A buoyancy, balance and stability challenge to the hypothesis of a semi-aquatic *Spinosaurus* Stromer, 1915 (Dinosauria:Theropoda)

Donald M Henderson Corresp. 1

1 Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada

Corresponding Author: Donald M Henderson
Email address: don.henderson@gov.ab.ca

A recent interpretation of the fossil remains of the enigmatic, large predatory dinosaur *Spinosaurus aegyptiacus* Stromer 1915 proposed that it was specially adapted for a semi-aquatic mode of life – a first for any predatory dinosaur. To test some aspects of this suggestion, a three-dimensional, digital model of the animal that incorporates regional density variations, lungs and air sacs was generated, and the flotation potential of the model was investigated using specially written software. It was found that *Spinosaurus* would have been able to float with its head clear of the water surface, although it was laterally unstable and would tend to roll onto its side. Similarly detailed models of another spinosaurid *Baryonyx* (*Suchomimus*) *tenerensis* Sereno et al. 1998, along with models of the more distantly related *Tyrannosaurus rex* Osborn 1905, *Allosaurus fragilis* Marsh 1877, *Struthiomimus altus* Lambe 1902 and *Coelophysis bauri* Cope 1887 were also able to float in positions that enabled the animals to breathe freely, showing that there is nothing exceptional about a floating *Spinosaurus* . Validation of the modelling methods was done with floated models of an alligator and an emperor penguin. The software also showed that the centre of mass of *Spinosaurus* was much closer to the hips than previously estimated, similar to that observed in other theropods, implying that this dinosaur would still have been a competent walker on land. With its pneumatised skeleton and a system of air sacs (modelled after birds), the *Spinosaurus* model was found to be unsinkable, even with its lungs deflated by 75%, and this would greatly hinder a semi-aquatic, pursuit predator. The conclusion is that *Spinosaurus* may have been specialized for a shoreline or shallow water mode of life, but would still have been a competent terrestrial animal.

1 A buoyancy, balance and stability challenge to the hypothesis of a semi-aquatic

2 *Spinosaurus* Stromer, 1915 (Dinosauria: Theropoda)

4 Donald M. Henderson

5 Royal Tyrrell Museum of Palaeontology

6 P.O. Box 7500

7 Drumheller, AB

8 Canada T0J 0Y0

9 don.henderson@gov.ab.ca

12   A buoyancy, balance and stability challenge to the hypothesis of a semi-aquatic

13   *Spinosaurus* Stromer, 1915 (Dinosauria: Theropoda)

15   ABSTRACT

16   A recent interpretation of the fossil remains of the enigmatic, large predatory dinosaur

17   *Spinosaurus aegyptiacus* Stromer 1915 proposed that it was specially adapted for a semi-

18   aquatic mode of life – a first for any predatory dinosaur. To test some aspects of this

19   suggestion, a three-dimensional, digital model of the animal that incorporates regional density

20   variations, lungs and air sacs was generated, and the flotation potential of the model was

21   investigated using specially written software. It was found that *Spinosaurus* would have been

22   able to float with its head clear of the water surface, although it was laterally unstable and

23   would tend to roll onto its side. Similarly detailed models of another spinosaurid *Baryonyx*

24   (*Suchomimus*) *tenerensis* Sereno et al. 1998, along with models of the more distantly related

25   *Tyrannosaurus rex* Osborn 1905, *Allosaurus fragilis* Marsh 1877, *Struthiomimus altus* Lambe

26   1902 and *Coelophysis bauri* Cope 1887 were also able to float in positions that enabled the

27   animals to breathe freely, showing that there is nothing exceptional about a floating

28   *Spinosaurus*. The software also showed that the centre of mass of *Spinosaurus* was much closer

29   to the hips than previously estimated, similar to that observed in other theropods, implying

30   that this dinosaur would still have been a competent walker on land. With its pneumatized

31   skeleton and a system of air sacs (modelled after birds), the *Spinosaurus* model was found to be

32   unsinkable, even with its lungs deflated by 75%, and this would greatly hinder a semi-aquatic,

33   pursuit predator. The conclusion is that *Spinosaurus* may have been specialized for a shoreline

34   or shallow water mode of life, but would still have been a competent terrestrial animal.

35   INTRODUCTION

36   At the time of their initial discoveries in the 19th century, there were conflicting views

37   about the preferred habitats of dinosaurs. The very largest ones, the sauropods, were claimed

38   by some authors to be capable of a fully terrestrial mode of life (eg. Mantell, 1850; Phillips,

39   1871), while others argued for an aquatic one (eg. Owen, 1875; Hatcher, 1901). The relatively

40   smaller hadrosaurs, while still impressively big when compared to most modern terrestrial

41   herbivores, were typically thought to be mainly aquatic. A series of anatomical features that

42   were interpreted to be adaptations for an amphibious life were regularly listed for these

43   animals (eg. Leidy, 1858; Cope, 1883) – webbed hands, deep tails for sculling, *etc*. In contrast,

44   theropods of all sizes were interpreted as fully terrestrial animals that could not swim. In fact,

45   the aquatic adaptations of hadrosaurs were frequently interpreted as a way to escape

46   predatory theropods by having the former dash to safety in the water, while the latter were left

47   frustrated and hungry on land (eg. Jackson, 1972). However, as early as the 1950s it was argued

48   that it was not physically realistic to interpret some dinosaurs as being aquatic, eg. sauropods

49   (Kermack, 1951). Beginning in the 1960s and 1970s with Ostrom's (1964) re-interpretation of

50   hadrosaurs as fully terrestrial animals, and Bakker's (1971) arguing for terrestrial sauropods, the

51   interpretation of all dinosaurs as fully terrestrial animals was starting to take hold. During the

52   past 47 years, as our knowledge of dinosaurs has increased exponentially (Wang & Dodson,

53   2006), this "terrestrialization" of dinosaurs has seemed unshakeable.

54   The idea that spinosaurids might have been piscivorous appears to have begun with

55   Taquet (1984). Since then there have been suggestions that *Spinosaurus* and its close relatives

56   might have had a strong association with aquatic environments. Charig and Milner (1987)

57   accepted the idea of the new english spinosaurid *Baryonyx walkeri* as a fish eater, but preferred

58   to keep the animal on shore. Amiot et al. (2010), based on analyses of oxygen isotope ratios

59   ($\delta^{18}O_p$) from biogenic apatites from a wide range of spinosaurid remains, proposed that

60   spinosaurids spent extended periods in freshwater. They also suggested that they may have fed

61   on both terrestrial and aquatic prey. Despite these suggestions, they did include the following

62   statement in their paper "However, their [spinosaurid] postcranial anatomy differs relatively

63   little from that of usual, large bipedal theropods, and is not particularly suggestive of aquatic

64   habits." (Amiot et al., 2010, p. 139).

65   Based on a skeletal reconstruction derived from one partial, associated skeleton and

66   several isolated, partial specimens from other localities of the Late Cretaceous dinosaur

67   *Spinosaurus aegyptiacus* (Stromer, 1915), and a functional interpretation of the resulting body

68   form, along with anatomical details, Ibrahim et al. (2014) made a case for this exceptionally

69   long and "sail-finned" dinosaur being a semi-aquatic predator, and particularly well-adapted for

70   pursing prey in the ancient rivers recorded by the Kem Kem beds rocks exposed in Morocco.

71   This interpretation of an extinct theropod as being semi-aquatic was much more forcefully

72   stated than previous suggestions, and generated much media attention (eg. Tarlach, 2014;

73   Coghlan, 2014).

74   Following after the article of Ibrahim et al. (2014), other authors took up the idea of

75   *Spinosaurus* as a piscivore, or even as an active aquatic predator. Vullo et al. (2016) outlined the

76   convergence in the shapes of the margins of the jaws and of the teeth of Spinosaurus and that

77 of the predatory pike conger eels (members of the family Muraenesocidae). These authors

78 cautiously suggested that spinosaurs would have been well adapted to forage in aquatic

79 settings like the eels, but did not say anything about semi-aquatic habits for spinosaurids. A

80 very speculative paper on the swimming abilities of *Spinosaurus* and the function of the dorsal

81 "sail" by Gimsa et al. (2016) employed qualitative comparisons between crocodilians, large,

82 predatory fishes (both chondrichthyan and osteichthyan) and *Spinosaurus*. The authors

83 envisaged *Spinosaurus* as an animal capable of becoming fully immersed and employing lateral

84 undulation in the pursuit of prey. These authors also hoped that more quantitative studies in

85 the form of hydrodynamical and biomechanical analyses would refine our understanding of the

86 functions of the peculiar anatomy spinosaurids.

87   The gross morphological features of extinct dinosaurs do not immediately suggest any

88 capacity for a mode of life that had an aquatic component. Their dorsal, and often their caudal

89 vertebrae as well, were tightly articulated with little capacity for lateral motion that could assist

90 with aquatic locomotion via lateral undulation. In particular, the theropod clade Tetanura

91 (*sensu* Gauthier, 1986) with their stiffened tails, would have been most unlikely to have been

92 tail-propelled. Spinosaurids belong to the latter clade (Carrano et al., 2010). The parasagittal

93 hind limbs of all dinosaurs, being held in place with the head of the femur deeply implanted in

94 the acetabulum, would also seem unlikely to have performed well in an aquatic setting.

95 Modern, semi-aquatic crocodilians evolved from thoroughly terrestrial animals, and show

96 changes in their spines and hips, especially their capacity to switch the hindlimb orientation

97 between a high walk and a semi-sprawl, that make them much better adapted to a semi-

98 aquatic life (Grigg & Kirshner, 2015). There are examples from around the world of dinosaur

99   fossils recovered from marine settings: hadrosaurs – *Eotrachodon orientalis* Prieto-Márquez et

100   al. 2016*;* theropods – *Scipionyx samniticus* dal Sasso & Signore 1998 and *Nothronychus*

101   *mckinleyi* Kirkland & Wolfe 2001; ankylosaurs – *Kunbarrasaurus ieversi* Leahey et al. 2015.

102   However, these examples are all interpreted as thoroughly terrestrial animals that got washed

103   out to sea.

104   The emphatic claim by Ibrahim et al. (2014) of a semi-aquatic theropod dinosaur

105   inspired further investigation of the aquatic potential of *Spinosaurus,* and some specially

106   written software was used to test the center of mass, buoyancy and equilibrium of an

107   immersed digital model of the animal. To put the results from an analysis of an immersed

108   *Spinosaurus* into context, the floating capabilities of five other theropods, including another

109   spinosaurid were also tested. The collective body masses of these five animals span almost four

110   orders of magnitude, allowing for the investigation of the effects of body size on the potential

111   for flotation and stability of immersed theropods.

112

113   MATERIALS AND METHODS

114   Five theropods, four of which were not closely related to each other or to *Spinosaurus*, were

115   chosen for comparison with the latter*.* These were *Coelophysis bauri* (Ceratosauria),

116   *Struthiomimus altus* (Ornithomimosauria), *Allosaurus fragilis* (Carnosauria), *Tyrannosaurus rex*

117   (Tyrannosauridae), and the spinosaurid *Baryonyx* (*Suchomimus*) *tenerensis* (Fig. 1). It has been

118   suggested that the fossil remains of *Suchomimus* are not distinct enough from *Baryonyx* to

119   merit the erection of a new genus (Holtz, 2012; Sues et al., 2002), and this suggestion is

120   followed here. The two criteria governing these choices of theropod for comparative purposes

121   were that the animals be known from enough skeletal material to produce reliable, whole body

122   reconstructions, and that they span a range of body sizes to enable investigation of the effects

123   of body size on the ability of theropods to float. There are allometric changes in body shapes as

124   theropods increase in size over time, with the trunk region becoming deeper, broader and

125   relatively shorter, and the hind limbs becoming more massive (Henderson & Snively, 2004). It

126   was felt important to check if these changes in body proportions would affect the ability of the

127   animals to float.

128   For all six theropod models, the axial body and limb shapes used in their construction

129   were obtained using the three-dimensional, mathematical slicing method of Henderson (1999).

130   The illustrations used as sources for the models are listed in Table 1.The basic axial body tissue

131   density of the models was set to be the same as that of water – 1000 gm/l. However, this was

132   modified in certain regions to reflect aspects of theropod anatomy. The system of air sacs

133   within the bodies of extant birds represents about 15% of their axial body volume (Proctor &

134   Lynch, 1993), and this observation was used to adjust the basic axial body densities of the

135   models. From fossil evidence of extensive pneumatisation of the skeletons of extinct theropod

136   dinosaurs, and the inference that these animals had a system of air sacs similar to those of

137   extant birds (O'Connor & Claessens, 2005), the pre-caudal, axial densities of the models were

138   reduced by 15% to 850 gm/l to incorporate the density reductions associated with the

139   presumed air sacs in the hips, trunk, and neck. Lacking evidence for differences in the sizes and

140   relative proportions of air sacs in extinct theropods, the most parsimonius assumption is that

141   they were all of similar construction and proportions. The presence of pneumatised bones in

142   theropod skulls, along with the nasal and oral cavities, led to the same reduced density value

143   being assumed for the heads. A lung cavity was also produced for each model and located in

144   the antero-dorsal portion of the thorax. For all the models the lung volume was set at

145   approximately 9% of the axial body volume based on observations of living reptiles (Gans &

146   Clark, 1976). The theropods used in the present study are assumed to have been non-flying, so

147   the use of a lung volume scaling seen in living birds (eg. Schmidt-Nielsen, 1989, Table 9.2) was

148   not considered appropriate. The mass deficits represented by the lungs were incorporated into

149   the determination of the buoyant states of the models. Lastly, the limbs with their substantial

150   bone component were assigned a slightly higher density of 1050 gm/l.

151   Among the distinctive features of *Spinosaurus* is the large dorsal "sail" (fig. 1E). Given

152   the size and position of the sail, and its potential to affect the equilibrium of a floating

153   *Spinosaurus*, special attention was given to its construction and mass estimation, and this was

154   guided by the comments on the sail by Ibrahim et al. (2014). Figure 2 presents details of the sail

155   relevant to the construction of its model. Digitizing the outline of the entire sail, and computing

156   its lateral area by the triangular decomposition method outlined in (Henderson, 2002), gives a

157   value of 6.60 m^2. Digitizing the perimeters of the neural spines associated with the

158   reconstruction of the sail shown in Ibrahim et al. (2014, figure 2), and computing their net area,

159   reveals that the combined lateral areas of these bones, 2.45 m^2, is equivalent to slightly more

160   than one third of the lateral area of the entire sail. The volume of bone comprising the sail is

161   given by the product of the lateral area of the neural spines multiplied by an assumed

162   transverse thickness of 2.25 cm, giving a value of 0.0550 m^3. Lacking information to the

163   contrary, the sail was assumed to be covered with skin to a depth of 1 cm on both sides, giving

164   a total thickness of 4.25 cm. The total volume of the sail is the product of its full lateral area,

165   6.60 m², and its estimated maximum thickness, and this gives a value of 0.281 m³. Subtracting

166   the volume of the bony component of the sail from the total sail volume gives a volume

167   measure for the soft tissue component. The soft and bony tissues of the sail were assumed to

168   have densities of 1,000 and 2,000 gm/l, respectively. With the above volume and density values

169   for the soft and hard components of the sail, the total mass of the sail was estimated to be 335

170   kg. The centroid of the sail was computed during the estimation of its lateral area (Henderson,

171   2002), and taken to be the center of mass (CM) of the sail. The mass of the sail represents

172   approximately 7.5% of the axial body mass, and almost 80% of the mass deficit represented by

173   the lung cavity (Table 2). Assuming a density of 1000 gm/l, the mass of the 1cm thick layer of

174   skin on one side of the sail is 66 kg. Doubling the thickness of the skin on both sides would

175   increase the sail mass fraction to approximately 8.5% of the axial body mass. The mass and CM

176   of the sail were considered necessary components to ensure an accurate determination of the

177   floating state of *Spinosaurus*.

178   The mathematical and computational methods used to simulate the immersion of a

179   model tetrapod, and the analysis of a model's floating characteristics, were developed in

180   Henderson (2003). To ensure that the modelling and the software can replicate the orientation

181   and depth of immersion of a large reptile that can be observed floating today, the software was

182   tested using a model of the semi-aquatic American alligator (*Alligator mississippiensis* Daudin

183   1802) (Henderson, 2003) (Fig. 3). Crocodylians share a common ancestry with theropods as

184   both are members of Archosauria. Additionally, the alligator has an elongate body with a

185   substantial, muscular tail similar to that inferred for theropods. As was done with the theropod

186   models, a lung volume equal to 9% of the axial body volume was generated for the alligator

187   model. Unlike what was done for the theropods, the axial body and limb densities were

188   maintained at 1050 gm/L as crocodilians lack the system of air sacs inferred for theropods.

189   It was suggested by a reviewer that a test of the software and methods should also be

190   done with a living, aquatic, predatory theropod, ie. a diving bird, to see how it would compare

191   to *Spinosaurus*. This was done with a model of an emperor penguin (*Aptenodytes forsteri* Gray

192   1844). The model was derived from frontal and lateral views of an adult using the 3D-slicing

193   technique, and included both the hind and fore limbs. The total body length from the tip of

194   beak to the tip of the tail was 1.25m. The post-cervical axial body density was set to 1000 gm/l,

195   while the neck and head were set to 800 gm/l. Penguins do not have the system of air sacs

196   found in other birds and have denser bones (Simpson 1976), hence the higher axial body

197   density. The limb densities were set to 1050 gm/l. A lung volume was generated using the bird

198   lung scaling relationships of Schmidt-Nielsen (1989).

199   It was suggested by another reviewer to test the lateral stability of the floating

200   *Spinosaurus* model, and it was decided to do the same test on the alligator model as well. As

201   their limbs are denser than the freshwater that the models are floating in, the buoyant force

202   arises in relation to the amount of water displaced by the less density axial body. An elliptical

203   disk representing the average cross-section of the axial body of a model was produced by

204   computing the average dorso-ventral and medio-lateral radii from the two slices defining the

205   axial body immediately posterior and anterior to the longitudinal position of the CM in the

206   floating model. This elliptical shape was done as a "super-ellipse" where the exponent was 2.5

207   instead of the usual 2. This produces cross-sections of slightly flatter tops, bottoms and sides

208   than a normal ellipse, and is more biologically plausible than a regular ellipse (Motani,

209   2001).The disk represents a transverse section of the floating axial body, and the competing

210   forces of gravity and buoyancy were assumed to act in the plane of the disk. The mass of the

211   disk is the product of its area, thickness and density, with the value of the latter being the mean

212   density of the whole model with a full lung. The center of mass of the test disk was taken to be

213   its centroid. An iterative process of analysis involved determining the degree of immersion of

214   the slice to compute the magnitude of the upwards buoyant force and the two-dimensional

215   location of the center of buoyancy. The positively-directed buoyant force was added to the

216   unchanging negatively-directed weight force, and if the result was positive the disk was moved

217   up by an amount proportional to the magnitude of the difference. Conversely, if the result was

218   negative, the disk was moved downwards. Any horizontal separation between the centers of

219   buoyancy and gravity represented a moment arm for the buoyant force and would produce a

220   turning moment on the disk acting about the CM. After adjusting the vertical position and

221   angular orientation of the disk, the process of testing and shifting was repeated. The disk was

222   considered to be in a final, stable equilibrium state when the difference between the gravity

223   and buoyant forces was less than 1% of the weight force and the torque acting on the disk was

224   less than 0.5% of a predefined reference torque. See Henderson (2003) for more complete

225   details on bringing a floating model to equilibrium.

226   As another test of the lateral stability of the alligator and *Spinosaurus* models, the

227   traditional naval architecture parameter of the metacentric height (Comstock, 1967) was

228   computed for the full body models and this required two additional parameters to be extracted

229   from the models. The first is the water plane for a model, and this was taken as the area

230   representing the intersection of the floating model with the water surface. As lateral stability is

231   the topic of interest, the second moment of area of the water plane was computed with

232   respect to the longitudinal (X) axis located in the sagittal plane. The second parameter is the

233   volume of the immersed portion of the body, and this was extracted from a model's geometry

234   by noting the degree of immersion of each of the sets of cylindrical disks forming the axial body.

235   The metacentric height, KM, is usually defined as the distance above the keel of a boat, but in

236   the present situation it was taken as the distance above the ventral surface of the belly at the

237   longitudinal position of the center of mass. KM was computed with the following expression:

238   (1) $$KM = KB + \frac{I_x}{V}$$

239   where KB is the distance of the center of buoyancy from the ventral surface, I_x is second

240   moment of area of the water plane, and V is the volume of the immersed portion.

241   For the present study, all but one of the flotation simulations were done with the

242   assumption that the models were in freshwater with a density of 1000 gm/l. The only exception

243   was with the penguin which was floated in seawater with a density of 1026 gm/l.

244   The potential effects of increased limb bone density on the mass and overall density of a

245   floating theropod were checked using three-dimensional, digital models of the non-pedal bones

246   of the hindlimb of *Allosaurus fragilis*. The bone geometries were taken from illustrations of the

247   femur, tibia, fibula and metatarsals of Madsen (1976), and their digital models were generated

248   using the methods of Henderson (1999). These bones were analyzed in association with the

249   three-dimensional mesh representing the muscles and fleshed out hindlimb of the *Allosaurus*

250   model of figure 1.

251

252   RESULTS

253   The whole body and component masses computed for the six theropod models, the

254   alligator and the penguin are presented in Table 2. The striding, non-floating theropod models

255   of figure 1 all show their centers of mass (CM) located just ahead of the hip sockets, but above

256   and between the leading and trailing feet, demonstrating that the animals are balanced with no

257   tendency to tip forward or back. This same is true for the highly attenuated, restored body

258   form of *Spinosaurus*. Even with its rather short legs, the CM of *Spinosaurus* is still positioned

259   above the leading foot, showing that with appropriate stride lengths, this animal could still walk

260   on land (Gatesy et al,. 2009).

261   The upper pair of images of figure 3 presents the basic mesh form of the alligator model

262   in dorsal and lateral views, together with a grey cylinder indicating the size and position of the

263   lung cavity. The estimated total mass of the 3.07 m long model is 122 kg, and these values are

264   similar to those observed for a 2.89 m female alligator that weighed 129 kg. (Woodward et al.,

265   1995). Further demonstrations of the validity of the alligator model and its computed

266   parameters can be found in Henderson (2003). The lower pair of images of figure 3 show the

267   model in stable, floating equilibrium with a fully inflated lung. This final state closely replicates

268   the observed resting positions of both crocodiles and alligators when resting at the water

269   surface (Grigg & Kirshner, 2015, Chapter 4). With the model of a floating alligator successfully

270   replicating aspects of a living one, this provides a level of confidence for what is predicted for

271   the extinct theropods.

272   Figure 4 shows the penguin model with a full lung floating in seawater with a density of 1026

273   gm/l, and exhibiting stable equilibrium at the surface. The mean body density of the model was 968

274   gm/l, and the computed total body mass was 46.3kg. Living emperor penguins with a body length of

275   1.22m are observed to have body masses of up to 45kg (Wikipedia, accessed January 8, 2018). The

276   model body orientation and depth of immersion match observations of living emperor penguins at the

277   surface (Kooyman et al. 1971), and provides another indication of the reliability of the modelling

278   process. Deflating the model penguin lung by 90% resulted in a mean body density of 989 gm/l, which is

279   still not high enough to make the model negatively buoyant and enable sinking. However, emperor

280   penguins have been observed to inhale prior to diving (Kooyman et al. 1971), so the lung deflation test is

281   not particularly relevant. With their highly derived wings and powerful pectoral muscles, penguins are

282   able to overcome the positive buoyancy associated with a full lung and propel themselves downwards

283   underwater (Lovvorn 2001).

284   For the present study, a criterion for judging whether a normally terrestrial animal was

285   unlikely to drown and could maintain a stable body orientation while immersed was that the

286   head, and the nostrils in particular, were clear of the water surface so that the animal could see

287   and breathe. Figure 5 presents the final, equilibrium floating states for the two spinosaurid

288   models with full lungs. In each case, the models float with their heads and nostrils above the

289   water, and their centers of mass and buoyancy are nearly coincident. As postulated by Ibrahim

290   et al. (2014), the sail of *Spinosaurus* does stay visible while the animal is floating. The

291   orientations of the heads and necks of these models were not altered from the basic,

292   "terrestrial" versions shown in figure 1. The mass of the low crest associated with the *Baryonyx*

293   (*Suchomimus*) model represents 2.2% of the axial body mass. This smaller mass, when

294   compared to the larger 7.5% relative mass of the *Spinosaurus* sail, and combined with the fact

295   the center of the crest lies close to the CM of the whole body, leads to the position and mass of

296   the *Baryonyx* (*Suchomimus*) crest having only a very minor effect on the overall, final CM of the

297   model.

298   Figure 6 presents the floating equilibrium states of the four other comparative theropod

299   models. The first thing to notice is that all four animals/models can float, and that their heads

300   are clear of the water surface. The heads of the *Coelophysis* and *Tyrannosaurus* models needed

301   to be dorsiflexed by 20° and 15°, respectively, to elevate them enough so that the tips of their

302   snouts (nostrils) were above the water surface. These head elevations were done via a series

303   small increments applied to the each of the model slices defining the necks, until the sum of the

304   rotations applied to individual slices equaled the required total head lifting angle. An additional

305   feature is that the floating states appear to be independent of body size, with the same

306   proportions of the bodies being exposed above the water line. The only apparent difference is

307   that the *Coelophysis* model floats with body tipped much more forward, when compared to the

308   others. This may be related to two aspects of the body shape of *Coelophysis*. The much more

309   attenuated, and slender axial body, with less of the body mass concentrated about the hips,

310   and the much longer neck, which will not only represent a larger fraction of the total body

311   mass, but in combination with the head, will also exert a stronger turning moment on the body.

312   Figure 7 shows the results of the lateral stability test conducted for the alligator model

313   with the disk representing the transverse section of the body at the longitudinal position of the

314   whole body CM. Although not shown, when this disk was placed in water without any lateral

315   tipping, it came to stable equilibrium with 95.25% of the disk immersed and remained upright.

316   The mass density of the disk is 952 gm/l. For the lateral stability test the model disk was tipped

317   sideways by 20° (figure 7, frame no. 0). This resulted in a small, although not visible, horizontal

318   separation between the CM (grey '+') and the CB (white '◊'). The shape of the whole cross-

319   section and its immersed portion, and the relative positions of the CM and CB, resulted in the

320   disk returning to equilibrium with the original topside uppermost (Figure 7, frame no. 42). The

321   vertical positions of the centers of buoyancy and mass, relative to the water surface in this final

322   state were -0.167 m and -0.159 m, respectively. The lengthy number of cycles needed to return

323   to equilibrium, 42 (also the answer to "life, the universe and everything" (Adams, 1982)), is

324   interpreted to be the result of the CM and CB being almost coincident and the moment arm of

325   the restoring buoyant forces being very small. The final degree of immersion was the same

326   95.25% as before. This capacity for stability and self-righting when floating at the surface is

327   what could be expected for a semi-aquatic animal that habitually spent extended periods at the

328   water surface. Confirmation of this dynamic stability was observed directly in a floating, and

329   occasionally gently paddling and rolling caimans (*Caiman crocodylus*) that remained upright at

330   the Vancouver Aquarium (Graham Amazon Gallery), Stanley Park, Vancouver, British Columbia

331   (pers. obs. January 2, 2018).

332   When not tipped sideways, the disk representing the *Spinosaurus* cross-section

333   remained upright, with 82.8% immersion. The mass density of the disk is 833 gm/l and ideally

334   the disk should have come to equilibrium with 83.3% immersion. The modelled value of 82.8%

335   is only off by 0.6% of the expected value, and this discrepancy is interpreted to arise from

336   modelling process and the asymptotic nature of how the disk is brought to equilibrium. Figure 8

337   shows what happened when the *Spinosaurus* disk was tipped sideways by 20° - the disk quickly

338   rolled over onto its side, with the final, equilibrium vertical positions of its CB and CM being -

339   0.301 m and -0.239 m, respectively. This test demonstrates that the body of a floating

340   *Spinosaurus* would have been liable to tip when nudged, and suggests that *Spinosaurus* must

341   have had to apply constant limb action to maintain an upright posture when in water when

342   subject to any disturbances at the surface. This does not appear to be an attribute of an animal

343   well- adapted for a semi-aquatic life.

344   Further confirmations of the conditions of stable and unstable equilibrium of the

345   alligator and *Spinosaurus*, respectively, were provided by the determinations of their

346   metacentric heights. A metacentric height located below the center of mass of an immersed

347   object indicates an unstable situation. Figure 9 presents graphically the locations of the centers

348   of buoyancy (KB), centers of mass (KG), and the metacentric heights (KM) of these two models.

349   Similar to what was found with the disk version of the alligator body (figure 7), these three

350   quantities in the alligator are all virtually coincident with one another, with just millimeters

351   separating them. Although the KM of the alligator is above the KG, the separation is less than

352   2mm, and this latter distance represents less than 0.5% of the 36cm body depth at the location

353   of the whole body center of mass. The closeness of the three quantities indicates that any

354   moment arms associated with misaligned buoyant and gravitational forces will be extremely

355   small. In contrast, the positions of KB, KM, and KG of the *Spinosaurus* model clearly

356   demonstrate an unstable situation, with the center of gravity located 12cm above the

357   metacentric height.

358   Figure 10 shows the fleshed-out form of the model hindlimb of the *Allosaurus* model

359   from figure 1 along with its larger limb bones. The volume of the hindlimb mesh was found to

360   be 0.1152 m^3, and with the assigned density of 1050 kg/m^3, it has a mass of 121 kg. The bones

361   have a combined volume of 0.01052 m^3, and subtracting this from the total volume leaves a

362   flesh (non-bone) volume of 0.1047 m^3. The mass of the leg can be expressed as:

363   (2)   leg_mass = flesh_volume * flesh_density + bone_volume * bone_density

364   Given that the total leg mass and the flesh and bone volumes are known, and assuming that the

365   flesh density is 1000 gm/l, one can solve (1) for the bone density. This gives a bone density for

366   the *Allosaurus* leg model of 1547 gm/l, approximately 50% more than that of water. Assuming

367   that compact bone has a density of approximately 2000 gm/l, the reduced bone density is

368   consistent with an open medullary cavity in the bones. The mass of the bones is computed as

369   their volume multiplied by their density, and comes to 16.28 kg. The bones of the single

370   hindlimb represent 1.69% of the total body mass estimated for the *Allosaurus* model of 963 kg

371   (Table 2). With the availability of the bone volumes, the effects of increasing the density of the

372   bones to increase their mass can be analyzed. Assuming that the bones are solid with a density

373   of 2000 gm/l, one gets a heavier bone mass of 21.04 kg which now represents 2.248% of total

374   body mass, an increase of just over half of one percent of total mass. The leg of the new

375   restoration of *Spinosaurus* is estimated to have a mass of 295 kg, more than twice that of the

376   *Allosaurus* model. However, the body mass of the animal is seven times as great as that of

377   *Allosaurus* at 6500 kg, and the hind limb represents just 4.54% of total body mass. Assuming

378   the same bone to flesh proportions in the hindlimbs of *Spinosaurus* and *Allosaurus*, any

379   increase in the mass of the relatively smaller hindlimbs of *Spinosaurus* via solid bones will be an

380   even smaller fraction of total body mass than that estimated for *Allosaurus*. Given the inherent

381   uncertainties of the various densities of the various body regions, and their true volumes,

382   exceptional evidence would be needed to demonstrate that the increase in body mass by a few

383   percent by having denser limb bones would significantly affect the ability of a *Spinosaurus* to

384   immerse itself.

385

386   DISCUSSION

387   Ibrahim et al. (2014) list details of *Spinosaurus aegyptiacus* and its ancient environment that

388   plausibly suggest this dinosaur was specialized for a semi-aquatic mode of life. These details

389   include: highly unusual adaptations such as a higher bone compactness than seen in alligators;

390   peculiar morphology of the pes; extremely retracted position of nares; oxygen isotope analyses

391   strongly suggesting a semiaquatic; presence of abundant giant fishes; very few remains of

392   plant-eating dinosaurs in the Kem Kem beds and other equivalent sequences in North Africa;

393   and seemingly optimal conditions for large, fish-eating tetrapods and fish-based food webs.

394   However, while no amount of evidence can prove the validity of a hypothesis, and it only takes

395   one contradictory observation to potentially falsify it. The three problems with the hypothesis

396   of a semi-aquatic Spinosaurus identified in the current work would appear to seriously weaken

397   the hypothesis of Ibrahim et al.

398   Contrary to the claim by Ibrahim et al. (2014) that the CM of *Spinosaurus* was centrally

399   located in the trunk region, this study finds the CM much closer to the hips than previously

400   estimated. In fact, it is less than the relative CM distance determined for the *Tyrannosaurus*

401   model (Table 2 – Horizontal Relative CM Position). This is interpreted to be a consequence of

402   the new restoration of *Spinosaurus* and the associated muscle mass of its substantially longer

403   tail when compared to that of *Tyrannosaurus*. Having a CM closer to its hips indicates that

404   *Spinosaurus* would still be competent as a terrestrial biped since the CM would be above

405   and/or between the supporting feet while walking (Henderson & Nicholls, 2015). A validation of

406   the present method for determination of the CM in theropods comes from an estimate of the

407   CMs of a standing pigeon and ostrich (Henderson, 2010). With densities appropriate for birds

408   assigned to the heads, necks, trunks and limbs of models of the latter two animals, their CMs

409   were found to lie directly above and between the feet enabling the animals to stand in a stable

410   fashion (Henderson, 2010, figure 1), as can be observed in the living forms.

411   In an attempt to replicate the more anteriorly located CM for *Spinosaurus* reported by

412   Ibrahim et al. (2014), two alternate versions of determination the CM were tried. The first

413   attempt involved determining the centroid of the the two-dimensional lateral profile of the

414   axial body. This 2D centroid is located towards the rear of trunk region, and slightly posterior to

415   the ventral bulge associated with the pubis (figure 11A). A second used just the axial body of

416   the three-dimensional model and assumed a uniform density, no pneumatic cavities, and no

417   lung cavity. The resulting 3D CM was again located towards the rear of the trunk region, but

418   just ahead of the ventral bulge associated with the distal end of the pubis (figure 11B). None of

419   the three computed values for the CM for *Spinosaurus* in the present study can match that

420   reported by Ibrahim et al. (2014).

421   *Spinosaurus* is certainly able to float and breathe with the head above water (Figure 5A),

422   However, there is nothing special about the state of the immersed *Spinosaurus*. With the

423   modest 15° upwards tilt of its head relative to that of the basic terrestrial form (figure 1F), the

424   *Tyrannosaurus* is also able to float and breathe (figure 6D). Furthermore, the *Tyrannosaurus*

425   model is 51% heavier and slightly denser than the *Spinosaurus* one (Table 2), yet is able to keep

426   most of the head clear of the water surface. The floating equilibrium states of the four other,

427   lighter models – *Baryonyx* (*Suchomimus*) (figure 5B), *Coelophysis* (figure 6A), *Struthiomimus*

428   (figure 6B), *Allosaurus* (figure 6C) – are consistent with the floating states of the two, heavier,

429   longer animals. These results are not unexpected, as most terrestrial tetrapods can successfully

430   float and swim (see Henderson & Naish, (2010) for review).

431   It was found that the alligator model would sink when the lungs were deflated by 40-

432   50% (Henderson, 2003). However, the lower mean densities of the two spinosaurid models,

433   relative to that of the alligator, immediately suggests that they might not be able to sink and

434   become fully immersed. This was tested by deflating the lung of the *Spinosaurus* model by 75%.

435   This had the effect of increasing the mean density of the model from its basic value of 823 gm/l

436   to 885 gm/l. It should be mentioned that the lung deflation process was associated with an

437   elevation of ventral abdominal region of the model body so that the volume decrease of the

438   axial body was reflecting the volume decrease of the lung. With the increased density, the

439   model reached buoyant equilibrium at the lower depth of 48 cm, compared to the 37 cm when

440 the lung was fully inflated. However, the new density is still less than that of water, 1000 gm/l,

441 indicating that the animal would still be buoyant. Extant semi-aquatic birds and reptiles such as

442 penguins, loons, ducks, cormorants, sea snakes, marine iguanas, crocodilians and both marine

443 and freshwater turtles ALL have the ability, and the apparent need, to become submersed to

444 enable the pursuit of prey, or in the case of the marine iguana, forage on the sea bed. The same

445 is true of semi-aquatic mammals such as otters, musk rats, waters shrews, beavers, hippos and

446 polar bears. Not being able to become fully immersed for any of these taxa listed would be a

447 major impediment. The inability of a *Spinosaurus* to sink underwater would severely limit its

448 ability to effectively capture aquatic prey, and conflicts with the suggestion that *Spinosaurus*

449 was specialized for a semi-aquatic life.

450 As a test of how sensitive the buoyant *Spinosaurus* model was to the assumed presence

451 of avian style air sacs and pneumatized bone, an alternate model lacking these features was

452 tried. This model assigned a uniform axial density of 1000 gm/l from the tip of the tail to the tip

453 of the snout. The limb and sail densities were unchanged, and the same lung was retained. This

454 resulted in a denser (918 gm/l) and heavier (7160 kg) model. Deflating the lungs of this denser

455 model by 75% resulted in an even greater mean body density of 986 gm/l, and deeper depth of

456 immersion for the CM at 0.696 m, but this model was still not able to sink as its density was still

457 less than that of fresh water. If it could be shown that the mass deficit represented by the

458 lungs and air sacs was offset by the increased mass of a denser skeleton that might help the

459 claim of a semi-aquatic *Spinosaurus*.

460   It should not be forgotten that the restoration of *Spinosaurus* by Ibrahim et al. (2014) is

461   based on the composition and scaling of the remains of several animals from different

462   localities, along with missing details supplied from other spinosaurids such as *Baryonyx*

463   (*Suchomimus*), *Irritator* and *Ichthyovenator* (caption for Figure S3, Supplementary Materials,

464   Ibrahim et al., 2014). In particular, the hind limbs of the new restoration, although from a single

465   individual, were not associated with a complete dorsal axial skeleton. The color codings of the

466   vertebrae used in the reconstruction (Ibrahim et al. 2014, Figure S3, Supplementary Materials)

467   clearly show that the majority of the vertebrae come from other animals and locations. The

468   only partially contiguous set of vertebrate are those of the anterior and mid dorsals and the

469   incomplete sacrum from the original specimen described by Stromer (1915). With the axial

470   body providing the majority of the body mass, any systematic errors in the restoration of body

471   length will affect estimates of total body mass and relative limb/body proportions. The restored

472   hindlimb proportions of *Spinosaurus* do appear to be rather small when compared to the rest of

473   the body, and when compared with the hind limb-body proportions seen in other theropods.

474   Figure 12 shows a plot of relative masses of single hind limbs, expressed as a percentage of

475   total body mass for the six animals of the present study. For the computation of the mean and

476   standard deviations shown in figure 12, the values for *Spinosaurus* were not included. The

477   relative hindlimb mass of the restored *Spinosaurus*, 4.88%, is less than half the mean relative

478   mass computed for the other five of 12.6% (stan.dev. = 1.87%). It might be argued that the

479   qualitative reconstructions of the forms of the hindlimbs of the models might be highly

480   subjective, and subject to bias. However, some qualitative aspects of the plot argue for its

481   general plausibility. *Struthiomimus*, interpreted to be highly cursorial (Russell, 1972), and

482   assumed to have extensive hindlimb musculature for running, has the highest relative leg mass

483   with it plotting more than one standard deviation above the mean (the dashed line of figure

484   12). The heaviest animal of the present study, *Tyrannosaurus*, has the second highest relative

485   limb mass, while lightest animal, *Coelophysis*, has a relative leg mass less than the mean value.

486   Modern, semi-aquatic crocodilians have relatively smaller hind *and* forelimbs when

487   compared to their more terrestrial ancestors eg. *Sebecus* (Pol et al., 2012), *Terrestrisuchus*

488   (Crush, 1984). This reduction in limb size is interpreted as an adaption to reduce drag while

489   swimming, and reflects the dominance of axial musculature for aquatic propulsion (Grigg &

490   Kirshner, 2015). If the reduced hindlimbs of the new restoration of *Spinosaurus* are an

491   indication of a more aquatic mode of life (Ibrahim et al., 2014), one would expect that the

492   forelimbs would also be reduced, similar to what is seen in the crocodilians. However, the

493   forelimbs as restored for Spinosaurus are large enough to reach the ground. Complete

494   forelimbs were not found in association with the hindlimbs or the axial body, and the color

495   codings in the supplementary information figure S3 of Ibrahim et al. (2014) clearly

496   demonstrates the disparate origins of the forelimb elements in the new restoration. The only

497   two minor exceptions to the mixed origins of the forelimb elements comes from a manual

498   phalanx 2 and an incomplete base of phalanx 3 from digit II that were found with the new

499   specimen. If isometric scaling based on the dimensions of these two elements was used to set

500   the sizes of the other bones, then it needs to be demonstrated that the assumed scaling

501   relationship is valid. The exceptionally large size of *Spinosaurus* compared to other theropods

502   indicates that non-linear, non-isometric changes in bone sizes and their relative proportions in

503   the forelimbs are a distinct possibility, and this undermines confidence in the new restorations.

504   Despite the above problems with having *Spinosaurus* as an animal that spent substantial

505   amounts of time immersed in water, it is still reasonable to interpret the animal as having some

506   connection with aquatic environments. Charig and Milner (1997) noted the gharial-like aspects

507   of the skull and dentition of another well-known spinosaurid, *Baryonyx walkeri*, and proposed

508   that *Baryonyx* was wading in the shallows snatching fish with its specialized jaws. The very

509   robust arms and manual claws of *Baryonyx* were also suggested as another way for the animal

510   to procure aquatic prey without having to become fully immersed - similar to modern grizzly

511   bears (Charig & Milner, 1997). Amiot et al. (2010) used stable isotope geochemistry analysis of

512   oxygen in the teeth of spinosaurids to show that they must have spent significant time in water

513   and must have included some aquatically derived prey as part of a more generalist diet. Ibrahim

514   *et al*. (2014) made a series of observations of the skull and teeth of *Spinosaurus* that suggested

515   it was well adapted to sense, pursue, and capture aquatic prey. However, given the findings of

516   the present study, the more conservative, and more terrestrially linked, *Baryonyx* model of

517   Charig and Milner would also seem to be the one for the interpretation of the mode of life of

518   *Spinosaurus aegyptiacus*.

519

520   CONCLUSION

521   The combination of a CM close to the hips that still enabled effective terrestrial locomotion, an

522   inability to become negatively buoyant, and a body (when immersed) with a tendency to roll

523   onto its side unless constantly resisted by limb use, suggests that *Spinosaurus* was not highly

524   specialized for a semi-aquatic mode of life. Furthermore, the floating characteristics of the

525   *Spinosaurus* model were similar to those of models of other predatory dinosaurs, indicating

526   that there was nothing special about the buoyant characteristics of this animal, and that other

527   theropods could have successfully taken to water to the same degree as well. Terrestrial

528   activity would still have been part of its normal life of *Spinosaurus*, similar to the interpretations

529   given for other large predatory dinosaurs. Lastly, the new reconstruction of *Spinosaurus* is

530   based on a composition of remains from multiple individuals of varying sizes and proportions

531   that come from different locations, and were scaled to match the presumed proportions of a

532   single individual. This does not seem like a good platform for building hypotheses about what

533   this animal was like as a once living organism.

534   ACKNOWLEDGEMENTS

535   I thank Jim Gardner (Royal Tyrrell Museum of Palaeontology) for reading an earlier draft of the

536   text. The constructive comments and suggestions of reviewers C. Palmer, V. Allen, and I.M.

537   Anonymous made for a much improved study.

538   REFERENCES

539   **Adams D. 1982.** *The Hitchhiker's Guide to the Galaxy: Life the universe and everything*. London,

540   England: Pan Books.

541   **Amiot R, Buffetaut E, Lecuyer C, Wang X, Boudad L, Ding Z, Fourel F, Hutt S, Martineau F,**

542   **Medeiros MA, Mo J, Simon L, Suteethorn V, Sweetman S, Tong H, Zhang F, Zhou Z. 2010.**

543   Oxygen isotope evidence for semi-aquatic habits among spinosaurid theropods. *Geology*

544   **39**:139-142.

545   **Bakker RT. 1971.** The ecology of brontosaurs. *Nature* 229:172–174.

546   **Carrano MT, Benson RBJ, Sampson SD. 2010.** The phylogeny of Tetanurae (Dinosauria:

547   Theropoda). *Journal of Systematic Palaeontology* **10**:211-300.

548   **Charig AJ, Milner AC. 1997.** *Baryonyx walkeri*; a fish-eating dinosaur from the Wealden of

549   Surrey. *Bulletin of the Natural History Museum of London Geology* **53**:11-70.

550   **Coghlan A. 2014.** Giant dinosaur was a swimming hunter. *New Scientist*, Issue No. 2987,

551   September 20, 2014.

552   **Comstock, JP. 1967.** *Principles of Naval Architecture*. Society of Naval Architects and Marine

553   Engineers, New York.

554   **Cope ED. 1883.** On the characters of the skull in the Hadrosauridae. *Proceedings of the*

555   *Academy of Natural Sciences of Philadelphia* **35**:97-107.

556   **Cope ED. 1887.** The Dinosaurian Genus Coelurus. *The American Naturalist.* **xxi 5**:367-369.

557   **Crush PJ. 1984**. A late Upper Triassic sphenosuchid crocodilian from Wales. Palaeontology 27:

558   131-157.

559   **Currie P J. 1997.** Theropods. In: Farlow JO & Brett-Surman MK, eds. *The complete dinosaur.*

560   Indianapolis, IN: Indiana University Press, 216–233.

561   **Dal Sasso C, Signore M. 1998.** Exceptional soft tissue preservation in a theropod dinosaur from

562   Italy. Nature **392**:383-387.

563   **Daudin FM. 1802.** Histoire naturelle, générale et particulière, des reptiles : ouvrage faisant suite

564   à l'Histoire naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée

565   par C.S. Sonnini. Imprimerie de F. Dufart, Paris.

566   **Gans C, Clark B. 1976.** Studies on the ventilation of Caiman crocodylus (Crocodilia: Reptilia).

567   *Respiration Physiology* **26**:285-301.

568   **Gatesy SM, Baker M, Hutchinson JR. 2009.** Constraint-based exclusion of limb poses for

569   reconstructing theropod dinosaur locomotion. *Journal of Vertebrate Paleontology* 29:535–

570   544. (doi:10.1671/039.029.0213)

571   **Gauthier JA. 1986.** *Saurischian monophyly and the origin of birds. In: Padian, K, ed. The Origin*

572   *of Birds and the Evolution of Flight. Memoirs of the California Academy of Sciences* **8**:1–55

573   **Gimsa J, Sleigh R, Gimsa U. 2016.** The riddle of *Spinosaurus aegypticus*' dorsal sail. Geological

574   Magazine **153**:544-547.

575   **Grigg G, Kirshner D. 2015.** *Biology and evolution of crocodylians*. Ithaca, New York: Cornell

576   University Press.

577   **Hatcher JG. 1901.** Diplodocus Marsh, its osteology, taxonomy, and probable habits, with a

578   restoration of the skeleton. *Memoirs of the Carnegie Museum* **1**:1-64.

579   **Henderson DM. 1999.** Estimating the masses and centers of mass of extinct animals by 3-D

580   mathematical slicing. *Paleobiology* **25**:88-106.

581   **Henderson DM. 2002.** The eyes have it: the sizes, shapes, and orientations of theropod orbits

582   as indicators of skull strength and bite force. *Journal of Vertebrate Paleontology* 22:766-

583   778.

584   **Henderson DM. 2003.** Effects of stomach stones on the buoyancy and equilibrium of a floating

585   crocodilian: a computational analysis. *Canadian Journal of Zoology* **81**:1346-1357.

586   **Henderson DM, Snively ED. 2004.** *Tyrannosaurus* en pointe: allometry minimized rotational

587   inertia of large carnivorous dinosaurs. *Biology Letters* (*Proceedings of the Royal Society of*

588   *London, B* Supplement) **271**:555-560.

589   **Henderson DM. 2010.** Pterosaur body mass estimates from three-dimensional mathematical

590   slicing. *Journal of Vertebrate Paleontology* **30**:768-785.

591   **Henderson DM, Naish D. 2010.** Predicting the buoyancy, equilibrium and potential swimming

592   abilities of giraffes by computational analysis. *Journal of Theoretical Biology* **265**:151-159.

593   **Henderson DM, Nicholls R. 2015.** Balance and strength - estimating the maximum prey-lifting

594   potential of the large predatory dinosaur *Carcharodontosaurus saharicus*. *The Anatomical*

595   *Record* **298**:1367-1375.

596   **Holtz TR Jr. 2012.** *Theropods.* In: Farlow JO & Brett-Surman MK, eds. The Complete Dinosaur 2nd

597   ed. Bloomington and Indianapolis, IA: Indiana University Press, 346-378.

598   **Ibrahim N, Sereno PC, dal Sasso C, Maganuco S, Fabbri M, Martill DM, Zouhri S, Myhrvold N,**

599   **Lurino DA. 2014.** Semiaquatic adaptations in a giant predatory dinosaur. *Science* **345**:1232-

600   1236.

601   **Jackson K. 1972.** *Dinosaurs*. Washington, DC: National Geographic Society – Books for Young

602   Explorers.

603   **Kermack KA. 1951.** A note on the habits of sauropods. *Annals and magazine of natural history*

604   **4**:830-832.

605   **Kirkland JI, Wolfe DG. 2001.** First definitive therizinosaurid (Dinosauria; Theropoda) from North

606   America. *Journal of Vertebrate Paleontology* **21**:410-414.

607   **Kooyman GL, Drabek CM, Elsner R, Campbell WB. 1971.** Diving behaviour of the Emperor

608   Penguin *Aptenodytes forsteri*. *The Auk* 88:775–795.

609   ***Leahey LG, Molnar RE, Carpenter K, Witmer LM, Salisbury SW. 2015.*** Cranial osteology of the

610   ankylosaurian dinosaur formerly known as *Minmi* sp. (Ornithischia: Thyreophora) from the

611   Lower Cretaceous Allaru Mudstone of Richmond, Queensland, Australia. *PeerJ 3:e1475.*

612   doi:10.7717/peerj.1475

613   ***Lambe LM. 1902.*** *On vertebrata of the mid-Cretaceous of the Northwest Territory. 2. New*

614   *genera and species from the Belly River Series (mid-Cretaceous). Contributions to Canadian*

615   *Palaeontology. **3**:25-81.*

616   **Leidy J. 1858.** *Hadrosaurus foulki*, a new saurian from the Cretaceous of New Jersey.

617   *Proceedings of the Academy of Natural Sciences of Philadelphia* **1858**:215-218.

618   **Lovvorn JR. 2001.** Upstroke thrust, drag effects, and stroke-glide cycles in wing-propelled

619   swimming by birds. *American Zoologist* **41**:154–165. doi:10.1093/icb/41.2.154.

620   **Madsen JH. 1976.** *Allosaurus fragilis*: a revised osteology. Bulletin 109, Utah Geological Survey

621   (reprinted 1993).

622   **Mantell GA. 1850.** On the Pelorosaurus; an undescribed gigantic terrestrial reptile whose

623   remains are associated with those of the Iguanodon and other saurian in the strata of the

624   Tilgate Forest, Sussex. *Philosophical Transactions of the Royal Society of London* **140**:379-

625   390.

626   **Marsh OC. 1877.** Notice of new dinosaurian reptiles from the Jurassic formation. *American*

627   *Journal of Science and Arts.* **14**: 514–516

628   **Motani R. 2001.** Estimating body mass from silhouettes: testing the assumption of elliptical

629   body cross-sections. *Paleobiology* **27**:735-750.

630   **Neill WT. 1971.** *The last of the ruling reptiles: alligators, crocodiles, and their kin.* New York:

631   Columbia University Press.

632   **O'Connor P, Claessens LPAM. 2005.** Basic avian pulmonary design and flow-through ventilation

633   in non-avian theropod dinosaurs. *Nature* **436**:253-256.

634   **Osborn HF. 1905.** *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs. *Bulletin of the*

635   *AMNH.* New York City: American Museum of Natural History. 21:259–265.

636   **Ostrom JH. 1964.** A reconsideration of the paleoecology of hadrosaurian dinosaurs. *American*

637   *Journal of Science* **262**:975-997.

638   **Owen R. 1875.** Monographs on the fossil Reptilia of the Mesozoic formations. Part II. (Genera

639   *Bothriospondylus, Cetiosaurus, Omosaurus*). *Palaeontographical Society Monograph* **29**:15-

640   94.

641   **Paul GS.** 1988. *Predatory dinosaurs of the world*. New York: Simon and Schuster.

642   **Phillips J. 1871**. Geology of Oxford and the Valley of the Thames. Oxford: Clarendon Press.

643 **Pol D, Leardi JM, Lecuona A, Krause M. 2012.** Postcranial anatomy of Sebecus icaeorhinus

644 (Crocodyliformes, Sebecidae) from the Eocene of Patagonia. *Journal of Vertebrate*

645 *Paleontology* **32**: 328–354.

646 **Prieto-Márquez A, Erickson GM, Ebersole JA. 2016.** A primitive hadrosaurid from southeastern

647 North America and the origin and early evolution of 'duck-billed' dinosaurs. *Journal of*

648 *Vertebrate Paleontology* **36**:doi:10.1080/02724634.2015.1054495.

649 **Proctor NS, Lynch PJ. 1993.** *Manual of Ornithology*. New Haven, CT: Yale University Press.

650 **Russell DA. 1972.** Ostrich dinosaurs from the Late Cretaceous of western Canada. *Canadian*

651 *Journal of Earth Sciences* **9**:375-402.

652 **Schmidt-Nielsen K. 1989.** *Scaling: why is animal size so important.* Cambridge: Cambridge

653 University Press.

654 **Sereno PC, Beck AL, Dutheil DB, Gado B, Larsson HCE, Lyon GH, Marcot JD, Rauhut OWM,**

655 **Sadleir RW, Sidor CA, Varricchio DD, Wilson GP, Wilson JA. 1998.** A long-snouted predatory

656 dinosaur from Africa and the evolution of spinosaurids. ***Science*** **282**:1298–1302.

657 **Simpson GG. 1976.** *Penguins: past and present, here and there.* New Haven, CT: Yale University

658 Press.

659 **Stromer E. 1915.** Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II.

660 Wirbelter-Reste der Baharije-Stufe (unterstes Cenoman). 3. Das Original de Theropoden

661 Spinosaurus aegyptiacus nov. gen., nov. spec. *Abhandlungen der Konglich Bayerischen*

662 *Akademie der Wissenschaften, Mathematisch-physikaliche Classe,* 28(3) Abhandlung:1-32.

663   **Sues H-D, Frey E, Martill DM, Scott DM. 2002.** *Irritator challengeri,* a spinosaurid (Dinosauria:

664   Theropoda) from the Lower Cretaceous of Brazil. *Journal of Vertebrate Paleontology*

665   **22**:535–547.

666   **Tarlach G. 2014.** The first dinosaur to menace both land and water. Discover Magazine

667   January/February.

668   **Taquet P. 1984.** A curious specialization of the skull of some Cretaceous carnivorous dinosaurs:

669   the long and narrow snout of spinosaurids. Comptes Rendus Academie Sciences Paris,

670   Sciences de la Terre Série IIA 299: 217-222.

671   **Vullo R, Allain R, Cavin L. 2016.** Convergent evolution of jaws between spinosaurid dinosaurs

672   and pike conger eels. Acta Palaeontologica Polonica 61: 825-828.

673   **Wang SC, Dodson P. 2006.** Estimating The Diversity Of Dinosaurs. *Proceedings of the National*

674   *Academy Of Sciences Of The United States Of America.* **10**:13601-13605.

675   **Woodward AR, White JH, Linda SB. 1995.** *Maximum size of the alligator (Alligator*

676   *mississippiensis). Journal of Herpetology* 29:507-513.

677

678   FIGURE CAPTIONS

679   Figure 1 Dorsal and lateral views of the theropod models used for flotation tests. (A)

680   *Coelophysis bauri*; (B) *Struthiomimus altus*; (C) *Allosaurus fragilis*; (D) *Baryonyx* (*Suchomimus*)

681   *tenerensis*; (E) *Spinosaurus aegyptiacus*; (F) *Tyrannosaurus rex*. Animals in order of increasing

682   mass. Lung volumes and positions are represented by the dark gray cylinders in the chest

683   regions. Black '+' denotes the computed center of mass. See Tables 1 and 2 for model image

684   sources and model details, respectively.

685   Figure 2 Detailed view of the *Spinosaurus* "sail" and its associated neural spines (after Ibrahim

686   et al. (2014)). These details were used to determine the relative fractions of the bony and soft

687   tissue components of the sail which were then used to compute the mass and center of mass of

688   the sail. These latter two values were components in the final calculations of the mass, center

689   of mass, and buoyant characteristics of the complete *Spinosaurus* model. Small white '+'s are

690   the centroids of the individual spines. Large black '+' is the centroid of the entire sail. See

691   Methods for details of the calculations.

692   Figure 3 Three-dimensional alligator (*Alligator mississippiensis*) model as a validation of the

693   methods. (A) basic model; (B) floating model that has attained buoyant equilibrium with a fully

694   inflated lung. Thin, horizontal black line is the water surface. Light colored dorsal regions are

695   "dry" and exposed to the air. Black '+' denotes the center of mass, while the white '◊' indicates

696   the center of buoyancy. These figures are derived and updated from Henderson (2003). See

697   Tables 1 and 2 for details of the model and its floating state.

698   Figure 4 Dorsal, lateral and anterior views of the floating model of the emperor penguin

699   (*Aptenodytes forsteri*). This example of an extant, aquatic, predatory theropod was done as

700   another test of the validity of the methods employed with the extinct theropods. The model is

701   in its final, equilibrium flotation state with a full lung, and replicates the situation seen in living

702   emperor penguins floating at the water surface. Unlike all the other flotation tests, this one is

703   done with seawater of density 1026 gm/l. Colours and symbols as per figure 3. See Table 2 for

704   details of the model and its floating state.

705   Figure 5 Floating spinosaurids in lateral and dorsal views. (A) *Spinosaurus aegyptiacus*; (B)

706   *Baryonyx* (*Suchomimus*) *tenerensis*. Determination of the buoyant state required knowing the

707   masses and centers of mass of the axial body (accounting the presence of a lung), all four limbs,

708   and in both cases, the dorsal "sail". See Table 2 for model details.

709   Figure 6 Floating theropods with masses ranging from 10.3 kg to 9360 kg. (A) *Coelophysis bauri* ;

710   (B) *Struthiomimus altus*; (C) *Allosaurus fragilis*; (D) *Tyrannosaurus rex*. See figure 3 explanation

711   of symbols. All models floated with full lungs. See Table 2 for model details.

712   Figure 7. A test of the lateral stability of the floating *Alligator* model using a disk representing

713   the transverse section of the immersed axial body at the position of the CM from the floating

714   model of figure 3B. The disk was given a 20° sideways tip, but slowly returned to an upright

715   orientation by passive self-righting. Gray '+' indicates center of mass (centroid) of disk and

716   white '◊' is the center of buoyancy. Green indicates the "dry" area above the waterline, while

717   the blue is the "wet", immersed portion.

718   Figure 8. A test of lateral stability of the floating *Spinosaurus* model using a disk representing

719   the cross-sectional area of the axial body at the position of the CM from the floating model of

720   figure 5A. The disk was given a 20° sideways tip and subsequently rolled onto its side to a new

721   position of stable equilibrium. Symbols and colors as per figure 7.

722   Figure 9 Graphical views of the metacentric heights (KM '□') determined for the floating

723   alligator and *Spinosaurus* models. A center of gravity above the metacentric height indicates an

724   unstable situation, which is clearly the case for the *Spinosaurus*. Centers of buoyancy and

725   gravity are indicated by KB '◊' and KG '+', respectively. Stated measurements are relative to the

726   water line and are in meters. See Methods and Results sections for more details.

727   Figure 10 Centers of mass determinations for the axial body of *Spinosaurus* using two different

728   methods: (A) two-dimensional silhouette with constant areal density; (B) Three-dimensional

729   mesh without lung cavity or air sacs. In neither case does the CM reside at the midpoint of the

730   trunk region as claimed by Ibrahim et al. (2014). See Discussion section.

731   Figure 11 Isometric views of hindlimb model of *Allosaurus fragilis* using the right limb from

732   figure 1C and three-dimensional models of the large limb bones based on illustrations in

733   Madsen (1976). The volumes of these shapes, combined with the appropriate densities, were

734   used to investigate the effects of higher than normal bone densities on the mass and density of

735   the host animal. See Discussion.

736   Figure 12 Relative mass fractions of the hindlimbs of the theropods in the present study

737   highlighting the small size of the restored *Spinosaurus* hindlimbs. Dashed line represents the

738   mean value of 12.6%. Gray band spans plus and minus one standard deviation about the mean.

739   The *Spinosaurus* limb mass was not used in the calculation of the mean and standard deviation.

740   A.f – *Allosaurus fragilis*, B.t – *Baryonyx* (*Suchomimus*) *tenerensis*, C.b – *Coelophysis bauri*, S.a –

741   *Struthiomimus altus*, S.ae – *Spinosaurus aegyptiacus*, T.r – *Tyrannosaurus rex*.

Sources of illustrations used to generate the theropod and alligator body forms.

Table 1. Sources of illustrations used to generate the theropod and alligator body forms.

Taxon	Image sources
Alligator mississippiensis	Neill (1971)
Coelophysis bauri	Paul (1988) and Currie (1997)
Struthiomimus altus	Paul (1988)
Allosaurus fragilis	Paul (1988)
Baryonyx (Suchomimus) tenerensis	Sereno *et al*. (1988) and Hartman (in Holtz 2012)
Spinosaurus aegyptiacus	Ibrahim *et al*. (2014)
Tyrannosaurus rex	Paul (1988) and Currie (1997)

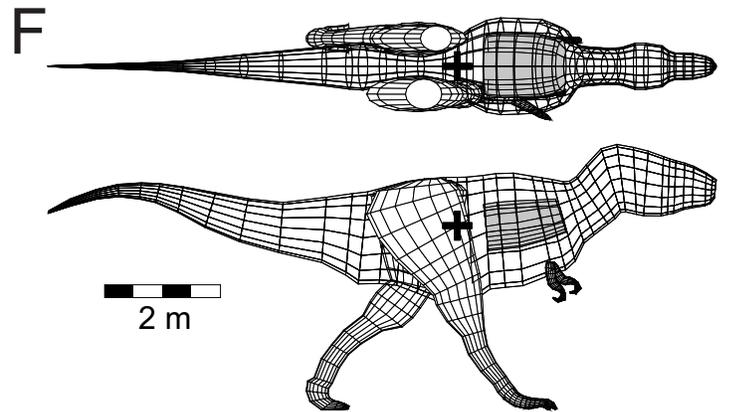
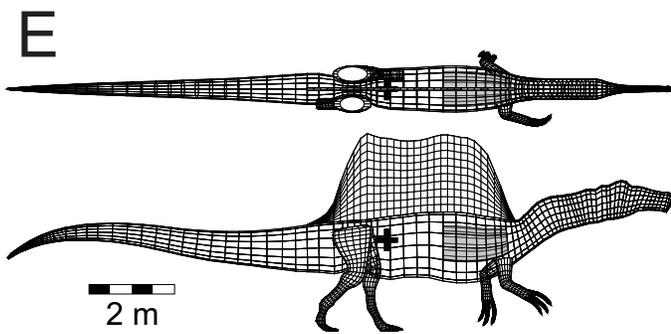
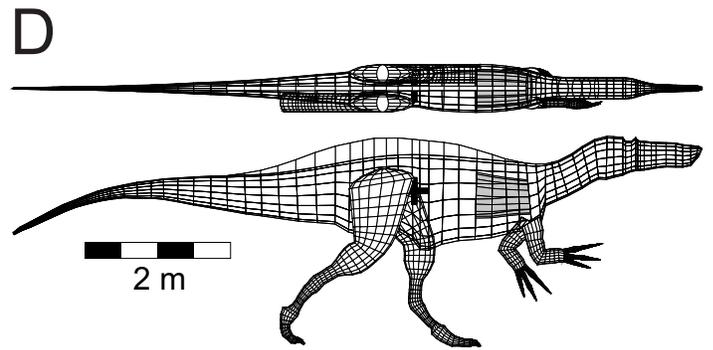
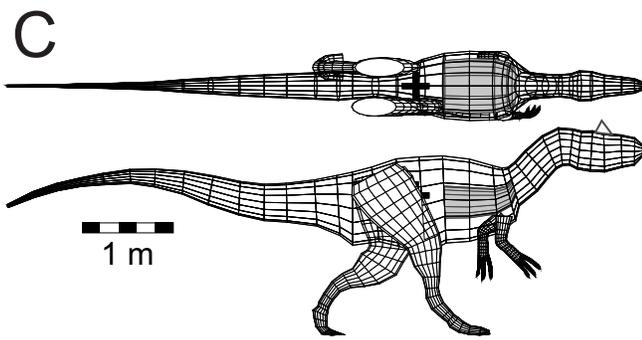
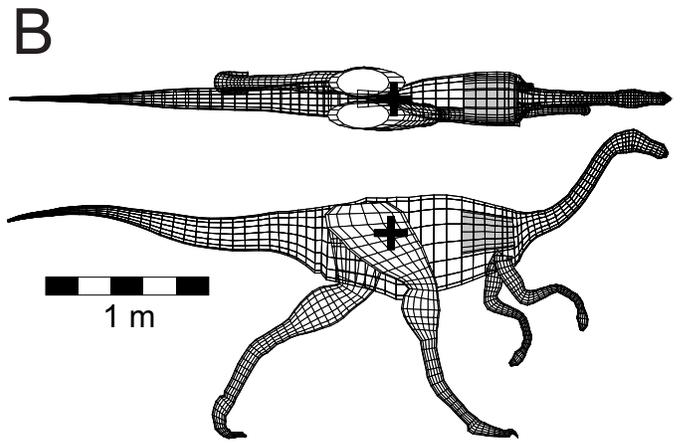
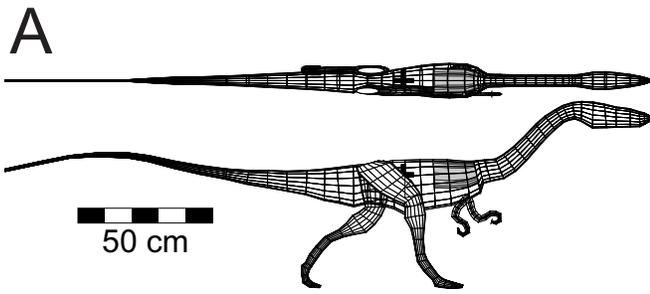
Body lengths, total mass and component masses for the eight models used in the present study. Listed alphabetically by genus from left to right.

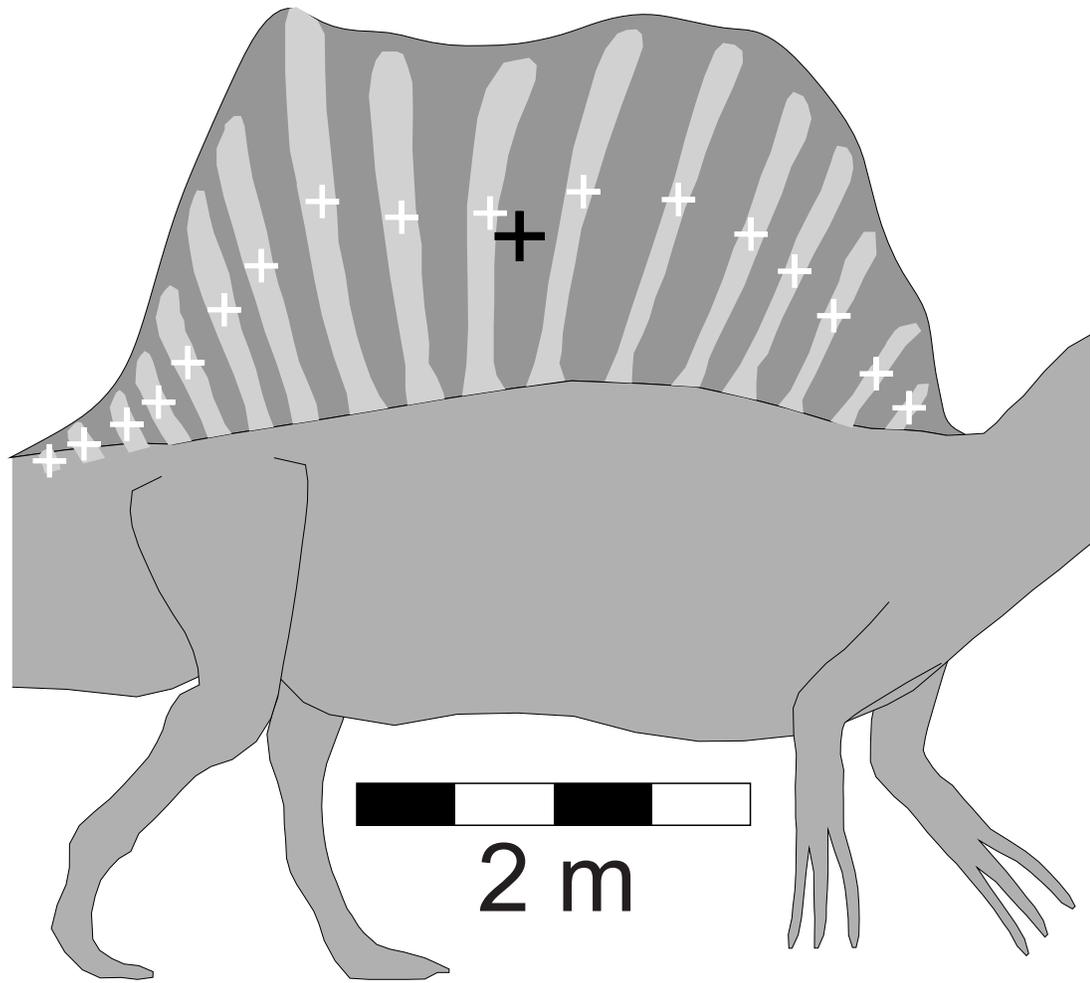
Table 2 Body lengths, total mass and component masses for the eight models used in the present study.

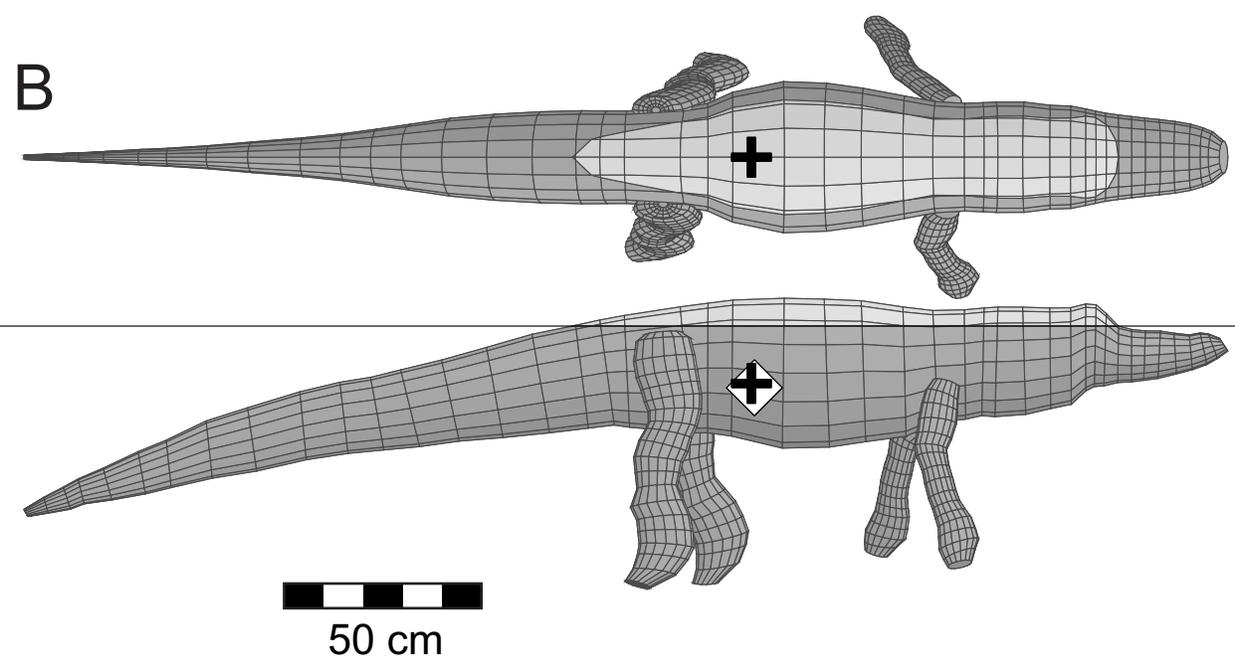
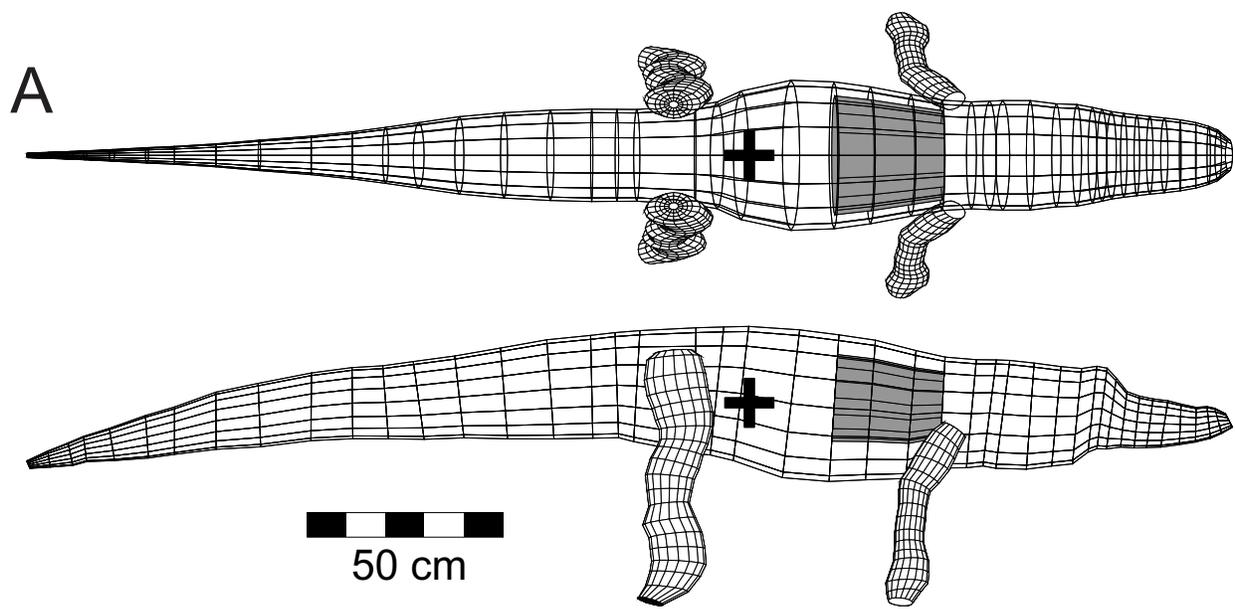
	Alligator mississippiensis	Aptenodytes forsteri	Allosaurus fragilis	Baryonyx (Suchomimus) tenerensis	Coelophysis bauri	Spinosaurus aegyptiacus	Struthiomimus altus	Tyrannosaurus rex
Length (m)	3.07	1.25	7.35	9.78	2.52	16.0	4.35	12.0
Total Mass (kg)	133	46.3	963	2.14×10^3	10.3	6,500	201	9,750
Mean body density (kg/m³)	952	968	818	840	828	833	858	851
Axial mass (kg)[1]	106	44.2	757	1.29×10^3	7.77	5470	119	6030
Single Arm Mass (kg)	1.58	0.354	7.12	20.0	0.0413	54.0	3.67	10.3
Single Leg mass (kg)	4.88	0.704	121	216	1.20	295	40.7	1,430
Lung Volume (l) (% axial volume)	11.4 (9.10)	1.05 (23.5)	97.8 (9.98)	149 (9.09)	1.08 (10.8)	662 (10.0)	14.5 (9.53)	837 (10.5)
CM (x,y)[2]	(1.86, -0.146)	(0.539, -0.118)	(4.50,0.645)	(5.50,0.814)	(1.48,0.148)	(8.85,1.00)	(2.35,0.416)	(7.01,1.35)
Horizontal Relative CM (%)[3]	27.7	71.6	19.2	19.0	27.2	20.9	15.3	28.6

1. Axial mass reduced by an equivalent mass of water represented by the lung cavity and excludes the mass of the sail for *Spinosaurus*.
2. Center of Mass: horizontal position expressed as meters from the tip of the tail, vertical position is meters above lowest point of the axial body. For *Alligator* and *Aptenodytes* vertical CM is from floating models and measured relative to water surface.
3. Horizontal Relative CM: distance in front of acetabulum expressed as a percentage of the gleno-acetabular distance.

Dorsal and lateral views of the theropod models used for flotation tests.

(A) *Coelophysis bauri* ; (B) *Struthiomimus altus* ; (C) *Allosaurus fragilis* ; (D) *Baryonyx* (*Suchomimus*) *tenerensis* ; (E) *Spinosaurus aegyptiacus* ; (F) *Tyrannosaurus rex* . Animals in order of increasing mass. Lung volumes and positions are represented by the dark gray cylinders in the chest regions. Black '+' denotes the computed center of mass. See Tables 1 and 2 for model image sources and model details, respectively.

Detailed view of the *Spinosaurus* "sail" and its associated neural spines (after Ibrahim et al. (2014)).

These details were used to determine the relative fractions of the bony and soft tissue components of the sail which were then used to compute the mass and center of mass of the sail. These latter two values were components in the final calculations of the mass, center of mass, and buoyant characteristics of the complete *Spinosaurus* model. Small white '+'s are the centroids of the individual spines. Large black '+' is the centroid of the entire sail. See Methods for details of the calculations.

Three-dimensional alligator (*Alligator mississippiensis*) model as a validation of the methods.

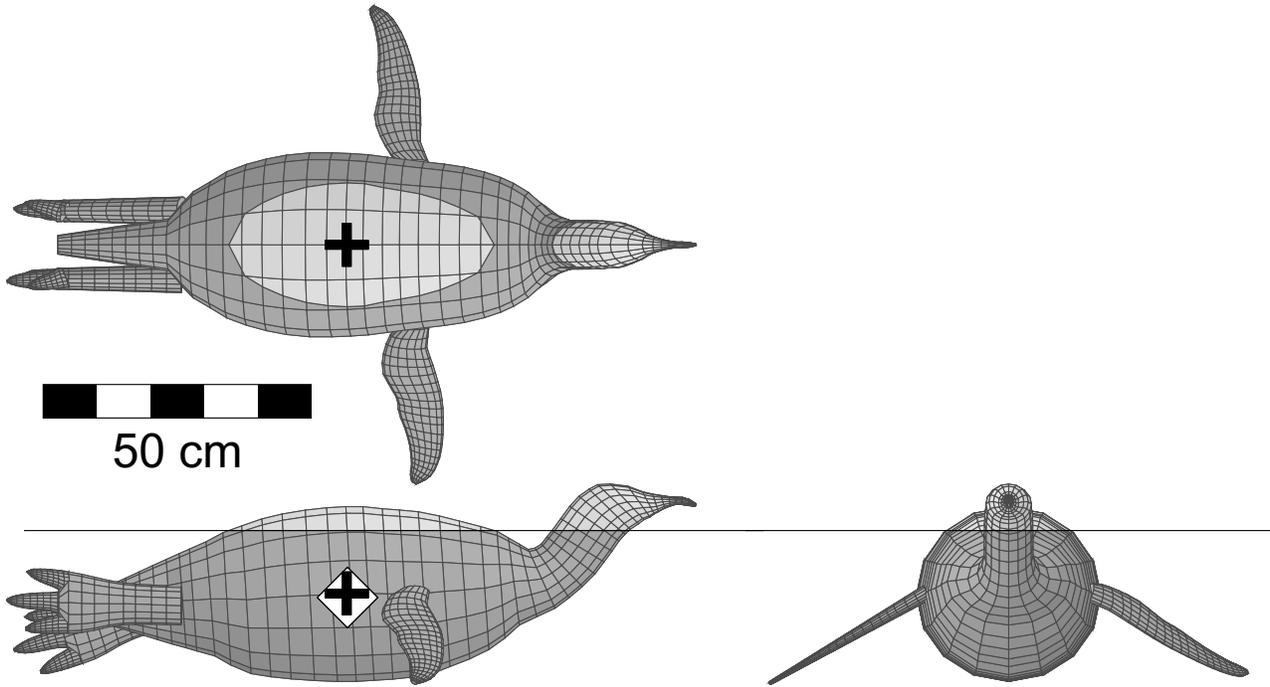
(A) basic model; (B) floating model that has attained buoyant equilibrium with a fully inflated lung. Thin, horizontal black line is the water surface. Light colored dorsal regions are "dry" and exposed to the air. Black '+' denotes the center of mass, while the white '◊' indicates the center of buoyancy. These figures are derived and updated from Henderson (2003). See Tables 1 and 2 for details of the model and its floating state.

A

B

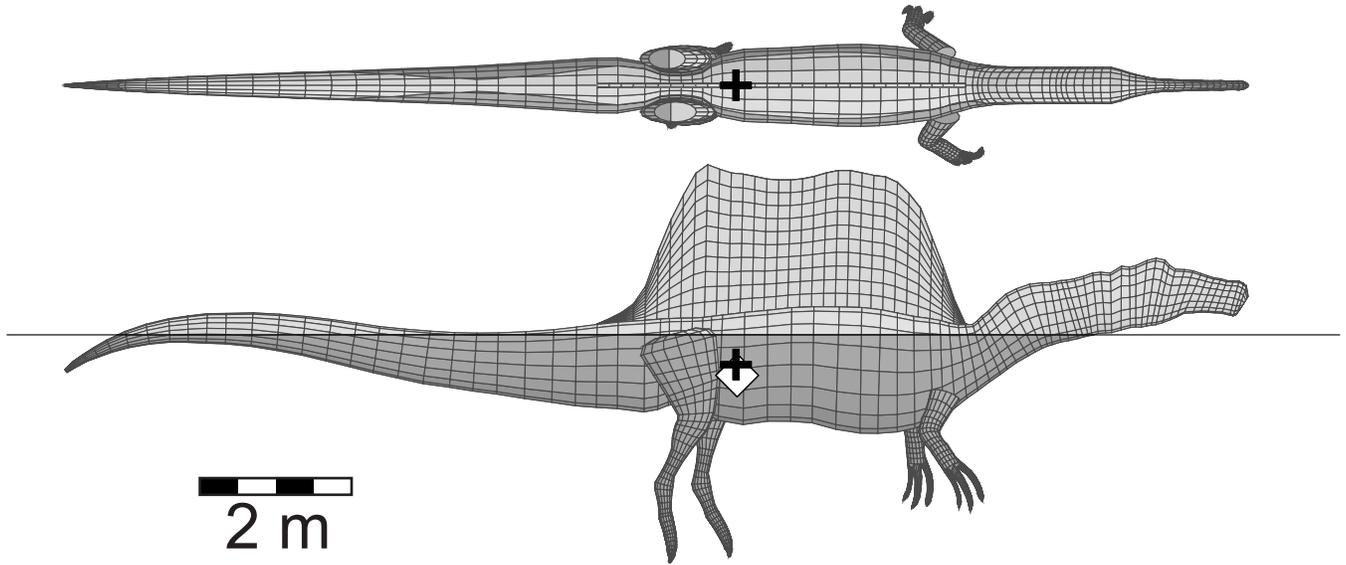
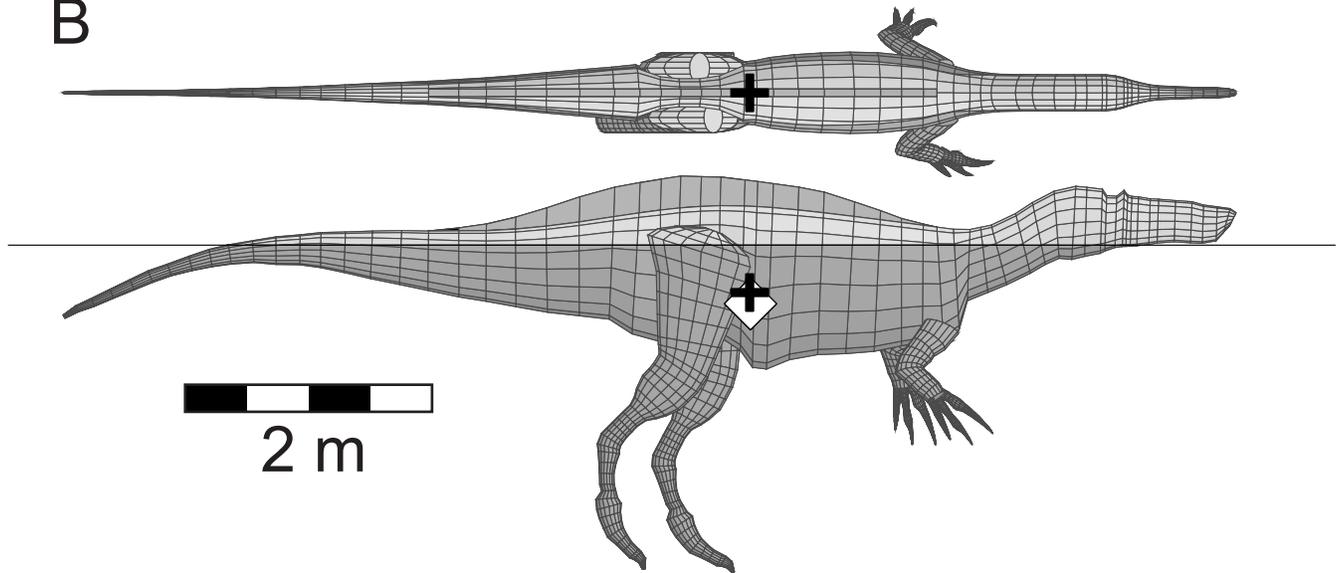
50 cm

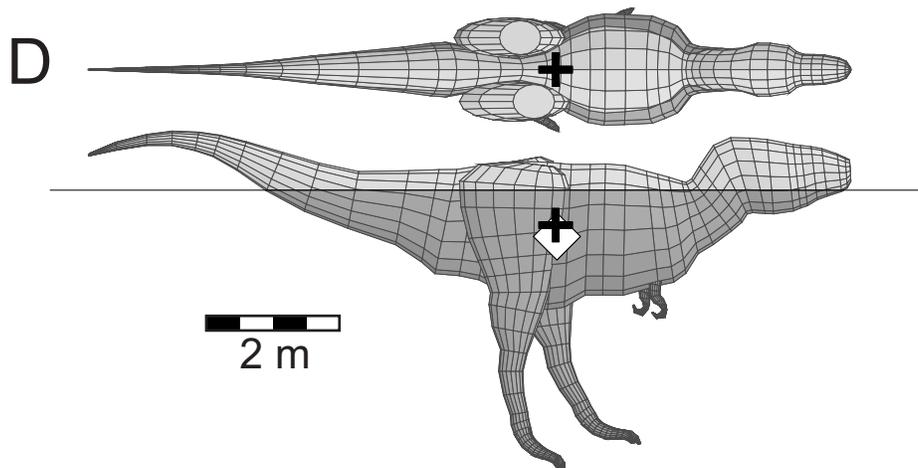
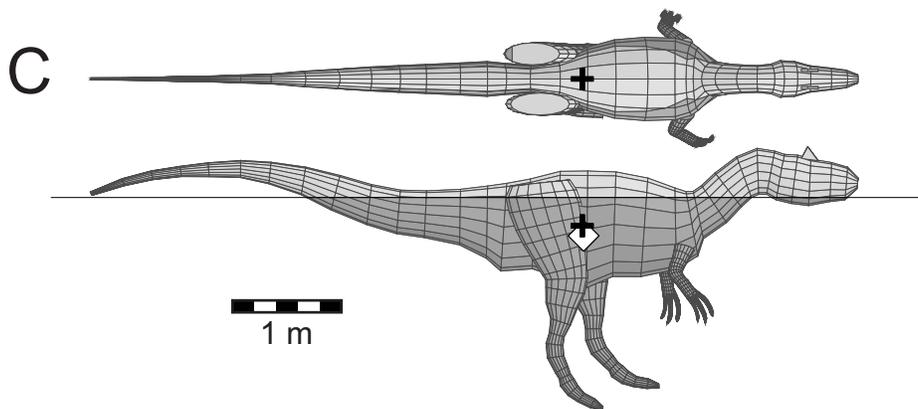
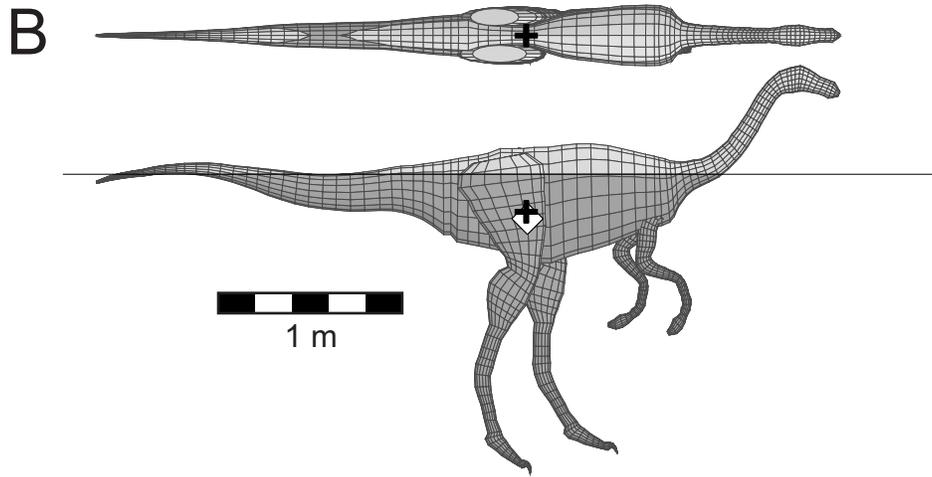
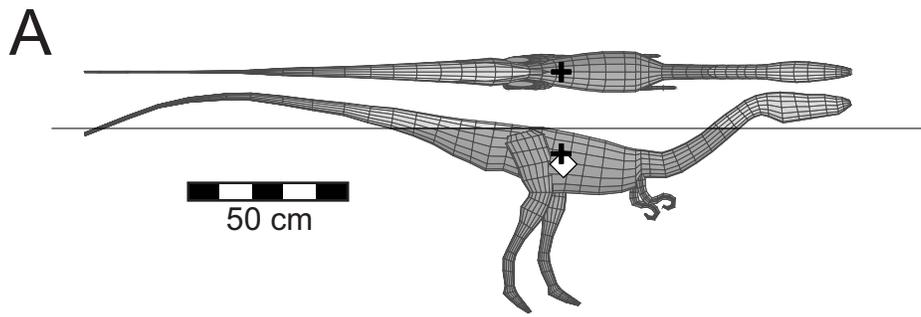
50 cm

Dorsal, lateral and anterior views of the floating model of the emperor penguin (*Aptenodytes forsteri*).

This example of an extant, aquatic, predatory theropod was done as another test of the validity of the methods employed with the extinct theropods. The model is in its final, equilibrium flotation state with a full lung, and replicates the situation seen in living emperor penguins floating at the water surface. Unlike all the other flotation tests, this one is done with seawater of density 1026 gm/l. Colours and symbols as per figure 3. See Table 2 for details of the model and its floating state.

50 cm

Floating spinosaurids in lateral and dorsal views.

(A) *Spinosaurus aegyptiacus* ; (B) *Baryonyx* (*Suchomimus*) *tenerensis* . Determination of the buoyant state required knowing the masses and centers of mass of the axial body (accounting the presence of a lung), all four limbs, and in both cases, the dorsal "sail". See Table 2 for model details.

Floating theropods with masses ranging from 10.3 kg to 9360 kg.

(A) *Coelophysis bauri* ; (B) *Struthiomimus altus* ; (C) *Allosaurus fragilis* ; (D) *Tyrannosaurus rex* . See figure 3 explanation of symbols. All models floated with full lungs. See Table 2 for model details.

A

50 cm

B

1 m

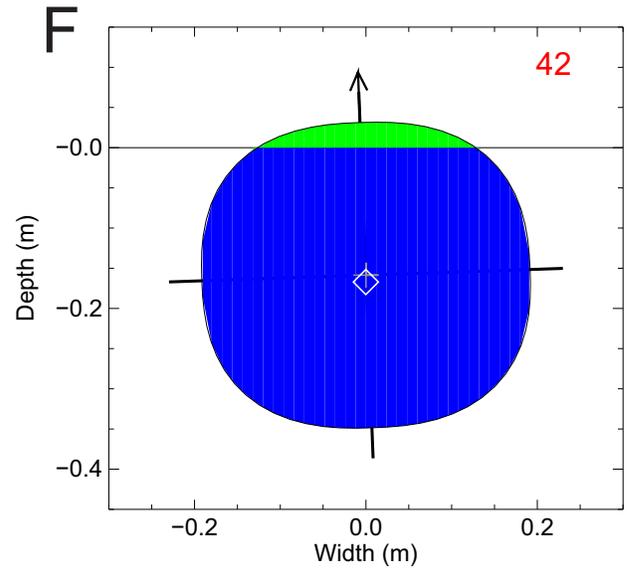
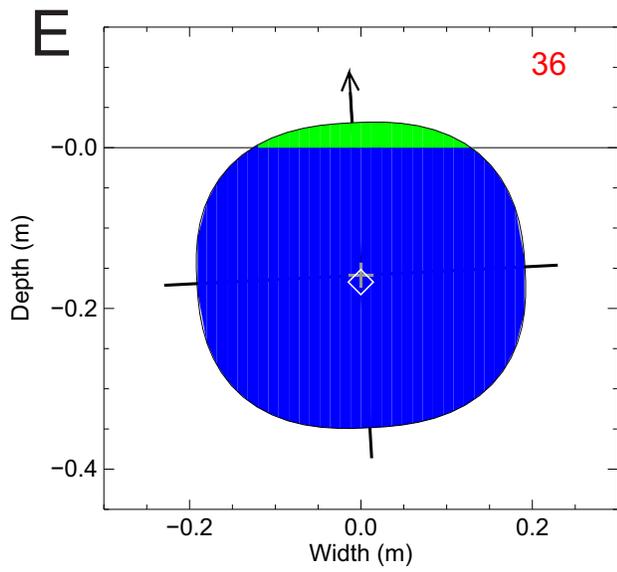
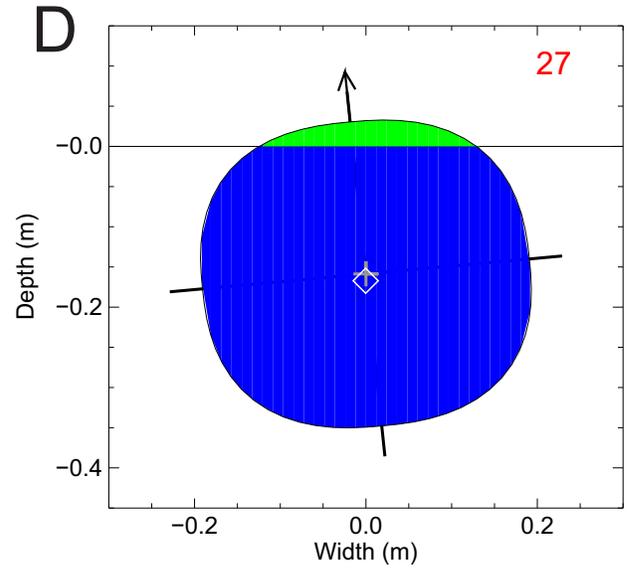
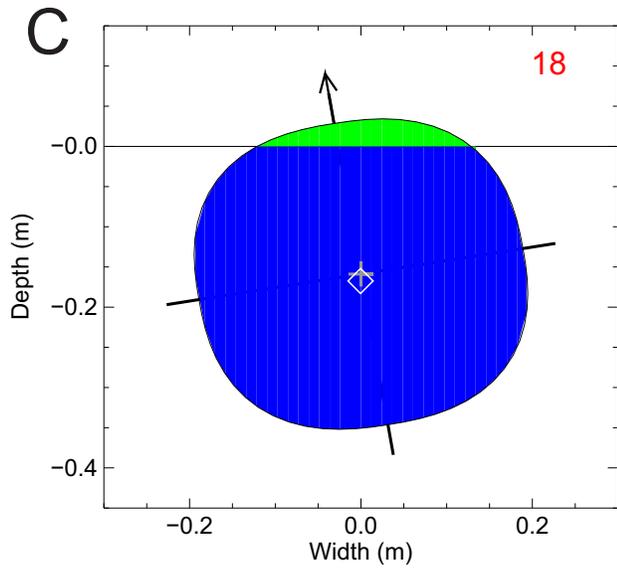
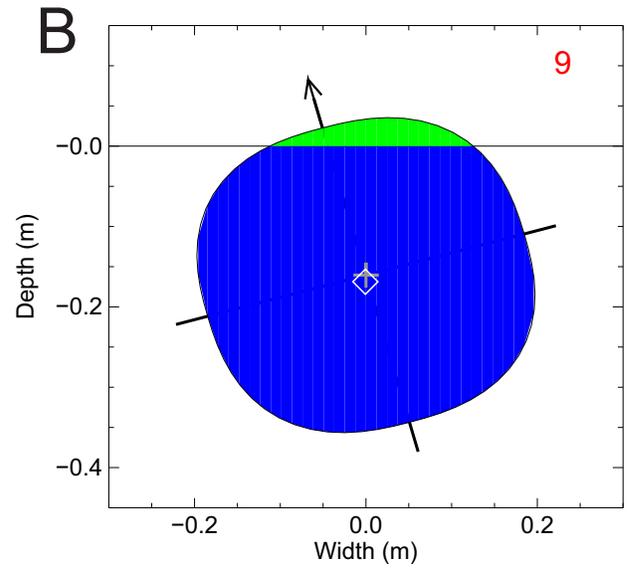
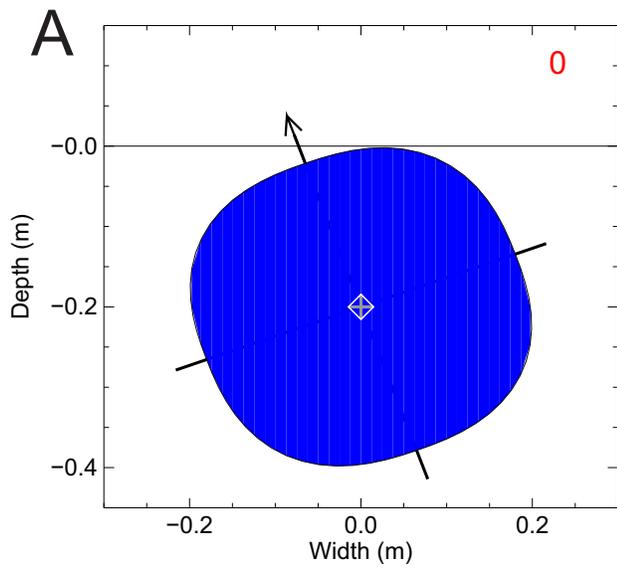
C

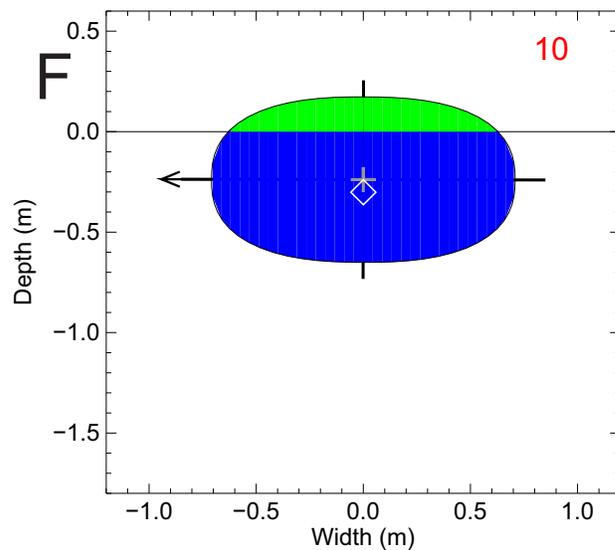
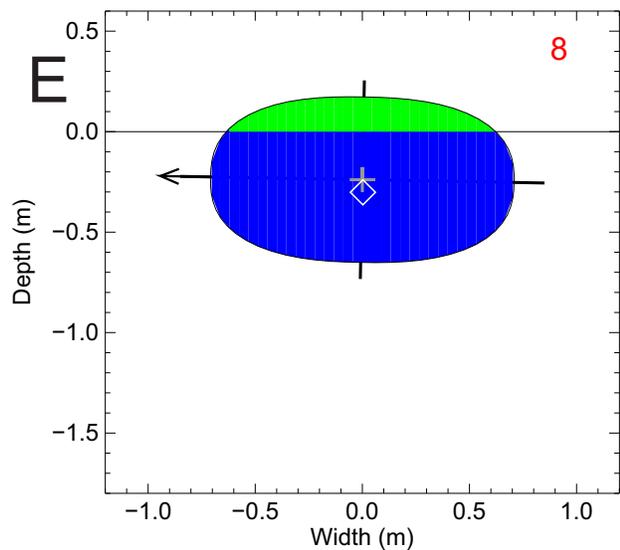
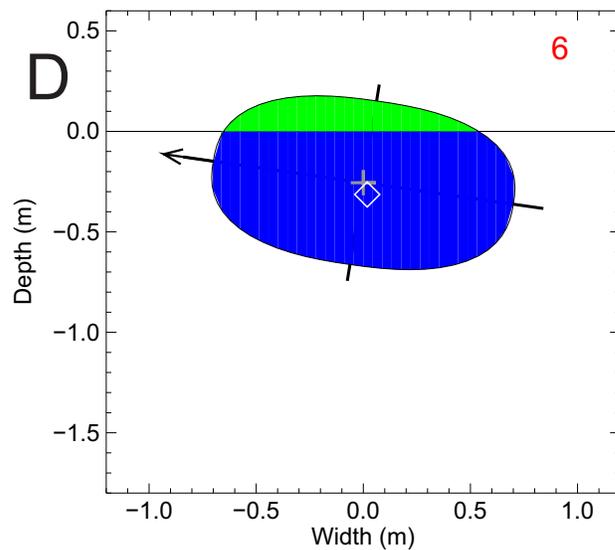
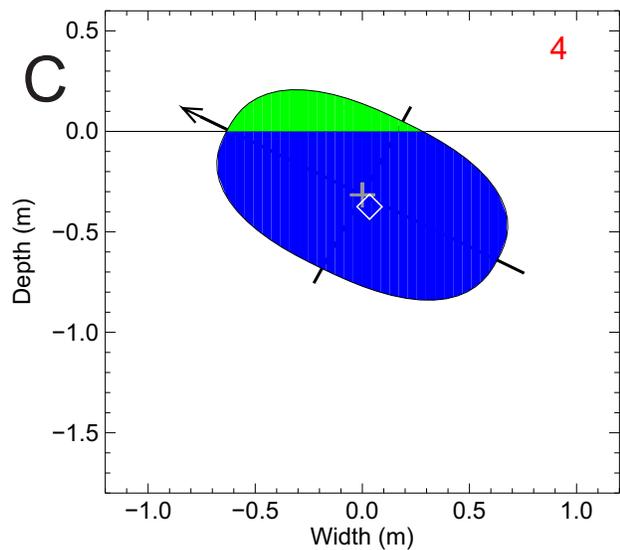
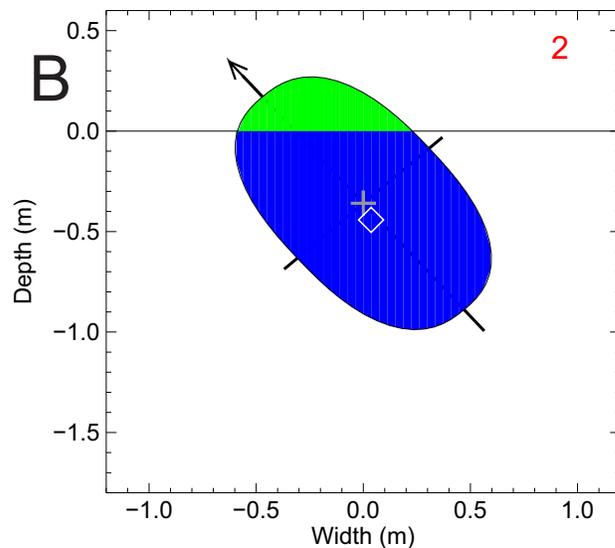
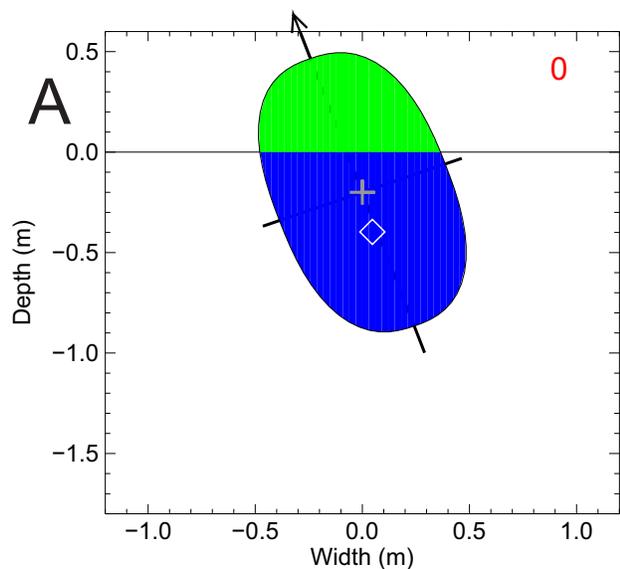
1 m

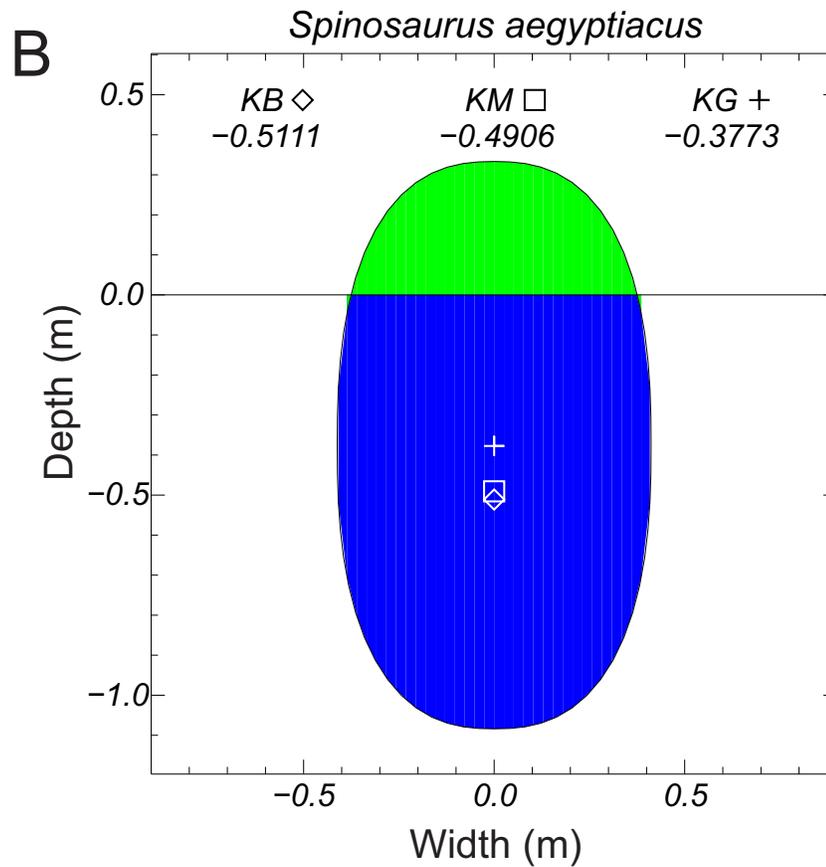
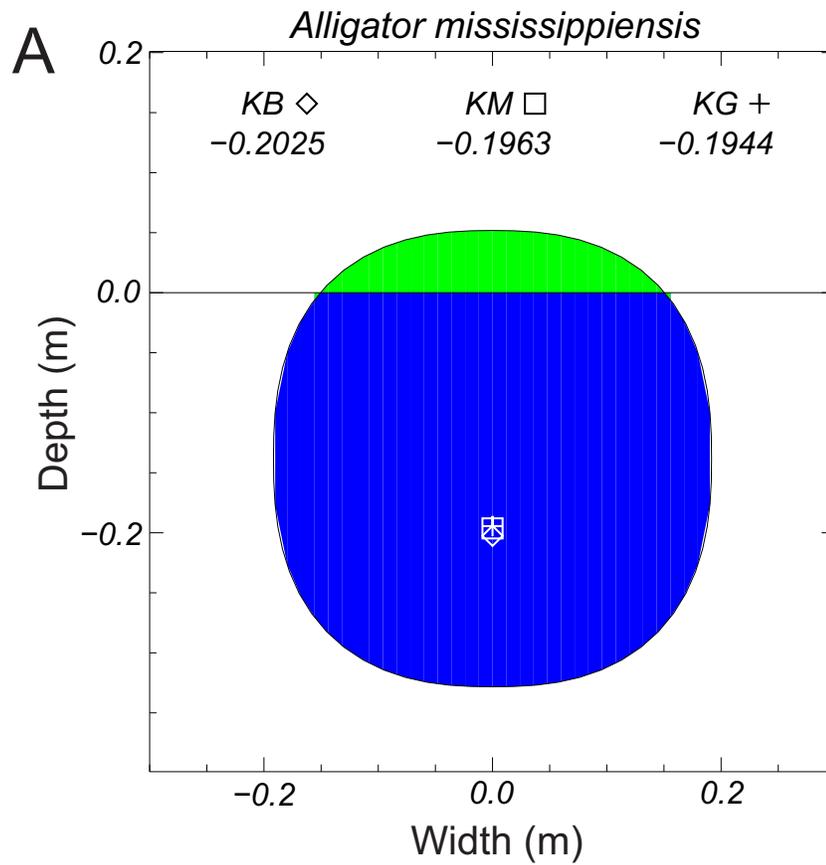
D

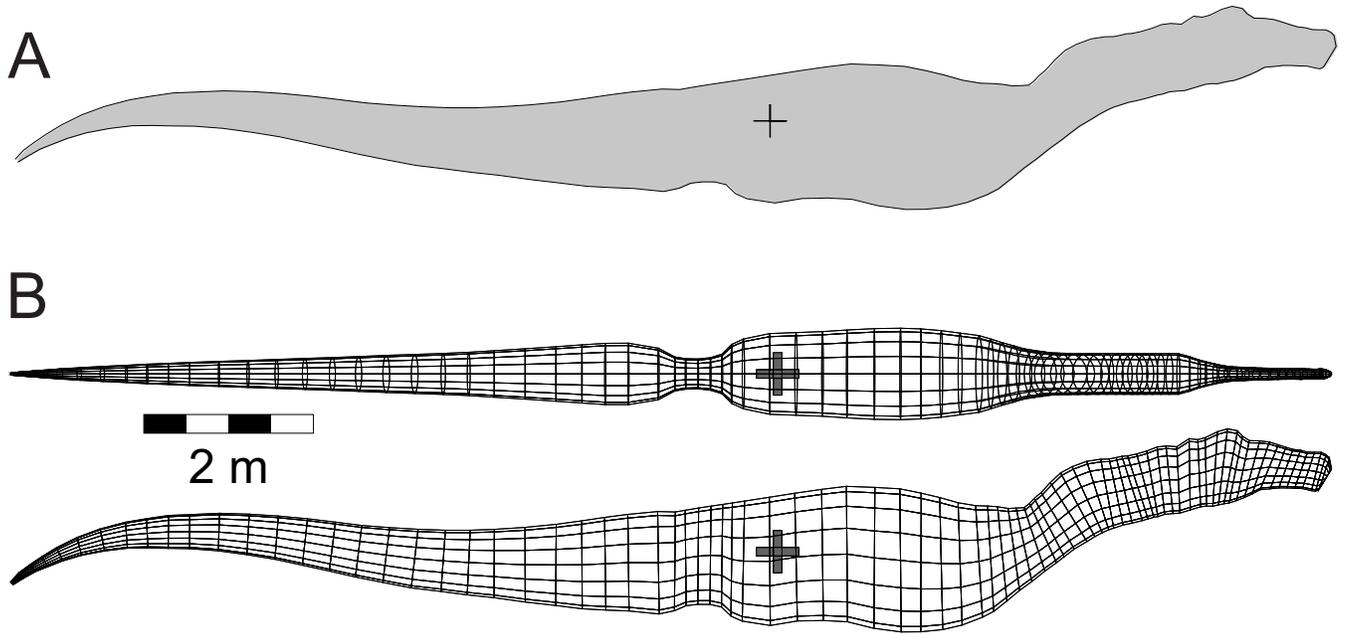
2 m

A test of the lateral stability of the floating *Alligator* model using a disk representing the transverse section of the immersed axial body at the position of the CM from the floating model of Figure 3B.

The disk was given a 20° sideways tip, but slowly returned to an upright orientation by passive self-righting. Gray '+' indicates center of mass (centroid) of disk and white '◊' is the center of buoyancy. Green indicates the "dry" area above the waterline, while the blue is the "wet", immersed portion.

A test of lateral stability of the floating *Spinosaurus* model using a disk representing the cross-sectional area of the axial body at the position of the CM from the floating model of Figure 5A.

The disk was given a 20° sideways tip and subsequently rolled onto its side to a new position of stable equilibrium. Symbols and colors as per figure 7.

Graphical views of the metacentric heights (KM '□') determined for the floating models.

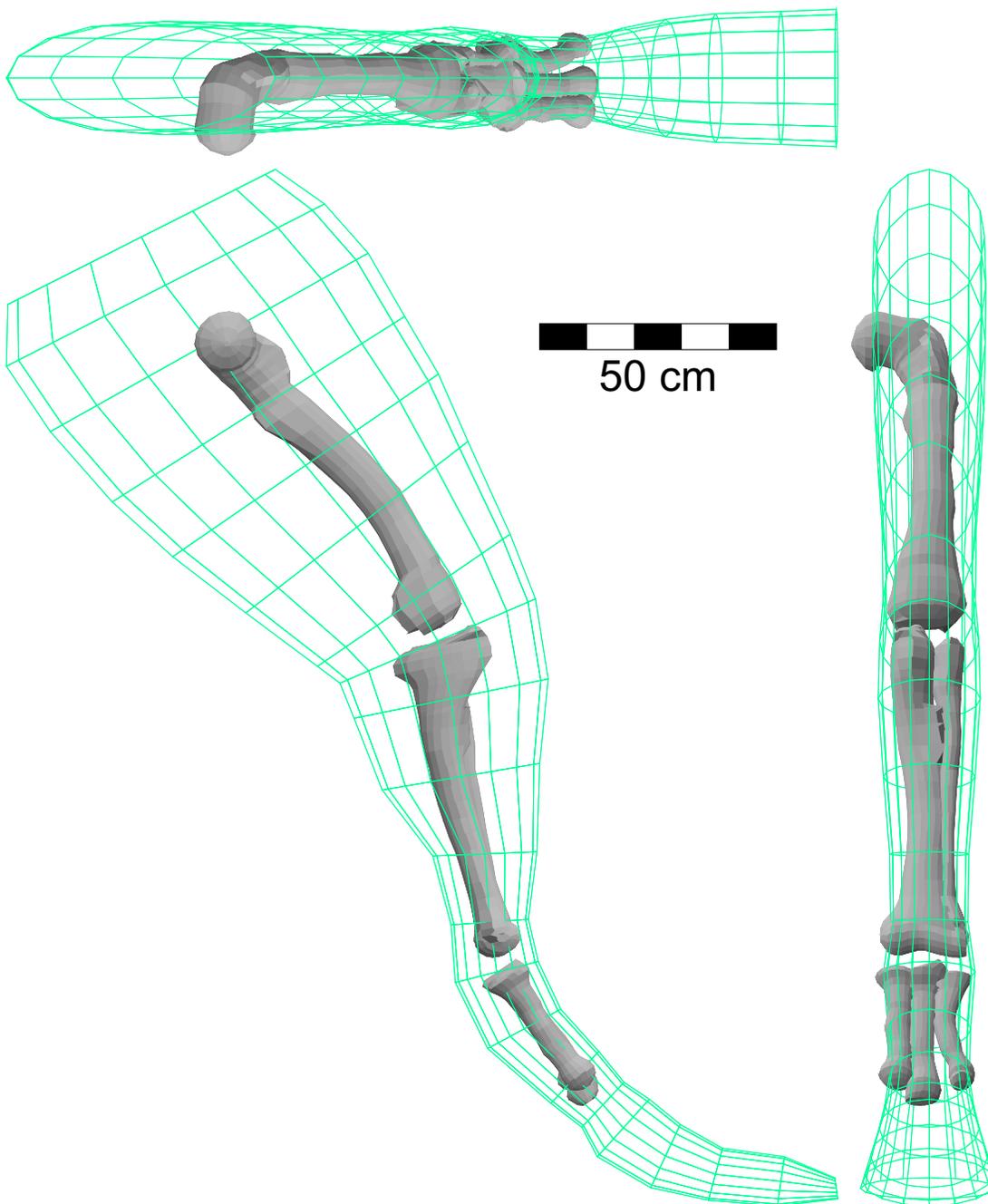
(A) American alligator. (B) *Spinosaurus*. A center of gravity above the metacentric height indicates an unstable situation, which is clearly the case for the *Spinosaurus* . Centers of buoyancy and gravity are indicated by KB '◊' and KG '+', respectively. Stated measurements are relative to the water line and are in meters. See Methods and Results sections for more details.

Centersof mass determinations for the axial body of *Spinosaurus* using two different methods:

(A) two-dimensional silhouette with constant areal density; (B) Three-dimensional mesh without lung cavity or air sacs. In neither case does the CM reside at the midpoint of the trunk region as claimed by Ibrahim et al. (2014). See Discussion section.

A

B

2 m

Isometricviews of hindlimb model of *Allosaurusfragilis* using the right limb from figure
1C and three-dimensional modelsof the large limb bones based on illustrations in
Madsen (1976).

The volumes of these shapes, combined with the appropriate densities, were used to investigate the effects
of higher than normal bone densities on the mass and density of the host animal. See Discussion.

50 cm

Relative mass fractions of the hindlimbs of the theropods in the present study highlighting the small size of the restored *Spinosaurus* hindlimbs.

Dashed line represents the mean value of 12.6%. Gray band spans plus and minus one standard deviation about the mean. The *Spinosaurus* limb mass was not used in the calculation of the mean and standard deviation. A.f – *Allosaurus fragilis*, B.t – *Baryonyx* (*Suchomimus*) *tenerensis*, C.b – *Coelophysis bauri*, S.a – *Struthiomimus altus*, S.ae – *Spinosaurus aegyptiacus*, T.r – *Tyrannosaurus rex*.

Relative Hindleg Mass