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1 **SEMI-AQUATIC ADAPTATIONS IN A SPINOSAUR FROM THE LOWER**
2 **CRETACEOUS OF BRAZIL**

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15 **ABSTRACT**

16 Spinosaurinae are known to have a strong relationship with aquatic environments,
17 involving several anatomical adaptations. Nonetheless, this group of theropods
18 remains enigmatic, due to the relative incompleteness of its fossil record. A large
19 partial tibia from the Aptian-Albian Romualdo Formation, Northeast Brazil, is herein
20 described through anatomical comparisons and paleohistological analyzes. It features
21 characteristics previously only observed in *Spinosaurus aegyptiacus*, which includes
22 a reduced fibular crest and an osteosclerotic condition. The later, a character
23 supported as correlated with semi-aquatic habits in many limbed vertebrates. The
24 results presented here support high bone compactness being already present in
25 Brazilian Spinosaurinae millions of years before the Moroccan *Spinosaurus*.

26 Furthermore, histological analyses demonstrate the Romualdo Formation specimen
27 was a young subadult still growing fast by the time of its death, and suggests Araripe
28 Basin Spinosaurinae could have grown larger than previously thought. This work
29 contributes to a better paleobiological and ecological understanding of South
30 American spinosaurs, and helps fill a gap in the macroevolutionary comprehension of
31 Spinosaurinae. Ultimately, it also contributes to further advancing the
32 paleoecological characterization of the Romualdo Formation.

33 **Keywords:** Paleohistology, Araripe Basin, Theropoda, Megalosauroida,
34 Spinosaurinae.

35 INTRODUCTION

36 Spinosauridae remains a poorly known group due to the incompleteness of its fossil
37 record. However, in recent years, new specimens and different approaches have
38 provided a wider understanding of the clade (e.g., Amiot *et al.*, 2010a; Kellner *et al.*,
39 2011; Allain *et al.*, 2012; Cuff & Rayfield, 2013; Ibrahim *et al.*, 2014; Hendrickx *et*
40 *al.*, 2016; Sales & Schultz, 2017). Most of the knowledge on Spinosauridae comes
41 from North African (mostly from Morocco and Niger) and west European taxa
42 (Spain, Portugal and England; eg. Canudo *et al.*, 2008), and comparatively little
43 information has been published about South-American representatives. The South-
44 American records are mostly restricted to the Cenomanian Alcântara Formation (São
45 Luís-Grajaú Basin) (Medeiros & Schultz, 2002; Medeiros, 2006; Kellner *et al.*, 2011)
46 and the Aptian-Albian Romualdo Formation (Araripe Basin) (Kellner & Campos,
47 1996; Sues *et al.*, 2002) of Northeast Brazil. However, there is also a single tooth
48 attributed to Spinosauridae recently found in Feliz Deserto Formation, Sergipe-

49 Alagoas Basin, also in NE Brazil, in Berriasian–Valanginian strata (Sales et al.,
 50 2017), which would represent the oldest Spinosauridae record in South America.
 51 Spinosaur theropods have been associated with coastal environments (Rayfield et al.,
 52 2007; Ibrahim et al., 2014; Sales et al., 2016) and by presenting a semi-aquatic life
 53 style (Charig & Milner, 1997; Sereno et al., 1998; Dal Sasso et al., 2005; Amiot et
 54 al., 2010; Ibrahim et al. 2014). In a recent work, Ibrahim and colleges (2014)
 55 described new materials from Morocco (including the neotype) belonging to
 56 *Spinosaurus aegyptiacus* with several semi-aquatic adaptations including retraction
 57 of the fleshy nostrils to a position near the mid-region of the skull; an elongate neck
 58 and trunk shifting the center of mass to the knee joint; short pelvic girdle and
 59 hindlimbs; and high density of the limb bones. The bone density in *Spinosaurus*
 60 suggests that this species could have a buoyancy control in water (Ibrahim et al.,
 61 2014). However, this feature is only found in *S. aegyptiacus* so far, and other species
 62 (e.g., *Suchomimus tenerensis*) should have had a more terrestrial lifestyle (Ibrahim et
 63 al., 2014). Histological analyses are important to obtain information on extinct
 64 animals including developmental stages, growth rates, and physiological details
 65 (Chinsamy, 2005; Sander et al., 2011; Padian & Lamm, 2013; Ibrahim et al., 2014;
 66 Ghilardi et al., 2016; Cerda et al., 2017), allowing a comprehensive biological and
 67 ecological understanding.
 68 Therefore, in this contribution we described a new material attributed to an
 69 indeterminate spinosaur from Araripe Basin, and performed a histological
 70 examination in order to interpret its lifestyle and to compare with terrestrial and
 71 semi-aquatic animals.

72 GEOLOGICAL SETTINGS

73 The Araripe Basin is located in the northeastern-most portion of South America, in
 74 Brazil, between longitudes 38°30' to 40°55' W and latitudes 7°07' to 7°49' S (WGS-
 75 84), comprising parts of Ceará, Pernambuco, and Piauí states (Neumann & Cabrera,
 76 1999) (Fig. 1). The Santana Group is part of the post-rift basin sequence, and
 77 comprises (from bottom to top) lacustrine carbonate sediments, coastal and
 78 transitional evaporites, and shallow marine/saline lagoon shales of the Crato, Ipubi,
 79 and Romualdo formations, respectively (Neumann & Cabrera, 1999). The Romualdo
 80 Formation (upper Aptian-lower Albian; Ponte, 1992) encompasses interbedded
 81 shales, marls, and limestones with abundant calcareous concretions containing fossils
 82 (Valença et al., 2003). These concretions often enclose fossils with exceptional three-
 83 dimensional and soft tissue preservation (Martill, 1988; Maisey, 1991).

84 The Romualdo Formation is particularly well known for the great variety and
 85 quantity of fossil fishes (Maisey, 1991; Fara et al., 2005). Nevertheless, it also
 86 yielded fossil plants and invertebrates (e.g., Coimbra et al., 2002; Lima et al., 2012;
 87 Pinheiro et al., 2014), besides crocodyliform, chelonian and pterosaur remains (e.g.,
 88 Price, 1959; Wellnhofer, 1991; Oliveira & Kellner, 2007; Kellner et al., 2013).
 89 Dinosaur fossils are rare (Kellner, 1996; Bittencourt & Langer, 2010), and only
 90 theropod material has been recovered so far (Bittencourt & Kellner, 2010). The
 91 Romualdo Formation dinosaurs include: two Spinosaurinae, *Irritator challengeri*
 92 Martill et al., 1996 and *Angaturama limai* Kellner & Campos, 1996; an indeterminate
 93 coelurosaur, *Santanaraptor placidus* Kellner, 1999; a large compsognathid,
 94 *Mirischia asymmetrica* Naish et al., 2004; and a megaraptoran (Rolando et al., 2017).
 95 Spinosaurinae fossils are unequivocally the most common dinosaur remains found in
 96 this geological context to date (Bittencourt & Kellner, 2010). Spinosauridae fossils
 97 include two partial skulls (Martill et al., 1996; Kellner & Campos, 1996; Sues et al.,

2002); a sacro-caudal vertebral sequence associated with chevrons (Bittencourt & Kellner, 2004); a rib tentatively assigned to the clade (Machado & Kellner, 2007); a pelvis, parts of anterior and posterior limbs, and further sacral and caudal vertebrae still undescribed (Campos & Kellner, 1991; Kellner, 1996; Kellner, 2001; Machado & Kellner, 2005; Machado, 2010). The two Romualdo Formation spinosaurids were erected on the recovered cranial material. The *I. challengerii* consists on an incomplete articulated skull with associated mandibles, lacking the anterior portion of the rostrum and the anterior part of both mandibles, and *A. limai* consists of the tip of a rostrum, comprising both pre-maxillae and the anterior-most portions of both maxillae. Several authors consider *A. limai* to be a junior synonym of *I. challengerii* (Charig et al., 1997; Sereno et al., 1998; Buffetaut & Ouaja, 2002; Sues et al., 2002, Dal Sasso et al., 2005; Ibrahim et al., 2014). However, Kellner & Campos (2000), Machado & Kellner (2005), and Sales & Schultz (2017) assume this as a premature conclusion because, although both species have a minimal overlapping features, and therefore are considered different individuals, further information on skulls are need to suggest the synonymy (Sales & Schultz, 2017).. Thus, the question will remain open until more complete cranial material is found (Hone & Holtz, 2017; Sales & Schultz, 2017).

MATERIALS AND METHODS

Institutional abbreviations: **AODF**, Australian Age of Dinosaurs Museum, Queensland, Australia; **DGM/MCT**, Museu de Ciências da Terra/Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil; **LPP**, Laboratório de Paleoeologia e Paleoicnologia, Universidade Federal de São Carlos, Brazil; **MCNA**, Museo de Ciencias Naturales de Álava/Arabako Natur Zietzien Museoa, Vitoria-Gasteiz, Spain; **ML**, Museu da Lourinhã, Portugal; **MN**, Museu Nacional,

123 Universidade Federal do Rio de Janeiro, Brazil; **MNFSAC**, Faculté des Sciences Aïn
 124 Chock, Casablanca, Morocco; **MNN**, Musée National du Niger, Niamey, Niger;
 125 **MPEF**, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; **MSNM**, Museo
 126 di Storia Naturale di Milano, Italy; **OUM**, Oxford University Museum, England;
 127 **PVL**, Fundación Miguel Lillo, Tucumán, Argentina; **SMNS**, Staatliches Museum für
 128 Naturkunde Stuttgart, Germany; **UCMP**, Museum of Paleontology, University of
 129 California, Berkeley, USA; **UMNH**, Utah Museum of Natural History, Salt Lake
 130 City, USA.

131 The studied specimen (LPP-PV-0042; Fig. 2) corresponds to a fragmentary left tibia.
 132 The material is deposited at the Laboratório de Paleoecologia e Paleoicnologia (LPP)
 133 paleontological collection of the Universidade Federal de São Carlos (UFSCar), São
 134 Carlos, São Paulo state, Brazil.

135 **CT-Scan**

136 A 3D reconstruction of the specimen was obtained using a Philips Diamond Select
 137 Brilliance CT 16-slice medical scanner with more than 1000 slices and a voxel size
 138 of 1 mm at UFSCar University Hospital. The software *3D-Slicer* v4.6 was used to
 139 visualize and segment the images. Bone density analysis was conducted in *Bone*
 140 *Profiler* (Girondot & Laurin, 2003).

141 **Bone histology**

142 For the histological study we followed the standard methodology presented by Lamm
 143 (2013). The specimen was replicated in resin and CT-Scanned before being
 144 sectioned. The fossil was transversely sectioned at the distal-most point of the
 145 preserved diaphysis and then embedded in resin for polishing until the thickness of
 146 the section was variable from ca. 40 μm to 100 μm . The thin-section was observed in

147 and photographed with the petrographic microscope Leica DM750P with camera
 148 Leica MC170HD and the imaging software LAS (Leica Application Suite) v4.4. We
 149 later corrected the images for brightness and contrast using Adobe Photoshop CC.
 150 The composite images were prepared in Corel Draw X6.

151 The histological nomenclature used herein is in accordance with Francillion-Vieillot
 152 et al. (1990) and Padian & Lamm (2013).

153 **SYSTEMATIC PALEONTOLOGY**

154 Dinosauria Owen, 1842

155 Theropoda Marsh, 1881

156 Tetanurae Gauthier, 1986

157 Megalosauroidea Fitzinger, 1843

158 Spinosauridae Stromer 1915

159 Spinosaurinae Stromer, 1915

160 gen. et. sp. indet.

161 **Referred material:** LPP-PV-0042, a fragmentary tibia.

162 **Locality and horizon:** Exact geological and geographical provenance is unknown,
 163 but the fossil was collected in the Araripe area, Northeast Brazil. Outcrops of the
 164 Lower Cretaceous Santana Group (Araripe Basin) are worldwide known for
 165 providing well-preserved fossils and are located in the Araripe region. In the Santana
 166 Group, three-dimensional fossils with calcite mineralization are unique to the
 167 Romualdo Formation (Aptian-Albian), whereas Crato Formation (Aptian) is well

known to provide fossils in laminated limestone. The specimen here described is attributed to the Romualdo Formation due to its three-dimensional preservation condition and typical calcite infilling of this unit. It was prepared from concretion by original owner. Also, the lack of crushing suggests that the specimen is not from the Crato Fm.

RESULTS

Morphological description

The fossil consists of partial diaphysis and metaphysis of a left tibia (Fig.2). The shaft becomes wider while the internal density decreases toward the proximal end (Fig.2K). In cross-section, the bone is anteriorly flat or slightly convex near the diaphysis, but it gets distinctively drop-shaped as the shaft expands through the metaphysis. The anterior surface is broad, flat and rugose, suggesting muscular attachment (*tibialis anterior* muscle). The fibular crest is almost straight and only slightly curved proximally towards the posterior side of the specimen. The fibular crest is somewhat reduced and low. Distinct osteosclerosis, or thickening of the cortical bone, can be recognized in distal cross-section.

The preserved total length of the specimen is 150 mm. The proximal-most cross-section has 84 mm in length and 66 mm in width; while the distal-most extremity has a transverse section of 76 X 46 mm. The reconstructed maximum length of the tibia is 60 ± 3 cm, based on *Spinosaurus aegyptiacus* Stromer, 1915 (FSAC-KK 11888; Ibrahim et al., 2014) and *Suchomimus tenerensis* Sereno et al., 1998 (MNN GDF500).

Petrography

191 Electron microscopy was conducted with an Oxford X-act EDS attached to a Fei
 192 Quanta 250 SEM. The analysis of LPP-PV-0042 indicates the abundance of calcium
 193 and absence of silicon in the bone matrix, a condition commonly observed in the
 194 Romualdo Formation fossils (e.g., Aureliano et al., 2014; see Fig.S1, in
 195 Supplementary material). Thin sections also demonstrate calcite infilling of the
 196 vascular spaces typical of this geological unit (Fig.3).

197 **Histological analyses**

198 There are no preparation marks on surface, but there are truncated osteons in one
 199 region of the bone surface. Other regions appear uncompromised. Truncation was
 200 caused either by pre-burial transport, by post-exhumation transport or by preparation.
 201 The medullary cavity of the bone is reduced and filled with spongiosa (Fig.3D). The
 202 cortical thickness ratio is very high ($CT/CaM = 0.097$ *sensu* Mitchell & Sander,
 203 2014; global bone compactness from tomography = 0.872; Fig.2.F, K). The extent
 204 and type of vascularization vary considerably across thin sections. In the posterior
 205 half of the bone, the cortex is predominantly primary in nature with a laminar to
 206 plexiform arrangement of the vascularization in fibrolamellar bone tissue (Fig.3A).
 207 Reticular organization of the vascularization can be found at the posterolateral outer
 208 cortex of the bone (Fig.3B), also in fibrolamellar bone tissue. Curiously, the
 209 anteromedial area of the internal bone wall is composed of tissue not formed in
 210 laminae, and a predominance of longitudinally oriented vascular canals within a
 211 woven matrix with numerous secondary osteons extending outwards to the cortex
 212 surface (Fig.3C). The tissue in this area is probably due to the insertion of the *tibialis*
 213 *anterior* muscle. The transition between the medullary cavity and the cortex is
 214 gradual, due to the presence of many resorption cavities in the inner cortex.
 215 Resorption cavities tend to decrease in density and size towards the external surface

216 of the cortex, and they are more abundant in the anteromedial area of the cross-
217 section. Their outline changes from irregular to rounded or elliptical. In the
218 fibrolamellar bone, primary vascular canals are only partially filled by lamellar bone.
219 In the region with laminar to plexiform fibrolamellar bone, zonation can be observed
220 but not every cycle is clearly distinguishable, however. Between four and eight lines
221 of arrested growth (LAGs) are identified (Fig.3.E). The spacing between LAGs
222 decreases towards the surface of the bone. It is clear that no external fundamental
223 system (EFS) is present despite the surface damage in some regions.

224 Horner & Padian (2004) similarly observed that large *Tyrannosaurus rex* Osborn,
225 1905 specimens presented several LAGs but did not show an outer avascular layer
226 (EFS) that would indicate effective cessation of growth. These concluded that those
227 large bodied, seemingly mature individuals were still growing, although at a lower
228 rate. Similarly, LPP-PV-0042 shows no EFS, but was still growing moderately fast
229 by the time of its death, as suggested by the prevalence of primary tissue at the
230 apposition front.

231 In sum, the increasing organization of vascular canals toward the outer surface in
232 LPP-PV-0042, the presence of some Haversian systems, the decreasing spacing
233 between LAGs and the absence of an EFS observed in the thin sections of the tibia
234 suggest this individual was subadult at the moment of its death. The subadult status is
235 here interpreted as an ontogenetic stage which the individual has not yet reached full
236 sized and sexual maturity (Mitchell & Sander, 2014). Furthermore, by applying the
237 three-front model of Mitchell & Sander (2014) to the posterior area of the bone, the
238 subadult status is reinforced (Fig.3.F). Although this model was developed for
239 sauropod dinosaurs, it can be applied to other dinosaurs and large mammals
240 (Mitchell & Sander 2014). The balance between the Haversian front and the

241 resorption front, both of which are slower than the apposition front is typical for
 242 subadult dinosaurs (Fig.3.F, Mitchell & Sander 2014, fig. 15).

243 **Taphonomy**

244 The specimen, besides fragmentary, also exhibits signs of abrasion. Both features,
 245 however, can be interpreted as modern artifacts, since fractures are obtuse, never
 246 sharp, and the abraded area is porous and brittle (Reif, 1971). It is common for large
 247 Romualdo concretions to break into several pieces and these become loose on the
 248 surface, undergoing erosion (e.g., Kellner et al., 2013). This could have happened
 249 with the referred material. Besides, sedimentological characteristics of the Romualdo
 250 Formation do not support a high energy transportation model.

251 **DISCUSSION**

252 **Taxonomy and comparisons**

253 The anatomical features of LPP-PV-0042 support the presence of a large
 254 Spinosaurinae in the Romualdo Formation, expanding the fossil record of this group
 255 in this geological unit.

256 The transverse diaphysis section of the analyzed specimen differs from most
 257 theropods. In taxa including *Pycnonemosaurus nevesi* Kellner & Campos, 2002,
 258 *Allosaurus fragilis* Marsh, 1887, and *Tyrannosaurus rex* (e.g., Horner & Padian,
 259 2004; Delcourt, 2017; see Fig.5), for example, the tibiae have an oval or subcircular
 260 in mid-shaft cross-section. LPP-PV-0042, however, is anteriorly flat (slightly
 261 convex), similar to what is observed in *S. aegyptiacus*, some megaraptorans
 262 (*Australovenator wintonensis* Hocknull et al., 2009, and *Aerosteon riocoloradensis*
 263 Sereno et al., 2008) and a few other theropods like *Neovenator salerii* Hutt et al.,

1996 and *Chilantaisaurus tashuikouensis* Hu, 1964 (e.g., White et al., 2013; Brusatte et al., 2008; see Table S1).

The sharp-ridged fibular crest present in LPP-PV-0042 is considered an unambiguous synapomorphy of Tetanurae theropods (Holtz, 1994). This feature is not present in abelisaurids and other ceratosaurians as well as in basal theropods, sauropods, and ornithischians (e.g., Holz, 1994; Naish, 1999; Rauhut, 2005; Carrano et al., 2012). The fibular crest of the Romualdo Formation specimen differs from allosauroids (e.g., *Allosaurus fragilis*, *Aerosteon* and *Giganotosaurus carolinii* Coria & Salgado, 1995), as well as from that of the megalosauroids *Torvosaurus gurneyi* Hendrickx & Mateus, 2014, *Piatnitzkysaurus floresi* Bonaparte, 1986, and *Eustreptospondylus oxoniensis* Walker, 1964 (Sadleir et al., 2008), because it is not well developed as in those taxa. In the spinosaurid *S. tenerensis* (MNN GDF500; Sereno et al., 1998), the fibular crest is large and bulbous (see Fig.4.C), differing from LPP-PV-0042, in which it is much smaller. Nevertheless, the reduced fibular crest of LPP-PV-0042 resembles that of *Spinosaurus* (FSAC-KK 11888), which is low and distally broad (Fig.4.B and Fig.S2). The reduced fibular crest might have been associated with the reduction of the knee joint for the vertical limb support as seen in *Spinosaurus* (Ibrahim et al., 2014) and probably also in this Romualdo taxon.

Regarding bone density, the extremely thick-walled cortical bone observed in the referred specimen is a feature currently only shared with *S. aegyptiacus* (Ibrahim et al., 2014) among other non-avian theropods (see further discussion in the next topic).

Although the robust appendicular bone proportion has been considered a typical feature of megalosauroids (Carrano et al., 2012), here we prefer not to take this into consideration for the taxonomic identification of LPP-PV-0042. As shown by Grillo

288 & Delcourt (2017), the apparent robustness of abelisauroid tibiae was misinterpreted
289 based just in a qualitative examination, and there is a strong correlation among the
290 tibia length, tibia shaft anteroposterior diameter and tibia shaft width. Thus, statistical
291 analyses of megalosauroid allometry should be done before including robustness as a
292 taxonomic character.

293 Even though several spinosaurid specimens have been recovered from the Romualdo
294 Formation beds, most of them remain undescribed (Machado & Kellner, 2005;
295 Machado, 2010). No appendicular elements have been formally published so far, and
296 the unpublished specimens (see Machado & Kellner, 2005; Machado et al., 2008;
297 Machado & Kellner, 2009) could not be directly assessed for comparison. A
298 proximal epiphysis of a right tibia attributable to Spinosaurinae described in Elaine
299 Machado's Msc thesis (Machado, 2010; Fig.3.B, MN4819-V). However, this
300 specimen was not useful, because the preserved portion did not overlap with LPP-
301 PV-0042 anatomically because it is missing the fibular crest (contrary to Machado,
302 2010).

303 Lastly, it is worth considering that LPP-PV-0042 differs from crocodylian tibiae in
304 its straight shaft, as well as because it displays an anterolateral sharp ridge, and the
305 cross-section near the diaphysis is not circular (see Snyder, 2007; Woodward et al.,
306 2014). The specimen described here cannot be considered a pterosaur or a bird either,
307 because its shaft lacks the well expressed medullary cavity and extremely thin
308 compact bone typical of these groups (e.g., Kellner et al., 2013; Aureliano et al.,
309 2014). Moreover, even in the largest birds, the fibular crest is not as apparent (i.e.
310 robust) as it is in this specimen (see Naish, 1999).

311 **Bone histology and evolutionary implications for the group**

312 Spinosauridae had a strong relationship to aquatic environments involving several
 313 adaptations in the cranial and axial skeleton (Holtz, 1998; Bertin, 2010; Ibrahim et
 314 al., 2014; Hone & Holtz, 2017). Some of these adaptations include conical teeth with
 315 sub-circular transverse sections; concave anterior portion of the upper jaw; laterally
 316 expanded anterior portion of upper and lower jaws; and elongated snout usually
 317 associated with piscivory (Charig & Milner, 1986; Taylor, 1987; Kellner & Campos,
 318 1996). Other features including size and position of nares and high bone compactness
 319 have also been pointed out as associated with the evolution of a semi-aquatic lifestyle
 320 in this group (Dal Sasso et al., 2005; Ibrahim et al., 2014; Sales & Schultz, 2017).

321 High bone compactness is a feature strongly correlated with semi-aquatic and aquatic
 322 habits in limbed vertebrates (Krilloff et al. 2008; Houssaye, 2009; Quemeneur et al.,
 323 2013; Houssaye et al. 2016). It occurs in different degrees and varies among different
 324 parts of the skeleton (Fish & Stein, 1991; Krilloff et al. 2008; Houssaye, 2009;
 325 Houssaye et al. 2016). Bone ballast is a primary function of this specialization, which
 326 means that dense bones are used for reducing buoyancy by compensating for the air-
 327 filled lung (Taylor, 2000). Similar evolutionary pathways involving independent
 328 acquisition of this character are independently observed in several mammal groups
 329 (Wall, 1983; Madar, 2007; Amson et al., 2014), some birds (Ksepka et al., 2015), and
 330 some marine reptiles (Hugi & Sánchez-Villagra, 2012; Houssaye, 2013). In all of
 331 them, bone compactness clearly increases in taxa adapted to life in shallow water.

332 In theropods, the large open medullary cavity in long bones apparently is a
 333 plesiomorphic feature (Ibrahim et al., 2014). Theropods are known to have ‘hollow
 334 bones’ since the early divergence of the bird branch (Ibrahim et al., 2014). Among
 335 non-avian theropods, semi-aquatic adaptations based on anatomical and
 336 osteohistological characters have previously only been observed in *S. aegyptiacus*

(Ibrahim et al., 2014). However, the high bone compactness value observed in the specimen described here (0.872) is strikingly similar to the one observed in FSAC-KK 11888 (0.968, based on a femur; Ibrahim et al., 2014), suggesting a similar adaptation. Although variations in bone compactness are known between appendicular elements (Fish & Stein, 1991; Kriloff et al. 2008; Houssaye, 2009; Houssaye et al. 2016), this does not invalidate the direct comparison made here, nor does the fact that those two former taxa (FSAC-KK 11888 and LPP-PV-0042) have much higher bone compactness than other theropods and most dinosaurs (see Fig.5).

The osteosclerotic condition in LPP-PV-0042 shows that this feature was already present in Brazilian Spinosaurinae during the early Albian, at least 10 myr before the Moroccan *Spinosaurus* (Cenomanian in age). This observation expands the occurrence of high bone compactness in Spinosaurinae as well as the suggested link to a semi-aquatic lifestyle in this group. Using the principle of phylogenetic bracketing (Bryant & Russell, 1992), osteosclerosis may be present in the entire Spinosaurinae clade, a hypothesis that must be empirically tested by observing more material related to the clade. Baryonychinae (*sensu* Sereno et al., 1998) appears to have a plesiomorphic condition regarding this state, as noted by Ibrahim et al. (2014) based on the analysis of *Suchomimus* (femur global compactness = 0.670), but sampling inside this group also needs to be expanded.

Finally, the evolution of large sizes (10-15 m length) in Spinosaurinae may also have been reinforced by the evolution of semi-aquatic preferences, which should be tested elsewhere using biomechanical and statistical analyses and it is beyond the scope of this paper.

360 **Comments on the Araripe Basin Spinosaurinae**

Figure 6.1.1 summarizes all Spinosauridae specimens recovered from the Romualdo Formation to date. A notable feature is the variation in size among sampled individuals. The total length (TL) of the reconstruction of LPP-PV-0042 is estimated to be 10 ± 3 m, based on the TL of *Spinosaurus* (~15 m, Ibrahim et al. 2014) and *Suchomimus* (~11 m, Sereno et al. 1998). The new specimen represented a much larger individual than MN4819-V (TL ~5.9 m, Machado et al., 2008), which can be easily observed by comparing both tibiae. LPP-PV-0042 was also probably larger than *I. challengerii* holotype (TL ~6.5 m, on Sales & Schultz, 2017; despite Paul, 2010, and Holz, 2011, proposition of 7.5-8 m TL) at the time of death and of roughly comparable size to the *A. limai* type specimen (TL ~8.3 m, from Sales & Schultz, 2017, scaling) (Fig.6.1.2).

As already mentioned, histological evidence indicates that LPP-PV-0042 was a subadult at the time of death. Thus, the specimen suggests that the Romualdo Formation Spinosaurinae could have reached larger sizes than previously thought. It is not possible to estimate how much the referred individual could still have grown, since the ontogeny and growth dynamics of spinosaurs are currently unknown. However, histological analyses of other Araripe specimens have the potential to clarify Spinosauridae ontogeny parameters and also to shed light on controversial aspects in Brazilian Spinosaurinae taxonomy.

Sales and Schultz (2017) suggested that Brazilian Spinosauridae apparently demonstrate several intermediate conditions between Baryonychinae and Spinosaurinae. The link between this information and the osteohistological condition described here add relevance to the study of the Araripe Basin forms. Both anatomical and osteohistological adaptations favorable to the interaction with the aquatic environment may have extended amphibious habits in Romualdo Formation

386 spinosaurs. This has great evolutionary relevance and means local and chrono-
387 correlated regional ecological contingencies (in both northeast Brazil and northwest
388 Africa), which may have favored this evolutionary pathway, need to be further
389 explored.

390 The potential of the Araripe Basin to provide more Spinosaurinae remains is great.
391 Almost yearly, new exceptional vertebrate and invertebrate fossils are discovered and
392 described from the basin (e.g., Kellner et al., 2013, Bantim et al., 2014, Pinheiro et
393 al., 2014, Maldanis et al., 2016, Freitas et al., 2016). Including a possible
394 Megalosauroida with affinities to Spinosauridae from the Ipubi Formation (which
395 underlies the Romualdo Formation) which is still undescribed (see Silva et al., 2013).
396 Controlled excavations carried out in recent years (Fara et al., 2005; Vila Nova et al.,
397 2011; Lima, 2013) probably will lead to important discoveries due proper
398 stratigraphic control.

399 Unfortunately all known Spinosaurinae material of the Araripe Basin came from
400 uncontrolled collecting, the primary purpose of which was (and still is) illegal trade.
401 Illegal because the trade of Brazilian fossils is prohibited by federal laws. Most of the
402 specimens mentioned were part of private collections and were fortuitously donated,
403 as is also the case of the specimen herein described. Illegal trade is still a problem in
404 the Araripe region, and the negative implications related to this activity (e.g., loss of
405 field data, alteration of specimens, loss to inaccessible private collections, etc.) need
406 to be strongly curtailed as they delay the advancement of paleontological knowledge.

407 The Romualdo Formation, in particular, offers a unique opportunity for the study of
408 Spinosaurinae paleobiology and paleoecology. Unlike other deposits where these
409 dinosaurs occur, the differential preservation of Santana Group fossils allows access

410 to many details about the ecosystem in which these dinosaurs lived, including
411 improved knowledge about the trophic web. In addition, the potential for soft tissue
412 preservation is great, which raises the possibility of unveiling rare details about the
413 biology, ecology and evolution of this fossil group.

414 **Romualdo Formation paleoecological inferences**

415 The articulated skull with mandibles of a Spinosaurinae found in the Romualdo
416 Formation (Kellner & Campos, 1996; Sues et al., 2002) suggests an autochthonous or
417 parautochthonous burial (see Voorhies, 1969). A floating carcass model, as already
418 suggested for some tetrapods of the Santana Group (Elgin and Frey, 2012), is not
419 plausible in this case. First, because the jaws were found tightly articulated to the
420 skull, which is unusual for floating carcasses (Liebig et al., 2003). Second, because
421 the osteosclerotic histological condition of the skeleton would cause the carcass to
422 rapidly sink. This leads us to conclude that most probably these organisms were
423 buried in their living environment and must be interpreted as part of the local
424 ecosystem.

425 The Romualdo Formation was deposited in a coastal lagoon influenced by
426 transgressive-regressive marine cycles (Custódio et al., 2017) and variable freshwater
427 influence (Antonietto et al., 2012). The terrestrial environment around the Romualdo
428 Formation is interpreted as arid to semi-arid, which is supported by the occurrence of
429 fossil plants with xeromorphic adaptations (Lima, 2013). The absence of herbivorous
430 dinosaurs in this geological context led Naish et al. (2004) to infer a possible low
431 productivity for the surrounding area, which probably would not sustain a resident
432 mega-herbivore fauna. Therefore, the main source of food for local large tetrapod
433 carnivores would have been the abundant aquatic fauna of the Romualdo

434 paleolagoon (e.g., Russell, 1996; Läng et al., 2013). Therefore, the Romualdo
435 Formation Spinosaurinae most likely have exploited the local diversity of fishes and
436 other aquatic organisms (see Maisey, 1991; Wenz et al., 1993).

437 This would imply in a shortening of the trophic web, similar to what was proposed
438 by Benyoucef et al. (2015), for the Grès Rouges Formation, Algeria. Figure 8 shows
439 an inferred trophic web for the Romualdo Formation.

440 The presence of several piscivorous organisms in the same community,
441 (crocodylomorphs, large fishes and various pterosaurs), could hypothetically have
442 caused overexploitation of the food resource, leading to high levels of competition
443 (see Begon et al., 2009). Nonetheless, the large size of the Spinosaurinae as well as
444 their unique physiological and morphological adaptations must have allowed them to
445 explore a different range of food items (see Cuff and Rayfield, 2013). Despite the
446 possible overlap of fundamental niches of local carnivores, the way the resources
447 were exploited (i.e. realized niche) must have differed significantly. Smaller-sized
448 species, for example, would not have been able to exploit larger food items.

449 Moreover, they may have explored different areas or even different depths of the
450 paleolagoon. The absence of large crocodylomorphs and other large aquatic
451 predators that could compete directly with spinosaurs in the Romualdo Formation
452 paleoecosystem must have facilitated the occupation of this niche by these dinosaurs
453 (e.g., Holtz, 1998; Amiot et al., 2010a; Hone and Holtz, 2017).

454 A sequence of cervical vertebrae of a large pterosaur from the Romualdo Formation
455 associated with a spinosaur tooth described by Buffetaut et al. (2004), indicate a
456 direct case of interaction between those organisms, and a possible case of
457 consumption. Thus, even with a diet interpreted mainly as piscivorous, predation on
458 pterosaurs could occasionally have occurred (see also Kellner, 2004). Beyond that,

small to medium-sized terrestrial dinosaurs, juveniles of the same species, crocodyliforms (both semi-aquatic and terrestrial), and turtles could also have been preyed on, placing Spinosaurinae as the top predators of the local environment. Figure 8 shows an artistic reconstruction of the Romualdo Formation paleoenvironment highlighting the semi-aquatic habit inferred for the local Spinosaurinae.

Coexistence of other large theropod groups such carcharodontosaurids and abelisaurids in sympatry with spinosaurs is known from other fossil deposits (Benton et al., 2000; Martill, 2007; Sereno & Brusatte, 2008; Amiot et al., 2010b; Ibrahim et al., 2014). However, no other large theropod has been found in the Romualdo Formation apart from spinosaurids so far, even after more than 40 years of geological exploration of the area. The preference for a coastal environment in Spinosauridae (Benyoucef et al., 2015; Sales et al., 2016) and the semi-aquatic lifestyle observed in the Cenomanian *Spinosaurus* (Ibrahim et al., 2014) probably occurred due to the clade's strong link to a piscivorous diet, and likely was reinforced by the presence of other large sympatric theropods in some contexts (see Amiot et al., 2010a; Benyoucef et al., 2015 and Sales et al., 2016 discussion). Since we do not yet have evidence of the later in the Araripe context, it is not possible to extend this explanatory hypothesis to the Brazilian paleoscenario.

CONCLUSION

The Romualdo Formation specimen LPP-PV-0042 comprises a fragmentary tibia with a reduced fibular crest and osteosclerotic histology previously only observed in *S. aegyptiacus*, supporting that this unique feature was already present in Brazilian

482 Spinosaurinae (basal Spinosaurinae) during the Aptian-Albian time, at least 10 myr
483 before the Moroccan *Spinosaurus*.

484 Histological analyses suggest LPP-PV-0042 was a young, fast growing subadult and
485 also that the bone microstructure varies a lot across the cross-section, probably due to
486 areas of muscle insertion. The latter observation suggests that caution is needed when
487 describing bone histology of dinosaurs, since only one slice from the shaft is not
488 always representative of the entire histology of the bone.

489 Furthermore, the current specimen represents one of the largest spinosaurs from this
490 unit so far (~10 m in reconstructed TL). It was larger than the *Irritator* holotype and
491 possibly larger than *Angaturama* holotype as well. Considering the subadult status
492 inferred from its histology, the referred individual would have grown even larger.

493 The Romualdo paleoenvironment could support large predators with semi-aquatic
494 habits due to its high productivity and diversity of aquatic species as an ecotone.
495 Spinosaurinae from Romualdo Formation probable occupied the position of apex
496 predators.

497 Thus, the skeletal element LPP-PV-0042 from the Romualdo Formation, although
498 fragmentary, has provided much information about Brazilian Spinosaurinae
499 paleobiology and ecology. Moreover, it gives new insight into the evolution of semi-
500 aquatic adaptations in this group, revealing the need to investigate other taxa within
501 the clade and expand the search for more spinosaur fossils.

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893 FIGURE CAPTIONS

894 **Figure 1.** On the left, detail of the Araripe Basin with the Santana Group and the
 895 main fossil localities of this unit highlighted (modified from Neumann & Cabrera,
 896 1999). On the right, South American context with geographical location of all
 897 geological units that yielded Spinosauridae fossils to date: **A**, Cenomanian Alcântara
 898 Formation (São Luís-Grajaú Basin) in coastal Maranhão state; **B**, Aptian-Albian
 899 Romualdo Formation (Araripe Basin) on the outback in the frontier between Ceará,
 900 Pernambuco and Piauí states; **C**, Berriasian-Valanginian Feliz Deserto Formation
 901 (Sergipe-Alagoas Basin) in eastern Sergipe state, all Brazil.

902 **Figure 2.** LPP-PV-0042, a fragmentary tibia of Spinosaurinae from the Lower
 903 Cretaceous of Brazil. **A, G**, lateral; **B, H**, posterior; **C, I**, medial; **D, J**, anterior; **E**,

904 proximal; and **F**, distal views. **G-J** represent the three-dimensional model from CT-
 905 scan data. **K**, reconstructed 3D model from CT-Scan with color bar highlighting
 906 distinct bone densities in posterior view with longitudinal slices in 1, 2, and 3.
 907 Abbreviation: **fcr**, fibular crest. Scale bar = 10 cm.

908 **Figure 3.** Transverse thin section and bone histology of LPP-PV-0042. **A**, External
 909 cortex from the posteromedial part of the bone showing typical fibro-lamellar bone
 910 with a plexiform arrangement of the vascularization. **B**, reticular organization of the
 911 vascularization and two growth marks in the outermost layer of cortex in the
 912 posterolateral area of cross-section. **C**, external cortex from the medial part of the
 913 bone showing secondary remodeling with Haversian channels and the absence of an
 914 EFS. **D**, polished transverse section showing the thick cortex (CT/CaM = 0.097;
 915 *sensu* Mitchell & Sander, 2014). **E**, external cortex showing the decreasing spacing
 916 of four (possibly eight) LAGs (arrows). **F**, a three-front model from E, indicating a
 917 subadult ontogenetic status to the specimen. Photographs taken under polarized light
 918 in A, B, C and E. A filter was applied in C to increase birefringence in 560λ .
 919 Abbreviations: **AF**, apposition front; **Ant**, anterior; **cb**, cancelous bone; **hb**,
 920 Haversian bone; **HSF**, Haversian substitution front; **Lat**, lateral; **Med**, medial; **pb**, p
 921 bone; **Pos**, posterior; **RF**, resorption front. Scale bar in A = 1 cm, in B-E = 1 mm.

922 **Figure 4.** Comparison of the proximal ends of left theropod tibiae in lateral view. **A**,
 923 Spinosaurinae indet. LPP-PV-0042. The blue solid line is the epiphysis
 924 reconstruction based on Spinosaurinae indet. MN4819-V (from Machado, 2010). The
 925 pink dashed line is the epiphysis reconstruction based on *Spinosaurus*. In green,
 926 epiphysis reconstruction based on *Suchomimus*. **B**, *Spinosaurus aegyptiacus* (FSAC-
 927 KK 11888; reversed) (Ibrahim et al., 2014). **C**, *Suchomimus tenerensis* (MNN
 928 GDF500) (Serenio et al., 1998). **D**, *Torvosaurus gurneyi* (ML 430) (Hendrickx &

929 Mateus, 2016). **E**, *Eustreptospondylus oxoniensis* (OUMNHJ.13558) (Sadleir et al.,
 930 2008). **F**, *Megalosaurus bucklandii* Mantel, 1827 (OUMNHJ.13505) (Carrano et al.,
 931 2012). **G**, *Condorraptor currumili* Rauhut, 2005 (MPEF-PV 1672). **H**,
 932 *Dilophosaurus* Welles, 1970 (UCMP V 4214) (Rauhut, 2005). **I**, *Piatnitzkysaurus*
 933 (PVL 4073) (Rauhut, 2005). **J**, *Australovenator* (AODF 604) (White et al., 2013). **K**,
 934 *Ceratosaurus* Marsh 1884 (UMNH VP 5278) (Rauhut, 2005). **L**, *Pycnonemosaurus*
 935 (DGM 8D9-R) (Delcourt, 2017). Abbreviations: **cc**, cnemial crest; **fer**, fibular crest;
 936 **lc**, lateral condyle; **lf**, lateral fossa. Scale bar = 10 cm.

937 **Figure 5.** Different tibial cross-sections in non-avian dinosaurs and *Alligator*. The
 938 reported values are global compactness obtained with **Bone Profiler**. Specimen
 939 numbers and references are in Tables S2-S3 (Supplementary material). Cross-
 940 sections not to scale.

941 **Figure 6. 1.** Spinosaurinae remains currently recovered from the Romualdo
 942 Formation, Araripe Basin, Brazil. Not to scale. **A**, USP GP/2T-5, holotype of *A.*
 943 *limai* (Kellner & Campos, 1996), fragmentary anterior tip of skull. **B**, SMNS 58022,
 944 holotype of *I. challengerii* (Sues et al., 2002) (originally mistakenly identified as a
 945 maniraptor by Martill et al., 1996), partial posterior portion of skull and mandible. **C**,
 946 MN 4743-V, incomplete indeterminate spinosaur sacral and caudal vertebrae series
 947 (S3, S4, S5, C1, C2, C3, C4, C4, C6) (Bittencourt & Kellner, 2004). **D**, MN 7021-V,
 948 indeterminate spinosaur rib (Machado & Kellner, 2007). **E**, MN 4819-V, incomplete
 949 indeterminate spinosaur pubis, pelvis, dorsal, sacral and caudal vertebrae (d, S1, S2,
 950 S3, S4, S5, C1), incomplete indeterminate spinosaur right manus, fragmentary right
 951 tibia and femur (Machado & Kellner, 2008; Machado & Kellner, 2009; Machado,
 952 2010). **F**, LPP-PV-0042, Spinosaurinae indet. metaphysis of left tibia described in
 953 this work. Skeletal reconstruction made by Tito Aureliano, based on the work by

954 Scott Hartman and Marcos Sales. **2.**, Romualdo Spinosaurinae specimens to scale. **A**,
 955 *Angaturama* USP GP/2T (~8.3 m, on the reconstruction by Sales & Schultz, 2017).
 956 **B**, *Irritator* SMNS 58022 (~6.5 m, from the reconstruction by Sales & Schultz,
 957 2017). **C**, Spinosaurinae indet. MN4819-V (~5.9 m; Machado et al., 2008). **D**,
 958 Spinosaurinae indet. LPP-PV-0042 (~10 m; this work). Scale bar in 7.2 is 1 m.

959 **Figure 7.** Inferred food web of the Aptian-Albian Romualdo Formation, Northeast
 960 Brazil. Vertebrate silhouettes are highlighted in black. Trophic relations are
 961 represented by arrows, of which solid bold red represent ecological interactions with
 962 direct fossil evidence from Romualdo Formation; solid black indicate putative
 963 trophic interactions with general theoretical support; and dashed grey represent weak
 964 or uncertain but plausible trophic links. **1**, Spinosaurinae; **2**, small to medium sized
 965 terrestrial theropods; **3**, pterosaurs; **4**, semi-aquatic crocodyliforms; **5**, terrestrial
 966 omnivorous crocodyliforms; **6**, semi-aquatic chelonians; **7**, large fishes; **8**, small
 967 fishes; **9**, plants; **10**, macroinvertebrates; **11**, plankton. See Text S1 in the
 968 Supplementary material for list of references. Spinosaurinae silhouette by Tito
 969 Aureliano. Other silhouettes from Phylopic (<http://phylopic.org/>), courtesy of
 970 Almandine (vectorized by T. Michael Keesey), FunkMonk (adapted), Hans
 971 Hillewaert, John Conway, Melissa Broussard, Nobu Tamura (vectorized by T.
 972 Michael Keesey), Olegivvit, Robert Gay and Sergio A. Muñoz-Gómez. See
 973 Supplementary material (Text S1) for references and further information.

974 **Figure 8.** Reconstruction of a Spinosaurinae at the Aptian-Albian lagunar/shallow
 975 marine environment of the Romualdo Formation, Araripe Basin, NE Brazil.
 976 Illustration by Julio Lacerda.

977

ACCEPTED MANUSCRIPT

Highlights

Spinosaur histology is here described for the first time.

Extreme bone compactness (osteosclerosis) was present in Brazilian Spinosaurinae.

These modifications appeared millions of years before the Moroccan *Spinosaurus*.

One of the largest spinosaur specimens from the Early Cretaceous of South America.