efficiency for each tail shape were calculated using standard fluid dynamic equations as in previous research^{43,44}. Mean thrust force (F_x) is calculated directly from transducer output from the Fx channel, and we accounted for transducer rotation resulting from the pitch motion to provide the force component directed upstream (positive thrust). Propulsive efficiency is calculated as the ratio of the thrust coefficient ($C_T = 2\overline{F_x}/\rho U^2 cs$) to the power coefficient ($C_p = 2\overline{P}/\rho U^3 cs$) where ρ is the fluid density, U swimming velocity, c foil chord, and s the tail span. Effectively, this metric assesses the extent to which input power is translated into thrust.

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