

1 *Spinosaurus* is not an aquatic 2 dinosaur

3 Paul C. Sereno^{1,2,*}, Nathan Myhrvold³, Donald M. Henderson⁴, Frank E. Fish⁵,
4 Daniel Vidal⁶, Stephanie L. Baumgart¹, Tyler M. Keillor¹, Kiersten K. Formoso^{7,8},
5 Lauren L. Conroy¹

*For correspondence:

dinosaur@uchicago.edu (PCS)

Present address: ⁵Organismal
Biology and Anatomy, University of
Chicago, USA

6 ¹Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL
7 60637; ²Committee on Evolutionary Biology, University of Chicago, IL 60637;
8 ³Intellectual Ventures, 3150 139th Avenue Southeast, Bellevue, WA 98005; ⁴Royal
9 Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada, T0J 0Y; ⁵Department of
10 Biology, West Chester University, West Chester, PA 19383; ⁶Grupo de Biología Evolutiva,
11 UNED, 28040 Madrid, Spain; ⁷Department of Earth Sciences, University of Southern
12 California, Los Angeles, CA 90089; ⁸Dinosaur Institute, Natural History Museum of Los
13 Angeles County, Los Angeles, CA 90007

14
15 **Abstract** A predominantly fish-eating diet was envisioned for the sail-backed theropod
16 dinosaur, *Spinosaurus aegyptiacus*, when its elongate jaws with subconical teeth were unearthed a
17 century ago in Egypt. Recent discovery of the high-spined tail of that skeleton, however, led to a
18 bolder conjecture, that *S. aegyptiacus* was the first fully aquatic dinosaur. The ‘aquatic hypothesis’
19 posits that *S. aegyptiacus* was a slow quadruped on land but a capable pursuit predator in coastal
20 waters, powered by an expanded tail. We test these functional claims with skeletal and flesh
21 models of *S. aegyptiacus*. We assembled a CT-based skeletal reconstruction based on the fossils,
22 to which we added internal air and muscle to create a posable flesh model. That model shows
23 that on land *S. aegyptiacus* was bipedal and in deep water was an unstable, slow surface swimmer
24 (<1 m/s) too buoyant to dive. Living reptiles with similar spine-supported sails over trunk and tail
25 in living reptiles are used for display rather than aquatic propulsion, and nearly all extant
26 secondary swimmers have reduced limbs and fleshy tail flukes. New fossils also show that
27 *Spinosaurus* ranged far inland. Two stages are clarified in the evolution of *Spinosaurus*, which is
28 best understood as a semiaquatic bipedal ambush piscivore that frequented the margins of
29 coastal and inland waterways.

31 Introduction

32 In 1915 Ernst von Stromer announced the discovery in Egypt’s Western Desert of the elongate
33 jaws and partial skeleton of a large sail-backed predator, *Spinosaurus aegyptiacus* (Stromer, 1915).
34 Other bones found nearby (Stromer, 1934) contributed to Stromer’s (1936) initial reconstruction of
35 *S. aegyptiacus* as a sail-backed, piscivorous biped, shortly before all of these bones were destroyed
36 in WWII (Nothdurft and Smith, 2002; Smith et al., 2006). Over the last 30 years, additional skull
37 and postcranial bones came to light in western Morocco in beds of similar age to those in Egypt
38 (Russell, 1996; Dal Sasso et al., 2005; Smyth et al., 2020; Ibrahim et al., 2020b). Central among these
39 finds was a partial skeleton (designated the neotype) that allowed a more complete reconstruction,
40 confirming its interpretation as a semiaquatic piscivore (Ibrahim et al., 2014).

41 As skeletal information on the unusual predator improved, so has speculation as to whether *S.*

42 *aegyptiacus* was better adapted to life in water as an aquatic predator, based on inferences from
43 oxygen isotopes in enamel (*Amiot et al., 2010*), the dental rosette likened to the jaws of a conger
44 eel (*Vullo et al., 2016*), the alleged elevated positioning of the orbits in the skull for visibility while
45 largely submerged (*Arden et al., 2019*), the hypothetical underwater role of the trunk sail (*Gimsa
46 et al., 2016*), and the infilling of the medullary cavities of hind limb bones that may have functioned
47 as ballast (*Ibrahim et al., 2014; Aureliano et al., 2018*).

48 **The aquatic hypothesis**

49 Recent discovery of the tall-spined tail bones of the neotypic skeleton reinvigorated the interpre-
50 tation of *S. aegyptiacus* as the first fully aquatic dinosaur (*Ibrahim et al., 2020a*) here dubbed the
51 ‘aquatic hypothesis,’ which makes three basic propositions. Unlike any other theropod, according
52 to the hypothesis, *S. aegyptiacus* (1) reverted to a quadrupedal stance on land, ostensibly knuckle-
53 walking with long-fingered, long-clawed forelimbs, while (2) functioning in water as a capable, div-
54 ing pursuit predator, using an expanded tail as a “novel propulsor organ”. Its adaptations for “deep-
55 water propulsion” were reasserted by quantitative analysis of bone density that suggested *S. ae-
56 gyptiacus* was a frequent diver (*Fabbri et al., 2022*), an interpretation that has been challenged
57 (*Myhrvold et al., in press*). A deep-diving pursuit predator of large body size, furthermore, would
58 be found exclusively in (3) deep-water coastal or marine habitats rather than also ranging into
59 freshwater, inland environments. We test these three central propositions.

60 Critique of the aquatic hypothesis thus far has focused on an alternative functional explana-
61 tion for the high-spined tail (as a display structure) and qualitative functional interpretations of its
62 skeletal anatomy (*Hone and Holtz, 2021*). Biomechanical evaluation of the aquatic functionality of *S.
63 aegyptiacus* remains rudimentary. The propulsive capacity of the tail in water was judged to be bet-
64 ter than terrestrial counterparts by oscillating miniature plastic tail cut-outs in water (*Ibrahim et al.,
65 2020a*), a limited approximation of the biomechanical properties of an anguilliform tail (*Lighthill,
66 1969; van Rees et al., 2013; Gutarra and Rahman, 2022*) and failed to take into account the bizarre
67 anterior half of the animal. The center of body mass, a critical functional parameter, has been es-
68 timated for *S. aegyptiacus* three times, each estimate pointing to a different location ranging from
69 the middle of the trunk to a position over the hind limbs (*Henderson, 2018; Ibrahim et al., 2014,
70 2020a*). Quantitative comparisons have not been made regarding the size or surface area of the
71 limbs, hind feet and tail of *S. aegyptiacus* to counterparts in extant primary or secondary swimmers.

72 Adequate evaluation of the aquatic hypothesis, thus, requires more realistic biomechanical
73 tests, quantitative body, axial and limb comparisons between *S. aegyptiacus* and extant primary
74 and secondary swimmers, and a survey of bone structure beyond the femur and shaft of a dorsal
75 rib. Such tests and comparisons require an accurate 3D digital flesh model of *S. aegyptiacus*, which,
76 in turn, requires an accurate skeletal model. Hence, we began this study by assembling a com-
77 plete set of CT scans of the fossil bones for *S. aegyptiacus* and its African forerunner, *Suchomimus
78 tenerensis* (*Sereno et al., 1998*).

79 **Aquaphilic terminology**

80 Aquatic status is central to the ‘aquatic hypothesis.’ *S. aegyptiacus*, the hypothesis holds, is the
81 first non-avian dinosaur bearing skeletal adaptations devoted to lifestyle and locomotion in water,
82 some of which inhibited terrestrial function. The contention is that *S. aegyptiacus* was not only a
83 diving pursuit predator in the open water column, but also a quadruped on land with long-clawed
84 forelimbs poorly adapted for weight support. A later publication seemed to downgrade that central
85 claim by suggesting that any vertebrate with “aquatic habits,” such as wading, submergence or
86 diving, had an “aquatic lifestyle” (*Fabbri et al., 2022*). That broadened usage of “aquatic lifestyle,”
87 however, blurs the longstanding use of aquatic as applied to lifestyle (*Pacini and Harper, 2008*). We
88 outline below traditional usage of aquaphilic terms, which we follow.

89 The adjective “aquatic” is used either as a broad categorization of *lifestyle* or, in more limited ca-
90 pacity, in reference to an *adaptation* of a species or group. In the former case, a vertebrate with an

91 “aquatic lifestyle” or “aquatic ecology” is adapted for life primarily, or solely, in water with severely
92 reduced functional capacity on land (*Pacini and Harper, 2008*). *Aquatic vertebrates* (e.g., bony fish,
93 sea turtles, whales) live exclusively or primarily in water and exhibit profound cranial, axial or ap-
94 pendicular modifications for life in water, especially at larger body sizes (*Webb, 1984; Webb and*
95 *De Buffrénil, 1990; Hood, 2020*). For example, extant whales are secondarily aquatic mammals
96 that spend all of their lives at sea and exhibit profound skeletal modifications for aquatic sensory
97 and locomotor function. A marine turtle, similarly, is considered an aquatic reptile, regardless of
98 whether it clambers ashore briefly to lay eggs, because the vast majority of its life is spent in water
99 using profoundly modified limbs for aquatic locomotion (flippers) that function poorly on land.

100 An aquaphilic animal with less profound adaptations to an aqueous arena is said to be *semi-*
101 *aquatic* (or semi-aquatic), no matter the proportion of aquatic foodstuffs in its diet, the proportion
102 of time spent in water, or the proficiency of swimming or diving. Nearly all semiaquatic vertebrates
103 are secondarily aquaphilic, having acquired aquatic adaptations over time to enhance functional
104 capacity in water without seriously compromising terrestrial function (*Howell, 1930; Hood, 2020*).
105 Indeed, semiaquatic animals are also semiterrestrial (*Fish, 2016*). Freshwater turtles, for exam-
106 ple, are regarded as semiaquatic reptiles because they frequent water rather than live exclusively
107 within an aqueous habitat, are sometimes found in inland habitats, and exhibit an array of less pro-
108 found modifications (e.g., interdigital webbing) for locomotion in water (*Pacini and Harper, 2008*).
109 Extant crocodylians and many waterbirds, likewise, are capable swimmers and divers but retain ex-
110 cellent functional capacity on land. Auks (Alcidae), among the most water-adapted of semiaquatic
111 avians, are agile wing-propelled, pursuit divers with an awkward upright posture on land resem-
112 bling penguins, but they retain the ability to fly and inhabit land for extended periods (*Nettleship,*
113 *1996*). On the other hand, the flightless penguins (Sphenisciformes) are considered aquatic due
114 to their more profound skeletal modifications for swimming and deep diving and more limited
115 terrestrial functionality, although still retaining the capability to trek inland and stand for consider-
116 able durations while brooding. As nearly all semiaquatic vertebrates have an aquatic diet and the
117 ability to swim or dive, more profound functional allegiance to water is requisite for an “aquatic”
118 appellation (*Pacini and Harper, 2008*).

119 An *aquatic adaptation* of an organism refers to the function of a particular feature, not the over-
120 all lifestyle of an organism. That feature should have current utility and primary function in water
121 (*Houssaye and Fish, 2016*). Aquatic adaptations are presumed to have evolved their functionality
122 in response to water and cannot also have special functional utility in a subaerial setting. For exam-
123 ple, the downsized, retracted external nares in *S. aegyptiacus* would prevent water intake through
124 the nostrils while feeding with the snout submerged. There has yet been offered no plausible alter-
125 native explanation involving terrestrial function for the downsizing and retraction of the external
126 nares in spinosaurids, a unique condition among non-avian theropods. The hypertrophied neural
127 spines of the tail of *S. aegyptiacus*, in contrast, are ambiguous as an “aquatic adaptation,” because
128 expanded tails can function both as aquatic propulsors and terrestrial display structures. For the
129 expanded tail to be an “aquatic adaptation,” its morphological construction and biomechanical
130 function demonstrate its primary utility and capability in water, as shown in extant tail-powered
131 primarily or secondarily aquatic vertebrates (e.g., newts, crocodylians, beavers, otters; (*Fish et al.,*
132 *2021*). The same must be shown or inferred to be the case in extinct secondarily aquatic verte-
133 brates (*Gutarra and Rahman, 2022*). We have not found such substantiating evidence in tail form
134 and inferred function in *S. aegyptiacus* or other spinosaurids for the heightened tail to be substan-
135 tiated as an aquatic adaptation (see below).

136 **Our approach**

137 To test the aquatic hypothesis for *S. aegyptiacus*, we began with CT scans of spinosaurid fossils from
138 sites in Africa to build high-resolution 3D skeletal models of *S. aegyptiacus* (*Figure 1A*) and its fore-
139 runner *Suchomimus tenerensis* (*Figure 1F*). Many vertebrae and long bones in both genera show
140 significant internal pneumatic (air) or medullary (marrow) space, which has ramifications for buoy-

141 ancy. When compared to the 2D silhouette drawing used in the aquatic hypothesis (*Ibrahim et al.*,
142 **2020a**), our CT-based 3D skeletal model of *S. aegyptiacus* differs significantly in skeletal proportions.

143 We enveloped the skeletal model in flesh informed by CT scans revealing the muscle volume
144 and air spaces in extant reptilian and avian analogs. To create a 3D flesh model for *S. aegyptiacus*
145 (**Figure 2A, B**), internal air spaces (trachea, lungs, air sacs) were shaped and positioned as in extant
146 analogs. We created three options for internal air volume based on extant squamate, crocodylian
147 and avian conditions (**Figure 2C**) and assigned densities to body partitions based on local tissue
148 types and air space. We calculated the surface area and volume of the flesh model as well as its
149 component body parts.

150 We posed this integrated flesh model in bipedal, hybrid- and axial-powered poses, the latter
151 two based on the swimming postures of extant semiaquatic reptiles (*Grigg and Kirshner, 2015*,
152 **Figure 2B**). We calculated *center of mass* (CM) and *center of buoyancy* (CB) to evaluate the habitual
153 two- or four-legged stance of *S. aegyptiacus* on land (**Figure 1A**), the depth of water at the point
154 of flotation (**Figure 2D**), and the neutral position of the flesh model in deeper water (**Figure 2A,**
155 **B**). Using biomechanical formulae (*Lighthill, 1969*) and data from extant alligators (*Fish, 1984*), we
156 estimated the maximum force output of its tail, which was used to calculate maximum swimming
157 velocity at the surface and underwater (**Figure 3A**). We also evaluated its stability, maneuverability
158 and diving potential in water (**Figure 3B**), with all of these functional capacities compared to extant
159 large-bodied aquatic vertebrates.

160 We turned to extant analogs to consider the structure and function of similar spine-supported
161 sails over the trunk and tail in lizards and the form of tail vertebrae in tail-powered secondary swim-
162 mers (**Figure 4**). We also considered the relative size (surface area) of appendages in a range of sec-
163 ondary swimmers (**Figure 5**), and how the surface area of foot paddles and tail scale in crocodylians
164 (**Figure 6**).

165 Lastly, we turned to the spinosaurid fossil record to look at the habitats where spinosaurid
166 fossils have been found. We reviewed their distribution (**Figure 7**) to determine if spinosaurids,
167 and *S. aegyptiacus* in particular, were restricted to coastal, marine habitats like all large secondarily
168 aquatic vertebrates. We updated spinosaurid phylogeny in order to discern major stages in the
169 evolution of spinosaurid piscivorous adaptations and sail structures (**Figure 8**), incorporating the
170 latest finds including new fossils of *Spinosaurus* from Niger.

171 Institutional abbreviations

172 BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; FMNH, Field
173 Museum of Natural History, Chicago, USA; FSAC, Faculté des Sciences Ain Chock, University of
174 Casablanca, Casablanca, Morocco; KU, The University of Kansas, Museum of Natural History, Lawrence,
175 USA; MNBH, Musée National de Boubou Hama, Niamey, Niger; MNHN, Muséum national d'Histoire
176 naturelle, Paris, France; NMC, Canadian Museum of Nature, Ottawa, Canada; UCMP, University
177 of California, Museum of Paleontology, Berkeley, USA; UCRC, University of Chicago Research Col-
178 lection, Chicago, USA; UF, University of Florida, University of Florida Collections, Gainesville, USA;
179 UMMZ, University of Michigan, Museum of Zoology, Ann Arbor, USA; WDC, Wildlife Discovery Cen-
180 ter, Lake Forest, USA.

181 Results

182 Spinosaurid skeletal models

183 Our skeletal reconstruction of *S. aegyptiacus* is just under 14 m long (**Figure 1A**), which is more than
184 1 m shorter than previously reported (*Ibrahim et al., 2014*). Major differences are apparent when
185 compared to the 2D graphical reconstruction of the aquatic hypothesis (*Ibrahim et al., 2020a*). In
186 their reconstruction, the length of the presacral column, depth of the ribcage, and length of the
187 forelimb were overestimated by approximately 10%, 25% and 30%, respectively, over dimensions
188 based on CT-scanned fossils. When translated to a flesh model, all of these proportional over-

189 estimates (heavier neck, trunk, forelimb) shift the center of mass anteriorly (see Materials and
190 Methods).

191 The hind limb long bones (femur, tibia, fibula, metatarsals) in *S. aegyptiacus* lack the medullary
192 cavity common to most dinosaurs and theropods in particular. When first discovered, the infilled
193 hind limb bones in *S. aegyptiacus* were interpreted as ballast for swimming (*Ibrahim et al., 2014*).
194 The infilled condition, however, is variable as shown by the narrow medullary cavity in a femur
195 of another individual slightly larger than the neotype (*Myhrvold et al., in press*). The bone infill-
196 ing, furthermore, is fibrolamellar and cancellous, similar to the infilled medullary cavities of other
197 large-bodied terrestrial dinosaurs (*Vanderven et al., 2014*) and mammals (*Houssaye et al., 2016*).
198 In contrast, dense pachystotic bone composes the solid and sometimes swollen bones of some
199 secondarily aquatic vertebrates that use increased skeletal mass as ballast (*Houssaye, 2009*).

200 Medullary space is present in most forelimb bones in both *S. aegyptiacus* and *S. tenerensis* (*Fig-*
201 *ure 1D, H*). The centra of anterior caudal vertebrae are occupied by a large medullary space (*Fig-*
202 *ure 1C, J*), and large air-filled pneumatic spaces are present in the centra and neural arches of
203 cervical vertebrae (*Evers et al. (2015); Figure 1B*). Collectively, these less dense, internal marrow-
204 and air-filled spaces in *S. aegyptiacus* more than offset the added mass of infilled medullary space in
205 the relatively reduced hind limb long bones (*Figure 1E*). Hind limb bone infilling is better explained
206 as compensation for the reduced size of the hind limb long bones that must support a body mass
207 at the upper end of the range for theropods. Bending strength increases by as much as 35% when
208 the medullary cavity is infilled (see *Appendix 1*).

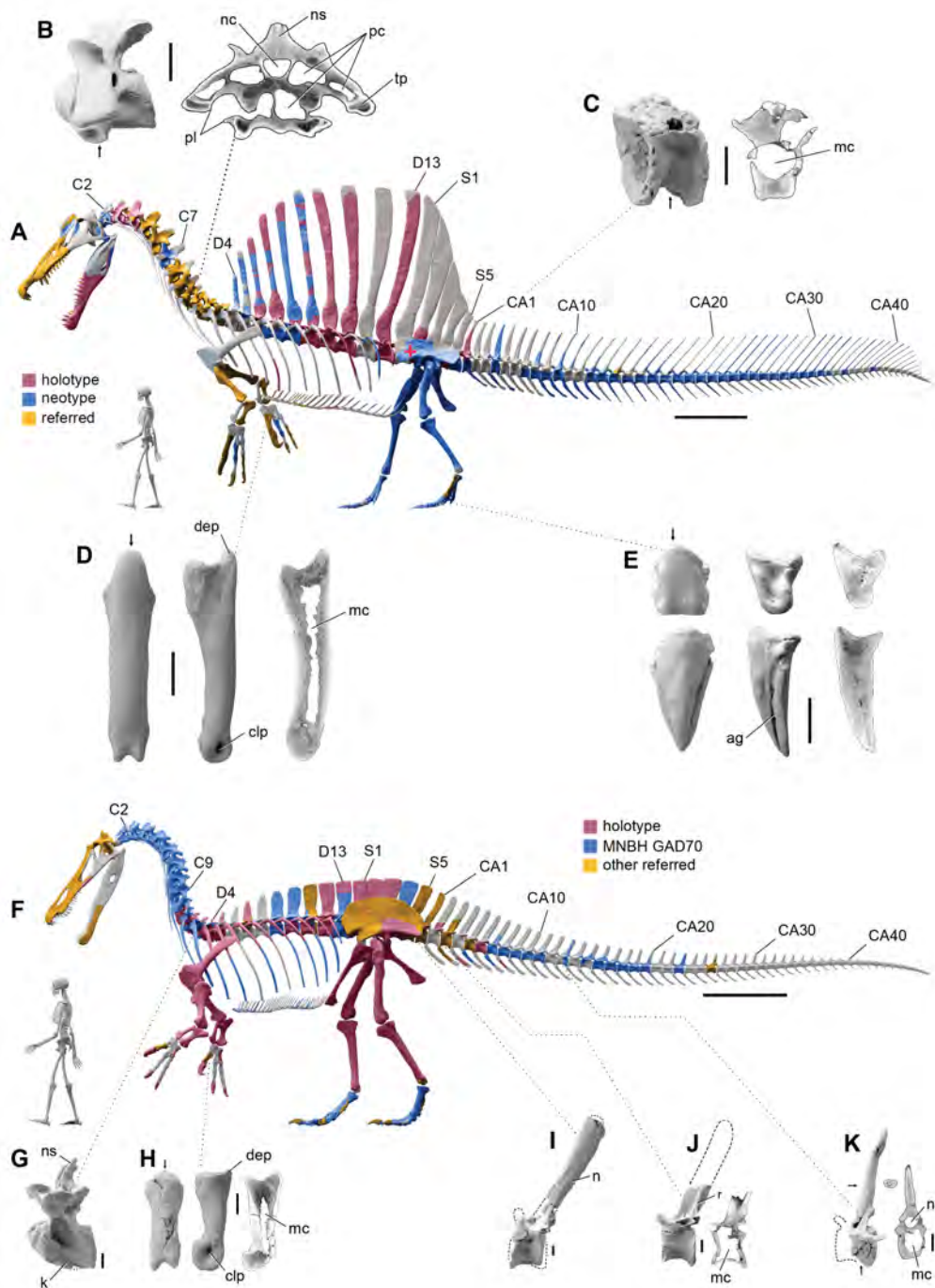


Figure 1. Digital skeletal reconstructions of the African spinosaurids *Spinosaurus aegyptiacus* and *Suchomimus tenerensis*. (A) *Spinosaurus aegyptiacus* (early Late Cretaceous, Cenomanian, ca. 95 Ma) showing known bones based on the holotype (BSPG 1912 VIII 19, red), neotype (FSAC-KK 11888, blue), and referred specimens (yellow) and the center of mass (cross) of the flesh model in bipedal stance (overlap priority: neotype, holotype, referred bones). (B) Cervical 9 (BSPG 2011 I 115) in lateral view and coronal cross-section showing internal air space. (C) Caudal 1 centrum (FSAC-KK 11888) in anterolateral view and coronal CT cross-section. (D) Right manual phalanx I-1 (UCRC PV8) in dorsal, lateral and sagittal CT cross-sectional views. (E) Pedal phalanges IV-4, IV-ungual (FSAC-KK 11888) in dorsal, lateral and sagittal CT. (F) *Suchomimus tenerensis* (mid Cretaceous, Aptian-Albian, ca. 110 Ma) showing known bones based on the holotype (MNBH GAD500, red), a partial skeleton (MNBH GAD70, blue), and other referred specimens (yellow) and the center of mass (cross) of the flesh model in a bipedal stance (overlap priority: holotype, MNBH GAD70, referred bones). (G) Dorsal 3 in lateral view (MNBH GAD70). (H) Left manual phalanx I-1 (MNBH GAD503) in dorsal, lateral and sagittal CT cross-sectional views. (I) Caudal 1 vertebra in lateral view (MNBH GAD71). (J) Caudal ~3 vertebrae in lateral view (MNBH GAD85). (K) Caudal ~13 vertebrae in lateral view with CT cross-sections (coronal, horizontal) of the hollow centrum and neural spine (MNBH GAD70). ag, attachment groove; C2, 7, 9, cervical vertebra 2, 7, 9; CA1, 10, 20, 30, 40, caudal vertebra 1, 10, 20, 30, 40; clp, collateral ligament pit; D4, 13, dorsal vertebra 4, 13; dip, dorsal intercondylar process; k, keel; mc, medullary cavity; nc, neural canal; ns, neural spine; pc, pneumatic cavity; pl, pleurocoel; r, ridge; S1, 5, sacral vertebra 1, 5. Dashed lines indicate contour of missing bone, arrows indicate plane of CT-sectional views, and scale bars equal 2 m (A, F), 5 cm (B, C), 3 cm (D, E, H-K) with human skeletons 1.8 m tall (A, F).

209 ***S. aegyptiacus* flesh model form and function**

210 We added flesh to the skeletal model and divided the flesh model into body partitions adjusted for
211 density. Muscle volume was guided by CT cross-sections from extant lizards, crocodylians and birds
212 (Figure 2B), and internal air space (pharynx-trachea, lungs, paraxial air sacs) was modeled on lizard,
213 crocodylian and avian conditions (Figure 2C; see Materials and Methods, Appendix 2). Whole-body
214 and body part surface area and volume were calculated, and body partitions were assigned density
215 comparable to that in extant analogs (see Materials and Methods). For biomechanical analysis, we
216 positioned the integrated flesh model in bipedal stance (Figure 1A) as well as hybrid- and axial-
217 powered swimming poses (Grigg and Kirshner (2015); Figure 2A, B).

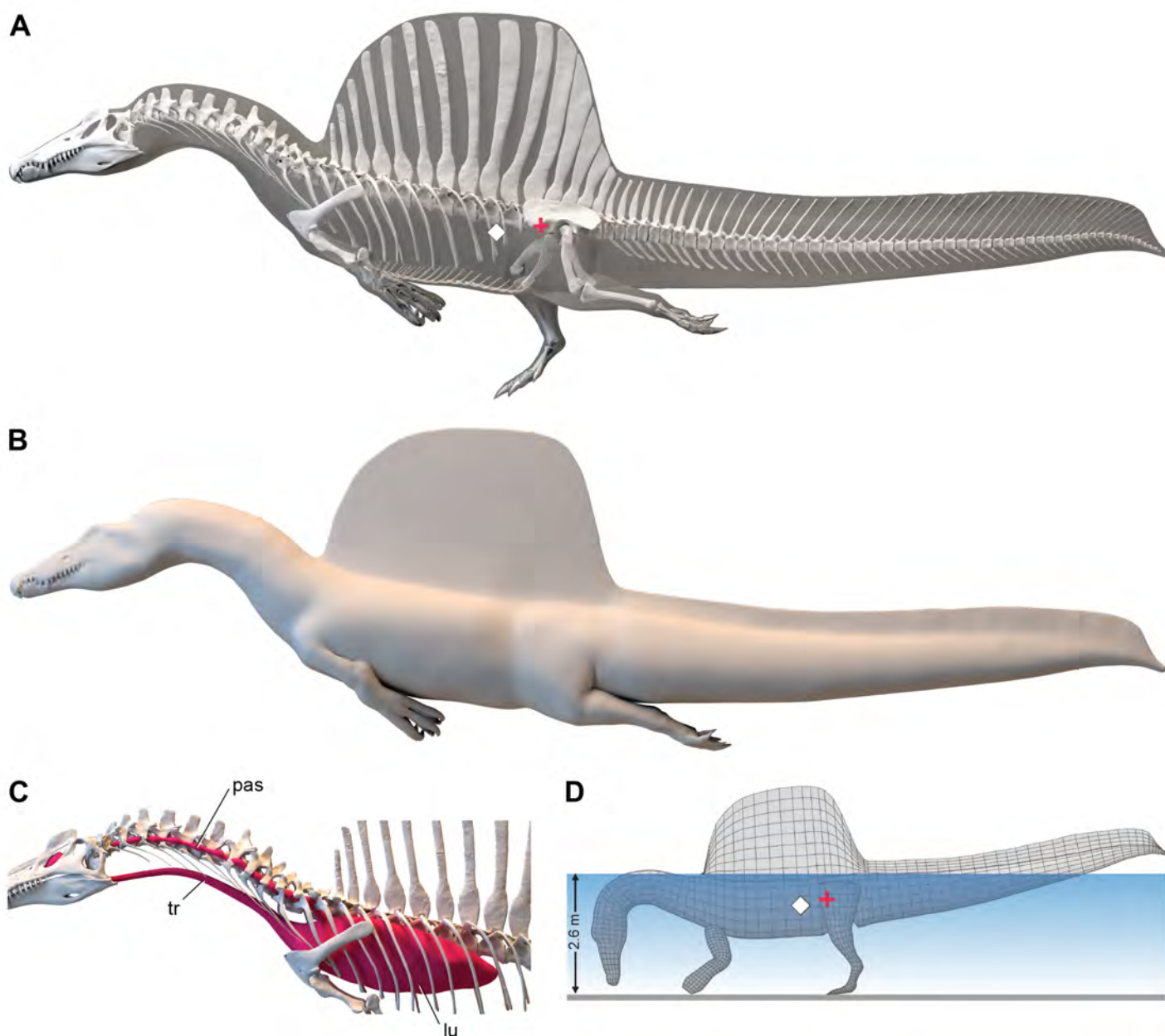


Figure 2. Digital flesh model of *Spinosaurus aegyptiacus*. (A) Translucent flesh model in hybrid swimming pose showing centers of mass (cross) and buoyancy (diamond). (B) Opaque flesh model in axial swimming pose with adducted limbs. (C) Modeled air spaces (“medium” option) include pharynx-trachea, lungs and paraxial air sacs. (D) Wading-strike pose at the point of flotation (2.6 m water depth) showing centers of mass (cross) and buoyancy (diamond). Abbreviations: lu, lungs; pas, paraxial air sacs; tr, trachea.

218 The *center of mass* (CM) and *center of buoyancy* (CB) of the flesh model were determined to
 219 evaluate habitual stance on land and in shallow water (**Figure 1A**), the water depth at the point of
 220 flotation (**Figure 2D**), and its swimming velocity, stability, maneuverability, and diving potential in
 221 deeper water (**Figure 3**). No matter the included volume of internal air space, CM is positioned over
 222 the ground contact of symmetrically-positioned hind feet (**Figure 1A**, red cross). Thus, *S. aegyptiacus*
 223 had a bipedal stance on land as previously suggested (**Henderson, 2018**), contrary to the aquatic
 224 hypothesis (**Ibrahim et al., 2020a**). Consistent with a bipedal stance, the manus is adapted for prey
 225 capture and manipulation (elongate hollow phalanges, scythe-shaped unguis) rather than weight
 226 support (**Figure 1A, D**).

227 Adult *S. aegyptiacus* can feed while standing in water with flotation occurring in water deeper
 228 than ~2.6 m (**Figure 2D**). In hybrid or axial swimming poses, trunk air space tilts the anterior end
 229 of the model upward (**Figure 2A, B**). With density-adjusted body partitions and avian-like internal
 230 air space, the flesh model of *S. aegyptiacus* has a body mass of 7,390 kg and an average density of
 231 833 kg/m³ (see Materials and Methods), which is considerably less than the density of freshwater
 232 (1,000 kg/m³) and saltwater (1,026 kg/m³) or the average density of living crocodylians (1080 kg/m³;
 233 **Grigg and Kirshner (2015)**).

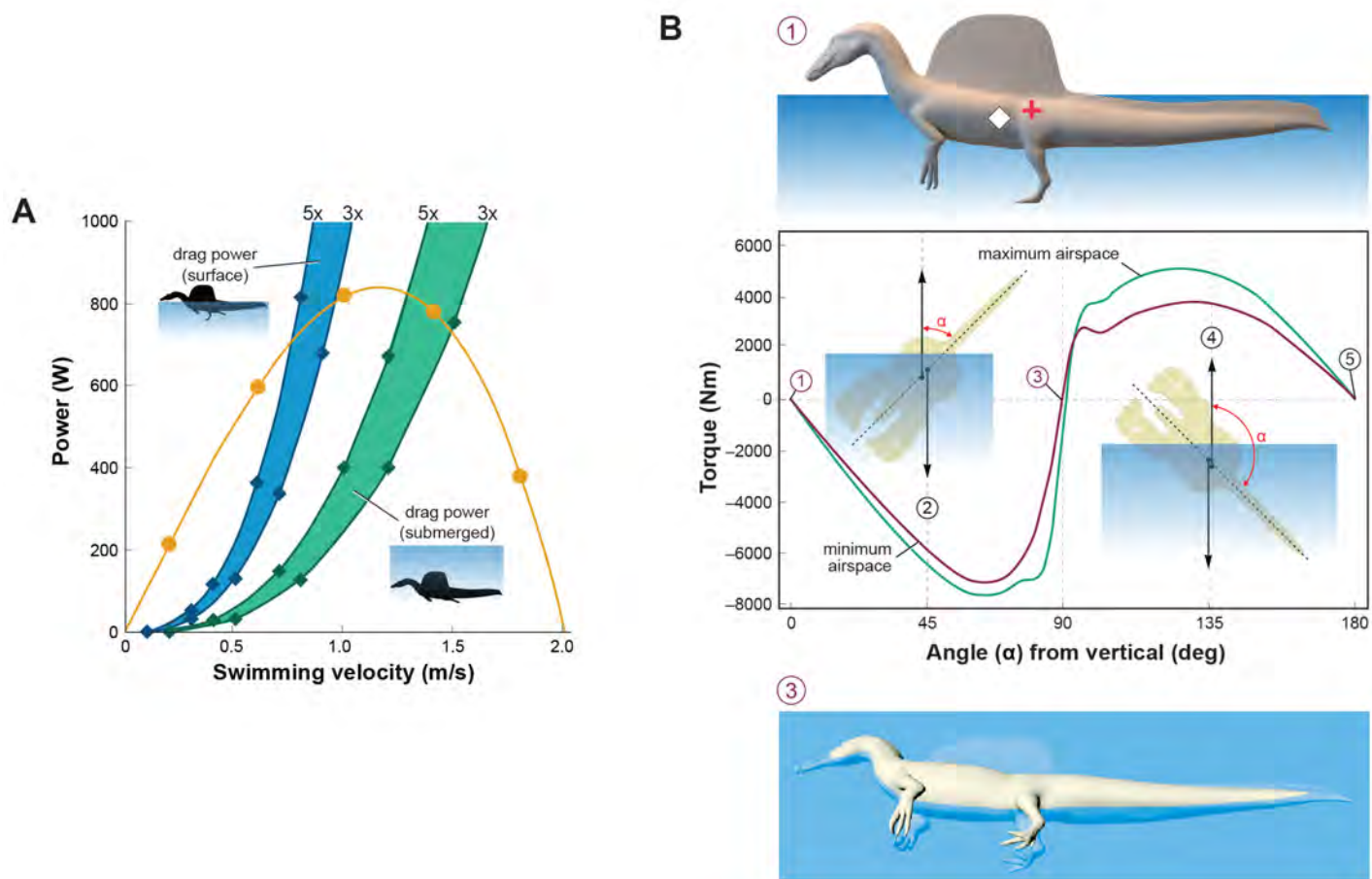


Figure 3. Biomechanical evaluation of *S. aegyptiacus* in water. (A) Tail thrust (yellow curve) and opposing drag forces as a function of swimming velocity at the surface (blue) and submerged (green), with drag during undulation estimated at 3 and 5 times stationary drag. **(B)** Stability curve for the flesh model of *S. aegyptiacus* in water showing torque between the centers of mass (cross) and buoyancy (diamond), unstable equilibria when upright or upside down (positions 1, 5), and a stable equilibrium on its side (position 3) irrespective of the volume of internal air space. Curves are shown for flesh models with minimum (magenta) and maximum (green) air spaces with a dashed line showing the vertical body axis and vector arrows for buoyancy (up) and center of mass (down).

234 *Swimming velocity* at the surface and underwater in extant lizards and crocodylians is powered
235 by foot paddling and axial undulation (hybrid swimming) and at moderate to maximum (critical)
236 speeds by axial undulation alone (axial swimming) (Fish, 1984; Grigg and Kirshner, 2015). We used
237 Lighthill's (1969) bulk momentum formula to estimate maximum surface and underwater swim-
238 ming velocity for the flesh model of *S. aegyptiacus*. Assuming a fully compliant *Alligator*-like tail (tail
239 amplitude: 0.24/body length, tail wavelength: 0.57/body length and tailbeat frequency: 0.25 Hz;
240 Fish (1984); Sato et al. (2007)), tail thrust (P_t) and maximum velocity (U) can be determined:

$$P_t = -164.93 + 1899.1U - 896.35U^2 \quad (1)$$

241 A body drag coefficient of 0.0035 assuming turbulent conditions was estimated for a Reynolds 242
number of 752,400 at a swimming speed of 1.0 m/s. The total power from estimates of drag in-243
creased three-to-five fold to account for undulation of the tail, near-surface wave formation and 244
increased sail drag when underwater (Figure 3A). The addition of the sail increases the drag on the 245
body of *S. aegyptiacus* by 33.4%. The intersection of the thrust power curve and drag power curves, 246
where the animal would be swimming at a constant velocity, indicates slow maximum velocity at 247
the surface (~0.8 m/s) and only slightly greater when submerged (~1.4 m/s) (Figure 3A). Maximum 248
tail thrust in *S. aegyptiacus* is 820 watts (683 N or 154 lbs), a relatively low value for the consider-249
able caudal muscle mass in this large theropod (Snivel and Russell, 2007). Only a minor amount 250
of caudal muscle power, however, is imparted to the water as thrust during undulation. As a re-251
sult, maximum velocity is only 1.2 m/s, an order of magnitude less than extant large-bodied (>1m) 252
pursuit predators. These species (mackerel sharks, billfish, dolphins and killer whales) are capable 253
of maximum velocities of 10 to 33 m/s (Tinsley, 1964; Fish, 1998; Fish and Rohr, 1999; Iosilevskii 254
and Weihs, 2008).

255 *Stability* and the capacity to right are important in water. When positioned upright in water,
256 the trunk sail of *S. aegyptiacus* is emergent (Figure 3B, position 1). The flesh model, however, is
257 particularly susceptible to long-axis rotation given the proximity of CM and CB, with stable equilib-
258 rium attained when floating on its side (Figure 3B, position 3). Righting requires substantial torque
259 (~5,000 Nm) that is impossible to generate with vertical limbs and a tail with far less maximum force
260 output (~700 N). This stability predicament remains even with the smallest internal air space. The
261 absence of vertical stability and righting potential in water stands in stark contrast to the condition
262 in extant crocodylians and marine mammals (Fish, 1998; Grigg and Kirshner, 2015).

263 *Maneuverability* in water (acceleration, turning radius and speed) wanes as body length increases
264 (Domenici, 2001; Parson et al., 2011; Domenici et al., 2014; Hirt et al., 2017; Gutarra and Rahman,
265 2022), which is further compromised in *S. aegyptiacus* by its rigid trunk and expansive, unretractable
266 sail. In contrast, large-bodied secondary swimmers capable of pursuit predation in open water
267 have fusiform body forms with a narrow caudal peduncle for efficient tail propulsion (ichthyosaurs,
268 cetaceans), control surfaces for reorientation, and narrow extensions (bills) to enhance velocity
269 in close encounters with smaller more maneuverable prey (Maresh et al., 2004; Domenici et al.,
270 2014). Besides some waterbirds, semiaquatic pursuit predators are rare and include only the small-
271 bodied (<2 m), exceptionally maneuverable otters that employ undulatory swimming (Fish, 1994).

272 *Diving* with an incompressible trunk requires a propulsive force (F_p) greater than buoyancy. For
273 *S. aegyptiacus*, in addition, a depth of ~10 m is needed to avoid wave drag (Figure 3A, bottom). The
274 propulsive force required to dive is approximately 17,000 N:

$$F_p = V_{\text{Body}} \times (\rho_{\text{Saltwater}} - \bar{\rho}_{\text{FleshModel}}) \times g \quad (2)$$

275

$$16,909\text{N} = 8.94\text{m}^3 \times (1026 - 833\text{kg}/\text{m}^3) \times 9.8\text{m}/\text{s}^2 \quad (3)$$

276 or approximately 25 times the maximum force output of the tail (ρ , density; $\bar{\rho}$, average density;
277 g , gravitational acceleration). Even with lizard-like internal air space, diving still requires approxi-
278 mately 15 times maximum force output of the tail. To initiate a dive, furthermore, the tail would

279 be lifted into the air as the body rotates about CB (**Figure 2D**), reducing significant tail thrust. The
280 now common depictions of *S. aegyptiacus* as a diving underwater pursuit predator contradict a
281 range of physical parameters and calculations, which collectively characterize this dinosaur as a
282 slow, unstable, and awkward surface swimmer incapable of submergence.

283 **Axial comparisons to aquatic vertebrates and sail-backed reptiles**

284 Axial flexibility is requisite for axial-propulsion in primary or secondary swimmers. However, in *S.*
285 *aegyptiacus*, trunk and sacral vertebrae are immobilized by interlocking articulations (hyposphene-
286 hypantrum), an expansive rigid dorsal sail composed of closely spaced neural spines and fused
287 sacral centra (**Figure 1A**).

288 The caudal neural spines in *S. aegyptiacus* stiffen a bone-supported tail sail by an echelon of
289 neural spines that cross several vertebral segments (**Figure 4A**). The caudal centra in *S. aegyptiacus*
290 have nearly uniform subquadrate proportions along the majority of the tail in lateral view. These
291 salient features of the tail suggest that it functioned more as a pliant billboard than flexible fluke.

292 No primary or secondary vertebrate swimmer has a comparable drag-magnifying, rigid dorsal
293 sail, including sailfish, the dorsal fin of which is fully retractable and composed of pliable spines in
294 membrane (**Domenici et al., 2014**). However, cranial crests and spine-supported torso-to-caudal
295 sails have evolved multiple times among extant lizard (agamids, iguanians, chameleons) for in-
296 traspecific display rather than aquatic propulsion. Semiaquatic sailfin and basilisk lizards (**Fig-**
297 **ure 4B**), for example, do not use their sails while swimming, spend very little time submerged,
298 and are not aquatic pursuit predators.

299 In contrast, the distal tail of secondary swimmers such as crocodylians (**Grigg and Kirshner,**
300 **2015**), mosasaurs (**Lindgren et al., 2013**) and cetaceans (**Fish, 1998**) is expanded with pliable soft
301 tissues free of bone to form a flexible caudal paddle or fluke (**Figure 4C**). Likewise, caudal centra pro-
302 portions in most secondary swimmers grade from subquadrate to spool-shaped in the distal half
303 of the tail to increase flexibility and undulatory amplitude (**Figure 4D**). Mosasaurs show a more de-
304 rived piscine pattern of more uniform, disc-shaped centra (**Lindgren et al. (2013)**; see **Appendix 2**).

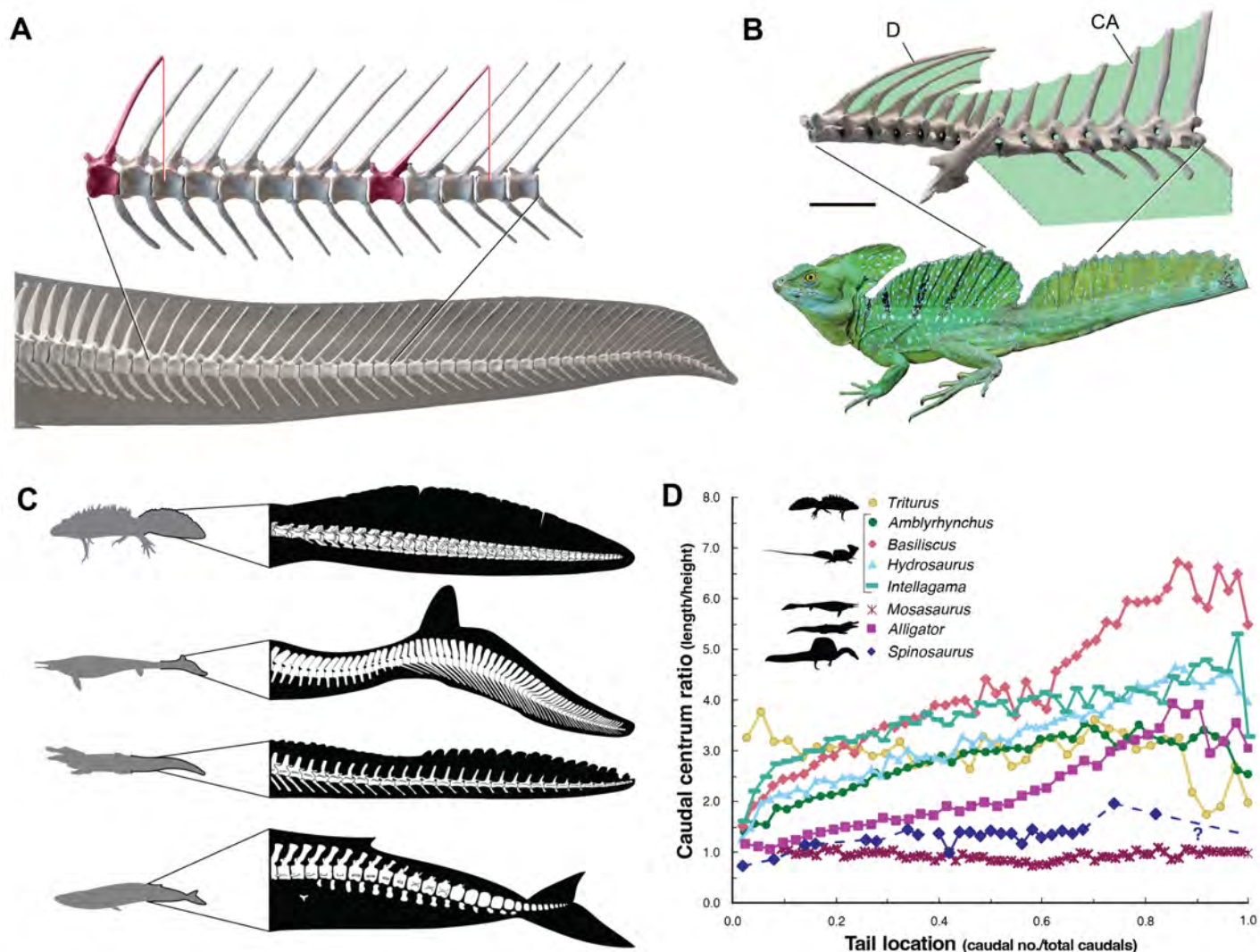


Figure 4. Skeletal comparisons between *S. aegyptiacus*, a basilisk lizard and secondarily aquatic vertebrates. (A) Tail in *S. aegyptiacus* showing overlap of individual neural spines (red) with more posterior vertebral segments. **(B)** Sail structure in the green basilisk (CT-scan enlargement) and in vivo form and coloration of the median head crest and sail (*Basiliscus plumifrons* FMNH 112993). **(C)** Tail flukes in a newt, mosasaur, crocodylian and whale. **(D)** Centrum proportions along the tail in the northern crested newt (*Triturus cristatus* FMNH 48926), semiaquatic lizards (marine iguana *Amblyrhynchus cristatus* UF 41558, common basilisk *Basiliscus basiliscus* UMMZ 121461, Australian water dragon *Intellagama lesueurii* FMNH 57512, sailfin lizard *Hydrosaurus amboinensis* KU 314941), an extinct mosasaurid (*Mosasaurus* sp. UCMP 61221; Lindgren et al. (2013)), an alligator (*Alligator mississippiensis* UF 21461), and *Spinosaurus* (*S. aegyptiacus* FSAC-KK 11888). Data in Appendix 2.

305 **Appendage comparisons to vertebrate secondary swimmers**

306 Appendage surface area in secondarily aquatic axial swimmers is minimized to reduce drag, be-
 307 cause terrestrial limbs are inefficient aquatic propulsors. Appendage surface area in *S. aegyptiacus*,
 308 in contrast, is substantially greater than in reptilian and mammalian secondary swimmers and
 309 even exceeds that of the terrestrial predators *Allosaurus* and *Tyrannosaurus* (Figure 5).

310 Interdigital webbing is used by some secondarily aquatic swimmers to increase the area of the
 311 foot paddle (Fish, 2004). Extant crocodylians use their limbs in paddling only at launch and slow
 312 speed before tucking them against the body (Grigg and Kirshner, 2015). Crocodylian interdigital
 313 webbing, which is better developed and always present in the hindfoot (Figure 6C, D), only modestly
 314 increases surface area (<20%). Across a range of body size, we show that crocodylian paddle area
 315 scales isometrically (Figure 6F; see Appendix 3). Thus, the crocodylian foot paddle becomes even

316 less effective as a propulsor with increasing body size. Nonetheless, a crocodylian of spinosaur
 317 size would have a foot paddle area an order of magnitude greater than is possible in *S. aegyptia-*
 318 *cus* (Figure 6E). Even a fully webbed hind foot in *S. aegyptiacus* (Figure 6A) is far too small to have
 319 functioned as a significant aquatic propulsor or for stabilizing control.

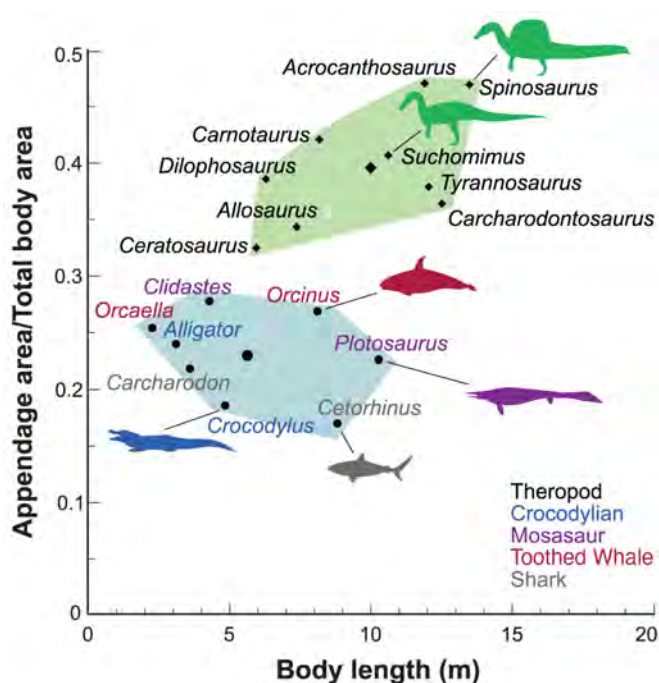


Figure 5. Appendage versus total body surface area in aquatic and semiaquatic vertebrates. *Spinosaurus aegyptiacus* and other non-avian theropods (green hull, diamonds) have appendages with considerable surface area compared to aquatic and semiaquatic vertebrates (blue hull, circles).

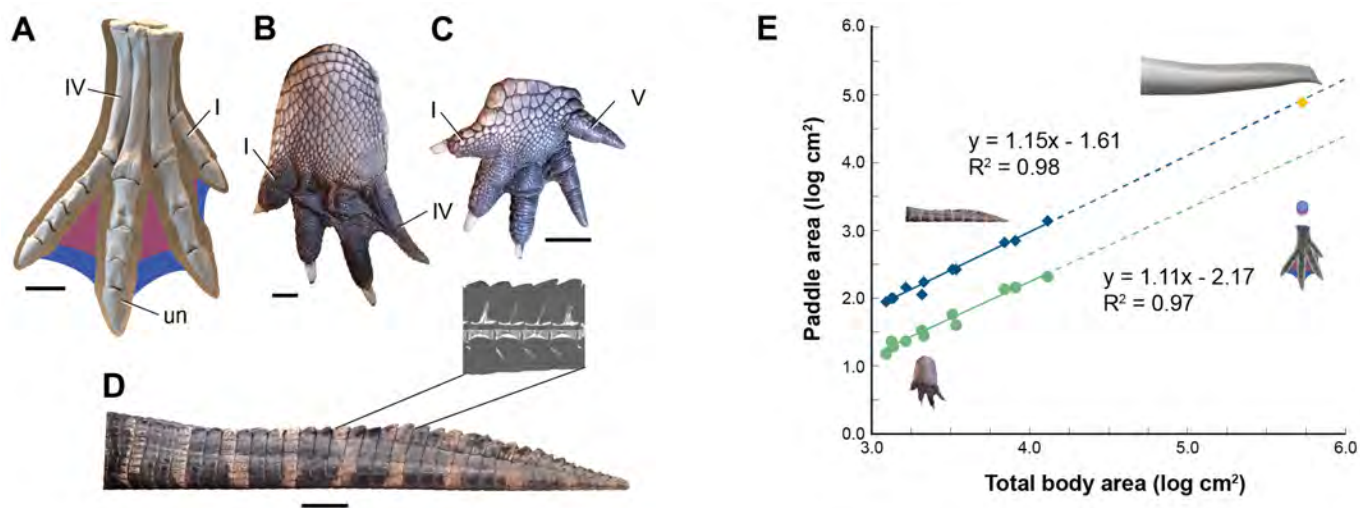


Figure 6. Appendage surface area and scaling of paddle surface areas in crocodylians. (A) Right hind foot of *S. aegyptiacus* (FSAC-KK 11888) showing the outlines of digital flesh based on the living ostrich (*Struthio camelus*) as well as partial (pink) and full (blue) interdigital webbing. (B) Hindfoot of an adult *Alligator mississippiensis* (WDC) in ventral view. (C) Forefoot of an adult *Alligator mississippiensis* (WDC) in ventral view. (D) Tail of an adult *Alligator mississippiensis* (WDC) in lateral view with CT visualization of vertebrae within the fleshy tail fluke. (E) Log-log plot of surface areas of webbed hindfoot and side of the tail as a function of total body area in a growth series for *Alligator mississippiensis* (hindfoot, green dots; tail, blue diamonds) and adult *S. aegyptiacus* (hindfoot, purple-blue dots; tail, yellow diamond). Abbreviations: I, IV, V digits I, IV, V, un, ungual. Scale bars are 10 cm (A) and 3 cm (B-D).

320 Paleohabitats and evolution

321 Most *Spinosaurus* fossils come from marginal basins along northern Africa in deltaic sediment laid
 322 down during an early Late Cretaceous transgression (**Figure 7A**, sites 1, 2). These deposits, however,
 323 also include the majority of non-spinosaurid dinosaur remains, all of which may have been trans-
 324 ported to some degree from inland habitats to coastal delta deposits. Because fossil transport is
 325 one way (downstream), documenting the inland fossil record is key to understanding true habitat
 326 range. We recently discovered fossils pertaining to *Spinosaurus* in two inland basins in Niger far
 327 from a marine coastline (**Figure 7A**, site 3). They were buried in fluvial overbank deposits alongside
 328 terrestrial herbivores (rebbachisaurid and titanosaurian sauropods) (see **Appendix 4**).

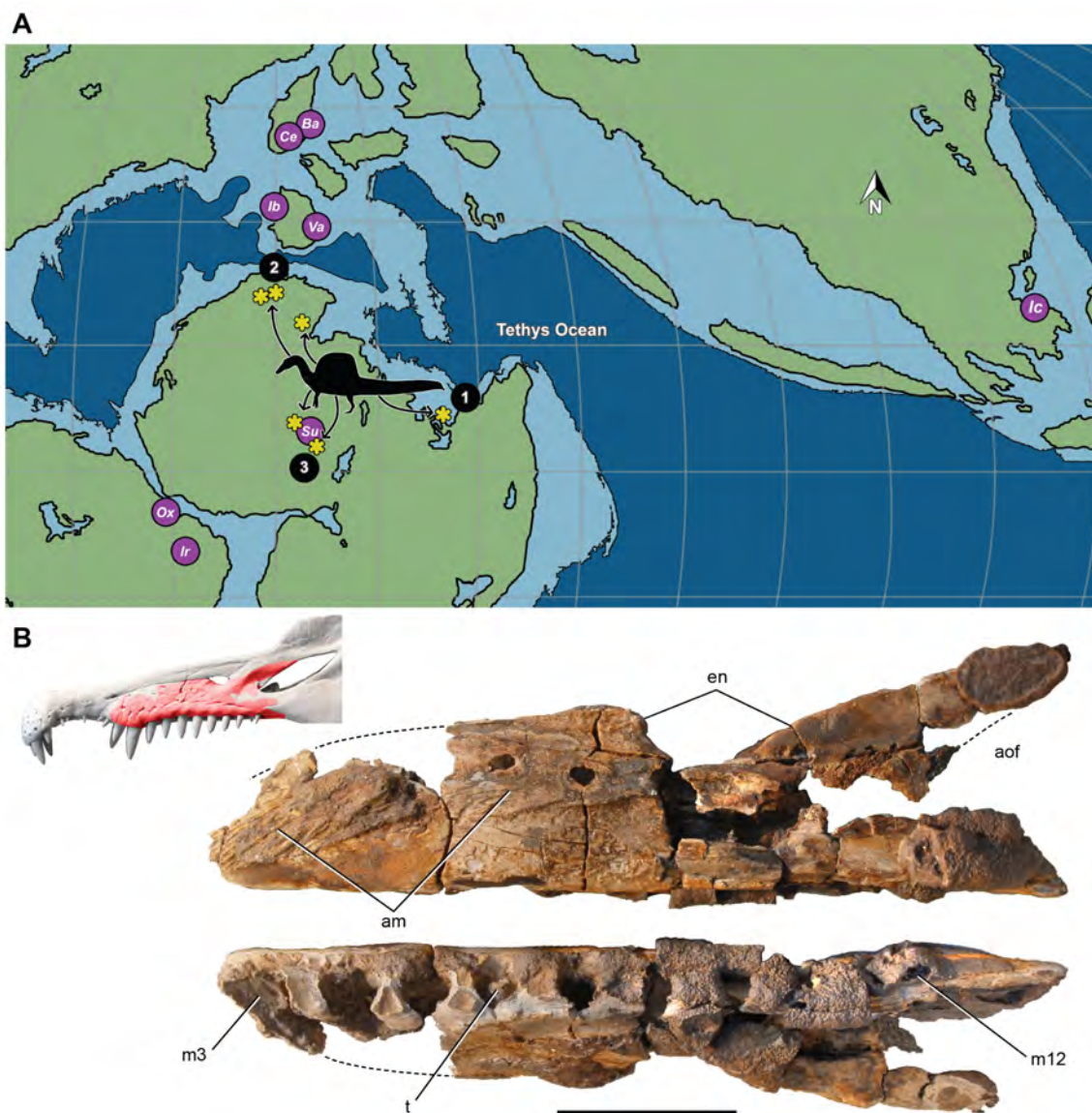


Figure 7. Paleogeographic location of spinosaurid fossils. (A) Paleogeographic map (early Albian, ~110 Mya; *Scotese (2014)*), showing the circum-Tethyan fossil localities for baryonychines (*Baryonyx*, *Suchomimus*) and spinosaurines (*Ichthyovenator*, *Vallibonavenatrix*, *Oxalaia*, *Irritator/Angaturama*, *Spinosaurus*). *Spinosaurus* localities (yellow asterisks) range across northern Africa from coastal (sites 1, 2) to inland (site 3) sites. **(B)** *Spinosaurus* sp. right maxilla (MNBH EGA1) from Égáro North (central Niger) in medial (top) and ventral (bottom) views and shown (red) superposed on the snout of *Spinosaurus aegyptiacus*. Abbreviations: 1, *S. aegyptiacus* holotype (Bahariya, Egypt); 2, *S. aegyptiacus* neotype (Zrigat, Morocco); 3, *Spinosaurus* sp. (Égáro North, Niger); am, articular rugosities for opposing maxilla; aofe, antorbital fenestra; Ba, *Baryonyx walkeri*; en, external naris; Ic, *Ichthyovenator laosensis*; Ir, *Irritator challenger/Angaturama limai*; m3, 12, maxillary tooth alveolus 3, 12; Ox, *Oxalaia quilombensis*; Su, *Suchomimus tenerensis*; t, tooth; Va, *Vallibonavenatrix cani*. Scale bar is 10 cm.

329 The inland location of these fossils undermines the interpretation of *S. aegyptiacus* as a “highly
330 specialized aquatic predator that pursued and caught its prey in the water column” (*Ibrahim et al.*,
331 **2020a**). All large-bodied secondarily aquatic vertebrates — both extant (e.g., sea turtles, sireni-
332 ans, seals, whales) and extinct (e.g., protostegid turtles, ichthyosaurs, metriorhynchoid crocodylo-
333 morphs, plesiosaurs) - are marine; none have been shown to live in both saltwater and freshwater
334 habitats. Secondarily aquatic vertebrates that live in freshwater habitats (*Evers and Benson, 2019*;
335 *Motani and Vermeij, 2021*). Secondarily aquatic vertebrates that live in freshwater habitats have
336 marine antecedents and are all small-bodied, such as river dolphins (<2.5 m length; *Hamilton et al.*
337 (2001)), small lakebound seals (<2 m; *Fulton and Strobeck (2010)*), the riverbound Amazonian man-
338 attee (<2.5 m; *Guterres-Pazin (2014)*), and a few mosasaurs and plesiosaurs of modest body size
339 (*Gao et al., 2016*). In contrast, large-bodied semiaquatic reptiles frequent coastal and inland lo-
340 cales today and in the past. *Sarcosuchus imperator* is among the largest of semiaquatic reptiles
341 (~12 m length; *Sereno et al. (2001)*) and lived in the same inland basin as *S. tenerensis*. The fossil
342 record supports our interpretation of *Spinosaurus* as a semiaquatic bipedal ambush predator that
343 frequented the margins of both coastal and inland waterways.

344 The large body size of *S. aegyptiacus* and antecedent species such as *S. tenerensis* also mitigates
345 against an aquatic interpretation for the former, as it would constitute the only instance among
346 vertebrates where the evolution of a secondarily aquatic species occurred at body size greater
347 than 2-3 m. All other large-bodied secondarily aquatic vertebrates (e.g., ichthyosaurs, plesiosaurs,
348 metriorhynchoid crocodylomorphs, protostegid turtles, mosasaurs, sirenians, whales) transitioned
349 to an aquatic lifestyle at small body size, radiating subsequently within the marine realm to larger
350 body size (*Domning, 2000; Polcyn et al., 2014; Moon and Stubbs, 2020; Motani and Vermeij, 2021*;
351 *Thewissen et al., 2009*).

352 Phylogenetic analysis of an enlarged dataset for spinosaurids clarifies piscivorous adaptations
353 in the earliest spinosaurids (stage 1) that enhance prey capture in shallow water and heighten
354 visual display (*Figure 8; Appendix 5*). In the skull, these include an elongate snout tipped with a
355 dental rosette for snaring fish, retracted external nares to inhibit water intake, and a prominent
356 nasal crest (*Charig and Milner, 1997; Sereno et al., 1998*). The ornamental crest over the snout is
357 accompanied by the evolution of a postcranial sail of varying height supported by neural spines of
358 the posterior dorsals, sacrals and caudal vertebrae (*Stromer, 1915; Sereno et al., 1998; Allain et al.,*
359 **2012; Barker et al., 2021**). The earliest spinosaurids, in addition, have “cervicalized” anterior trunk
360 vertebrae to enhance ventroflexion and the effective length of the neck, presumably as an adapta-
361 tion to feeding in water (*Hone and Holtz, 2021*). Using the second dorsal vertebrae of the terrestrial
362 predator *Allosaurus* for comparison, the homologous vertebra in spinosaurids shows marked mod-
363 ification (anterior face is convex, prominent ventral keel for muscular attachment, neural spine is
364 reduced, zygapophyses large and planar). Giraffids, for a similar purpose, have “cervicalized” the
365 first thoracic vertebra to facilitate dorsiflexion and effective neck length (*Lankester, 1908; Danowitz*
366 *et al., 2015; Müller et al., 2021*).

367 Other features present in stage 1 indicate that baryonychines (e.g., *Suchomimus, Baryonyx, Cer-*
368 *atosuchops*) have a low nasal crest and swollen brow ridges as ornamentation on the skull for
369 display or agonistic purposes, respectively. Neural spines over the trunk and tail are heightened
370 to a varying degree (*Figure 1B*). Spinosaurines (*Figure 1A; Figure 8*, stage 2) exhibit further special-
371 izations for display (heightened cranial crest, low cervical sail, hypertrophied torso-to-caudal sail)
372 and piscivory (spaced teeth with smooth carinae, smaller, more retracted external nares, scythe-
373 shaped manual unguals).

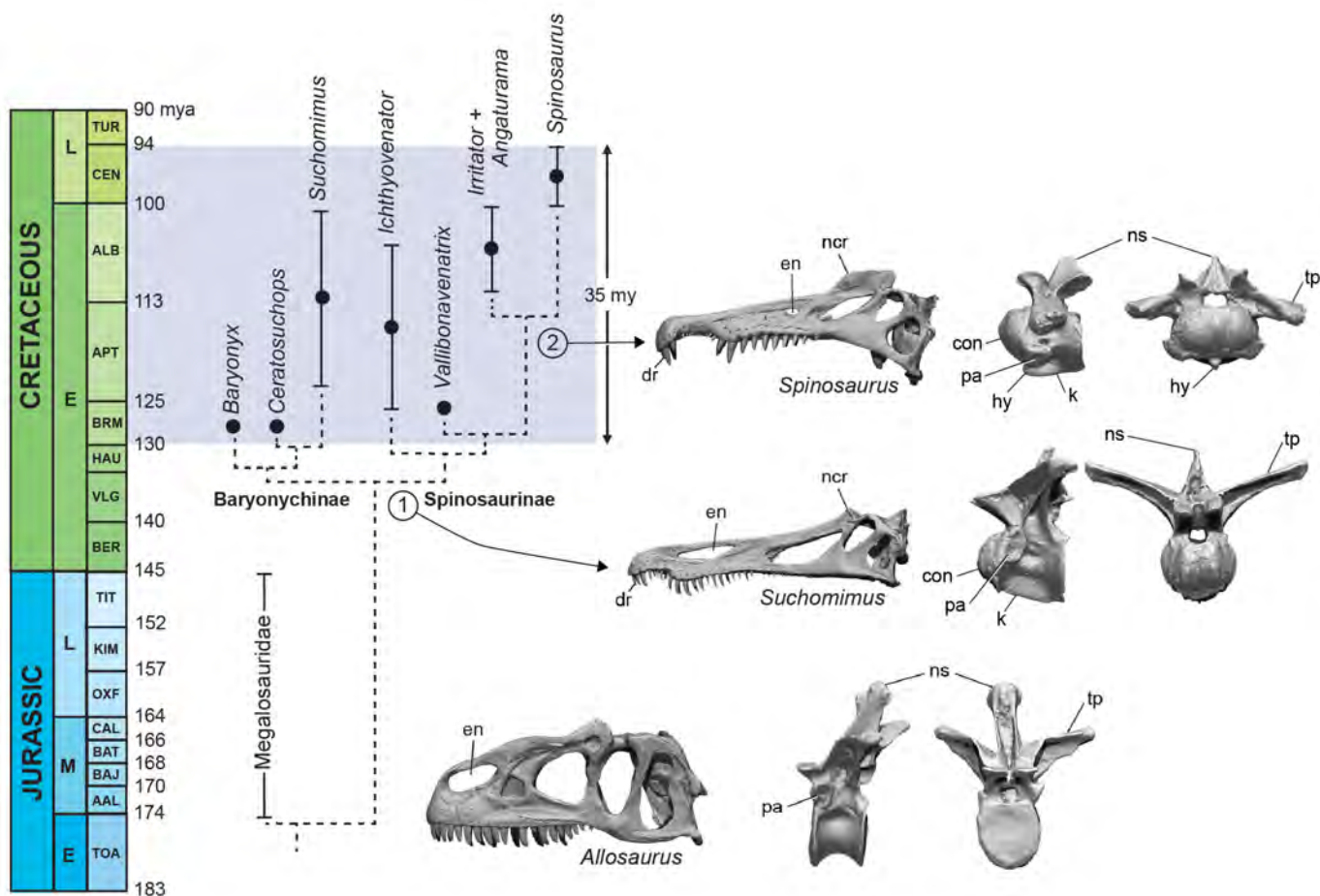


Figure 8. Calibrated phylogeny of spinosaurids (Barremian to Cenomanian, ~35 My). Updated phylogenetic analysis of spinosaurids resolves two stages in the evolution of piscivory and display. We show key cranial adaptations in the skull and highlight changes at the anterior end of the trunk to enhance neck ventroflexion (second dorsal vertebra in lateral and anterior views). Bottom, the fully terrestrial theropod *Allosaurus fragilis* (Madsen, 1976); middle, the baryonychine spinosaurid *Suchomimus tenerensis* (MNBH GAD70); top, the spinosaurine *Spinosaurus aegyptiacus* (BSPG 1912 VIII 19). Abbreviations: con, condyle; dr, dental rosette; en, external naris; hy, hypophysis; k, keel; ncr, nasal crest; ns, neural spine; pa, parapophysis; tp, transverse process.

Conclusions

374
375
376
377
378
379
380
381
382
383
384
385
386
387
388
389

1. Adult *S. aegyptiacus* had a body length of approximately 14 m with the axial column in neutral pose.
2. The reduced hind limb long bones in *S. aegyptiacus* are infilled to a varying degree probably as an adaptation to weight support on land, because the added mass from infilling is more than offset by significant paraxial pneumaticity along the length of the presacral column. Medullary cavities, in addition, are common in forelimb long bones and in anterior caudal centra.
3. The segment-crossing caudal neural spines in *S. aegyptiacus* suggest that its tail functioned more as a pliant billboard than flexible fluke. Similar spine-supported torso-to-caudal sails in extant reptiles are used for display rather than in swimming. The expanded keels on the tail of extant and extinct vertebrate secondary swimmers, in contrast, is composed mostly of pliable soft tissues free of bone.
4. *S. aegyptiacus*, like *S. tenerensis* and other spinosaurids, was bipedal on land with its center of mass positioned over its hind feet. The long-clawed forelimbs of *S. aegyptiacus* were not used in weight support on land.

- 390 5. An adult flesh model of *S. aegyptiacus* has a body mass of ~7400 kg and average density of
391 ~830 kg/m³, which is considerably less than the density of saltwater (1,026 kg/m³).
- 392 6. *S. aegyptiacus* could wade into shallow water for feeding with flotation occurring at water
393 depth greater than ~2.6 m.
- 394 7. *S. aegyptiacus* was incapable of diving, given its buoyancy and incompressible trunk. Full sub-
395 mergence would require 15-25 times the maximum force output of its tail, depending on
396 estimated lung volume.
- 397 8. *S. aegyptiacus* was unstable in deeper water with little ability to right itself, swim, or maneuver
398 underwater. Maximum power from its tail, assuming it could undulate as in *Alligator*, is less
399 than 700N, which would generate a top speed of ~1m/s, an order of magnitude slower than
400 extant large-bodied pursuit predators.
- 401 9. All extant and extinct large-bodied (>2m long) secondarily aquatic vertebrates are strictly ma-
402 rine, whereas fossils pertaining to *Spinosaurus* have been found in inland basins distant from
403 a marine coast.
- 404 10. Transition to a semiaquatic lifestyle, as occurred in the evolution of spinosaurid theropods,
405 can occur at any body size. In contrast, transition to an aquatic lifestyle among tetrapods
406 has only occurred at relatively small body size (<3 m) with subsequent radiation once in the
407 marine realm into larger body sizes.
- 408 11. *S. aegyptiacus* is interpreted as a semiaquatic shoreline ambush predator more closely tied
409 to waterways than baryonychine spinosaurids.
- 410 12. Spinosaurids flourished over a relatively brief Cretaceous interval (~35 My) in circum-Tethyan
411 habitats with minimal impact on aquatic habitats globally.
- 412 13. Two phases are apparent in evolution of aquatic adaptations among spinosaurids, the second
413 distinguishing spinosaurines as the most semiaquatic (but not aquatic) non-avian dinosaurs.

414 **Materials and Methods**

415 **Skeletal reconstruction**

416 The composite skeletal reconstruction of *S. aegyptiacus* is based principally on bones of holotypic
417 and neotypic specimens supplemented by associated and isolated bones from Cenomanian-age
418 formations in Egypt, Morocco and Niger (**Figure 1A**). The two most important specimens include
419 the subadult partial skeleton composing the holotype (BSP 9012 VIII 19) from the Western Desert
420 of Egypt (**Stromer, 1915; Smith et al., 2006**) and a subadult partial skeleton designated as the neo-
421 type from the Kem Kem Group in Morocco (FSAC-KK 11888; **Ibrahim et al. (2014, 2020b)**). A third re-
422 ferred specimen from Egypt was also considered (BSPG 1922 X45, "*Spinosaurus B*"; **Stromer (1934)**).
423 These are the only associated specimens known for *Spinosaurus aegyptiacus* on which to base the
424 skeletal reconstruction, the relative size calculated from overlapping bones (**Table 1**). Of these
425 three specimens, only the bones of the neotype are preserved, all of which have been CT-scanned
426 except for recently discovered bones of the tail (**Ibrahim et al., 2020a**). Noteworthy isolated spec-
427 imens have been recovered from the Kem Kem Group in Morocco, including a large snout and
428 manual phalanx used to gauge maximum adult body size.

Table 1. Relative size of specimens in the skeletal reconstruction of *S. aegyptiacus*. Relative sizes of key specimens used in the skeletal model of *S. aegyptiacus* (nos. 1-4) and select bones (nos. 5, 6) from Egypt and Morocco. All are scaled to the size of the adult snout (MSMN V4047).

No.	Specimen	Maturity	Relative Size	Linear Up-sizing	Description
1	BSPG 1912 VIII 19	subadult	76%	1.32	Holotype (destroyed) preserving dentaries, presacral, sacral and caudal vertebrae including the dorsal sail (<i>Stromer, 1915</i>)
2	FSAC-KK 11888	subadult	76%	1.32	Neotype preserving skull bones, partial limbs, dorsal sail and most of the tail (<i>Ibrahim et al., 2014</i>)
3	BSPG 1922 X 45	subadult	66%	1.51	" <i>Spinosaurus B</i> " (destroyed) fragmentary specimen with 5 partial dorsals (~D1 centrum, mid dorsal centrum, partial ~D13 vertebra), 7 partial caudal vertebrae, and both tibiae (<i>Stromer, 1934</i>)
4	MSMN V4047	adult	100%	—	Isolated snout with broken teeth (<i>Dal Sasso et al., 2005</i>)
5	UCRC PV8	adult	80%	1.25	Large manual phalanx I-1 (28.0 cm length) of an adult within reach but still smaller than the 35 cm length estimated on the basis of the proportions in the manus of <i>Angaturama</i> (? = <i>Irritator</i>) scaled to the adult snout (<i>Aureliano et al., 2018</i>)
6	UCRC PV24	adult	75%	1.33	Large Kem Kem vertebra, ~C9, from Gara Sbaa (centrum length 11.6 cm, centrum width 14.0 cm)

429 We incorporated all CT-scanned bones of the neotype and reconstructions (based on litho-
 430 graphic plates and photographs) of bones of the holotype and referred specimen from Egypt. For
 431 unknown bones without sequential adjacency as a guide, other spinosaurids were consulted for
 432 shape and proportion. In the case of overlapping bones, priority was given to the neotype (blue)
 433 followed by the holotype (red) and referred specimens (yellow). Bones without representation
 434 among specimens attributed to *Spinosaurus aegyptiacus* are shaded gray (*Figure 1A*).

435 **Skeletal reconstructions compared**

436 We compared our digital skeletal model of *S. aegyptiacus* to the recently published two-dimensional
 437 silhouette skeletal reconstruction in the aquatic hypothesis (*Ibrahim et al., 2020a*), both of which
 438 are based primarily on holotypic and neotypic specimens (*Figure 9*). We registered the reconstruc-
 439 tions to each other by superimposing the four longest complete bones of the neotype (femur, tibia,
 440 ilium, ischium). Significant differences are apparent in several dimensions with major implications
 441 for the calculation of center of mass and buoyancy.

442 When aligned at the hip, sacral and caudal columns have nearly identical length, but the pre-
 443 sacral column is significantly longer (~10%) in the reconstruction of the aquatic hypothesis. The
 444 extra length of the presacral column is located in the neck between C2-10 and torso between D4-
 445 13. The trunk in our digital skeletal model is also not as deep as that in skeletal silhouette drawing,
 446 as can be seen by aligning the skeletons along the dorsal column (*Figure 9C*). The contour of the
 447 belly marked by the gastral basket and the coracoids of the pectoral girdle extend farther ven-
 448 trally (~25%) than the ends of the pubes, unlike our digital reconstruction or that of most other
 449 silhouette reconstructions for non-avian theropods. The length of the ribcage in our model are
 450 consistent with the only well preserved spinosaurid ribcage known to date (*Suchomimus tenerensis*,
 451 MNBH GAD70).

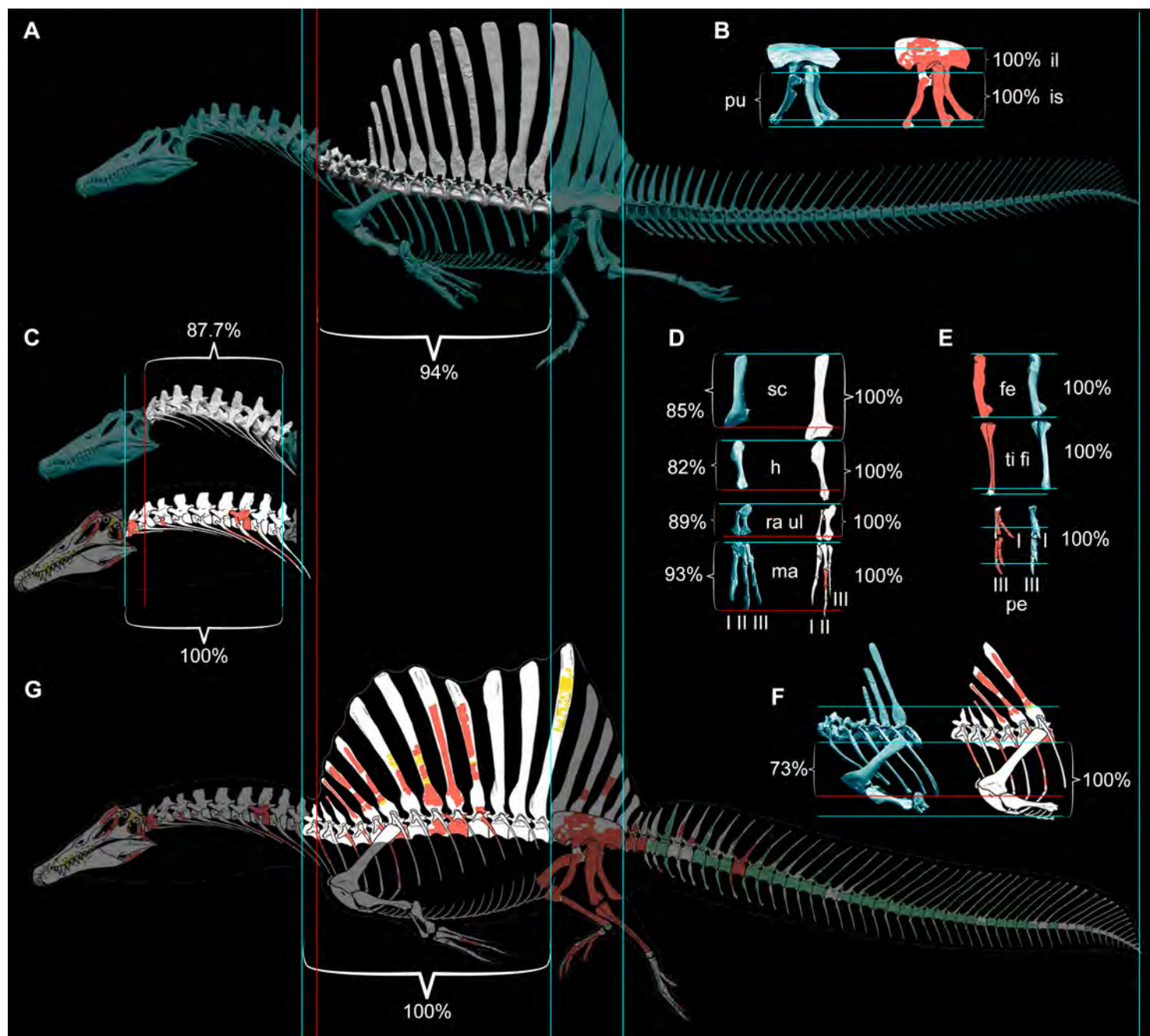


Figure 9. Comparison of skeletal reconstructions for *S. aegyptiacus* in left lateral view (A) Digital skeletal reconstruction from this study in left lateral view. **(B)** Pelvic girdle. **(C)** Cervical column (C1-10). **(D)** Pectoral girdle and forelimb. **(E)** Hind limb. **(F)** Anterior trunk. **(G)** Silhouette skeletal drawing from the aquatic hypothesis (from Ibrahim et al. (2020a)). On one side of each length comparison, one or two blue lines are shown that register the alternative reconstructions. The opposing end of each length comparison either has a single blue line (when comparisons match, both 100%) or a red line as well for the shorter one (<100%). Skeletal reconstructions (A,G) are aligned by the anterior and posterior margins of the ilium and measured to the cervicodorsal junction (C10-D1); the pelvic girdle (B) is aligned along the ventral edge of the sacral centra and base of the neural spines and measured to the distal ends of the pubis and ischium; the cervical column (C) is aligned at the cervicodorsal junction (C10-D1) and measured to the anterior end of the axis (C2); the scapula and components of the forelimb (humerus, ulna, manual digit II, manual phalanx II-1) (D) are aligned at the distal end of the blade and their proximal ends, respectively, and measured to the opposing end of the bone; the components of the hind limb (femur, tibia, pedal digits I, III) (E) are aligned at their proximal ends and measured to the opposing end of the bone; and anterior trunk depth (F) is aligned along the ventral edge of the centrum and neck of the spine of D6 and measured to the ventral edge of the coracoid. All limb bones compared are from the left side with the exception of the pes, which is from the better preserved right side of the neotype. Abbreviations: I, II, III, digits I-III; II-1, phalanx II-1; fe, femur; h, humerus; il, ilium; is, ischium; ma, manus; pe, pes; pu, pubis; sc, scapula; ti, tibia; ul, ulna.

452 Finally, the forelimb in the skeletal silhouette drawing is approximately 30% longer than that in
453 our digital reconstruction (**Figure 9A**). The neotype is the only associated specimen of *S. aegyptiacus*
454 preserving bones from the forelimb (partial manual digit II). The preserved manual phalanges are
455 slender with deeply cleft distal condyles, which allows reference of additional phalanges of similar
456 form from the Kem Kem Group (**Figure 1D**). Our reconstruction of the manus is based on a recently
457 described forelimb of the close relative *Irritator* (= *Angaturama*; **Machado and Kellner (2009)**; **Aure-**
458 **liano et al. (2018)**). The proportions of more proximal forelimb segments and the pectoral girdle
459 are based on the holotypic specimens of *Baryonyx* and *Suchomimus*. The forelimb in *S. aegyptiacus*
460 is robust and long relative to other non-avian theropods, although considerably shorter than in
461 some previous reconstructions (**Ibrahim et al., 2014, 2020a**).

462 The longer presacral proportions, deeper torso, and longer forelimb of the skeletal reconstruc-
463 tion and flesh model used by the aquatic hypothesis cantilever significant additional body mass an-
464 terior to the hip joint. That additional front-loading appears to be the main factor generating their
465 mid trunk location for center of mass and the basis for regarding *S. aegyptiacus* as quadrupedal on
466 land (**Ibrahim et al., 2020a**).

467 **Flesh reconstruction of axial musculature**

468 To estimate the volume of axial musculature in *S. aegyptiacus* (**Figure 10**), we referenced CT-based
469 studies on the ostrich (*Struthio*; **Wedel (2003)**; **Snively and Russell (2007)**; **Persons IV et al. (2020)**)
470 and alligator *Alligator* (**Cong, 1998**; **Mallison et al., 2015**). To estimate caudal muscle mass, we used
471 CT scans of various reptiles including the sail-backed basilisk lizard, *Basiliscus plumifrons* (**Figure 11**,
472 **Table 2-5**).

473 For epaxial muscle mass in *S. aegyptiacus*, we estimated its vertical extent as twice centrum
474 height, measuring upward from the base of the neural spine. The transverse width of epaxial
475 musculature was estimated to be a little less than that of the hypaxial muscles, widest ventrally
476 and tapering to the midline dorsally. For hypaxial muscle mass in *S. aegyptiacus*, we estimated
477 its vertical depth at approximately twice chevron length in the anterior tail and 1.5 times chevron
478 length in mid and posterior portions of the tail. We estimate the transverse width of hypaxial
479 muscles as twice the length of the transverse processes. CT cross-sections of extant reptiles show
480 that considerable muscle mass is present beyond the distal end of caudal transverse processes in
481 anterior and middle portions of the tail (**Figure 10**).

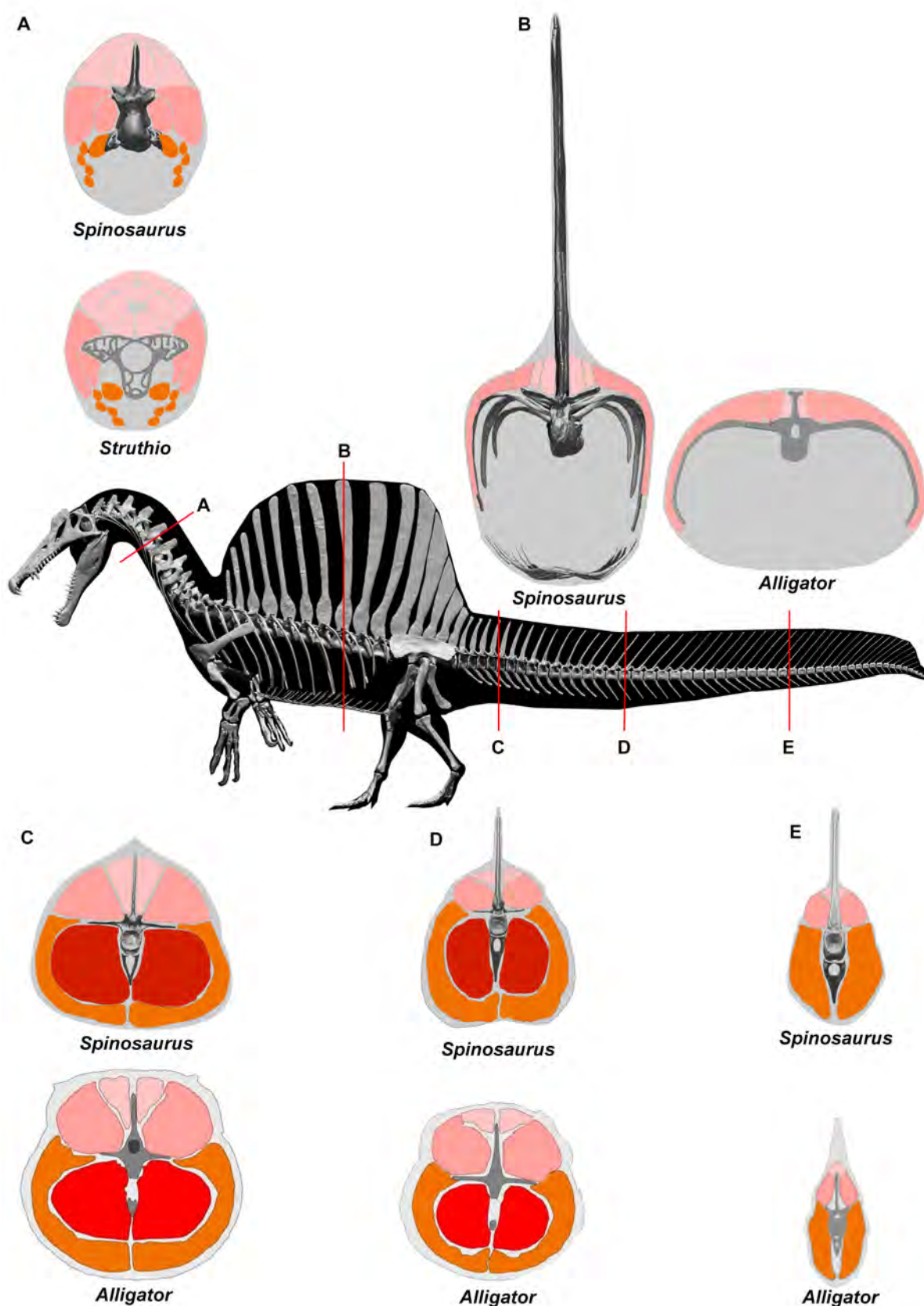


Figure 10. Cross sections for the flesh model of *S. aegyptiacus* compared to CT-based cross sections from ostrich and alligator (after *Wedel (2003); Böhmer et al. (2019); Mallison et al. (2015); Cong (1998)*). Cross sections at (A) Mid neck, (B) Mid trunk, (C) Anterior tail, (D) Mid tail, and (E) Distal tail. Epaxial muscles pink; hypaxial muscles orange; caudofemoralis muscle in red.

482 Several cross-sections from *Basiliscus plumifrons* (crested basilisk) provided valuable insights
483 on the distribution of axial muscles in a lizard with a dorsal-to-caudal sail (**Figure 11, Table 2-5**).
484 Epaxial musculature in the trunk and tail comprises less than one-third of total axial muscle vol-
485 ume (**Table 2**). Caudal neural spines project beyond the epaxial musculature to support the sail to
486 a greater extent in mid and distal portions of the tail. At the base of the tail (CA4), approximately
487 one-third (29.3%) of the neural spine projects dorsally supporting the sail. At mid tail (CA15), ap-
488 proximately three-quarters (76.8%) of the neural spine projects dorsally supporting the sail. The
489 hypaxial musculature extends well below the distal end of the chevrons. At the base of the tail (CA4),
490 the chevron lies internal to approximately one-half (52.6%) of hypaxial muscle depth, with the re-
491 mainder (47.4%) distal to the end of the chevron. Farther along the tail (CA10-15), the chevrons
492 are proportionately longer, supporting approximately two-thirds (67%) of hypaxial muscle depth
493 with approximately one-third of hypaxial musculature beyond the distal end of the chevron. These
494 cross-sections confirm the presence of considerable muscle mass ventral to the distal end of the
495 chevrons in anterior through mid portions of the tail (**Figure 10, Figure 11**).

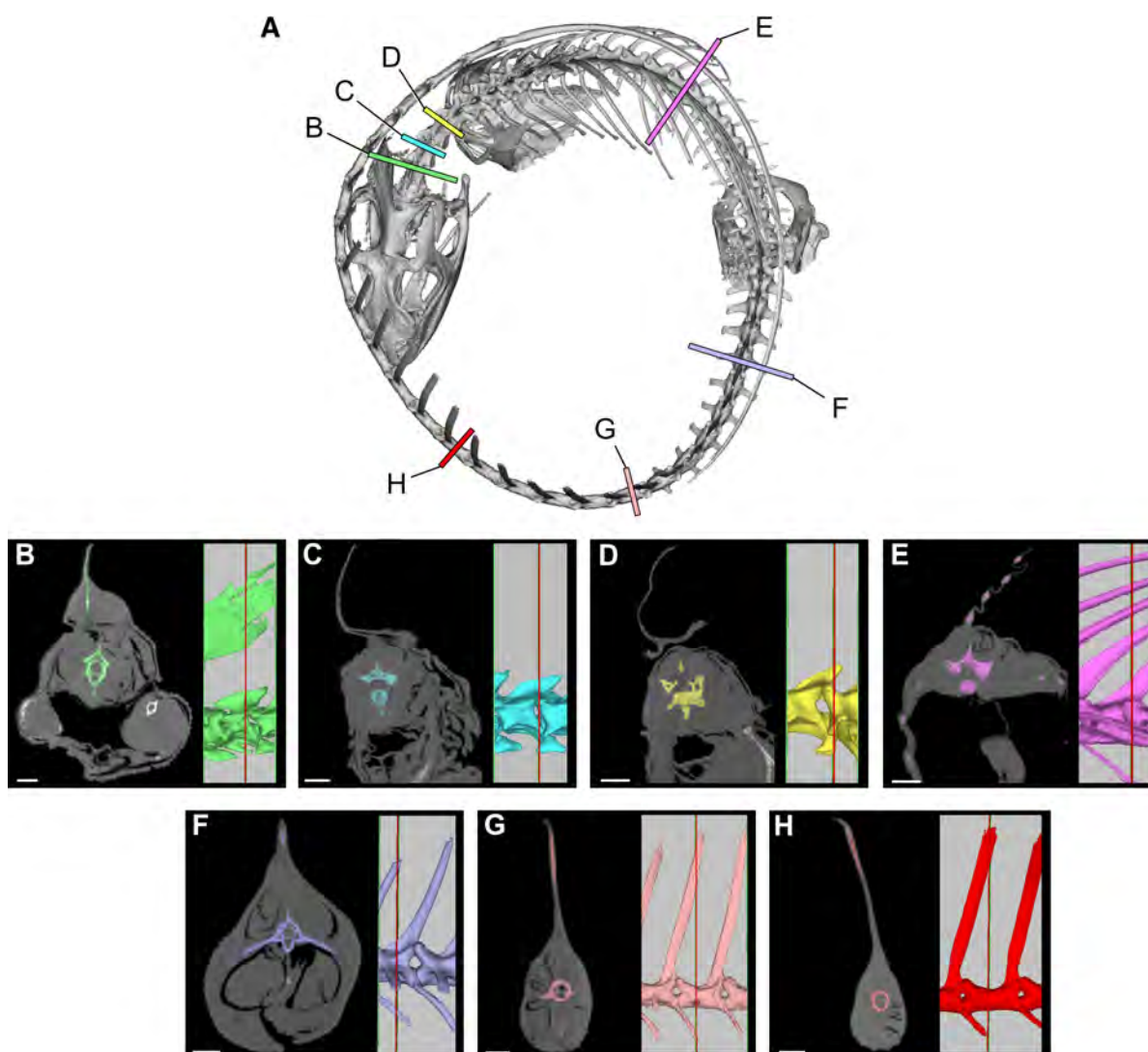


Figure 11. Cross-sections from a CT scan of a male *Basiliscus plumifrons* FMNH 112993. (A) Skeleton showing position of computed-tomographic sections of the axial column. **(B)** Anterior cervical region (C2). **(C)** Mid cervical region (C3). **(D)** Posterior cervical and anterior dorsal region (C4-D1). **(E)** Mid dorsal region (D12). **(F)** Anterior caudal region (CA4). **(G)** Caudal region at most posterior transverse process (CA10). **(H)** Mid caudal region (CA15). CT scan data available on Morphosource.org. Abbreviations: C, cervical; CA, caudal; D, dorsal. Scale bars, 5mm.

Table 2. Axial muscle area in the crested basilisk. Area measurements of epaxial and hypaxial musculature along the axial column in the crested basilisk *Basiliscus plumifrons* (FMNH 112993). C, cervical; D, dorsal; CA, caudal.

Location	Total area	Epaxial area		Hypaxial area	
	mm ²	mm ²	% total	mm ²	% total
Anterior neck (C2)	180.4	83.9	46.5	96.5	53.5
Mid neck (C3)	139.7	54.9	39.3	84.8	60.7
Posterior neck (C4-D1)	202.1	69.8	34.7	132.3	65.3
Mid dorsal (D12)	212	60	28.3	152	71.7
Basal tail (CA4)	434	153.8	35.4	280.2	64.6
Anterior tail (CA10, last transverse process)	221.7	63.5	28.6	158.2	71.4
Mid tail (CA15)	97.8	29.8	29.8	68	70.2

Table 3. Axial muscle and transverse process length in the crested basilisk. Transverse processes versus muscle width in the tail cross-sections in the crested basilisk *Basiliscus plumifrons* (FMNH 112993). Measurements are from the midline to the distal end of the transverse process (or centrum margin when there is no process) and to the lateral surface of the tail.

Location	Measurement	Total (mm)	% bone and muscle	% muscle only
CA4	transverse process width	16.8	62.9	37.1
	total width	26.7		
CA10	transverse process width	8.1	57	43
	total width	14.2		
CA15	centrum width	3.5	36.8	63.2
	total width	9.5		

Table 4. Epaxial muscle height and neural spine height in the crested basilisk. Height of neural spines versus epaxial musculature in tail cross-sections in the crested basilisk *Basiliscus plumifrons* (FMNH 112993). Measurements are from the dorsal surface of the centrum to the top of the epaxial muscle and to the distal end of the neural spine.

Location	Measurement	Total (mm)	% neural spine adjacent to muscle	% neural spine above muscle
CA4	neural spine height	18.4	70.7	29.3
	epaxial mm. height	13.0		
CA10	neural(1) spine height	33.6	32.1	67.9
	epaxial mm. height	10.8		
CA15	neural spine height	34.5	23.2	76.8
	epaxial mm. height	8.0		

Table 5. Hypaxial muscle depth and chevron length in the crested basilisk. Chevron length versus hypaxial muscle depth in tail cross-sections in the crested basilisk *Basiliscus plumifrons* (FMNH 112993). Measurements are from the ventral surface of the centrum to the distal tip of the chevron and to the ventral surface of the tail.

Location	Measurement	Total (mm)	% chevron length	% muscle below chevron
CA4	chevron depth	9	52.6	47.4
	hypaxial depth	17.1		
CA10	chevron depth	7.1	67	33
	hypaxial depth	10.6		
CA15	chevron depth	4.8	67.6	32.4
	hypaxial depth	7.1		

496 **Flesh model density partitions, dimensions and properties**

497 The digital skeletal model was wrapped in flesh (using ZBrush) guided by recent documentation of
 498 muscle mass in CT scans of various modern analogs (Wedel, 2003; Snively and Russell, 2007; Malli-
 499 son et al., 2015; Persons IV et al., 2020; Díez Díaz et al., 2020). We inserted anatomically-shaped and
 500 -positioned air spaces (pharynx-trachea, paraxial air sacs, lungs) of optional volumes (minimum-
 501 lizard, medium-crocodylian, maximum-avian) within the head, neck and torso (Figure 2C). For ad-
 502 ditional measurements, we added a “mesh” over the flesh model (Henderson (1999); Figure 2D).

503 We divided the flesh model into six parts (axial body-presacral, axial-caudal, dorsal-to-caudal
 504 sail, forelimbs, hindlimbs, lungs) in order to assign appropriate densities (Table 6). Densities were
 505 assigned to body parts based on their estimated composition, using values for tissues ranging from
 506 fat (900 gm/l) to compact bone (2,000 gm/l). The average whole body density for *S. aegyptiacus*,
 507 833 gm/l (Table 6), compares favorably to whole body density estimates for various non-avian di-
 508 nosaurs (800-900 gm/l). We have compiled various functional dimensions of the adult flesh model
 509 (Table 7), and we divided the flesh model into 10 body parts, for which we list volumes and external
 510 surface areas (excluding cut surfaces) (Table 8).

Table 6. Density, volume and mass in the flesh model of *S. aegyptiacus*. Whole body and body part densities, volumes and masses for the new mesh adult flesh model of *S. aegyptiacus*.

No.	Body Partition	Average density (kg/m ³)	% of Axial volume without sail	Mass (kg)
1	Whole body	833	—	7,390
2	Axial body (excluding lung/sail)	788	100	5,794
3	Axial head-trunk (not lung/sail/tail)	850	64.8	3,209
4	Axial tail (not sail)	1,000	35.2	2,585
5	Forelimb (paired)	1,050	3.8	108
6	Hind limb (paired)	1,050	11.1	590
7	Dorsocaudal sail	1,196	8.5	441
8	Lungs	0	12.5	0

Table 7. Flesh model functional dimensions in *S. aegyptiacus*. Functional dimensions for the adult flesh model of *S. aegyptiacus* in sculling pose.

No.	Dimension	Measure (m)
1	Total body length (sculling pose)	13.53
2	Body length minus tail (sculling pose)	6.92
3	Head length	1.57
4	Neck length (sculling pose)	2.18
5	Trunk depth (mid trunk, without sail)	1.28
6	Trunk sail depth (mid trunk)	1.93
7	Trunk sail length (maximum at base)	3.53
8	Tail length	6.61

Table 8. Flesh model volume and surface area in *S. aegyptiacus*. Adult flesh model whole body and body part volumes and surface areas as measured in MeshLab. Surface area of body parts does not include cut surfaces.

No.	Body Part	Volume (m ³)	Surface Area (m ²)
1	Whole body	8.94	54.06
2	Body above waterline (floating)	1.65	22.58
3	Body below waterline (floating)	7.27	31.38
4	Head	0.21	2.23
5	Neck	0.78	4.37
6	Trunk	4.01	11.44
7	Trunk sail (both sides, external edge)	0.40	10.06
8	Forelimb (both)	0.24	3.86
9	Hind limb (both)	0.45	5.29
10	Tail	2.81	16.56
11	Tail with axial muscle	2.71	13.27
12	Tail sail only	0.10	3.17
13	Airspace-minimum (~4% volume)	0.37	4.86
14	Airspace-medium (~8% body volume)	0.67	6.63
15	Airspace-maximum (~12% body volume)	1.08	8.66

511 We registered center of mass (CM) as the horizontal distance from the apex of the acetabu-
 512 lum (*x*-coordinate) and the vertical distance from the ground surface under the sole of the foot
 513 (*y*-coordinate) (**Table 9**, no. 4). This is the fourth estimation of center of mass for *S. aegyptiacus*, and
 514 we argue here the most accurate. We prefer a measure from the acetabulum rather than the distal
 515 tail tip, which as in *S. aegyptiacus* is often a matter of speculation given the rarity of completely pre-
 516 served caudal columns (**Hone, 2012**). For the acetabulum, we recommend using its “apex” rather
 517 than its “cranial end” (**Ibrahim et al., 2020a**) for three reasons. First, the apex of the acetabulum is a
 518 more easily recognized landmark than the poorly defined anterior edge (or rim) of the acetabulum.
 519 Second, the apex rather than the “cranial end” of the acetabulum, is a more functionally intuitive
 520 point from which to measure center of mass, given its proximity to the rotational point for body
 521 mass centered over the hind limbs. And third, the dorsal (proximal) articular end of the femoral
 522 head is close to the apex of the acetabulum, and so length the femur and the distance that CM lies
 523 farther forward can be directly compared (CM located anteriorly beyond femoral length excludes
 524 stable bipedal posture with a relatively horizontal dorsosacral column).

Table 9. Center of mass (CM) calculations for *S. aegyptiacus*. There have been four estimates for the location of CM in flesh models of *S. aegyptiacus* using four different points of origin as a reference. Because three were based on an adult flesh model, we convert the one study based on a subadult (number 3) to reflect its position in an adult flesh model.

No.	Author/Result	x-origin	CM (cm)		Notes
			(x = anterior to origin)		
			x	y	
1	<i>Ibrahim et al. (2014); quadruped</i>	hip joint	>81	—	Based on an adult flesh model, no coordinates given, CM shown graphically under D10 and said to be anterior to hip/knee joints at a distance greater than femur length (MeshLab calculation error)
2	<i>Henderson (2018); biped</i>	tip of tail	8,850	100	Based on a 3D mesh model based on the adult skeletal model of Ibrahim et al. (2014) with estimated length 16 m long; y-coordinate origin is “lowest point of axial body”
3	<i>Ibrahim et al. (2020a); quadruped</i>	“cranial rim” of acetabulum	72.5 - 82.5 (adult = 95.7-108.9)	-81 (106.9)	Based on a flesh model of the subadult neotype with femur length of 62.5 cm (actual 61.0 cm); y-coordinate measures to substrate
4	this paper; <i>biped</i>	apex of the acetabulum	15.3	-240	Based on an adult flesh model with avian-style internal air spaces and femur length of 81.0 cm; y-coordinate measures to substrate

Table 10. Estimated internal air space in *S. aegyptiacus*. Air space options for the adult flesh model of *S. aegyptiacus* and their effect on whole body density, body mass (BM), and center of mass (CM). The x-coordinate for CM is measured from the apex of the acetabulum.

No.	Air space option	Part of whole-body volume (%)	Mean whole-body density (Gm/l)	BM (kg)	CM x-coordinate (cm)
1	Minimum (lizard-like)	4	909	8,013	28.5
2	Medium (croc-like)	8	875	7,716	23.2
3	Maximum (bird-like)	12.5	833	7,390	15.3

525 With avian-like air space (“maximum”), CM is positioned only 15.3 cm anterior to the apex of the
526 acetabulum and clearly over the pedal phalanges of the foot for a bipedal stance (**Table 10**). The
527 smallest air space option modeled on lizards (“minimum,” only 4% of body volume) generates the
528 heaviest torso and displaces CM anteriorly 13.2 cm to a distance of 28.5 cm from the apex of the
529 acetabulum (**Table 10**). In this location, CM is still approximately 12 cm short of the midpoint along
530 the length of the femur (~40 cm; femoral length is 81 cm in adult *S. aegyptiacus*). In this worst-case
531 scenario regarding internal air volume, CM is still positioned over the pedal phalanges of the hind
532 limb. Our flesh model does not support an obligatory quadrupedal pose on land for *S. aegyptiacus*.

533 Acknowledgments

534 We thank A Resetar, J Mata and D Coldren of the Field Museum of Natural History, R Carmichael
535 of the Wildlife Center and R Bavrisha of the Chicago Herpetological Society for access to recent
536 preserved and live reptile specimens; Morphosource, oVert TCN, UMMZ, KU, and UF for access

537 to and archiving of CT scans; R Shonk and A Schulte for digital modeling; E Fitzgerald for fossil
538 preparation; J Mallon for photography; and E Saitta, E Johnson-Ransom, DB Dutheil, SW Evers, E
539 Snively, and J Schwartz for comments on the manuscript. This research was supported by Bob and
540 Ellen Vladem and SC Johnson.

541 **Additional information**

542 **Author contributions**

543 Conceptualization, PCS, NM, DMH, FEF, DV, SLB and KKF; Initial draft, PCS; Review and editing, DMH,
544 DV, SLB, FEF, KKF and NM; Biomechanical simulation, DMH, NM and FEF; Fossil CT imaging, skeletal
545 and flesh model reconstruction, TMK, LLC and DV; Modern analog CT imaging and data collection,
546 SLB, DV; Final figures, LLC and PCS with contributions from SLB, DMH, FEF, DV and NM; Phylogenetic
547 analysis, DV and PCS.

548 **Author ORCIDs**

549 **Paul C Sereno** <https://orcid.org/0000-0001-7958-3701>

550 **Nathan Myhrvold** <https://orcid.org/0000-0003-3994-5143>

551 **Donald M Henderson** <https://orcid.org/0000-0002-2411-3611>

552 **Frank E Fish** <https://orcid.org/0000-0001-5973-3282>

553 **Stephanie L Baumgart** <https://orcid.org/0000-0001-9534-7389>

554 **Daniel Vidal** <https://orcid.org/0000-0002-6054-1357>

555 **Kiersten K Formoso** <https://orcid.org/0000-0002-3519-2503>

556 **Lauren Conroy** <https://orcid.org/0000-0002-2799-4792>

557 **Decision letter and Author response**

558 Decision letter

559 Author response

560 **Additional files**

561 **Supplementary files**

562 **Data availability**

563 All data generated or analyzed in this study are included in the paper, Appendices, and
564 Morphosource.

565 **References**

566 **Allain R**, Xaisanavong T, Richir P, Khentavong B. The first definitive Asian spinosaurid (Dinosauria: Theropoda)
567 from the Early Cretaceous of Laos. *Naturwissenschaften*. 2012; 99(5):369–377. <https://doi.org/10.1007/s00114-012-0911-7>, doi: 10.1007/s00114-012-0911-7.

569 **Amiot R**, Buffetaut E, Lécuyer C, Wang X, Boudad L, Ding Z, Fourel F, Hutt S, Martineau F, Medeiros MA, Mo
570 J, Simon L, Suteethorn V, Sweetman S, Tong H, Zhang F, Zhou Z. Oxygen isotope evidence for semi-aquatic
571 habits among spinosaurid theropods. *Geology*. 2010; 38(2):139–142. <https://doi.org/10.1130/G30402.1>, doi:
572 [10.1130/G30402.1](https://doi.org/10.1130/G30402.1).

573 **Arden TMS**, Klein CG, Zouhri S, Longrich NR. Aquatic adaptation in the skull of carnivorous dinosaurs
574 (Theropoda: Spinosauridae) and the evolution of aquatic habits in spinosaurids. *Cretaceous Re-*
575 *search*. 2019; 93:275–284. <https://www.sciencedirect.com/science/article/pii/S0195667117303427>, doi:
576 [10.1016/j.cretres.2018.06.013](https://doi.org/10.1016/j.cretres.2018.06.013).

577 **Aureliano T**, Ghilardi AM, Buck PV, Fabbri M, Samathi A, Delcourt R, Fernandes MA, Sander M. Semi-aquatic
578 adaptations in a spinosaur from the Lower Cretaceous of Brazil. *Cretaceous Research*. 2018; 90:283–295.
579 <https://www.sciencedirect.com/science/article/pii/S0195667117305153>, doi: [10.1016/j.cretres.2018.04.024](https://doi.org/10.1016/j.cretres.2018.04.024).

- 580 **Barker CT**, Hone DWE, Naish D, Cau A, Lockwood JAF, Foster B, Clarkin CE, Schneider P, Gostling NJ. New
581 spinosaurids from the Wessex Formation (Early Cretaceous, UK) and the European origins of Spinosauri-
582 dae. *Scientific Reports*. 2021; 11(1):19340. <https://www.nature.com/articles/s41598-021-97870-8>, doi:
583 <https://doi.org/10.1038/s41598-021-97870-8>.
- 584 **Benson RBJ**, Carrano MT, Brusatte SL. A new clade of archaic large-bodied predatory dinosaurs (Theropoda:
585 Allosauroidea) that survived to the latest Mesozoic. *Naturwissenschaften*. 2009; 97(1):71. [https://doi.org/10.](https://doi.org/10.1007/s00114-009-0614-x)
586 [1007/s00114-009-0614-x](https://doi.org/10.1007/s00114-009-0614-x), doi: 10.1007/s00114-009-0614-x.
- 587 **Brusatte SL**, Norell MA, Carr TD, Erickson GM, Hutchinson JR, Balanoff AM, Bever GS, Choiniere JN, Makovicky
588 PJ, Xu X. Tyrannosaur paleobiology: New research on ancient exemplar organisms. *Science*. 2010;
589 329(5998):1481–1485. <http://www.science.org/doi/10.1126/science.1193304>, doi: 10.1126/science.1193304.
- 590 **Brusatte SL**, Sereno PC. A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian
591 of Niger and a revision of the genus. *Journal of Vertebrate Paleontology*. 2007; 27(4):902–916. [https://](https://www.tandfonline.com/doi/abs/10.1671/0272-4634%282007%2927%5B902%3AANSOCD%5D2.0.CO%3B2)
592 www.tandfonline.com/doi/abs/10.1671/0272-4634%282007%2927%5B902%3AANSOCD%5D2.0.CO%3B2, doi:
593 [10.1671/0272-4634\(2007\)27\[902:ANSOCD\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2007)27[902:ANSOCD]2.0.CO;2).
- 594 **Böhmer C**, Fabre AC, Taverne M, Herbin M, Peigné S, Herrel A. Functional relationship between myology
595 and ecology in carnivores: do forelimb muscles reflect adaptations to prehension? *Biological Journal of*
596 *the Linnean Society*. 2019; 127(3):661–680. <https://doi.org/10.1093/biolinnean/blz036>, doi: 10.1093/biolinnean/blz036.
597
- 598 **Carrano MT**, Benson RBJ, Sampson SD. The phylogeny of Tetanurae (Dinosauria: Theropoda). *Journal*
599 *of Systematic Palaeontology*. 2012; 10(2):211–300. <https://doi.org/10.1080/14772019.2011.630927>, doi:
600 [10.1080/14772019.2011.630927](https://doi.org/10.1080/14772019.2011.630927).
- 601 **Cau A**, Beyrand V, Voeten DFAE, Fernandez V, Tafforeau P, Stein K, Barsbold R, Tsogtbaatar K, Currie PJ, Gode-
602 froit P. Synchrotron scanning reveals amphibious ecomorphology in a new clade of bird-like dinosaurs.
603 *Nature*. 2017; 552(7685):395–399. <http://www.nature.com/articles/nature24679>, doi: 10.1038/nature24679.
- 604 **Charig A**, Milner AC. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural*
605 *History Museum Geology series*. 1997; 53:11–70. <https://www.biodiversitylibrary.org/part/75343>.
- 606 **Chure DJ**, Madsen JH. Variation in aspects of the tympanic pneumatic system in a population of *Allosaurus*
607 *fragilis* from the Morrison Formation (Upper Jurassic). *Journal of Vertebrate Paleontology*. 1996; 16(1):63–66.
608 <https://doi.org/10.1080/02724634.1996.10011284>, doi: 10.1080/02724634.1996.10011284.
- 609 **Cong L**. The Gross Anatomy of *Alligator sinensis* Fauvel [in Chinese with English summary]. China Science and
610 Technology Press; 1998.
- 611 **Dal Sasso C**, Maganuco S, Buffetaut E, Mendez MA. New information on the skull of the enigmatic theropod
612 *Spinosaurus*, with remarks on its size and affinities. *Journal of Vertebrate Paleontology*. 2005; 25(4):888–
613 896. [https://www.tandfonline.com/doi/abs/10.1671/0272-4634%282005%29025%5B0888%3ANIOTSO%5D2.0.](https://www.tandfonline.com/doi/abs/10.1671/0272-4634%282005%29025%5B0888%3ANIOTSO%5D2.0.CO%3B2)
614 [CO%3B2](https://doi.org/10.1671/0272-4634(2005)025[0888:NIOTSO]2.0.CO;2), doi: 10.1671/0272-4634(2005)025[0888:NIOTSO]2.0.CO;2.
- 615 **Danowitz M**, Vasilyev A, Kortlandt V, Solounias N. Fossil evidence and stages of elongation of the *Giraffa*
616 *camelopardalis* neck. *Royal Society Open Science*. 2015; 2(10):150393. [https://royalsocietypublishing.org/doi/](https://royalsocietypublishing.org/doi/10.1098/rsos.150393)
617 [10.1098/rsos.150393](https://doi.org/10.1098/rsos.150393), doi: 10.1098/rsos.150393.
- 618 **Domenici P**, Wilson ADM, Kurvers RHJM, Marras S, Herbert-Read JE, Steffensen JF, Krause S, Viblanc PE, Couil-
619 laud P, Krause J. How sailfish use their bills to capture schooling prey. *Proceedings of the Royal Society B: Bio-*
620 *logical Sciences*. 2014; 281(1784):20140444. <https://royalsocietypublishing.org/doi/full/10.1098/rspb.2014.0444>,
621 doi: 10.1098/rspb.2014.0444.
- 622 **Domenici P**. The scaling of locomotor performance in predator-prey encounters: from fish to killer whales.
623 *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*. 2001; 131(1):169–182.
624 <https://www.sciencedirect.com/science/article/pii/S1095643301004652>, doi: 10.1016/S1095-6433(01)00465-2.
- 625 **Domning DP**. The readaptation of Eocene sirenians to life in water. *Historical Biology*.
626 2000; 14(1-2):115–119. <https://www.tandfonline.com/doi/abs/10.1080/10292380009380559>, doi:
627 <https://doi.org/10.1080/10292380009380559>.
- 628 **Díez Díaz V**, Demuth OE, Schwarz D, Mallison H. The tail of the Late Jurassic sauropod *Giraffatitan brancai*: dig-
629 ital reconstruction of its epaxial and hypaxial musculature, and implications for tail biomechanics. *Frontiers*
630 *in Earth Science*. 2020; 8. <https://www.frontiersin.org/article/10.3389/feart.2020.00160>.

- 631 **Evers SW**, Benson RBJ. A new phylogenetic hypothesis of turtles with implications for the timing and number
632 of evolutionary transitions to marine lifestyles in the group. *Palaeontology*. 2019; 62(1):93–134. [http://](http://onlinelibrary.wiley.com/doi/abs/10.1111/pala.12384)
633 onlinelibrary.wiley.com/doi/abs/10.1111/pala.12384, doi: 10.1111/pala.12384.
- 634 **Evers SW**, Rauhut OWM, Milner AC, McFeeters B, Allain R. A reappraisal of the morphology and systematic
635 position of the theropod dinosaur *Sigilmassasaurus* from the “middle” Cretaceous of Morocco. *PeerJ*. 2015;
636 3:e1323. <https://peerj.com/articles/1323>, doi: 10.7717/peerj.1323.
- 637 **Fabbri M**, Navalón G, Benson RBJ, Pol D, O’Connor J, Bhullar BAS, Erickson GM, Norell MA, Orkney A, Lamanna
638 MC, Zouhri S, Becker J, Emke A, Dal Sasso C, Bindellini G, Maganuco S, Auditore M, Ibrahim N. Subaqueous
639 foraging among carnivorous dinosaurs. *Nature*. 2022; 603(7903):852–857. [https://www.nature.com/articles/](https://www.nature.com/articles/s41586-022-04528-0)
640 [s41586-022-04528-0](https://www.nature.com/articles/s41586-022-04528-0), doi: 10.1038/s41586-022-04528-0.
- 641 **Farlow JO**, Smith MB, Robinson JM. Body mass, bone “strength indicator,” and cursorial potential of *Tyran-*
642 *nosaurus rex*. *Journal of Vertebrate Paleontology*. 1995; 15(4):713–725. [https://doi.org/10.1080/02724634.](https://doi.org/10.1080/02724634.1995.10011257)
643 [1995.10011257](https://doi.org/10.1080/02724634.1995.10011257), doi: 10.1080/02724634.1995.10011257.
- 644 **Fish FE**, Rohr JJ. Review of dolphin hydrodynamics and swimming performance. *Space and Naval Warfare*
645 *Systems Command San Diego CA*. 1999; p. 187. <https://apps.dtic.mil/sti/citations/ADA369158>.
- 646 **Fish F**. Comparative kinematics and hydrodynamics of odontocete cetaceans: morphological and ecological
647 correlates with swimming performance. *Journal of Experimental Biology*. 1998; 201(20):2867–2877. <https://doi.org/10.1242/jeb.201.20.2867>, doi: 10.1242/jeb.201.20.2867.
- 648 [/doi.org/10.1242/jeb.201.20.2867](https://doi.org/10.1242/jeb.201.20.2867), doi: 10.1242/jeb.201.20.2867.
- 649 **Fish FE**. Kinematics of undulatory swimming in the American alligator. *Copeia*. 1984; 1984(4):839–843. <http://www.jstor.org/stable/1445326>, doi: 10.2307/1445326.
- 650 [/www.jstor.org/stable/1445326](http://www.jstor.org/stable/1445326), doi: 10.2307/1445326.
- 651 **Fish FE**. Association of propulsive swimming mode with behavior in river otters (*Lutra canadensis*). *Journal of*
652 *Mammalogy*. 1994; 75(4):989–997. <https://doi.org/10.2307/1382481>, doi: 10.2307/1382481.
- 653 **Fish FE**. Structure and mechanics of nonpiscine control surfaces. *IEEE Journal of Oceanic Engineering*. 2004;
654 29(3):605–621. <https://ieeexplore.ieee.org/abstract/document/1353414>, doi: 10.1109/JOE.2004.833213.
- 655 **Fish FE**. Secondary evolution of aquatic propulsion in higher vertebrates: validation and prospect. *In-*
656 *tegrative and Comparative Biology*. 2016; 56(6):1285–1297. <https://doi.org/10.1093/icb/icw123>, doi:
657 10.1093/icb/icw123.
- 658 **Fish FE**, Rybczynski N, Lauder GV, Duff CM. The role of the tail or lack thereof in the evolution of tetrapod
659 aquatic propulsion. *Biological Journal of the Linnean Society*. 2021; 61(2):398–413. [https://doi.org/10.1093/](https://doi.org/10.1093/icb/icab021)
660 [icb/icab021](https://doi.org/10.1093/icb/icab021), doi: 10.1093/icb/icab021.
- 661 **Fulton TL**, Strobeck C. Multiple markers and multiple individuals refine true seal phylogeny and bring molecules
662 and morphology back in line. *Proceedings of the Royal Society B: Biological Sciences*. 2010; 277(1684):1065–
663 1070. [https://royalsocietypublishing.org/doi/10.1098/rspb.2009.1783?url_](https://royalsocietypublishing.org/doi/10.1098/rspb.2009.1783?url_ver=Z39.88-2003&rfr_id=ori:rid:crossref.org&rfr_dat=cr_pub%20%20pubmed)
664 [ver=Z39.88-2003&rfr_id=ori:rid:](https://royalsocietypublishing.org/doi/10.1098/rspb.2009.1783?url_ver=Z39.88-2003&rfr_id=ori:rid:crossref.org&rfr_dat=cr_pub%20%20pubmed)
[crossref.org&rfr_dat=cr](https://royalsocietypublishing.org/doi/10.1098/rspb.2009.1783?url_ver=Z39.88-2003&rfr_id=ori:rid:crossref.org&rfr_dat=cr_pub%20%20pubmed)
[_pub%20%20pubmed](https://royalsocietypublishing.org/doi/10.1098/rspb.2009.1783?url_ver=Z39.88-2003&rfr_id=ori:rid:crossref.org&rfr_dat=cr_pub%20%20pubmed), doi: 10.1098/rspb.2009.1783.
- 665 **Gao T**, Li DQ, Li LF, Yang JT. The first record of freshwater plesiosaurian from the Middle Jurassic of Gansu,
666 NW China, with its implications to the local palaeobiogeography. *Journal of Palaeogeography*. 2016; 8(1):27.
667 <https://doi.org/10.1186/s42501-019-0043-5>, doi: 10.1186/s42501-019-0043-5.
- 668 **Gimsa J**, Sleight R, Gimsa U. The riddle of *Spinosaurus aegyptiacus*’ dorsal sail. *Geological Mag-*
669 *azine*. 2016; 153(3):544–547. [https://www.cambridge.org/core/journals/geological-magazine/](https://www.cambridge.org/core/journals/geological-magazine/article/riddle-of-spinosaurus-aegyptiacus-dorsal-sail/B19941405E1791A97230BCF003017B7B)
670 [article/riddle-of-spinosaurus-aegyptiacus-dorsal-sail/B19941405E1791A97230BCF003017B7B](https://www.cambridge.org/core/journals/geological-magazine/article/riddle-of-spinosaurus-aegyptiacus-dorsal-sail/B19941405E1791A97230BCF003017B7B), doi:
671 10.1017/S0016756815000801.
- 672 **Grigg G**, Kirshner D. *Biology and Evolution of Crocodylians*. Illustrated edition ed. Cornell University Press;
673 2015.
- 674 **Gutarra S**, Rahman IA. The locomotion of extinct secondarily aquatic tetrapods. *Biological Reviews*. 2022;
675 97(1):67–98. <http://onlinelibrary.wiley.com/doi/abs/10.1111/brv.12790>, doi: 10.1111/brv.12790.
- 676 **Guterres-Pazin MG**. Feeding ecology of the Amazonian manatee (*Trichechus inunguis*) in the Mami-
677 rauá and Amanã sustainable development reserves, Brazil. *Aquatic Mammals*. 2014; 40(2):139–
678 149. [http://aquaticmammalsjournal.org/index.php?option=com_](http://aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=682:feeding-ecology-of-the-amazonian-manatee-trichechus-inunguis-in-the-mamiraua-and-amana-sustainable-development-reser)
679 [content&view=article&id=682:](http://aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=682:feeding-ecology-of-the-amazonian-manatee-trichechus-inunguis-in-the-mamiraua-and-amana-sustainable-development-reser)
[feeding-ecology-of-the-amazonian-manatee-trichechus-inunguis-in-the-mamiraua-and-amana-sustainable-development-reser](http://aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=682:feeding-ecology-of-the-amazonian-manatee-trichechus-inunguis-in-the-mamiraua-and-amana-sustainable-development-reser)
680 [catid=55&Itemid=157">catid=55&Itemid=157](http://aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=682:feeding-ecology-of-the-amazonian-manatee-trichechus-inunguis-in-the-mamiraua-and-amana-sustainable-development-reser), doi: 10.1578/AM.40.2.2014.139.

- 681 **Hamilton H**, Caballero S, Collins AG, Brownell RL. Evolution of river dolphins. *Proceedings of the Royal Society*
682 *of London Series B: Biological Sciences*. 2001; 268(1466):549–556. <https://royalsocietypublishing.org/doi/10.1098/rspb.2000.1385>, doi: 10.1098/rspb.2000.1385.
- 684 **Henderson DM**. Estimating the masses and centers of mass of extinct animals by 3-D mathematical
685 slicing. *Paleobiology*. 1999; 25(1):88–106. [https://www.cambridge.org/core/journals/paleobiology/](https://www.cambridge.org/core/journals/paleobiology/article/abs/estimating-the-masses-and-centers-of-mass-of-extinct-animals-by-3d-mathematical-slicing/9AC05A1834580390840081FC7CB8B244)
686 [article/abs/estimating-the-masses-and-centers-of-mass-of-extinct-animals-by-3d-mathematical-slicing/](https://www.cambridge.org/core/journals/paleobiology/article/abs/estimating-the-masses-and-centers-of-mass-of-extinct-animals-by-3d-mathematical-slicing/9AC05A1834580390840081FC7CB8B244)
687 [9AC05A1834580390840081FC7CB8B244](https://www.cambridge.org/core/journals/paleobiology/article/abs/estimating-the-masses-and-centers-of-mass-of-extinct-animals-by-3d-mathematical-slicing/9AC05A1834580390840081FC7CB8B244), doi: 10.1666/0094-8373(1999)025<0088:ETMACO>2.3.CO;2.
- 688 **Henderson DM**. A buoyancy, balance and stability challenge to the hypothesis of a semi-aquatic *Spinosaurus*
689 Stromer, 1915 (Dinosauria: Theropoda). *PeerJ*. 2018; 6:e5409. <https://peerj.com/articles/5409>, doi:
690 [10.7717/peerj.5409](https://peerj.com/articles/5409).
- 691 **Hendrickx C**, Mateus O, Araújo R, Choiniere J. The distribution of dental features in non-avian theropod di-
692 nosaurs: Taxonomic potential, degree of homoplasy, and major evolutionary trends. *Palaeontologia Elec-*
693 *tronica*. 2019; 22(3):1–110. <https://palaeo-electronica.org/content/2019/2806-dental-features-in-theropods>, doi:
694 [10.26879/820](https://palaeo-electronica.org/content/2019/2806-dental-features-in-theropods).
- 695 **Hirt MR**, Jetz W, Rall BC, Brose U. A general scaling law reveals why the largest animals are not the fastest.
696 *Nature Ecology & Evolution*. 2017; 1(8):1116–1122. <https://www.nature.com/articles/s41559-017-0241-4>, doi:
697 [10.1038/s41559-017-0241-4](https://www.nature.com/articles/s41559-017-0241-4).
- 698 **Holtz T**. A new phylogeny of the carnivorous dinosaurs. *Gaia*. 2000; 15:5–61. doi: 10.26879/1110.
- 699 **Hone D**, Holtz T. Evaluating the ecology of *Spinosaurus*: shoreline generalist or aquatic pursuit specialist?
700 *Palaeontologia Electronica*. 2021; 24:1–28. doi: 10.26879/1110.
- 701 **Hone DWE**. Variation in the tail length of non-avian dinosaurs. *Journal of Vertebrate Paleontology*. 2012;
702 32(5):1082–1089. <http://www.jstor.org/stable/23251301>.
- 703 **Hood GA**. *Semi-aquatic Mammals: Ecology and Biology*. Johns Hopkins University Press; 2020.
- 704 **Houssaye A**. “Pachystosis” in aquatic amniotes: a review. *Integrative Zoology*. 2009; 4:325–340.
- 705 **Houssaye A**, Fish FE. Functional (secondary) adaptation to an aquatic life in vertebrates: an introduction to
706 the symposium. *Integrative and Comparative Biology*. 2016; 56(6):1266–1270. [https://doi.org/10.1093/icb/](https://doi.org/10.1093/icb/icw129)
707 [icw129](https://doi.org/10.1093/icb/icw129), doi: 10.1093/icb/icw129.
- 708 **Houssaye A**, Waskow K, Hayashi S, Cornette R, Lee AH, Hutchinson JR. Biomechanical evolution of solid bones
709 in large animals: a microanatomical investigation. *Biological Journal of the Linnean Society*. 2016; 117(2):350–
710 371. <http://onlinelibrary.wiley.com/doi/abs/10.1111/bij.12660>, doi: 10.1111/bij.12660.
- 711 **Howell AB**. *Aquatic Mammals: Their Adaptations to Life in the Water*. Charles C. Thomas; 1930.
- 712 **Ibrahim N**, Maganuco S, Dal Sasso C, Fabbri M, Auditore M, Bindellini G, Martill DM, Zouhri S, Mattarelli DA,
713 Unwin DM, Wiemann J, Bonadonna D, Amane A, Jakubczak J, Joger U, Lauder GV, Pierce SE. Tail-propelled
714 aquatic locomotion in a theropod dinosaur. *Nature*. 2020; 581(7806):67–70. [https://www.nature.com/articles/](https://www.nature.com/articles/s41586-020-2190-3)
715 [s41586-020-2190-3](https://www.nature.com/articles/s41586-020-2190-3), doi: 10.1038/s41586-020-2190-3.
- 716 **Ibrahim N**, Sereno PC, Dal Sasso C, Maganuco S, Fabbri M, Martill DM, Zouhri S, Myhrvold N, Iurino DA. Semi-
717 aquatic adaptations in a giant predatory dinosaur. *Science*. 2014; 345(6204):1613–1616. [http://www.science.](http://www.science.org/doi/10.1126/science.1258750)
718 [org/doi/10.1126/science.1258750](http://www.science.org/doi/10.1126/science.1258750), doi: 10.1126/science.1258750.
- 719 **Ibrahim N**, Sereno PC, Varricchio DJ, Martill DM, Duthel DB, Unwin DM, Baidder L, Larsson HCE, Zouhri S,
720 Kaoukaya A. Geology and paleontology of the Upper Cretaceous Kem Kem Group of eastern Morocco.
721 *ZooKeys*. 2020; 928:1–216. <https://zookeys.pensoft.net/article/47517/>, doi: 10.3897/zookeys.928.47517.
- 722 **Iosilevskii G**, Weihs D. Speed limits on swimming of fishes and cetaceans. *Journal of the Royal Society Interface*.
723 2008; 5(20):329–338. <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2607394/>, doi: 10.1098/rsif.2007.1073.
- 724 **Lankester R**. On certain points in the structure of the cervical vertebrae of the okapi and the giraffe. *Proceed-*
725 *ings of the Zoological Society of London*. 1908; 1908:320–334. <https://www.biodiversitylibrary.org/part/72436>,
726 doi: 10.1111/j.1096-3642.1908.tb01845.x.
- 727 **Lighthill MJ**. Hydromechanics of aquatic animal propulsion. *Annual Review of Fluid Mechanics*. 1969; 1(1):413–
728 446. <https://doi.org/10.1146/annurev.fl.01.010169.002213>, doi: 10.1146/annurev.fl.01.010169.002213.

- 729 **Lindgren J**, Kaddumi HF, Polcyn MJ. Soft tissue preservation in a fossil marine lizard with a bilobed
730 tail fin. *Nature Communications*. 2013; 4(1):2423. <https://www.nature.com/articles/ncomms3423>, doi:
731 10.1038/ncomms3423.
- 732 **Loewen MA**, Irmis RB, Sertich JJW, Currie PJ, Sampson SD. Tyrant dinosaur evolution tracks the rise and fall of
733 Late Cretaceous oceans. *PLOS ONE*. 2013; 8(11):e79420. [https://journals.plos.org/plosone/article?id=10.1371/](https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0079420)
734 [journal.pone.0079420](https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0079420), doi: 10.1371/journal.pone.0079420.
- 735 **Longrich NR**, Currie PJ. A microraptorine (Dinosauria–Dromaeosauridae) from the Late Cretaceous of North
736 America. *Proceedings of the National Academy of Sciences*. 2009; 106(13):5002–5007. [https://www.pnas.org/](https://www.pnas.org/doi/10.1073/pnas.0811664106)
737 [doi/10.1073/pnas.0811664106](https://www.pnas.org/doi/10.1073/pnas.0811664106), doi: 10.1073/pnas.0811664106.
- 738 **Machado EB**, Kellner AWA. On a spinosaurid manus (Dinosauria, Theropoda) from the Romualdo Formation
739 (Santana Group), Araripe Basin, Brazil. *Boletim Resumen, XXI Congresso brasileiro de Paleontologia*. 2009; p.
740 193.
- 741 **Madsen JH Jr.** *Allosaurus fragilis*: a revised osteology. *Utah Geological and Mining Survey Bulletin*.
742 1976; 109:1–163. [https://www.semanticscholar.org/paper/Allosaurus-Fragilis%3A-a-Revised-Osteology-Madsen/](https://www.semanticscholar.org/paper/Allosaurus-Fragilis%3A-a-Revised-Osteology-Madsen/7f145dfab1a6a66f15bdd22791dfec34d8b5c927)
743 [7f145dfab1a6a66f15bdd22791dfec34d8b5c927](https://www.semanticscholar.org/paper/Allosaurus-Fragilis%3A-a-Revised-Osteology-Madsen/7f145dfab1a6a66f15bdd22791dfec34d8b5c927).
- 744 **Malafaia E**, Gasulla JM, Escaso F, Narváez I, Sanz JL, Ortega F. New spinosaurid (Theropoda, Mega-
745 losauroida) remains from the Arcillas de Morella Formation (upper Barremian) of Morella, Spain. *Creta-
746 ceous Research*. 2018; 92:174–183. <https://www.sciencedirect.com/science/article/pii/S0195667118301162>,
747 doi: 10.1016/j.cretres.2018.08.006.
- 748 **Malafaia E**, Gasulla JM, Escaso F, Narváez I, Sanz JL, Ortega F. A new spinosaurid theropod (Dinosauria: Mega-
749 losauroida) from the upper Barremian of Vallibona, Spain: Implications for spinosaurid diversity in the Early
750 Cretaceous of the Iberian Peninsula. *Cretaceous Research*. 2020; 106:104221. [https://www.sciencedirect.com/](https://www.sciencedirect.com/science/article/pii/S0195667119301302)
751 [science/article/pii/S0195667119301302](https://www.sciencedirect.com/science/article/pii/S0195667119301302), doi: 10.1016/j.cretres.2019.104221.
- 752 **Mallison H**, Pittman M, Schwarz D. Using crocodylian tails as models for dinosaur tails. *PeerJ Preprints*. 2015;
753 3(e1339v1). <https://peerj.com/preprints/1339>, doi: <https://doi.org/10.7287/peerj.preprints.1339v1>.
- 754 **Maresh JL**, Fish FE, Nowacek DP, Nowacek SM. High performance turning capabilities during foraging by bot-
755 tlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science*. 2004; 30(3):498–509. [https://www.wcupa.](https://www.wcupa.edu/sciences-mathematics/biology/fFish/documents/2004MMSCDolphinTurn.pdf)
756 [edu/sciences-mathematics/biology/fFish/documents/2004MMSCDolphinTurn.pdf](https://www.wcupa.edu/sciences-mathematics/biology/fFish/documents/2004MMSCDolphinTurn.pdf).
- 757 **Moon BC**, Stubbs TL. Early high rates and disparity in the evolution of ichthyosaurs. *Communications Biology*.
758 2020; 3(1):1–8. <http://www.nature.com/articles/s42003-020-0779-6>, doi: 10.1038/s42003-020-0779-6.
- 759 **Motani R**, Vermeij GJ. Ecophysiological steps of marine adaptation in extant and extinct non-avian tetrapods.
760 *Biological Reviews*. 2021; 96(5):1769–1798. <http://onlinelibrary.wiley.com/doi/abs/10.1111/brv.12724>, doi:
761 10.1111/brv.12724.
- 762 **Myhrvold N**, Sereno PC, Baumgart SL, Formoso KK, Vidal D, Fish FE, Henderson DM. Spinosaurids as ‘subaque-
763 ous foragers’ undermined by selective sampling and problematic statistical inference. *Nature*. in press; <https://www.biorxiv.org/content/10.1101/2022.04.13.487781v1>, doi: <https://doi.org/10.1101/2022.04.13.487781>.
- 764 <https://www.biorxiv.org/content/10.1101/2022.04.13.487781v1>, doi: <https://doi.org/10.1101/2022.04.13.487781>.
- 765 **Müller MA**, Merten LJF, Böhmer C, Nyakatura JA. Pushing the boundary? Testing the “functional elongation
766 hypothesis” of the giraffe’s neck. *Evolution*. 2021; 75(3):641–655. [https://onlinelibrary.wiley.com/doi/abs/10.](https://onlinelibrary.wiley.com/doi/abs/10.1111/evo.14171)
767 [1111/evo.14171](https://onlinelibrary.wiley.com/doi/abs/10.1111/evo.14171), doi: 10.1111/evo.14171.
- 768 **Nettleship DN**. Family Alcidae (Auks). In: del Hoyo J, Elliott A, Sargatal J, editors. *Handbook of the Birds*
769 *of the World: Hoatzin to Auks*, vol. 3 Lynx Edicions; 1996.p. 679–722. [https://www.lynxeds.com/product/](https://www.lynxeds.com/product/handbook-of-the-birds-of-the-world-volume-3/)
770 [handbook-of-the-birds-of-the-world-volume-3/](https://www.lynxeds.com/product/handbook-of-the-birds-of-the-world-volume-3/).
- 771 **Nothdurft W**, Smith J. *The Lost Dinosaurs of Egypt*. 1st edition ed. Random House; 2002.
- 772 **O’Connor JK**. A systematic review of Enantiornithes (Aves: Ornithothoraces). *ProQuest Dissertations and*
773 *Theses*; 2009. <https://www.proquest.com/docview/304997622/abstract/9A2646E1717B463DPQ/1>.
- 774 **Pacini N**, Harper DM. Aquatic, semi-aquatic and riparian vertebrates. In: Dudgeon D, editor. *Tropical Stream*
775 *Ecology* Aquatic Ecology, Academic Press; 2008.p. 147–197. [https://www.sciencedirect.com/science/article/pii/](https://www.sciencedirect.com/science/article/pii/B978012088449050008X)
776 [B978012088449050008X](https://www.sciencedirect.com/science/article/pii/B978012088449050008X), doi: 10.1016/B978-012088449-0.50008-X.

- 777 **Parson JM**, Fish FE, Nicastro AJ. Turning performance of batoids: Limitations of a rigid body. *Journal of Experimental Marine Biology and Ecology*. 2011; 402(1):12–18. <https://www.sciencedirect.com/science/article/pii/S0022098111001225>, doi: 10.1016/j.jembe.2011.03.010.
- 780 **Persons IV WS**, Currie PJ, Erickson GM. An older and exceptionally large adult specimen of *Tyrannosaurus rex*. *The Anatomical Record*. 2020; 303(4):656–672. <https://onlinelibrary.wiley.com/doi/abs/10.1002/ar.24118>, doi: 10.1002/ar.24118.
- 783 **Polcyn MJ**, Jacobs LL, Araújo R, Schulp AS, Mateus O. Physical drivers of mosasaur evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 2014; 400:17–27. <https://www.sciencedirect.com/science/article/pii/S0031018213002514>, doi: 10.1016/j.palaeo.2013.05.018.
- 786 **Rauhut OWM**. A tyrannosauroid dinosaur from the Upper Jurassic of Portugal. *Palaeontology*. 2003; 46(5):903–910. <http://onlinelibrary.wiley.com/doi/abs/10.1111/1475-4983.00325>, doi: 10.1111/1475-4983.00325.
- 788 **Rauhut OWM**, Canudo JI, Castanera DA. Reappraisal of the Early Cretaceous theropod dinosaur *Camarillasaurus* from Spain. 17th European Association of Vertebrate Palaeontologists, Brussels, Belgium. 2019; .
- 791 **van Rees WM**, Gazzola M, Koumoutsakos P. Optimal shapes for anguilliform swimmers at intermediate Reynolds numbers. *Journal of Fluid Mechanics*. 2013; 722:R3. <https://www.cambridge.org/core/journals/journal-of-fluid-mechanics/article/abs/optimal-shapes-for-anguilliform-swimmers-at-intermediate-reynolds-numbers/82B0F4B119815A9AB0508E67A582A285>, doi: 10.1017/jfm.2013.157.
- 796 **Russell DA**. Isolated dinosaur bones from the Middle Cretaceous of the Tafilalt, Morocco. *Bulletin du Muséum national d'Histoire naturelle, 4ème série – section C – Sciences de la Terre, Paléontologie, Géologie, Minéralogie*. 1996; 18(2). <https://sciencepress.mnhn.fr/en/periodiques/bulletin-du-museum-national-d-histoire-naturelle-4eme-serie-section-c-sciences-de-la-terre-paleontologie-geologie-mineralogie/18/2-3/os-isoles-de-dinosaures-du-cretace-moyen-du-tafilalt-maroc>.
- 801 **Sales MAF**, Schultz CL. Spinosaur taxonomy and evolution of craniodental features: evidence from Brazil. *PLOS ONE*. 2017; 12(11):e0187070. <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0187070>, doi: 10.1371/journal.pone.0187070.
- 804 **Samathi A**, Sander PM, Chanthasit P. A spinosaurid from Thailand (Sao Khua Formation, Early Cretaceous) and a reassessment of *Camarillasaurus cirugedae* from the Early Cretaceous of Spain. *Historical Biology*. 2021; 33(12):3480–3494. <https://doi.org/10.1080/08912963.2021.1874372>, doi: 10.1080/08912963.2021.1874372.
- 807 **Sato K**, Watanuki Y, Takahashi A, Miller PJO, Tanaka H, Kawabe R, Ponganis PJ, Handrich Y, Akamatsu T, Watanabe Y, Mitani Y, Costa DP, Bost CA, Aoki K, Amano M, Trathan P, Shapiro A, Naito Y. Stroke frequency, but not swimming speed, is related to body size in free-ranging seabirds, pinnipeds and cetaceans. *Proceedings of the Royal Society B: Biological Sciences*. 2007; 274(1609):471–477. <https://royalsocietypublishing.org/doi/10.1098/rspb.2006.0005>, doi: 10.1098/rspb.2006.0005.
- 812 **Scotese C**. Atlas of Early Cretaceous paleogeographic maps. *PALEOMAP Atlas for ArcGIS: The Cretaceous*. 2014; 2. https://www.academia.edu/11245383/Atlas_of_Early_Cretaceous_Paleogeographic_Maps.
- 814 **Senter P**, Kirkland JJ, Bird J, Bartlett JA. A new troodontid theropod dinosaur from the Lower Cretaceous of Utah. *PLOS ONE*. 2010; 5(12):e14329. <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0014329>, doi: 10.1371/journal.pone.0014329.
- 817 **Sereno PC**, Larsson HC, Sidor CA, Gado B. The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa. *Science (New York, NY)*. 2001; 294(5546):1516–1519. doi: 10.1126/science.1066521.
- 819 **Sereno PC**, Beck AL, Dutheil DB, Gado B, Larsson HCE, Lyon GH, Marcot JD, Rauhut OWM, Sadleir RW, Sidor CA, Varricchio DD, Wilson GP, Wilson JA. A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. *Science*. 1998; 282(5392):1298–1302. <http://www.science.org/doi/10.1126/science.282.5392.1298>, doi: 10.1126/science.282.5392.1298.
- 823 **Smith JB**, Lamanna MC, Mayr H, Lacovara KJ. New information regarding the holotype of *Spinosaurus aegyptiacus* Stromer, 1915. *Journal of Paleontology*. 2006; 80(2):400–406. <https://www.cambridge.org/core/journals/journal-of-paleontology/article/abs/new-information-regarding-the-holotype-of-spinosaurus-aegyptiacus-stromer-1915/9FDDB86D49787D067B6830F8F4BC0AEB>, doi: 10.1666/0022-3360(2006)080[0400:NIRTHO]2.0.CO;2.

- 828 **Smyth RSH**, Ibrahim N, Martill DM. *Sigilmassasaurus* is *Spinosaurus*: A reappraisal of African spinosaurines. Cre-
829 taceous Research. 2020; 114:104520. <https://www.sciencedirect.com/science/article/pii/S0195667120302068>,
830 doi: 10.1016/j.cretres.2020.104520.
- 831 **Snively E**, Russell AP. Functional morphology of neck musculature in the Tyrannosauridae (Dinosauria,
832 Theropoda) as determined via a hierarchical inferential approach. Zoological Journal of the Linnean
833 Society. 2007; 151(4):759–808. <https://doi.org/10.1111/j.1096-3642.2007.00334.x>, doi: 10.1111/j.1096-
834 3642.2007.00334.x.
- 835 **Stromer E**. Ergebnisse der Forschungsreisen Prof. E. Stromer in den Wüsten Ägyptens. II. Wirbeltier-
836 Reste der Baharije-Stufe (unterstes Cenoman). 3. Das Original des Theropoden *Spinosaurus aegyptiacus*
837 nov. gen., nov. spec. Abhandlungen Königlich-Bayerische Akademie der Wissenschaften Mathematisch-
838 Naturwissenschaftliche Klasse. 1915; 28:1–32.
- 839 **Stromer E**. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste
840 der Baharije-Stufe (unterstes Cenoman). 13. Dinosauria von E. Stromer. Abhandlungen Königlich-Bayerische
841 Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Abteilung. 1934; 22:1–79.
- 842 **Stromer E**. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. VII. Baharije-Kessel
843 und -Stufe mit deren Fauna und Flora. Eine ergänzende Zusammenfassung. Abhandlungen der Bayerischen
844 Akademie der Wissenschaften Mathematisch Naturwissenschaftliche Abteilung. 1936; 33:1–102.
- 845 **Sánchez-Hernández B**, Benton MJ. Filling the ceratosaur gap: a new ceratosaurian thero-
846 pod from the Early Cretaceous of Spain. Acta Palaeontologica Polonica. 2012; 59(3):581–
847 600. [https://bioone.org/journals/acta-palaeontologica-polonica/volume-59/issue-3/app.2011.0144/
848 Filling-the-Ceratosaur-Gap--A-New-Ceratosaurian-Theropod-from/10.4202/app.2011.0144.full](https://bioone.org/journals/acta-palaeontologica-polonica/volume-59/issue-3/app.2011.0144/Filling-the-Ceratosaur-Gap--A-New-Ceratosaurian-Theropod-from/10.4202/app.2011.0144.full), doi:
849 <https://doi.org/10.4202/app.2011.0144>.
- 850 **Taquet P**, Russell DA. New data on spinosaurid dinosaurs from the Early Cretaceous of the Sahara. Comptes
851 Rendus de l'Académie des Sciences - Series IIA - Earth and Planetary Science. 1998; 327(5):347–353. <https://www.sciencedirect.com/science/article/pii/S1251805098800542>, doi: 10.1016/S1251-8050(98)80054-2.
852
- 853 **Thewissen JGM**, Cooper LN, Bajpai S. From land to water: the origin of whales, dolphins, and porpoises.
854 Evolution: Education and Outreach. 2009; 2(2):272–288. <https://doi.org/10.1007/s12052-009-0135-2>, doi:
855 10.1007/s12052-009-0135-2.
- 856 **Tinsley JB**. The Sailfish: Swashbuckler of the Open Seas. University of Florida Press; 1964.
- 857 **Tykoski RS**. Anatomy, ontogeny, and phylogeny of coelophysoid theropods. ProQuest Dissertations and The-
858 ses; 2005. <https://www.proquest.com/docview/305382545/abstract/313066F8A1A64CF3PQ/1>.
- 859 **Vanderven E**, Burns ME, Currie PJ. Histologic growth dynamic study of *Edmontosaurus regalis* (Dinosauria:
860 Hadrosauridae) from a bonebed assemblage of the Upper Cretaceous Horseshoe Canyon Formation, Ed-
861 monton, Alberta, Canada. Canadian Journal of Earth Sciences. 2014; 51(11):1023–1033. [https://cdsciencepub.
862 com/doi/10.1139/cjes-2014-0064](https://cdsciencepub.com/doi/10.1139/cjes-2014-0064), doi: 10.1139/cjes-2014-0064.
- 863 **Vullo R**, Allain R, Cavin L. Convergent evolution of jaws between spinosaurid dinosaurs and pike conger eels.
864 Acta Palaeontologica Polonica. 2016; 61:825–828. <http://www.app.pan.pl/article/item/app002842016.html>,
865 doi: 10.4202/app.00284.2016.
- 866 **Webb PW**. Body form, locomotion and foraging in aquatic vertebrates. American Zoologist. 1984; 24(1):107–
867 120. <https://doi.org/10.1093/icb/24.1.107>, doi: 10.1093/icb/24.1.107.
- 868 **Webb PW**, De Buffrénil V. Locomotion in the biology of large aquatic vertebrates. Transactions of the American
869 Fisheries Society. 1990; 119(4):629–641. [https://onlinelibrary.wiley.com/doi/abs/10.1577/1548-8659%281990%
870 29119%3C0629%3ALITBOL%3E2.3.CO%3B2](https://onlinelibrary.wiley.com/doi/abs/10.1577/1548-8659%281990%29119%3C0629%3ALITBOL%3E2.3.CO%3B2), doi: 10.1577/1548-8659(1990)119<0629:LITBOL>2.3.CO;2.
- 871 **Wedel MJ**. The evolution of vertebral pneumaticity in sauropod dinosaurs. Journal of Vertebrate Pale-
872 ontology. 2003; 23(2):344–357. <http://www.jstor.org/stable/4524322>, doi: [https://doi.org/10.1671/0272-
873 4634\(2003\)023\[0344:TEOVPI\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2003)023[0344:TEOVPI]2.0.CO;2).

874 Appendix 1

875 Long bone infilling in *Spinosaurus aegyptiacus*

876 In *S. aegyptiacus* the medullary cavities in the long bones of the hind limb are reduced in
877 diameter or infilled altogether by non-pachystotic bone. This condition, which is unusual
878 among non-avian dinosaurs, was initially thought to be an adaptation for decreasing buoy-
879 ancy (*Ibrahim et al., 2014; Fabbri et al., 2022*), although that function has been challenged
880 recently (*Myhrvold et al., in press*). Enhanced bone strength is an alternative explanation
881 for solid hind limb long bones in *S. aegyptiacus*, a bipedal theropod of very large body size
882 with a reduced hind limb. Solid long bones are known to occur in other large-bodied bipedal
883 and quadrupedal dinosaurs and mammals (*Vandervan et al., 2014; Housaye et al., 2016*).

884 To better understand this alternative explanation, we compare the increase in strength
885 of a femur with solid shaft compared to one of identical size with a hollow shaft, using the
886 section modulus as an indicator of the resistance to bending (*Farlow et al., 1995*). For a
887 solid circular cross-section, the section modulus (SM) is given by $\frac{\pi}{4}R^3$, where R is the outer
888 radius. When R has a value 1.0, SM is $\frac{\pi}{4}$, or 0.785 m³. The SM for a cylinder with a hollow
889 core is calculated by subtracting the SM of an inner cylinder comprising the hollowed space
890 from that of the outer cylinder.

891 An inner radius of 0.5 generates a hollow cylinder that decreases the solid cylinder vol-
892 ume with 25% and generates a SM of $\frac{\pi}{4}(1.0^3 - 0.5^3) = \frac{\pi}{4}(0.875)$. This is a reduction of approx-
893 imately 13% of SM . Many theropods, however, have hollow cores within long bones that
894 comprise 50% or more of the volume of the long bone. For a hollow core equal to 50%
895 of outer cylinder volume, the inner radius is 0.707. The section modulus, calculated by sub-
896 tracting SM for a cylinder of radius 0.707 from the full cylinder of radius 1.0, is $\frac{\pi}{4}(1.0^3 - 0.707^3)$,
897 or $\frac{\pi}{4}(0.646)$, a reduction of approximately 35% of the SM of a solid cylinder.

898 Thus, infilling of hind limb bones in *S. aegyptiacus* may have increased bending strength
899 by as much as 35%. The femur in *S. aegyptiacus*, in particular, may have been subjected to
900 substantial bending forces. The attachment flange for the caudofemoralis muscle is hyper-
901 trophied, occupying almost one-third of the length of the femoral shaft.

902 **Appendix 2**

903 **Extant and extinct comparative materials**

904 We used references in the literature, an extant amphibian and reptile specimens, and a
 905 mosasaur to estimate muscle mass in the flesh reconstruction of *S. aegyptiacus* and to mea-
 906 sure caudal centrum proportions along the tail (**Figure 2, Figure 4D**; Appendix 2 **Table 1,**
 907 **Table 2**).

908 **Appendix 2 Table 1.** Extant newt and squamate specimens used for muscle mass estimation and for
 909 logging centrum proportions along the tail. Specimen number hyperlinks go to Morphosource
 910 specimen pages with CT scans and 3D models.

Specimen No.	Taxon	Sex	Type	Purpose
FMNH 84926	<i>Triturus cristatus</i>	Male	Wet	Caudal centrum ratios, muscle mass estimation
FMNH 57512	<i>Intellagama lesueurii</i>	Male	Wet	Muscle mass estimation
FMNH 22389	<i>Intellagama lesueurii</i>	Male	Skeleton	Caudal centrum ratios, muscle mass estimation
KU 314941	<i>Hydrosaurus amboinensis</i>	Unknown; low neural spines (female/immature male)	Wet	Caudal centrum ratios
FMNH 52698	<i>Hydrosaurus pustulatus</i>	Male	Wet	Muscle mass estimation
FMNH 236131	<i>Hydrosaurus pustulatus</i>	Unknown; low neural spines (female/immature male)	Skeleton	Muscle mass estimation
FMNH 112993	<i>Basiliscus plumifrons</i>	Male	Wet	Muscle mass estimation
FMNH 257162	<i>Basiliscus plumifrons</i>	Male	Skeleton	Additional high resolution visualization
UMMZ 121461	<i>Basiliscus basiliscus</i>	Male	Wet	Caudal centrum ratios
UF 41558	<i>Amblyrhynchus cristatus</i>	Unknown	Wet	Caudal centrum ratios
FMNH 22042	<i>Amblyrhynchus cristatus</i>	Unknown; ?male (tallest caudal neural spines in FMNH collection)	Skeleton	Muscle mass estimation
UF 21461	<i>Alligator mississippiensis</i>	Unknown; juvenile	Wet	X-ray image of caudal centra in tail; caudal centrum ratios

Appendix 2 Table 2. Caudal centrum ratios along the tail in *S. aegyptiacus*, *Mosasaurus*, and extant semiaquatic amphibians and reptiles (**Figure 4D**).

CA#	L-H ratios								Relative distance (Caudal #/Total # of caudals)							
	Spino.	Mosa.	Ambly.	Alli.	Basil.	Hydro.	Trit.	Intel.	Spino.	Mosa.	Ambly.	Alli.	Basil.	Hydro.	Trit.	Intel.
1	0.73		1.40	1.14	1.52	1.25	3.26	1.60	0.02	0.01	0.02	0.02	0.02	0.02	0.03	0.02
2			1.56	1.11	1.92	1.50	3.78	2.21	0.04	0.03	0.04	0.05	0.04	0.04	0.05	0.04
3			1.55	1.05	2.05	1.97	3.18	2.48	0.06	0.04	0.06	0.07	0.06	0.05	0.08	0.06
4	0.84		1.88	1.18	2.30	2.05	3.20	2.73	0.08	0.05	0.09	0.10	0.08	0.07	0.11	0.08
5			1.86	1.22	2.44	2.14	2.88	2.78	0.10	0.07	0.11	0.12	0.10	0.09	0.14	0.10
6			1.96	1.33	2.50	2.14	3.08	2.83	0.12	0.08	0.13	0.15	0.12	0.11	0.16	0.13
7	1.12	1.06	2.06	1.38	2.55	2.26	3.05	2.98	0.14	0.09	0.15	0.17	0.14	0.13	0.19	0.15
8	1.15	1.03	2.10	1.43	2.72	2.17	3.11	2.99	0.16	0.11	0.17	0.20	0.16	0.14	0.22	0.17
9		0.95	2.13	1.49	2.87	2.41	3.07	3.22	0.18	0.12	0.19	0.22	0.18	0.16	0.24	0.19
10		0.97	2.19	1.52	2.89	2.45	2.90	3.26	0.20	0.14	0.21	0.24	0.20	0.18	0.27	0.21
11		0.98	2.29	1.53	3.14	2.34	2.95	3.17	0.22	0.15	0.23	0.27	0.22	0.20	0.30	0.23
12		0.93	2.37	1.67	2.94	2.50	3.17	3.28	0.24	0.16	0.26	0.29	0.24	0.21	0.32	0.25
13	1.24	1.07	2.57	1.62	3.27	2.48	2.73	3.34	0.26	0.18	0.28	0.32	0.25	0.23	0.35	0.27
14	1.21	1.04	2.52	1.65	3.35	2.43	2.77	3.21	0.28	0.19	0.30	0.34	0.27	0.25	0.38	0.29
15		1.06	2.59	1.74	3.49	2.64	2.85	3.51	0.30	0.20	0.32	0.37	0.29	0.27	0.41	0.31
16		0.91	2.67	1.72	3.46	2.52	2.95	3.64	0.32	0.22	0.34	0.39	0.31	0.29	0.43	0.33

17	1.43	0.92	2.74	1.91	3.55	2.94	2.65	3.52	0.34	0.23	0.36	0.41	0.33	0.30	0.46	0.35
18	1.33	0.95	2.80	1.81	3.66	2.82	3.29	3.73	0.36	0.24	0.38	0.44	0.35	0.32	0.49	0.38
19		0.99	2.91	1.89	3.73	3.03	3.14	3.61	0.38	0.26	0.40	0.46	0.37	0.34	0.51	0.40
20	1.37	0.98	2.77	1.97	3.89	2.85	2.70	3.50	0.40	0.27	0.43	0.49	0.39	0.36	0.54	0.42
21	0.97	0.99	2.94	1.89	3.91	2.89	2.82	3.73	0.42	0.28	0.45	0.51	0.41	0.38	0.57	0.44
22	1.40	0.98	2.99	1.95	3.99	2.87	3.16	3.69	0.44	0.30	0.47	0.54	0.43	0.39	0.59	0.46
23	1.38	1.02	2.99	2.12	4.01	2.82	3.27	3.93	0.46	0.31	0.49	0.56	0.45	0.41	0.62	0.48
24	1.32	0.92	3.00	2.21	3.74	2.96	2.92	3.90	0.48	0.32	0.51	0.59	0.47	0.43	0.65	0.50
25	1.41	0.88	3.05	2.25	4.40	3.29	3.22	3.96	0.50	0.34	0.53	0.61	0.49	0.45	0.68	0.52
26	1.36	0.90	3.05	2.49	4.14	3.12	3.63	3.72	0.52	0.35	0.55	0.63	0.51	0.46	0.70	0.54
27	1.35	0.93	3.02	2.63	4.25	3.31	3.45	3.99	0.54	0.36	0.57	0.66	0.53	0.48	0.73	0.56
28	1.15	0.90	3.24	2.79	3.69	3.13	3.36	4.03	0.56	0.38	0.60	0.68	0.55	0.50	0.76	0.58
29	1.44	0.83	3.27	2.70	4.37	3.25	3.03	4.14	0.58	0.39	0.62	0.71	0.57	0.52	0.78	0.60
30	1.29	0.89	3.31	2.99	3.97	3.18	3.11	4.06	0.60	0.41	0.64	0.73	0.59	0.54	0.81	0.63
31	1.34	0.97	3.22	3.10	3.82	3.37	3.23	3.77	0.62	0.42	0.66	0.76	0.61	0.55	0.84	0.65
32	1.42	0.82	3.54	3.21	4.56	3.48	3.27	4.22	0.64	0.43	0.68	0.78	0.63	0.57	0.86	0.67
33	1.36	0.94	3.44	3.32	4.76	3.46	2.19	3.86	0.66	0.45	0.70	0.8	0.65	0.59	0.89	0.69
34	1.45	0.88	3.31	3.45	4.87	3.48	1.75	4.25	0.68	0.46	0.72	0.83	0.67	0.61	0.92	0.71
35		0.89	3.07	3.92	5.09	3.59	1.89	4.11	0.70	0.47	0.74	0.85	0.69	0.63	0.95	0.73
36		0.89	3.25	3.72	5.19	3.68	2.70	4.00	0.72	0.49	0.77	0.88	0.71	0.64	0.97	0.75
37	1.96	0.82	3.50	3.90	5.54	3.71	1.98	4.21	0.74	0.50	0.79	0.90	0.73	0.66	1.00	0.77
38		0.82	3.31	2.96	5.50	3.65		4.17	0.76	0.51	0.81	0.93	0.75	0.68		0.79
39		0.82	3.22	3.19	5.94	3.82		4.13	0.78	0.53	0.83	0.95	0.76	0.70		0.81
40		0.82	3.19	3.54	5.93	3.71		3.95	0.80	0.54	0.85	0.98	0.78	0.71		0.83
41	1.74	0.77	3.07	3.06	5.95	3.91		4.45	0.82	0.55	0.87	1.00	0.8	0.73		0.85
42		0.79	3.25		5.99	4.06		4.31	0.84	0.57	0.89		0.82	0.75		0.88
43		0.72	3.42		6.22	3.99		4.67	0.86	0.58	0.91		0.84	0.77		0.90
44		0.75	3.29		6.73	4.32		4.80	0.88	0.59	0.94		0.86	0.79		0.92
45		0.74	3.16		6.64	4.24		4.59	0.90	0.61	0.96		0.88	0.80		0.94
46		0.80	2.63		6.00	4.33		4.56	0.92	0.62	0.98		0.90	0.82		0.96
47		0.83	2.53		5.82	4.42		5.31	0.94	0.64	1.00		0.92	0.84		0.98
48		0.90			6.61	4.66		3.27	0.96	0.65			0.94	0.86		1.00
49		0.88			6.16	4.61			0.98	0.66			0.96	0.88		
50		0.98			6.49	4.39			1.00	0.68			0.98	0.89		
51		0.95			5.49	4.29				0.69			1.00	0.91		
52		0.83				4.39				0.70				0.93		
53		0.91				4.52				0.72				0.95		
54		0.91				4.53				0.73				0.96		
55		0.88				4.18				0.74				0.98		
56		0.96				3.97				0.76				1.00		
57		0.89								0.77						
58		1.04								0.78						
59		0.96								0.80						
60		0.94								0.81						
61		1.08								0.82						
62		0.99								0.84						
63		0.86								0.85						
64		0.88								0.86						
65		1.06								0.88						
66		1.03								0.89						
67		0.96								0.91						
68		1.02								0.92						
69		1.01								0.93						
70		0.99								0.95						
71		1.00								0.96						
72		1.01								0.97						
73		1.01								0.99						
74		0.98								1.00						

912 **Appendix 3**

913 **Crocodylian foot paddle size and scaling**

914 We measured forefoot, hind foot, and tail areas in five species of extant crocodylians by
915 photographing appendages of individuals in captivity (Appendix 3 **Table 1**).

916 **Appendix 3 Table 1.** Forefoot, hind foot and tail area and other data in five species of extant
917 crocodylians. American alligator (1-7, *Alligator mississippiensis*); Schneider's dwarf crocodile (8,
918 *Paleosuchus trigonatus*); Broad-snouted caiman (9, *Caiman latirostris*); Spectacled caiman (10, *Caiman*
920 *crocodylus*); African dwarf crocodile (11, *Osteolemus tetraspis*).

921

No.	Total length (cm)	Snout-vent length (cm)	Skull length (cm)	Post. skull width (cm)	Tail length (cm)	Mass (kg)	Sex (m, f)	Age est. (yr)	Foot palm/sole, lateral tail areas, (cm ²)		
									hand	foot	tail
1	65	32	9	5.5	35.5	1.15	f	2	5.7	9.8	90.9
2	69	36	9.8	5.6	35	1.05	f	12	7	13.2	102.8
3	85	42.5	11.5	6.8	43	1.95	f	3	10.9	23.6	114.1
4	105.4	52.2	14	8.5	54.5	3.65	f	4	18.3	39.9	267.7
5	154	78	22	14.3	77.5	15.45	m	12	46.2	93.3	655.2
6	167	85	21.8	15.5	86.8	22.95	m	?	51.4	96	717.9
7	211.5	104.5	25.3	18.5	108	39.1	m	23	69.5	146.5	1372.5
8	86.3	47.6	12.6	8.5	37	2.85	f	5	8.4	19.8	172.1
9	75.5	38	8.6	6.3	38	1.55	f	3	5.8	18.3	141.6
10	108.8	55.5	14	10	55.5	4.95	f	5	12.1	29.6	272.1
11	68.2	33.3	9.4	6.2	32.4	1.15	f	4	6.3	17.1	99

922 Appendix 4

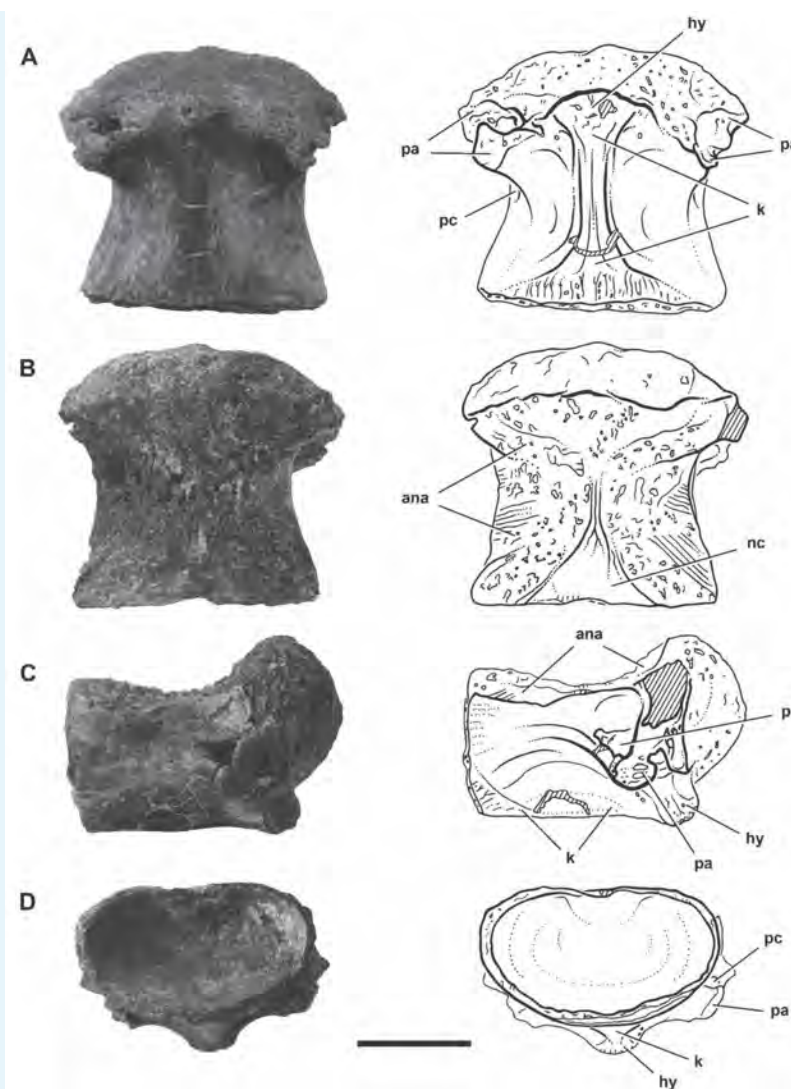
923 Inland fossils referable to *Spinosaurus*

924 Inland fossils referable to *Spinosaurus* sp. were discovered in 1970 at the locality Gara
925 Samani in the Béchar Basin of Algeria (Appendix 4 **Table 1**). The most complete specimen is
926 a snout (MNHN SAM 124) comparable in size to subadult *S. aegyptiacus* and eventually de-
927 scribed as *S. maroccanus* (**Taquet and Russell, 1998**). We consider its specific status in doubt.
928 *S. maroccanus* is based on isolated vertebrae from the Kem Kem Group in Morocco (**Russell,**
929 **1996**) and has recently has been reduced to a junior synonym of *S. aegyptiacus* (**Ibrahim**
930 **et al., 2020b**).

932 **Appendix 4 Table 1.** Fossil material referable to *Spinosaurus* from inland basins in Algeria and Niger.

Specimens	Description
MNHN SAM 124	Snout with preserved length of 62 cm (Gara Samani, Béchar Basin, Algeria) compared to ~1 m for adult snout MSNM V4047
MNHN SAM 125	Premaxilla fragment (Gara Samani, Béchar Basin, Algeria)
MNHN SAM 125-8	Two cervical vertebra, one dorsal vertebra (Gara Samani, Béchar Basin, Algeria)
MNBH IGU11	~D1 short, very low oval centrum with low parapophysis, very strong ventral keel (In Abangharit, Iullumedden Basin, Niger)
MNBH EGA1	Both maxillae and a portion of the alveolar edge of the right dentary with tooth roots within alveoli (Égaro North, Chad Basin, Niger)
MNBH EGA2	Isolated tooth with root (Égaro North, Chad Basin, Niger)

934 Inland fossils referable to *Spinosaurus* sp. come from two areas of outcrop of the Cenomanian-
935 age Echkar Formation in Niger (Appendix 4 **Table 1**). The first locality is near In Abangharit
936 northeast of Agadez that yielded isolated teeth and an anterior dorsal centrum initially re-
937 ferred to *Carcharodontosaurus iguidensis* (Appendix 4 **Figure 1**). Reassigned to *Spinosaurus*
938 sp., this vertebra is very close in form to the first dorsal centrum of *S. aegyptiacus* from Mo-
939 rocco (**Ibrahim et al., 2020b**, Fig. 128A-D) and Egypt (**Stromer, 1934**, Pl. 1, Fig. 2), although
940 differences suggest it may pertain to a distinct species. For the time being, reference is
941 made only to the genus *Spinosaurus*.



942

943

944

945

946

948

Appendix 4 Figure 1. Anterior dorsal centrum referable to *Spinosaurus* sp. (from (Brusatte and Sereno, 2007, Figure 9)). Photographs and line drawings of an anterior dorsal centrum (MNBH IGU11) from the Echkar Formation (Cenomanian) of Niger in ventral (A) dorsal (B), right lateral (C) and posterior (D) views. Cross-hatching indicates broken bone. ana, articular surface for the neural arch; hy, hypapophysis; k, ventral keel; nc, neural canal; pa, parapophysis; pc, pleurocoel. Scale bar, 5 cm.

949

950

951

952

953

954

955

956

957

958

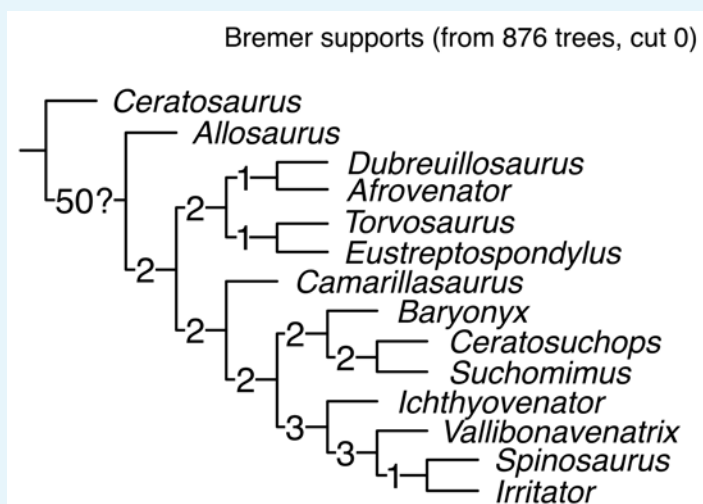
In 2019 a fragmentary snout preserving most of the right and left maxillae of *Spinosaurus* sp. was recovered from a second locality southeast of Agadez also in the Echkar Formation (Figure 7B). The material also includes a partial right dentary (MNBH EGA1) with subconical crowns and long tapering roots (MNBH EGA2). The jaw bones, which closely resemble *S. aegyptiacus* although possibly a new species, are comparable in size to the subadult holotypic and neotypic skeletons, or about 75% of the size of the large snout recovered in Morocco (Dal Sasso et al., 2005). They were found in overbank deposits near the remains of rebbachisaurid and titanosaurid sauropods and evidence of a vertebrate fauna common to Cenomanian sites across northern Africa (including *Carcharodontosaurus*, lungfish tooth plates, sawfish rostral teeth, etc.).

959 Appendix 5

960 Phylogenetic analysis of Spinosauroidea

961 Phylogenetic analysis

962 A phylogenetic analysis of Spinosauroidea was performed to examine phylogenetic pat-
963 terns within the clade and survey the distribution and evolution of putative display and
964 semiaquatic features. The analysis included 14 terminal taxa (8 spinosaurids) scored for
965 120 characters with *Allosaurus fragilis* and *Ceratosaurus nasicornis* as successive outgroups
966 and was analyzed with TNT set for a heuristic search (1000 Wagner tree replicates, 10 TBR;
967 Goloboff et al., 2008). The analysis yielded a single most-parsimonious tree of 156 steps
968 (Appendix 5 **Figure 1**).



969
970 **Appendix 5 Figure 1.** Phylogenetic tree for Spinosauroidea. Single most-parsimonious tree for 12
971 spinosauroid terminal taxa (8 spinosaurids) and 120 characters split evenly between the cranium
972 (49%) and postcranium (51%), showing decay values (CI = 0.81, RI = 0.86).

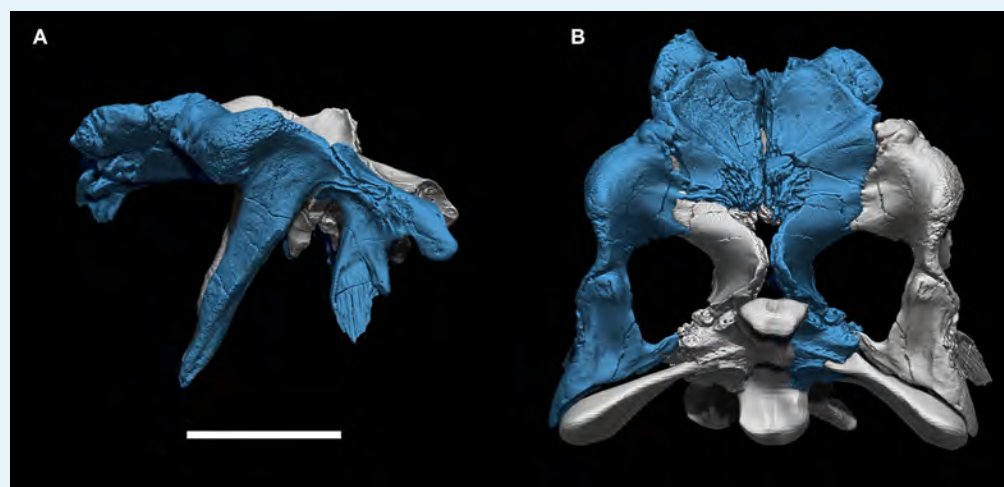
974 Although **Sales and Schultz (2017)** were unable to resolve a basal polytomy involving
975 *Baryonyx*, *Suchomimus* and spinosaurines (*Irritator*, *Spinosaurus*), other analyses follow **Sereno**
976 **et al. (1998)** splitting spinosaurid theropods into the subclades Baryonychinae and Spinosauri-
977 **nae (Allain et al., 2012; Carrano et al., 2012; Arden et al., 2019; Malafaia et al., 2018; Barker**
978 **et al., 2021)**. We obtain this result again here in an updated analysis of Spinosauroidea
979 based on a dataset of 120 characters, 24 of which are newly introduced. Larger-scale anal-
980 yses that incorporate theropods far afield and non-applicable character evidence do not
981 appear to have added any clarity or insights to an understanding of ingroup relationships
982 and morphological character change within Spinosauroidea.

983 *Camarillasaurus cirugedae* was originally described as a ceratosaur (**Sánchez-Hernández**
984 **and Benton, 2012**) and later reinterpreted as either a megalosaurid or spinosaurid (**Rauhut**
985 **et al., 2019; Malafaia et al., 2018; Samathi et al., 2021)**. Our analysis tentatively resolves *Ca-*
986 *marillasaurus* as the most basal spinosaurid, although further study and additional remains
987 of this fragmentary taxon are needed.

Fossil material from the Wessex Formation on the Isle of Wight was described recently as
two new baryonychines, *Ceratosuchops inferodios* and *Riperovenator milnerae* (**Barker et al.,**
2021), which differ in minor details where they overlap. Both are close in form to *Suchomimus*
tenerensis. Only the premaxillae and portions of the braincase of the holotypic specimens
of the new taxa overlap, and some doubt exists regarding their association as single speci-
mens, as neither hypodigm were found in association from single sites. The distinguishing

991
992
993
994
995
996
997
998
999
1000
1001
1002
1003

features in the premaxillae (low narial tuberosity in one but not preserved in the other) and in the shape/depth of fossae, relative thickness of laminae and other minutiae of the braincase could well be due to individual variation (*Chure and Madsen, 1996*), as several of these features seem to occur on one or the other side of a well-preserved braincase of *Suchomimus tenerensis* (MNBH GAD43) or are impossible to evaluate effectively. The configuration of the orbital margin and form of the swollen postorbital brow is similar in *Suchomimus tenerensis* and *Ceratosuchops*, which was cited as distinguishing feature of the latter. We tentatively score as a single taxon the Wessex spinosaurid material (shown as *Ceratosuchops* on the phylogeny), which is resolved as the sister taxon to *Suchomimus tenerensis* (Appendix 5 *Figure 2*).



1004
1005
1006
1007
1008

Appendix 5 Figure 2. Posterior skull roof of the baryonychine spinosaurid *Suchomimus tenerensis*. Composite restoration of the posterior skull roof of *Suchomimus tenerensis* in (A) lateral and (B) dorsal views showing a swollen postorbital brow and narrow orbital notch limiting the frontal orbital margin. Scale = 10 cm.

1010
1011
1012
1013
1014
1015
1016

The analysis positions *Ichthyovenator* (*Allain et al., 2012*) and *Vallibonavenatrix* (*Malafaia et al., 2018*) as successively closer to the spinosaurines *Irritator* and *Spinosaurus*. Postcranial remains from the Romualdo Formation of Brazil (*Aureliano et al., 2018*), which may pertain to the Brazilian genus *Irritator*, show derived spinosaurine features (e.g., posterior dorsal neural spines narrower than centrum length, iliac blade proportionately low, pubic process of the ilium ventrally directed). *Irritator* and *Spinosaurus* share straight tooth crowns, spaced tooth positions, more posteriorly positioned external nares, and an oval quadrate head.

1017
1018

Character list

Skull

1019
1020
1021
1022
1023
1024
1025
1026
1027
1028
1029

1. Snout (preorbital region of skull), length relative to antorbital fenestra length: less (0) or more (1) than three times. (*Sereno et al., 1998*, char. 7)
2. Jaws (premaxillae and dentary), anterior end, form: convergent (0); expanded into a premaxillary/ dentary rosette (1). (*Sereno et al., 1998*, char. 6)
3. Premaxilla, form of premaxilla-nasal suture: V-shaped (0); W-shaped (1). (*Carrano et al., 2012*, char. 5)
4. Premaxilla, external nares, proportions and position: shorter than premaxilla ventral to nares, angle between anterior and alveolar margins $> 75^\circ$ (0); longer than body ventral to nares (1). (*Carrano et al., 2012*, char. 6)
5. Premaxillae, inter-premaxillary suture at maturity, form: open (0); fused (1). (*Sereno et al., 1998*, char. 10)

- 1030 6. Premaxilla-maxilla articulation, form: scarf or butt joint (0); interlocking (1). (*Sereno*
1031 *et al., 1998*, char. 11)
- 1032 7. Premaxilla-maxilla suture, lateral surface, subnarial foramen, shape: foramen (0);
1033 dorsoventrally directed channel (1). (*Carrano et al., 2012*, char. 10)
- 1034 8. Premaxilla, ventral margin, shape in lateral view: straight to convex (0); concave (1).
1035 (*Cau et al., 2017*, char. 1485)
- 1036 9. Premaxilla, lateral and dorsal surface, extensive pitting of neurovascular foramina:
1037 absent (0); present (1). (*Barker et al., 2021*, char. 1796)
- 1038 10. Maxilla, anterior ramus, length relative to maximum depth: 70% (0); 100% or more (1).
1039 (*Sereno et al., 1998*, char. 1)
- 1040 11. Maxilla, contribution to the narial fossa: no contribution (0); contributes partially or
1041 totally (1). (modified from *Longrich and Currie (2009)*, char 7).
- 1042 12. Maxilla, antorbital fossa, width of ventral margin relative to depth of posterior ramus
1043 of maxilla: more (0) or less (1) than 30%. (*Sereno et al., 1998*, char. 40)
- 1044 13. Maxilla, antorbital fossa, anterior margin: rounded (0); squared (1). (*Carrano et al.,*
1045 *2012*, char. 23)
- 1046 14. Maxilla, subcircular depression in the anterior corner of the antorbital fossa: absent
1047 (0); present (1). (*Sereno et al., 1998*, char. 41)
- 1048 15. Maxilla, anteromedial process, shape: fluted prong (0); plate (1). (*Sereno et al., 1998*,
1049 char. 12)
- 1050 16. Maxilla, anteromedial process, anterior extension: as far as (0) or far anterior to (1)
1051 the anterior margin of the maxilla. (*Sereno et al., 1998*, char. 13)
- 1052 17. Maxilla, antorbital fossa, size relative to orbit: larger (0); smaller (1). (*Sereno et al.,*
1053 *1998*, char. 9)
- 1054 18. Maxilla, anteroventral margin, curvature: not curved (0); dorso-medially curved (1).
1055 (modified from *Cau et al. (2017)*, char 731; *Tykoski (2005)*)
- 1056 19. Nasal, posterior process, overlap of frontal in articulation: absent or limited (0); exten-
1057 sive, in particular medially, on almost or all the process dorsal surface (1). (modified
1058 from *Cau et al. (2017)*, char. 1500)
- 1059 20. Jugal, posterior ramus, depth relative to orbital ramus: less (0); more (1). (*Sereno et al.,*
1060 *1998*, char. 43)
- 1061 21. Lacrimal, anterior and ventral rami, angle of divergence: 75° to 90° (0); 30° to 45° (1).
1062 (*Sereno et al., 1998*, char. 15)
- 1063 22. Lacrimal foramen, position relative to ventral process: near the base (0); at mid-height
1064 (1). (*Sereno et al., 1998*, char. 42)
- 1065 23. Lacrimal, anterior ramus, length relative to ventral ramus: more (0) or less (1) than
1066 65%. (*Sereno et al., 1998*, char. 2)
- 1067 24. Postorbital, ventral process, cross section of distal half: subcircular (0); U-shaped (1).
1068 (*Sereno et al., 1998*, char. 44)
- 1069 25. Postorbital, supraorbital shelf (boss) formed mostly by palpebral: absent (0); present
1070 (1). (modified from *Carrano et al. (2012)*, char. 61)
- 1071 26. Frontal, postorbital facet, anterior depth: less than 2/5 facet length (0); more than 2/5
1072 facet length (1). (*Barker et al., 2021*, Supplementary 2)
- 1073 27. Frontal, shape of the lateral margin in dorsal view: describes a smooth transition be-
1074 tween the anterior half and the postorbital process (0); an abrupt transition between
1075 the anterior half and the postorbital process (1). (*Senter et al., 2010*, char. 44)
- 1076 28. Prefrontal, boss-like process: absent (0); present (1). (*Barker et al., 2021*, Supplemen-
1077 tary 2)
- 1078 29. Parietal, length: less than 3/4 of the frontal (0); subequal or more than 3/4 of the
1079 frontal (1). (*Cau et al., 2017*, char. 78)

- 1080 30. Quadrate, head, shape: oval (0); subquadrate (1). (*Sereno et al., 1998*, char. 27)
- 1081 31. Quadrate, foramen, size: foramen (0); broad fenestra (1). (*Sereno et al., 1998*, char. 28)
- 1082 32. Quadrate, medial foramina adjacent to condyles: absent (0); present (1). (*Carrano*
- 1083 *et al., 2012*, char. 84)
- 1084 33. Quadrate, foramen margin, placement: at mid-height or dorsal (0); ventral, close to
- 1085 mandibular condyles (1). (modified from *Loewen et al. (2013)*, char. 158)
- 1086 34. Basisphenoid, width of the interbasipterygoidal web: thin; 40 percent of occipital condyle
- 1087 width or less (0); thick, more than 40 percent occipital condyle width (1). (modified
- 1088 from *Barker et al. (2021)*, Supplementary 2)
- 1089 35. Basisphenoid, basiptyergoid process, exposure of the ventral surface in lateral view:
- 1090 thick (0); reduced (1). (*Barker et al., 2021*, Supplementary 2)
- 1091 36. Basisphenoid, basiptyergoid process, shape of lateral margin in ventral view: flat or
- 1092 slightly concave (0); convex (1). (*Barker et al., 2021*, Supplementary 2)
- 1093 37. Basioccipital, position of subcondylar recess: dorsoventrally tall, recess reaches the
- 1094 occipital condyle neck (0); ventrally restricted, surface directly below condyle convex
- 1095 (1). (*Barker et al., 2021*, Supplementary 2)
- 1096 38. Basioccipital, width of subcondylar recess relative to occipital condyle width: narrow,
- 1097 0.5 times or less (0); wide, greater than 0.5 times (1). (modified from (*Barker et al.,*
- 1098 *2021*, Supplementary 2))
- 1099 39. Basioccipital, thick crests bordering subcondylar recess laterally: present (0); absent
- 1100 (1). (*Barker et al., 2021*, Supplementary 2)
- 1101 40. Basioccipital, contribution to foramen magnum: large, exoccipitals widely separated
- 1102 (0); reduced, exoccipitals closely placed (1). (*Barker et al., 2021*, Supplementary 2)
- 1103 41. Basioccipital, proportions relative to basisphenoid (measured along midline ventral to
- 1104 occipital condyle to interbasipterygoidal web), in posterior view: shorter (0); longer (1).
- 1105 (*Barker et al., 2021*, Supplementary 2)
- 1106 42. Otoccipitals, angle of projection of paroccipital processes: posterolaterally (0); laterally
- 1107 or subhorizontal (1). (*Barker et al., 2021*, Supplementary 2)
- 1108 43. Splenial foramen, size: small (0); large (1). (*Sereno et al., 1998*, char. 16)
- 1109 44. Dentary, shape of anterior end in lateral view: blunt and unexpanded (0); dorsoven-
- 1110 trally expanded, rounded and slightly upturned (1); squared off in lateral view via an-
- 1111 teroventral process (2). (*Carrano et al., 2012*, char. 120)
- 1112 45. Premaxilla and anterior dentary, interdental septa spacing: regular (0); alternate (alve-
- 1113 oli result paired) (1). (modified from *Cau et al. (2017)*, char. 1614)

1114 Dental

- 1115 46. Teeth, distal, curvature: present, marked (0); reduced or non-curved (1). (*Sereno et al.*
- 1116 *(1998)*, char. 35; modified after *Hendrickx et al. (2019)*)
- 1117 47. Teeth, maxillary and dentary, serrations: present (0); absent (1). (*Sereno et al., 1998*,
- 1118 char. 17)
- 1119 48. Teeth, distal, midcrown cross-section: elliptical (0); circular (1). (*Sereno et al. (1998)*,
- 1120 char. 36; modified after *Hendrickx et al. (2019)*)
- 1121 49. Teeth, distal, crown striations (flutes/apicobasal ridges): absent (0); present (1). (*Sereno*
- 1122 *et al. (1998)*, char. 18; modified after *Hendrickx et al. (2019)*)
- 1123 50. Teeth, enamel ornamentation: absent (0); present (1). (modified from *Carrano et al.*
- 1124 *(2012)*, char. 143)
- 1125 51. Teeth, enamel ornamentation type: extending as bands across labial and lingual tooth
- 1126 surfaces (0); pronounced marginal enamel wrinkles (1); pronounced deeply veined/
- 1127 anastomous texture (2). (modified from *Carrano et al. (2012)*, char. 143)
52. Teeth, basalmost root shape: broad (0); strongly tapered (1). (*Sereno et al., 1998*,

1128
1129
1130
1131
1132
1133
1134
1135
1136
1137
1138
1139
1140

1141

1142
1143
1144
1145
1146
1147
1148
1149
1150
1151
1152
1153
1154
1155
1156
1157
1158
1159
1160
1161
1162
1163
1164
1165
1166
1167
1168
1169
1170
1171
1172
1173
1174
1175
1176

- char. 21)
53. Premaxilla, tooth count: 3 to 4 (0); 6 to 7 (1). (*Sereno et al., 1998*, char. 19)
54. Premaxillary tooth 1, size: slightly smaller (0) or much smaller (1) than crowns 2 and 3. (*Sereno et al., 1998*, char. 38)
55. Premaxilla, diastemata within the premaxillary rosette: narrow (0); broad (1). (*Sereno et al., 1998*, char. 39)
56. Maxillary teeth, mid-tooth spacing: adjacent (0); with intervening space/diastemata (1). (*Sereno et al., 1998*, char. 20)
57. Dentary, tooth count: up to 15 (0); ≥ 15 (1). (*Sereno et al., 1998*, char. 26)
58. Dentary teeth, spacing: adjacent (0); with intervening space (1). (*Sereno et al., 1998*, char. 37)
59. Paradental laminae: present (0); absent (1). (*Sereno et al., 1998*, char. 14)

Axial

60. Cervical vertebrae, middle, shape of anterior pneumatic foramina: round (0); antero-posteriorly elongate (1). (*Carrano et al., 2012*, char. 169)
61. Cervical vertebrae, posteriormost, ventral keel: absent or developed as a weak ridge (0); pronounced, around 1/3 the height of centrum and inset from lateral surfaces (1). NEW
62. Cervical vertebrae, prezygapophyseal facets, elongation related to width: as long as wide (0); longer than wide (1); wider than longer (2). NEW
63. Cervical vertebrae, middle and posterior centra width relative to centra height: taller than wide or round (0); wider than tall (1). NEW
64. Cervical vertebrae, anterior post-axial neural spines in lateral view: longer than tall (0); taller than long (1). (*Cau et al., 2017*, char. 212)
65. Dorsal vertebrae, anterior centra, depth of ventral keel relative to total centrum height: absent or less than $\frac{1}{4}$ (0); blade-shaped, more than $\frac{1}{4}$ (1). (*Sereno et al., 1998*, char. 22)
66. Dorsal vertebrae, anterior centra, ventral processes anterior to the keel (hypapophysis): poorly developed (0); strongly developed (1). (Modified by *Cau et al. (2017)* (char. 225) from *Rauhut (2003)*; *O'Connor (2009)*)
67. Dorsal vertebrae, middle, centra length relative to height: $1.4 <$ times centrum height (0); ≥ 1.4 times centrum height (1). NEW
68. Dorsal vertebrae, anterior parapophyses, size: less (0) or more (1) than half-depth of anterior facet of centrum. (*Cau et al., 2017*, char. 1740)
69. Dorsal vertebrae, anterior centra, pneumatic foramen, size relative to parapophysis: larger or equal (0); smaller (1). NEW
70. Dorsal vertebrae, anterior, prezygapophyseal facets, elongation related to width: as long as wide (0); longer than wide (1); wider than longer (2). NEW
71. Dorsal vertebrae, mid-posterior, excavated prezygo-para-diapophyseal fossa (prpdf) delimited by the paradiapophyseal lamina (ppdl): absent (0); present (1). NEW (after *Malafaia et al. (2020)*)
72. Dorsal vertebrae, middle and posterior centra, pneumatic foramina: absent (0); present (1). (modified from *Cau et al. (2017)*, char. 1350)
73. Dorsal vertebrae, height of neural spines relative to centrum height: low, $< 1.3x$ (0); moderate, $1.3-1.8x$ (1); tall, $< 1.8x$ (2). (modified from *Carrano et al. (2012)*, char. 193)
74. Dorsal vertebrae, posterior neural spines, basal webbing: absent (0); present (1). (*Sereno et al., 1998*, char. 24)
75. Dorsal vertebrae, posterior neural spines, accessory centrodiaepophyseal lamina: absent (0); present (1). (*Sereno et al., 1998*, char. 25)
76. Dorsal vertebrae, middle and posterior, neural spine antero-posterior length at base

1177

1178

relative to centrum length: subequal (0); shorter (1). NEW

1179

77. Dorsal vertebrae, middle-posterior parapophyses, development: distinct and well-developed (0); small, knob-like (1). (**Stromer, 1934**)

1180

1181

78. Dorsal vertebrae, accessory centrodiapophyseal lamina: absent (0); present (1). (modified from **Benson et al. (2009)**, char. 2015)

1182

1183

79. Sacrum, centrum pneumaticity: absent (0); present (1). (modified from **Carrano et al. (2012)**, char. 196)

1184

1185

80. Sacrum, centrum pneumaticity type: pleurocoelous fossae (0); pneumatic foramina (1). (modified from **Carrano et al. (2012)**, char. 196)

1186

1187

81. Sacrum, neural spines: without distal antero-posterior expansion (0); with distal expansion contacting adjacent spines (1). NEW

1188

1189

82. Caudal vertebrae, anterior, morphology of ventral surface: flat (0); groove (1); ridge (2). (**Carrano et al., 2012**, char. 202)

1190

1191

83. Caudal vertebrae, anterior, well-marked spino-diapophyseal lamina: absent (0); present (1). NEW

1192

1193

84. Caudal vertebrae, anterior neural arches, ventral rib laminae: absent (0); present (1). (**Cau et al., 2017**, char. 358)

1194

1195

85. Caudal vertebrae, anterior neural arches, anterolateral surface, deep triangular prezygocostal fossa delimited by two laminae: absent (0); present (1). (**Cau et al. (2017)**, char. 1605; modified from **Brusatte et al. (2010)**)

1196

1197

86. Caudal vertebrae, anterior neural arches, hyposphene: absent (0); present (1). (**Cau et al., 2017**, char. 359)

1198

1199

87. Caudal vertebrae, CFL and ilio-ischiocaudalis correlates: transition point at or beyond CA20 (0); transition point around CA15-19 (1). NEW

1200

1201

88. Caudal vertebrae, middle, height of neural spines relative to centrum height: low, $\geq 1.3x$ (0); moderate, 1.3-2.0x (1); tall, 2.0-4.0x (2); extreme elongation $> 4x$ (3). NEW

1202

1203

89. Caudal vertebrae, distal, height of neural spines relative to centrum height: low, $\geq 1.3x$ (0); moderate, 1.3-2.0x (1); tall, 2.0-4.0x (2); extreme elongation $> 4x$ (3). NEW

1204

1205

90. Caudal vertebrae, middle, morphology of neural spines: rod-like and posteriorly inclined (0); subrectangular and sheet-like (1); rod-like and vertical (2). (**Carrano et al., 2012**, char. 207)

1206

1207

91. Caudal vertebrae, middle, centrum elongation relative to centrum height: elongated $> 1.6x$ (0); not elongated $\leq 1.6x$ (1). NEW

1208

1209

92. Caudal vertebrae, middle and posterior, prezygapophyses: elongated, projected beyond the anterior rim of the centrum (0); shortened, barely reaching the anterior rim of the centrum (1). NEW (after observations in **Samathi et al. (2021)**)

1210

1211

93. Chevrons, anterior and posterior longitudinal groove: absent (0); present (1). NEW

1212

1213

94. Chevrons, anterior and posterior surfaces: without distinctive features (0); with longitudinal groove widened as a fossa (1). NEW

1214

1215

95. Chevrons, posterior elongation compared with anterior and middle ones: shorter (0); as elongated (1). NEW

1216

1217

96. Chevrons, anterior process: absent (0); present (1). (**Carrano et al., 2012**, char. 217)

1218

1219

1220 Appendicular

1220

1221

97. Coracoid, posterior process, shape: low and rounded (0); crescentic (1). (**Sereno et al., 1998**, char. 29)

1222

1223

98. Appendicular bones, marrow cavity: present (0); reduced to barely present (1). NEW

1224

1225

99. Humerus, deltopectoral crest, length relative to humeral length: less (0) or more (1) than 45%. (**Sereno et al., 1998**, char. 3)

100. Humerus, deltopectoral crest, orientation of apex: anterior (0), lateral (1). (**Sereno**

1274

1275

1276

1277

1278

1279

1280

1281

1282

1283

1284

1285

1286

1287

1288

1289

1290

1291

1292

1293

1294

1295

1296

1297

1298

1299

1300

1301

1302

1303

1304

1305

1306

1307

1308

1309

1310

1311

1312

1313

1314

1315

1316

1317

1318

1319

1320

1321

1322

1323

1324

0 1 0 0 1 0 0 0 0 0 0 & 1 0 & 1 0 0 0 0 ? 0 0 1 0 0 0 1 0 0 0 0 1 0 0 0 & 1 2 0 2 0 0 1 0 1 0 0 0
Eustreptospondylus 0 0 ? 1 0 0 0 0 0 1 0 1 ? 1 0 0 0 0 ? 1 0 1 1 1 0 0 0 0 0 0 0 0 0 ? ? ? 0 0 0 0 ?
0 ? 0 0 0 0 0 0 1 1 0 0 0 ? 0 0 0 0 1 0 ? 0 1 0 0 ? 0 0 0 0 ? 1 0 0 ? ? ? 0 ? 0 1 0 0 0 1 ? ? ? 0 0 ? ? ?
? ? 0 ? 1 0 0 0 ? ? ? 1 ? 3 1 1 ? ? 1 ? ? 0 0 & 1 ? 0 0
Torvosaurus 0 0 ? 1 0 0 0 0 0 1 0 1 0 1 0 0 0 0 ? 1 0 1 1 1 0 ? ? ? ? 0 0 1 0 ? ? ? ? ? ? ? ? ? ? 0 0 0
0 0 0 1 1 0 0 0 ? 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 & 1 1 0 0 0 0 0 1 0 0 1 0 0 1 0 ? 0 ? 0 0 ? 1 0 0 1
0 ? 1 0 0 0 1 0 1 1 0 3 1 1 1 0 1 0 1 0 0 0 0 0
Afrovenator 0 ? ? ? ? 0 ? ? ? 1 0 1 1 1 0 0 0 0 ? 1 0 1 0 1 0 ? ? ? ? 0 0 1 ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0
0 0 1 1 ? ? ? ? 0 ? ? ? 1 0 0 0 0 0 0 0 0 ? 0 0 0 0 0 0 0 0 ? ? ? ? ? ? ? ? ? ? 0 0 0 0 0 1 0 0 1 ? ? 0 0
0 0 ? ? 0 1 1 0 1 1 0 ? 1 0 1 0 0 0 ? 0
Dubreuillosaurus 0 0 ? 1 0 0 ? 0 0 1 0 1 1 ? 0 0 0 0 ? ? 0 ? 1 ? 0 0 ? ? ? ? ? ? ? ? ? ? ? ? 0 0 1 0 ? 0 1 0
0 0 0 0 0 1 1 0 0 0 ? 0 0 0 0 1 0 ? ? ? 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 1 ? ? 0 ? ? ? ? ? ? ? ? 0 0 1 0 0 1 ? ?
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? ? ?
Baryonyx 1 1 0 2 1 1 1 1 1 1 0 ? ? ? 1 1 1 1 ? ? 1 0 1 ? ? 0 0 ? 1 1 1 0 ? 0 0 0 0 1 0 0 0 1 1 1 0 0 0
1 1 1 2 1 1 0 0 1 1 0 1 1 1 1 0 0 1 0 0 1 0 1 0 0 2 1 1 0 0 1 ? ? ? ? 0 ? ? ? ? ? ? ? ? ? ? ? 1 1 ? 0 2 ? 1 1
1 1 1 1 1 ? 0 0 1 ? ? 1 ? 0 ? 1 ? ? ?
Suchomimus 1 1 0 2 1 1 1 1 1 1 0 ? ? 0 1 1 1 1 1 ? ? ? 1 0 1 1 1 1 1 1 1 1 0 ? 1 0 0 0 0 1 1 1 0 ? 1 0
0 0 1 1 1 2 1 1 0 0 1 1 0 1 1 1 1 0 0 1 0 0 & 1 1 0 1 0 0 2 1 1 0 0 1 1 1 1 0 0 & 1 0 0 0 0 2 ? 0 0 1 1
1 0 0 2 0 1 1 1 1 1 1 1 1 ? 0 1 0 1 0 1 0 0 0 1 0 1 0
Ichthyovenator ?
? ? ? ? ? ? ? ? ? ? ? 1 1 1 1 1 0 1 1 1 1 0 2 ? 1 1 1 0 ? ? 1 0 0 1 1 0 ? 2 ? 0 0 1 1 1 1 0 ? ? ? ? ? ? ?
? ? ? 0 ? 2 1 2 ? 1 1 0 ? ? ? ? ? ?
Camarillasaurus ?
1 0 ?
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 ?
Vallibonavenatrix ?
? ? ? ? ? ? ? ? ? ? ? 1 1 ? 1 ? 1 ? 1 1 ? ? 1 1 2 ? 1 1 ? 1 1 1 ? 1 1 ? ? 0 ? ? ? ? ? 1 ? 0 ? ? 0 1 ? ? ? ? ? ?
? ? ? 1 0 0 1 2 1 ? ? ? 0 ? ? ? ? ? ?
Irritator 1 1 ? 2 1 1 ? ? ? 1 1 ? 0 0 1 1 1 1 1 0 1 ? 1 1 0 & 1 0 0 1 1 0 1 0 1 0 1 0 1 0 0 0 0 0 0 ? ? ? 1
1 1 1 1 2 1 ? 1 1 1 0 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 2 ? ? 1 ? ? 1 1 1 ? ? ? ? ? ? ? ? 0 1 ? ? ? ? ? ? 1 ? ? ?
? ? ? 1 1 0 0 0 1 1 0 & 1 ? ? 0 ? ? ? ? ? ?
Spinosaurus 1 1 1 2 1 1 1 1 1 1 1 ? ? ? 1 1 ? 1 1 ? ? ? ? ? ? ? ? ? ? ? ? ? 0 1 0 1 ? ? ? ? ? ? ? ? ? ? 1 1 1 1 1
1 0 & 1 1 2 1 1 1 1 0 1 1 1 1 1 1 1 1 1 1 1 1 1 2 0 1 1 1 0 1 1 1 1 1 1 0 1 3 3 0 1 1 1 1 1 0 ?
1 ? ? ? ? ? ? 1 1 0 0 0 1 1 1 0 1 0 1 1 1 1 1
Ceratosuchops ? 1 0 2 1 1 1 1 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 1 1 1 1 1 ? ? ? ? ? 0 & 1 0 & 1 0 & 1 0 & 1
0 & 1 0 & 1 1 0 0 ? ? 0 0 0 1 1 1 2 ? 1 0 0 ? ? ? 1 ? 0 ? ? ? ? 2 1
? 0 1 1 1 1 0 ?

Apomorphy list

Spinosauridae (with *Camarillasaurus*)

- Ch. 48: 0 → 1 Maxillary lateral teeth with circular midcrown cross section.
- Ch. 92: 0 → 1 Middle and posterior caudal vertebrae with short prezygapophyses.
- Ch. 119: 0 → 1 Tibia with a proximal diaphysis with length+width ratio greater than 2.

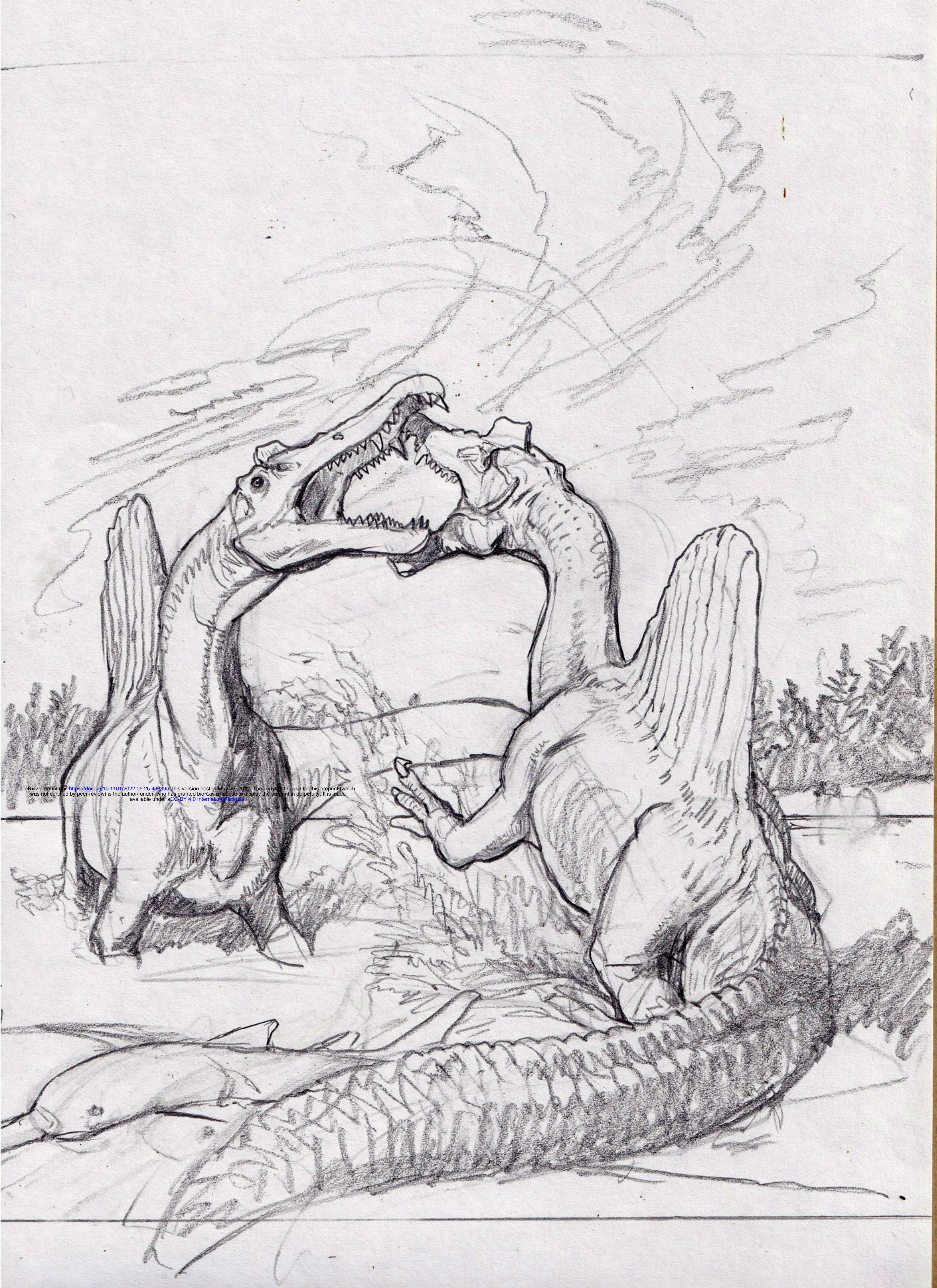
Spinosauridae (minus *Camarillasaurus*)

- Ch. 49: 0 → 1 Maxillary lateral teeth with fluting (apico-basal ridges).
- Ch. 94: 0 → 1 Anterior chevrons with longitudinal groove widened as a fossa.

Baryonychinae

- Ch. 3: 0 → 1 V-shaped premaxilla-nasal suture
- Ch. 30: 0 → 1 Square-shaped quadrate head
- Ch. 57: 0 → 1 30 dentary teeth.

1325	Ch. 64: 1 → 0 Middle cervical vertebrae with neural spines longer than tall
1326	Ch. 74: 0 → 1 Dorsal vertebrae, posterior neural spines with basal webbing
1327	Ch. 78: 0 → 1 Dorsal vertebrae with accessory centrodiaepophyseal lamina
1328	Ch. 97: 0 → 1 Coracoid with crescentic posterior process.
1329	Ceratosuchopsini (<i>Suchomimus</i> + <i>Ceratosuchops</i>)
1330	Ch. 26: 0 → 1 Frontal, postorbital facet depth more than 2/5 facet length.
1331	Ch. 27: 0 → 1 Frontal with abrupt transition between the anterior half and the postorbital
1332	process
1333	Ch. 40: 0 → 1 Basioccipital contribution to foramen magnum reduced, with exoccipitals
1334	closely placed.
1335	Spinosaurinae
1336	Ch. 63: 0 → 1 Middle and posterior cervical vertebrae with centra wider than tall
1337	Ch. 66: 0 → 1 Anterior dorsal vertebrae with strongly developed hypapophysis
1338	Ch. 69: 0 → 1 Anterior dorsal vertebrae with pneumatic foramen smaller than parapophy-
1339	sis
1340	Ch. 71: 0 → 1 Middle and posterior dorsal vertebrae with deeply excavated prezygo-
1341	para-diaepophyseal fossa (prpdf).
1342	Ch. 76: 0 → 1 Posterior dorsal vertebrae with neural spine base shorter than centrum
1343	Ch. 77: 0 → 1 Middle and posterior dorsal vertebrae with reduced, knob-like parapophy-
1344	ses
1345	Ch. 84: 0 → 1 Anterior caudal vertebrae with centro-costal laminae
1346	Ch. 85: 0 → 1 Anterior caudal vertebrae with prezygo-costal fossa delimited by two
1347	laminae.
1348	<i>Vallibonavenatrix</i> + (<i>Spinosaurus</i> + <i>Irritator</i>)
1349	Ch. 67: 0 → 1 Mid-dorsal vertebrae centra longer than 1.4 times centrum height
1350	Ch. 72: 0 → 1 Middle and posterior dorsal centra with large pneumatic foramina
1351	Ch. 83: 0 → 1 Anterior caudal vertebrae with well-marked spino-diaepophyseal lamina
1352	Ch. 91: 0 → 1 Shorter middle caudal centra.
1353	<i>Spinosaurus</i> + <i>Irritator</i>
1354	Ch. 109: 0 → 1 Ilium, orientation of pubic peduncle mostly anterior or 'kinked' double
1355	facet with anterior and ventral components.



bioRxiv preprint doi: <https://doi.org/10.1101/2022.05.25.493395>; this version posted May 26, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.



bioRxiv preprint doi: <https://doi.org/10.1101/2022.05.25.493395>; this version posted May 26, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.