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Micro-tomographic analysis of a scorpion fossil from the Aptian Crato Formation of North-Eastern Brazil

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17 Abstract

18

19 A scorpion fossil (*Protoischnurus axelrodorum*) from the Lower Cretaceous Crato Formation  
20 (Aptian, northeastern Brazil) is analyzed with computed microtomography. Its taphonomy and  
21 morphology is described and illustrated, a revised diagnosis of the genus is presented, and the  
22 phylogenetic relationships of this taxon are discussed. *Protoischnurus* belongs in the  
23 Scorpionoidea and is probably an early member of the Iurida crown group, possibly representing  
24 a stem hormurid.

25

26 Keywords: *Protoischnurus*, scorpion, Cretaceous, Brazil, CT-scan, Araripe Basin

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## 32 1. Introduction

33

34 Mesozoic scorpion fossils are exceptionally rare. The first Cretaceous scorpion ever  
35 described was *Araripescorpius ligabuei* Campos, 1986, from the Lower Cretaceous Crato  
36 Formation (Aptian, Araripe Basin, northeastern Brazil). 15 years later, a second taxon from the  
37 same horizon was described, as *Protoischnurus axelrodorum* Carvalho and Lourenço, 2001, and  
38 was placed in a new family (Protoischnuridae Carvalho and Lourenço, 2001). To date, these two  
39 taxa are still the only Cretaceous scorpions in lithified matrix to have been described, although  
40 several taxa preserved in Cretaceous amber have been described, from Lebanon, France, and  
41 Myanmar (Lourenço, 2001, 2002, 2003, 2012, 2016, 2018; Lourenço and Beigel, 2011;  
42 Lourenço and Velten, 2021; Xuan et al., 2022).

43 This is the first Cretaceous scorpion to have been investigated by computed  
44 microtomography, and is only the second scorpion fossil ever investigated this way (the first was  
45 a Carboniferous fossil in sideritic matrix; Legg et al., 2012). It is also the first scorpion fossil in  
46 limestone matrix to be analyzed microtomographically, highlighting the usefulness of this  
47 procedure for study of small fossil arthropods in carbonate matrix.

48 Cretaceous scorpions are important because of their close evolutionary relationships to  
49 modern forms. In the case of *Araripescorpius* and *Protoschinurus*, Carvalho and Lourenço  
50 (2001) observed that these taxa “could be classified together with some extant families within the  
51 Superfamily Scorpionoidea”. Subsequently, Baptista et al. (2006) considered that  
52 *Protoischnurus* is a stem scorpionoid and that *Araripescorpius* is a stem chactoid, both contained  
53 within the Parvorder Iurida Soleglad and Fet, 2003a. Menon (2007) assigned *Protoischnurus* to  
54 the scorpionoid family Hemiscorpiidae Pocock, 1893, and *Araripescorpius* to the chactoid

55 family Chactidae Pocock, 1893; i.e., among crown (rather than stem) scorpionoids and chactoids.  
56 However, the criteria currently used to assign fossil scorpions to groups, living or extinct, are  
57 mostly unsatisfactory, and an assessment of their interrelationships will only become possible  
58 within an acceptable theory of relationships of extant scorpions.

59 *Protoischnurus axelrodorum* Carvalho and Lourenço, 2001 was utilized to calibrate the  
60 minimum age for the Scorpiones node in the arthropod tree of life (112.6 Ma; Wolfe et al.,  
61 2016).

62

## 63 **2. Geological context of the material**

64

65 The Araripe Basin is a fault-bound interior sedimentary basin, located in the border area  
66 of Piauí, Ceará and Pernambuco States, in North-eastern Brazil (Fig. 1). The basin formed during  
67 the Mesozoic break up of Western Gondwana, which involved reactivation of Precambrian fault  
68 systems that generated many intracontinental basins within pull-apart grabens, of which Araripe  
69 is the widest (Matos, 1992; Carvalho, 2000). At a geologically later time, the Araripe graben was  
70 inverted to become a topographically high-standing horst (Marques et al., 2014). Within the  
71 Araripe Basin two sub-basins are recognized; the Feira Nova sub-basin in the East and the Crato  
72 sub-basin in the west (Ponte and Ponte Filho, 1996), separated by a structural high, the Dom  
73 Leme Horst (Assine et al., 2014; Scherer et al., 2014). The Cretaceous lithostratigraphic units  
74 within the Araripe Basin include both clastic and chemical deposits formed successively under  
75 changing fluvial, deltaic, lacustrine and marine conditions (Beurlen 1962; Ponte and Appi, 1990;  
76 Assine, 2007; Rios-Netto et al., 2012a, 2012b; Martill and Bechly, 2007; Varejão et al., 2021a,  
77 2021b; Maisey, 2000; Arai, 2014; Fürsich et al., 2019).

78           Within this basin, the Crato Formation (Lower Cretaceous; Aptian, Santana Group; Arai,  
79 2014; Coimbra and Freire, 2021) is represented by up to 70 meters thickness of laminated  
80 limestones, shales and fine sandstones that were deposited during arid climatic conditions in  
81 continental and lagoonal environments (Catto et al., 2016; Guerra-Sommer et al., 2021), with  
82 evidence of cyclic deposition under orbital influence (Gomes et al., 2021). The formation is  
83 mined extensively for commercial purposes in the vicinity of Santana do Cariri and Nova Olinda  
84 in Ceará State, and the majority of fossils reported from the Crato Formation are found in the  
85 laminated carbonates, including an impressive assemblage of continental and aquatic fossils  
86 (fungi, plants, mollusks, arthropods, fishes, amphibians, reptiles and birds; Maisey, 1991; Maisey  
87 and Carvalho, 1995; Martill et al., 2007; Barling et al., 2015; Carvalho et al., 2015a, 2015b;  
88 2019; Ribeiro et al., 2021), as well as dinosaur tracks (Carvalho et al., 2021).

89           The taxonomic diversity and exquisite preservation of these fossils allows the Crato  
90 Formation to be considered a conservation and concentration *Lagerstätte* (Crato *Lagerstätte*). It  
91 has been suggested that the exceptional preservation of fossils within laminated carbonates of  
92 this unit resulted from organic mediation of microorganisms (especially bacteria) immersed in a  
93 polysaccharide matrix within microbial mats (Carvalho et al., 2013, 2017; Iniesto et al., 2015,  
94 2016, 2017, 2018, 2021; Varejão et al., 2019); such mediation may have played a fundamental  
95 role in the creation of a microbial sarcophagus and mineralization of the organic remains (Dias  
96 and Carvalho, 2020, 2022). Scorpion fossils have been recovered from just below the middle of  
97 the laminated carbonate sequence (Fig. 1).

98

### 99 **3. Material and Methods**

100

101 We analyzed one almost complete individual of *Protoischnurus axelrodorum* Carvalho  
102 and Lourenço, 2001, consisting of the part and counterpart (Figs. 2, 3). The material is stored in  
103 the Macrofossil Collection, Geology Department, Institute of Geosciences, University Federal do  
104 Rio de Janeiro (UFRJ-DG), Brazil, Catalog number UFRJ-DG 101-Ac (Arachnida), part (UFRJ-  
105 DG 101-Ac-a) and counterpart (UFRJ-DG 101-Ac-b). This material is from the Pedra Branca  
106 Mine (7°7'28" S; 39°42'5" W), Municipality of Nova Olinda (CE, Brazil) found in fossil-rich  
107 Aptian limestones of the Crato Formation.

108 Like many fossil insects from the Crato Formation (Barling et al., 2015), the scorpion  
109 fossil is preserved as an orange to brown amorphous material, probably representing goethite  
110 (limonite) replacement of the original cuticle. The main body of the fossil has split horizontally,  
111 exposing the internal surfaces of the carapace and mesosoma in UFRJ-DG 101-Ac-a, and the  
112 internal surface of the sternal region in the counterpart. The metasomal segments are contained  
113 almost completely in UFRJ-DG 101-Ac-a, with only an external mold of the metasoma ventral  
114 surface in the counterpart. The external features of the fossil are largely 'face-down' in matrix  
115 and most cannot be observed directly, even under a microscope. The pedipalp chelae are both  
116 well preserved (Figs. 2, 3). The legs are also well preserved but were fractured through the  
117 patellae when the rock matrix was opened, so some parts of these appendages are preserved on  
118 the part and others on the counterpart (Fig. 2). The complete appendages are shown in the  
119 merged reconstitution of the part and counterpart (Fig. 3). The coxapophyses of the first paired  
120 legs are incomplete, but those of the second pair are almost complete. The sternites are better  
121 preserved on the left side and towards the midline of the fossil; the right parts of these elements  
122 are mostly missing, exposing the inner surfaces of the tergites in ventral view (Fig. 3B). All five  
123 metasomal segments and the telson with its vesicle and aculeus are preserved, but the dorsal

124 surfaces of the metasomal segments in the study specimen have caved in and are cracked  
125 longitudinally (Fig. 3A). The telson is very well preserved but is completely enclosed by matrix  
126 and cannot be seen in the fossil, only in the scan (Figs. 2,3).

127 *Taphonomy.* Based on taphonomic observations of scorpions outlined by McCoy and Brandt  
128 (2009), the studied specimen almost certainly represents the corpse of an individual which was  
129 carried into a lake either before or soon after death, rather than a molted carapace. According to  
130 McCoy and Brandt (2009), features associated with death include: chelicerae retracted, straight  
131 body line in dorsal view, metasoma extended straight back, pedipalps pulled in toward the  
132 prosoma, and legs folded against the prosoma and mesosoma. By contrast, features associated  
133 with molts following ecdysis include: extended chelicerae posture, curved body line and curved  
134 metasoma, pedipalps pulled well back from the prosoma in an extended position, and legs  
135 splayed. Additionally, there is often a gap below the carapace by which the scorpion exits the old  
136 exoskeleton (Gaban and Farley, 2002). In UFRJ-DG 101-Ac, the chelicerae are retracted, the  
137 body and metasoma are both straight (although the mesosoma and metasoma are slightly angled  
138 with respect to each other), the pedipalps are pulled in against the prosoma, the legs are pulled in  
139 against the prosoma and mesosoma (especially the last pair), and there is no evidence that the  
140 carapace has been displaced by ecdysis.

141 *Microtomography.* The specimen was subjected to computed microtomography (CT) at the  
142 Nuclear Instrumentation Laboratory in the Department of Nuclear Engineering (COPPE), at the  
143 Universidade Federal do Rio de Janeiro (UFRJ). Prior to scanning, the fossil was trimmed using  
144 a conventional rock saw to reduce the amount of matrix, and the part and counterpart were  
145 scanned separately to improve scan quality. Both pieces were scanned using identical parameters  
146 (180 kV, resolution 0.5  $\mu\text{m}$ ). The scans were processed in Mimics© Version 18.0 x64, on a



147 Dell© Precision 7710 Mobile Workstation. Separate reconstitutions of the part and counterpart  
148 pieces were created, as well as a merged reconstitution of the part and counterpart scans, which  
149 were aligned using Meshlab© Version 2022.02. Additionally, the carapace and elements of the  
150 pedipalps were reconstituted separately. Scan images were captured in Meshlab© Version  
151 2022.02, using the program's orthographic view option, and illustrations were prepared in Adobe  
152 Photoshop© Elements Version 10.

153 *Photography and measurement.* The specimen was also photographed under natural light with a  
154 Nikon D600 digital camera with an AF Micro-Nikkor 60mm F/2.8D lens. Measurements given  
155 in the paper were determined from the specimen by the AxioVision 4.8.2.0 software, using a  
156 Zeiss Stereo Discovery.V20 binocular microscope with a connected AxioCam MRc 5 digital  
157 camera, at the Laboratory of Paleontological Studies in the Department of Geology (UFRJ).

158 *Morphological terminology* follows Hjelle (1990), Prendini (2000), Sissom (1990), and Stahnke  
159 (1970); trichobothrial patterns follow Vachon (1974).

160

161

#### 162 **4. Systematic Paleontology**

163

164 Order Scorpiones Koch, 1837

165 Parvorder Iurida Söglad and Fet, 2003

166 Superfamily Scorpionoidea Latreille, 1802

167 Family Protoischnuridae Carvalho and Lourenço, 2001

168

169 Genus *Protoischnurus* Carvalho and Lourenço, 2001

170 Type species: *Protoischnurus axelrodorum* Carvalho and Lourenço, 2001 (by original  
171 designation).

172  
173 *Emended diagnosis* (based mostly on the new specimen UFRJ-DG 101-Ac): scorpion of medium  
174 size; robust pedipalp with the chela, patella and femur bounded by thick, prominent carinae  
175 ornamented with several tubercles; chela with two robust tubercles proximally, adjacent to  
176 patella; carinae of pedipalp femur ornamented with thick tubercles; chela fixed and free finger  
177 each with a single row of denticles; tibial spurs absent from legs; trichobothrial pattern of basic  
178 type “C” sensu Vachon (1974); spiracles slit-like; pectines moderately large, with 14-15 teeth;  
179 sublateral carinae of tergite VII extend obliquely downward posteriorly to meet the anterolateral  
180 border of metasoma segment I; no subaculear tooth on telson.

181

182 ***Protoischnurus axelrodorum* Carvalho and Lourenço, 2001**

183 Zoobank LSID urn:lsid:zoobank.org:pub:AD77F5C2-1BF6-496D-8E8D-8859B6E67D39

184

185 *Holotype*. MN-7601-I (a-b), Museu Nacional, Rio de Janeiro, Brazil; Lower Cretaceous, Aptian,  
186 Crato Formation, Araripe Basin, Brazil. NOTE: the holotype and one paratype specimen (MN-  
187 7600-I) are known to have withstood the fire which devastated the National Museum in 2018.  
188 However, both specimens were damaged and discolored by intense heat, and it is not known  
189 whether diagnostic morphological features described in Carvalho and Lourenço (2001) are still  
190 evident in the holotype specimen.

191 *Emended Diagnosis*. As for genus.

192 *Referred Material*. UFRJ-DG 101-Ac-a and -b, from the Macrofossil Collection, Department of

193 Geology, Universidade Federal do Rio de Janeiro; a complete adult individual of *Protoischnurus*  
194 *axelrodorum* Carvalho and Lourenço, 2001.

195 *Occurrence.* Early Cretaceous (Aptian) limestones of the Crato Formation, Pedra Branca Mine  
196 (7°7'28" S; 39°42'5" W), near Nova Olinda, Ceará State, northeastern Brazil.

197

198 *Systematic Note.* In the original description of *Protoischnurus axelrodorum* Carvalho and  
199 Lourenço, 2001, the diagnosis of the genus was identical to that of the family Protoischnuridae.  
200 Subsequently, other Cretaceous scorpion genera have been assigned to this family (e.g.,  
201 *Cretaceousormiops knodeli* Lourenço, 2018; *Cretaceousopisthacanthus smeeli* Lourenço and  
202 Velten, 2021), although these new genera differ morphologically from *Protoischnurus* (discussed  
203 below). The revised diagnosis of the genus presented here attempts to distinguish *Protoischnurus*  
204 from those forms. The holotype specimen (MN-7601-I) was unavailable for comparison, but was  
205 previously studied by the senior author for the original description.

206 *Description.* The dimensions of UFRJ-DG 101-Ac are as follows: total body length 36.35  
207 mm; prosoma length 5.2 mm, prosoma anterior width 5.08 mm, posterior width 6.29 mm;  
208 mesosoma length 14.6 mm; metasoma length 15.04 mm.

209 Carapace: The dorsal surface of the carapace is smooth, with total length of 5.2 mm, anterior  
210 width 5.08 mm, and posterior width of 6.29 mm (Fig. 4A, B). The carapace is strongly  
211 emarginated anteriorly and has paired notches anterolaterally, presumably for the lateral eyes  
212 (which are not preserved in the study specimen). Paired openings for the median eyes are located  
213 slightly anterior to the center of the carapace. A suturiform median longitudinal furrow is  
214 present, with anterior and posterior bifurcations (arrowed in Fig. 4B). Many Recent scorpionoid  
215 genera possess a similar suturiform median longitudinal furrow with Y-shaped branches at either

216 end (Stockwell, 1989, Prendini, 2000). In *Protoischnurus*, the anterior longitudinal furrow  
217 extends posteriorly between the median eyes and then divides, forming an inverted Y-shape that  
218 terminates before reaching the posterior margin of the carapace. A wide, somewhat deep  
219 posterior longitudinal furrow is also present between the Y-shaped posterior branches, becoming  
220 broader posteriorly to form paired posterior marginal furrows like those found in many recent  
221 scorpions. A shallow paired furrow extends from the anterolateral border of each median eye  
222 towards a pair of large symmetrical openings located approximately half-way between the  
223 median and lateral eyes. These openings may represent scan or image processing artifacts in thin  
224 or poorly mineralized regions of the carapace.

225 Mesosomal tergites: As in scorpions generally, seven tergites are present (Fig. 3A). These  
226 increase in length posteriorly, and the last one (VII) is tapered posteriorly, with rounded lateral  
227 margins. All the tergites have sublateral and lateral carinae but lack a median carina. The lateral  
228 carina on tergite VII becomes obsolete posteriorly, and the sublateral carina slopes downward  
229 posteriorly, ending below the level of the first metasomal segment. Medial to the sublateral  
230 carinae, on the posterior part of mesosoma segment VII is a pair of short, posteriorly convergent  
231 dorsolateral carinae, which meet the U-shaped anterior margin of metasoma sternite I and  
232 contribute to the mesosoma/metasoma articulation laterally (arrowed in Fig. 3A).

233 Sternum, genital operculum, pectines, and sternites (Figs. 3B, 5): The sternum is pentagonal,  
234 weakly concave laterally, and its posterior width is equal to or slightly wider than its anterior  
235 width (Fig. 5), not greatly widened as in some modern bothriurids (in which the sternum can be  
236 considerably wider than long; Soleglad and Fet, 2003b). Its posterior margin is incomplete in the  
237 study specimen, but it is possible that a posterior emargination was originally present. Presence  
238 of a posterior emargination on the sternum has been considered a synapomorphy of the Iurida

239 (Soleglad and Fet, 2003a,b). The genital operculum is wider than long, with a slightly elevated  
240 anterior margin. A gap between the left and right parts of the genital operculum in the study  
241 specimen may represent a posterior emargination. A narrow median longitudinal carina is  
242 present on the anterior sternites, becoming indistinct on sternite V and absent on sternites VI and  
243 VII (Fig. 3B). This unusual feature is not present in the holotype of *Protoischnurus axelrodorum*,  
244 which, like some modern scorpions, has smooth and unkeeled sternites (Carvalho and Lourenço,  
245 2001). It is unclear whether this keel represents a morphological feature, or is an artifact of  
246 preservation in the study specimen, so we refrained from including it in the emended diagnosis.  
247 Openings near the external margins of the sternites in the study specimen are interpreted as  
248 spiracular pores, although their shape was difficult to determine; they are slit-like in the holotype  
249 of *Protoischnurus axelrodorum*. The pectines are poorly resolved in the scan and the number of  
250 pectine teeth could not be accurately determined, although it appears to be greater than 10 (Fig.  
251 3B).

252 **Pedipalps:** Individual elements of both pedipalps are illustrated here in dorsal, retrolateral,  
253 ventral, and prolateral views (Figs. 6, 7). The chela, patella, and femur are all bounded by thick  
254 and prominent carinae dorsally. The pedipalp coxa is covered dorsally by the carapace, but can  
255 be observed in ventral view (Fig. 5). The chelicerae ought to be located close to the coxa, but  
256 these were not observed. Adjacent to the femur, the articular rim of the trochanter is raised and  
257 bears several low tubercles (Fig. 5). The femur is 6.32 mm long and 2.26 mm maximum width.  
258 The retrolateral surface of the femur bears rows of numerous dense tubercles along its dorsal and  
259 ventral margins (the dorsal row can be seen in Figure 6I and the ventral row in 6J). The patella is  
260 4.94 mm long and 2.67 maximum width. It bears somewhat prominent, rounded dorsal and  
261 ventral patellar spurs proximally (Figs. 6,7 E, G). The chela (including the fixed finger) is 8.65

262 mm long and 3.51 mm maximum width. The chela has two robust tubercles located proximally  
263 on its dorsal surface (arrowed in Figs. 6A, 7A), which represent vestigial subdigital and dorsal  
264 secondary carinae (for details, see Prendini, 2000). The fixed and movable fingers are of almost  
265 equal size, and both have sharp, weakly tuberculated cutting margins. The movable finger is  
266 narrow and elongated, with no basal or accessory teeth.

267 **Trichobothria:** Carvalho and Lourenço (2001) identified the following trichobothria in  
268 *Protoischnurus*: chela manus with four ventral  $V_1$ ,  $V_2$ ,  $V_3$ ,  $V_4$ ,  $eb$ , and  $Et_5$ ; tibia with two ventral  
269  $V_1$  and  $V_2$ ,  $et_1$  and  $est$ . Menon (2007) identified: chela ventral  $Et_1$ ,  $Est$ , and  $Esb$ ; chela dorsal  $dt$ ,  
270  $dst$ ,  $db$ ,  $dsb$ , and  $est$ ; patella dorsal  $I$ ,  $d_2$ , and  $d_1$ , external (retrolateral)  $et$ ,  $est$ ,  $em$ , and  $esb$ ; femur  
271  $I$ ,  $d$ , and  $e$ . Only some of these trichobothria could be identified in the study specimen (Figs. 6,7)  
272 but these agree with the ‘basic’ type “C” pattern of Vachon (1974).

273 **Legs:** Four pairs of legs (I-IV) are present. The prolateral and retrolateral margins of the femur of  
274 each leg are thickened to form rounded carinae, but the patella has only a retrolateral carina. The  
275 tibia is without a spur. No pedal spur was observed in the study specimen, and tarsal ungues are  
276 preserved only on the anteriormost legs.

277 **Metasoma:** Successive metasomal segments become progressively longer posteriorly, but the  
278 metasomal width is consistent, with a very slight taper posteriorly (the width of metasoma  
279 segment I is approx. 0.2x the length of the metasoma (excluding the telson); the width of  
280 segment V is approx. 0.15x). The last segment (V) is much longer than the previous ones,  
281 comprising approx. 34% of the metasoma total length (again excluding the telson). By contrast,  
282 segment I represents approx. 13%, segments II and III each form approx. 17%, and segment V  
283 represents approx. 19%. Paired longitudinal dorso-lateral carinae are present on each segment,  
284 bearing scattered low tubercles. Two apodemes are preserved at the end of the segment V and

285 can be observed in dorsal view (Fig. 8A). On the ventral surface, metasomal segments I-IV have  
286 two pairs of longitudinal carinae (these are less distinct on segment I), including  
287 ventrosubmedian carinae close to the midline (Fig. 8B). No tubercles are evident on the carinae  
288 of segment I and II; one or two tubercles are present on the ventrolateral carinae in segment III  
289 and three or four in segment IV. By contrast, the ventrolateral carinae on segment V are  
290 divergent posteriorly and are densely ornamented with numerous small tubercles. No median  
291 ventral carina was observed except on segment V, which has a low median carina ornamented  
292 with small tubercles. The telson has a distinct peduncle, vesicle, and sting. The telson vesicle is  
293 elongated and laterally flattened (Fig. 8C-F). The sting is short (its tip appears to be separated  
294 from the rest of the telson in the reconstitution, possibly because the intervening region was  
295 poorly mineralized). A subaculear tubercle is absent.

296

## 297 **5. Discussion**

298

299 Morphological characters of extant and fossil organisms are crucial to establishing their  
300 systematic position, ecological role and evolutionary trends. Unfortunately, some kinds of data  
301 utilized in phylogenetic analyses of modern scorpions are unavailable in fossils (e.g., ‘soft’  
302 morphology such as reproductive organs, and molecular sequence data), while others can be  
303 problematic to observe (e.g., trichobothrial positions). Nevertheless, Legg et al., (2012)  
304 demonstrated that computed microtomography and 3-D imaging could provide greatly improved  
305 morphological resolution of Carboniferous scorpion fossils in sideritic matrix. The present study  
306 demonstrates the utility of computed microtomography in studying scorpion fossils preserved in  
307 limestones, and adds considerably to our understanding of the preservation and morphology of

308 *Protoischnurus* from the Crato Formation of Brazil. Our observations support Schwermann et  
309 al.'s (2016) statement that mineralized fossils, even those with macroscopically poor  
310 preservation, can constitute a rich source of anatomical data for fossil arthropods when  
311 investigated using microtomographic methods. Our results also support McCoy and Brandt's  
312 (2009) proposal that fossil scorpion taphonomy can help distinguish between carcasses and  
313 molts.

314 Besides *Protoischnurus* from Brazil, two extinct scorpions from Early Cretaceous  
315 Burmese amber have been referred to the family Protoischnuridae (*Cretaceoushormiops*  
316 Lourenço, 2018; *Cretaceousopisthacanthus*, Lourenço and Velten, 2021). Based solely on the  
317 published descriptions (we have not examined the Burmese material), all three genera appear to  
318 share some features included in the original diagnosis of the family; e.g., no subaculear tooth on  
319 the telson; pectines moderate in size, tibial spurs absent; trichobothrial pattern of type C as  
320 defined by Vachon (1974). Unfortunately, these features can vary at the genus or even the  
321 species level among modern scorpions and their systematic value at family level is questionable.  
322 *Cretaceoushormiops* and *Cretaceousopisthacanthus* differ morphologically from  
323 *Protoischnurus*; in *Protoischnurus*, the spiracles are slit-like, whereas they are 'round to oval' in  
324 *Cretaceoushormiops* and 'oval to slit-like' in *Cretaceousopisthacanthus*; the pectines reportedly  
325 bear 14-15 teeth in *Protoischnurus* and *Cretaceoushormiops*, but only 10 are present in  
326 *Cretaceousopisthacanthus*; metasomal segments I-IV of *Protoischnurus* bear paired carinae  
327 ventrally, whereas only dorsal carinae were noted in *Cretaceousopisthacanthus*, and only dorsal  
328 and latero-dorsal carinae in *Cretaceoushormiops*; the dentate margin of the pedipalp fixed finger  
329 has a single linear row of small granules in *Protoischnurus* and *Cretaceoushormiops*, but two  
330 distinct rows are present in *Cretaceousopisthacanthus*. It is therefore problematic to assess the



331 family placement of *Cretaceousormiops* and *Cretaceousopisthacanthus* based solely on  
332 available data.

333 Carvalho and Lourenço (2001) remarked that *Protoischnurus* resembles the modern  
334 families Scorpionidae Latreille and Ischnuridae Simon (now Hormuridae Laurie, 1896; Monod  
335 and Prendini, 2014). *Protoischnurus* exhibits some features of the family Hormuridae as defined  
336 by Prendini (2000) (e.g., non-granular surfaces of the prosoma, mesosoma and metasoma;  
337 cheliceral dorsal distal denticle of movable finger subequal in length to the ventral distal  
338 denticle; telson vesicle of male is laterally flattened). Menon (2007) placed *Protoischnurus*  
339 within the family Hemiscorpiidae, subfamily Hormurinae Laurie, 1896 (now Hormuridae;  
340 Monod and Prendini [2014] restricted Hemiscorpiidae to *Hemiscorpius* alone, and  
341 accommodated Ischnuridae under the earlier name Hormuridae).

342 Baptista et al. (2006, fig. 35) positioned *Protoischnurus* on the scorpionoid stem within  
343 Iurida, for which orthobothriotaxy Type C and a posterior emargination of the sternum were  
344 considered apomorphic (Soleglad and Fet, 2003a; characters 1[5], 63[1]). Both of these features  
345 seem to be present in *Protoischnurus*. Given that an extinct taxon can be placed definitively  
346 within a crown group only if it exhibits synapomorphies of one of its subtended groups  
347 (Friedman and Brazeau, 2010), both *Araripescorpius* and *Protoischnurus* can be considered  
348 members of the Iurida crown group, apparently within different subtended groups (Hormuridae  
349 and Chactidae respectively), and *Protoischnurus* could be regarded as a stem hormurid.

350

## 351 **6. Concluding remarks**

352

353 Our observations concerning the taphonomy and preservation of the studied specimen

354 suggests that it represents an individual which died either before or soon after being carried into  
355 the lake in which the Crato limestones were deposited. Our findings also underscore the  
356 advantages of computed microtomography in the study of scorpion fossils preserved in  
357 limestone. From an evolutionary perspective, we conclude that *Protoischnurus* (and the family  
358 Protoischnuridae) belongs in the Scorpionoidea and represents an early member of the Iurida  
359 crown group, and we find some evidence supporting placement of *Protoischnurus* within the  
360 scorpionoid crown (e.g., as a stem hormurid).

361

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363

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378 Tecnológico in Brazil.

Journal Pre-proof

379 **References**

380

381 Arai, M., 2014. Aptian/Albian (Early Cretaceous) paleogeography of the South  
382 Atlantic: a paleontological perspective. *Brazilian Journal of Geology* 44 (2), 339-350.

383

384 Assine, M.L., 2007. Bacia do Araripe. *Boletim de Geociências da Petrobras* 15 (2), 371-  
385 389.

386

387 Assine, M.L., Perinotto, J.A.J., Custódio, M.A., Neumann, V.H., Varejão, F.G.,  
388 Mescolotti, P.C., 2014. Sequências deposicionais do Andar Alagoas da Bacia do  
389 Araripe, Nordeste do Brasil. *Boletim de Geociências Petrobras* 22 (1), 3-28.

390

391 Baptista, C., Santiago-Blay, J. A., Fet, V., Soleglad, M. E. 2006 . The Cretaceous scorpion  
392 genus, *Archaeobuthus*, revisited (Scorpiones: Archaeobuthidae). *Euscorpius* 35, 1-40.

393

394 Barling, N., Martill, D.M., Heads, S.W., Gallien, F. 2015. High fidelity preservation of fossil  
395 insects from the Crato Formation (Lower Cretaceous) of Brazil. *Cretaceous Research* 52, 605-  
396 622.

397

398 Beurlen, K., 1962. A geologia da Chapada do Araripe. *Anais da Academia Brasileira de*  
399 *Ciências* 34 (3), 365-370.

400

401 Campos, D.R.B. 1986. Primeiro registro fossil de Scorpionoidea na Chapada do Araripe

402 (Cretáceo Inferior), Brasil. *Annais de Academia Brasileira de Ciencias* 58, 135-137.  
403

404 Carvalho, I.S. 2000. Geological environments of dinosaur footprints in the intracratonic  
405 basins from Northeastern Brazil during the South Atlantic opening (Early Cretaceous).  
406 *Cretaceous Research* 21, 255-267.  
407

408 Carvalho, I.S., Agnolin, F., Rolando, M.A.A., Novas, F.E., Xavier-Neto, J., Freitas, F.I.,  
409 Andrade, J.A.F.G., 2019. A new genus of pipimorph frog (anura) from the early  
410 Cretaceous Crato Formation (Aptian) and the evolution of South American tongueless  
411 frogs. *Journal of South American Earth Sciences* 92, 222-233.  
412

413 Carvalho, I.S., Borghi, L., Fernandes, A.C.S., 2017. Microbial mediation in invertebrate  
414 trace fossil preservation in Sousa Basin (Early Cretaceous), Brazil. *Cretaceous Research*  
415 69, 136-146.  
416

417 Carvalho, I.S., Borghi, L., Leonardi, G., 2013. Preservation of dinosaur tracks induced  
418 by microbial mats in the Sousa Basin (Lower Cretaceous), Brazil. *Cretaceous Research*  
419 44, 112-121.  
420

421 Carvalho, I.S., Leonardi, G., Rios-Netto, A.M., Borghi, L., Freitas, A.P., Andrade, J.A.,  
422 Freitas, F.I., 2021. Dinosaur trampling from the Aptian of Araripe Basin, NE Brazil, as  
423 tools for paleoenvironmental interpretation. *Cretaceous Research* 117, 104626.  
424

- 425 Carvalho, I.S., Novas, F.E., Agnolín, F.L., Isasi, M.P., Freitas, F.I., Andrade, J.A.,  
426 2015a. A Mesozoic bird from Gondwana preserving feathers. *Nature Communications* 6  
427 (7141), 1-5.  
428
- 429 Carvalho, I.S., Novas, F.E., Agnolín, F.L., Isasi, M.P., Freitas, F.I., Andrade, J.A.,  
430 2015b. A new genus and species of enantiornithine bird from the Early Cretaceous of  
431 Brazil. *Brazilian Journal of Geology* 45 (2), 161-171.  
432
- 433 Carvalho, M.G.P. de, Lourenço, W. R., 2001. A new family of fossil scorpions from the Early  
434 Cretaceous of Brazil. *Comptes Rendus de l'Academie des Sciences de Paris, Earth and Planetary*  
435 *Sciences* 332, 711- 716.  
436
- 437 Catto, B., Jahnert, R.J., Warren, L.V., Varejão, F.G., Assine, M.L., 2016. The microbial  
438 nature of laminated limestones: Lessons from the Upper Aptian, Araripe Basin, Brazil.  
439 *Sedimentary Geology* 341, 304-315.  
440
- 441 Coimbra, J.C., Freire, T.M., 2021. Age of the Post-Rift Sequence I from the Araripe  
442 Basin, Lower Cretaceous, NE Brazil: Implications for spatio-temporal correlation.  
443 *Revista Brasileira de Paleontologia* 24 (1), 37-46.  
444
- 445 Dias, J.J., Carvalho, I.S., 2020. Remarkable fossil crickets preservation from Crato  
446 Formation (Aptian, Araripe Basin), a Lagerstätten from Brazil. *Journal of South*  
447 *American Earth Sciences* 98, 102443.

- 448
- 449 Dias, J.J., Carvalho, I.S., 2022. The role of microbial mats in the exquisite preservation  
450 of Aptian insect fossils from the Crato Lagerstätte, Brazil. *Cretaceous Research* 130,  
451 105068.
- 452
- 453 Dunlop, J.A., Legg, D.A., Selden, P.A., Fet, V., Schneider, J.W., Robler, R. 2016. Permian  
454 scorpions from the Petrified Forest of Chemnitz, Germany. *BMC Evolutionary Biology*  
455 16:72 DOI 10.1186/s12862-016-0634-z.
- 456
- 457 Friedman, M., Brazeau, M. D. 2010. A Reappraisal of the Origin and Basal Radiation of the  
458 Osteichthyes. *Journal of Vertebrate Paleontology* 30 (1), 36-56.
- 459
- 460 Fürsich, F.T., Custódio, M.A., Matos, A.M., Hethke, M., Quaglio, F., Warren, L.V.,  
461 Assine, M.L., Simões, M.G., 2019. Analysis of a late Aptian (Cretaceous) high-stress  
462 ecosystem: the Romualdo Formation of the Araripe Basin, northeastern Brazil.  
463 *Palaeogeography, Palaeoclimatology, Palaeoecology* 95, 268–296.
- 464
- 465 Gaban, R.D., Farley, R.E. 2002. Ecdysis in scorpions: supine behavior and exuvial ultrastructure.  
466 *Invertebrate Biology* 12, 136-147.
- 467
- 468 Gomes, J.M.P., Rios-Netto, A.M., Borghi, L., Carvalho, I.S., Filho, J.G.M., Sabaraense,  
469 L.D., Araújo, B.C., 2021. Cyclostratigraphic analysis of the early Cretaceous laminated  
470 limestones of the Araripe Basin, NE Brazil: Estimating sedimentary depositional rates.

471 Journal of South American Earth Sciences 112 (1), 103563.  
472  
473 Guerra-Sommer, M., Siegloch, A.M., Degani-Schmidt, I., Santos, A.C.S., Carvalho,  
474 I.S., Andrade, J.A.F.G., Freitas, F.I., 2021. Climate change during the deposition of the  
475 Aptian Santana Formation (Araripe Basin, Brazil): Preliminary data based on wood  
476 signatures. Journal of South American Earth Sciences 111, 103462.  
477  
478 Hjelle, J.T., 1990. Anatomy and morphology. In: Polis, G.A. (Ed.), The Biology of Scorpions.  
479 Stanford University Press, Stanford, 9-63.  
480  
481 Iniesto, M., Blanco-Moreno, C., Villalba, A., Buscalioni, A.D., Guerrero, M.C., López-  
482 Archilla, A.I., 2018. Plant Tissue Decay in Long-Term Experiments with Microbial  
483 Mats. Geosciences 8 (387), 1-21.  
484  
485 Iniesto, M., Buscalioni, A.D., Guerrero, M.C., Benzerara, K., Moreira, D., López-  
486 Archilla, A.L., 2016. Involvement of microbial mats in early fossilization by decay  
487 delay and formation of impressions and replicas of vertebrates and invertebrates.  
488 Scientific Reports 6, 1-12.  
489  
490 Iniesto, M., Gutiérrez-Silva, P., Dias, J.J., Carvalho, I.S., Buscalioni, A.D., López-  
491 Archilla, A.I., 2021. Soft tissue histology of insect larvae decayed in laboratory  
492 experiments using microbial mats: taphonomic comparison with Cretaceous fossil  
493 insects from the exceptionally preserved biota of Araripe, Brazil. Palaeogeography,



- 494 Palaeoclimatology, Palaeoecology 564, 110156.
- 495
- 496 Iniesto, M., Laguna, C., Florín, M., Guerrero, M.C., Chicote, A., Buscalioni, A.D.,  
497 López-Archilla, A.L., 2015. The impact of microbial mats and their microenvironmental  
498 conditions in early decay of fish. *Palaios* 30, 792-801.
- 499
- 500 Iniesto, M., Villalba, L., Buscalioni, A.D., Guerrero, M.C., López-Archilla, A.L., 2017.  
501 The effect of microbial mats in the decay of anurans with implications for  
502 understanding taphonomic processes in the fossil record. *Scientific Reports* 7, 1-12.
- 503
- 504 Koch, C. L. 1837. *Übersicht des Arachnidensystems*. CH Zehsche Buchhandlung, Nürnberg, 1,  
505 1–39.
- 506
- 507 Latreille, P. A. 1802. *Histoire naturelle, générale et particulière, des Crustacés et des Insectes*.  
508 *Ouvrage faisant suite à l’histoire naturelle générale et particulière, composée par Leclerc de*  
509 *Buffon, et redigée par C. S. Sonnini*. Imprimerie de F. Dufart, Paris, 3, 467 pp.
- 510
- 511 Laurie, M. 1896. Further notes on the anatomy and development of scorpions, and their bearing  
512 on the classification of the order. *Annals and Magazine of Natural History Series* 6, 18, 121–133.
- 513
- 514 Legg, D.A., Garwood, R.J., Dunlop, J.A., and Sutton, M.D., 2012. A taxonomic revision of  
515 orthosternous scorpions from the English Coal-measures aided by X-ray Micro-Tomography  
516 (XMT). *Palaeontologia Electronica* 15 (2), 14A, 16 pp.

517

518 Lourenço, W.R., 2001. A remarkable scorpion fossil from the amber of Lebanon. Implications  
519 for the phylogeny of Buthoidea. *Comptes Rendus de l'Academie de Sciences de Paris, Earth and*  
520 *Planetary Sciences* 332, 641-646.

521

522 Lourenço, W.R., 2002. The first scorpion fossil from the Cretaceous amber of Myanmar  
523 (Burma). New implications for the phylogeny of Buthoidea. *Comptes Rendus Paleovol* 1, 97-  
524 101.

525

526 Lourenço, W.R., 2003. The first scorpion fossil from the Cretaceous amber of France. New  
527 implication for the phylogeny of the Chactoidea. *Comptes Rendus Paleovol* 2, 213-219.

528

529 Lourenço, W.R., 2012. About the scorpion fossils from the Cretaceous amber of Myanmar  
530 (Burma) with the descriptions of a new family, genus and species. *Acta Biologica Paranaense* 41,  
531 75-87.

532

533 Lourenço, W.R., 2016. A preliminary synopsis on amber scorpions with special reference to  
534 Burmite species: an extraordinary development of our knowledge in only 20 years. *ZooKeys*  
535 600, 75-87.

536

537 Lourenço, W.R., 2018. A new remarkable scorpion genus and species from Cretaceous Burmese  
538 amber (Scorpiones: Protoischnuridae). *Revista Aracnologica Italiana* 18, 2-14.

539

- 540 Lourenço, W.R., Beigel, A., 2011. A new scorpion fossil from the Cretaceous amber of  
541 Myanmar (Burma). New phylogenetic implications. *Comptes Rendus Palevol* 10, 635-639.  
542
- 543 Lourenço, W.R., Velten, J., 2021. One more new genus and species of scorpion from Early  
544 Cretaceous Burmese amber (Scorpiones: Protoischnuridae). *Faunitaxys*, 9 (14), 1-5.  
545
- 546 Maisey, J.G., 1991. *Santana Fossils. An illustrated atlas.* Neptune, New Jersey, T.F.H.  
547 Publications, 459 pp.  
548
- 549 Maisey, J.G., 2000. Continental break up and the distribution of fishes of western  
550 Gondwana during the early Cretaceous. *Cretaceous Research* 21, 281–314.  
551
- 552 Maisey, J.G., Carvalho, M.D.G.P., 1995. First records of fossil sergestid decapods and  
553 fossil brachyuran crab larvae (Arthropoda, Crustacea), with remarks on some supposed  
554 palaemonid fossils, from the Santana Formation (Aptian- Albian, NE Brazil). *American*  
555 *Museum Novitates* 3132, 1–17.  
556
- 557 Marques, F.O., Nogueira, F.C.C., Bezerra, F.H.R., de Castro, D.L. 2014. The Araripe Basin in  
558 NE Brazil: An intracontinental graben inverted to a high-standing horst. *Tectonophysics* 630,  
559 251-264.  
560
- 561 Martill, D.M, Bechly, G., 2007. Introduction to the Crato Formation. In: Martill, D.,  
562 Bechly, G., Loveridge, R. (Eds.), *The Crato fossil beds of Brazil: window into an*

- 563 ancient world, Cambridge University Press, New York, pp. 3-7.
- 564
- 565 Martill, D., Bechly, G., Loveridge, R. 2007. The Crato Fossil Beds of Brazil: Window  
566 into an Ancient World. Cambridge: Cambridge University Press, pp. 475-524.
- 567
- 568 Matos, R.M.D., 1992. The northeast Brazilian rift system. *Tectonics* 11, 766–791.
- 569
- 570 McCoy, V.E., Brandt, D.S. 2009. Scorpion taphonomy: criteria for distinguishing fossil scorpion  
571 molts and carcasses, *Journal of Arachnology* 37(3), 312-320. <https://doi.org/10.1636/SH09-07.1>
- 572
- 573 Menon, F., 2007. Higher systematics of scorpions from the Crato Formation, Lower Cretaceous  
574 of Brazil. *Palaeontology* 50 (1), 185-195.
- 575
- 576 Monod, L., Prendini, L. 2014. Evidence for Eurogondwana: The roles of dispersal, extinction  
577 and vicariance in the evolution and biogeography of Indo-Pacific Hormuridae (Scorpiones:  
578 Scorpionoidea). *Cladistics* 31(1), 71-111.
- 579
- 580 Pocock, R.I. 1893. Notes on the classification of scorpions, followed by some observations on  
581 synonymy, with description of new genera and species. *Annals and Magazine of Natural History*  
582 *Series 6*, 12, 303–330.
- 583
- 584 Ponte, F.C., Appi, C.J., 1990. Proposta de revisão da coluna litoestratigráfica da Bacia  
585 do Araripe. In: *Congresso Brasileiro de Geologia*, 36, Natal, 1, pp. 211-226.

586

587 Ponte, F.C., Ponte Filho, F.C., 1996. Evolução tectônica e classificação da Bacia do Araripe. In:  
588 Boletim do 4 Simpósio Sobre o Cretáceo do Brasil. UNESP, Campus de Rio Claro, SP, pp. 123-  
589 133.

590

591 Prendini, L., 2000. Phylogeny and classification of the superfamily Scorpionoidea Latreille 1802  
592 (Chelicerata, Scorpiones): An exemplar approach. *Cladistics* 16 (1), 1-78.

593

594 Ribeiro, A.C., Ribeiro, G.C., Varejão, F.G., Battirola, L.D., Pessoa, E.P., Simões, M.G.,  
595 Warren, L.V., Riccomini, C., Poyato-Ariza, F.J., 2021. Towards an actualistic view of  
596 the Crato Konservat-Lagerstätte paleoenvironment: a new hypothesis as an early  
597 Cretaceous (Aptian) equatorial and semi-arid wetland. *Earth-Science Reviews* 216, 103573,  
598 ISSN 0012-8252, <https://doi.org/10.1016/j.earscirev.2021.103573>.

599

600 Rios-Netto, A.M., Paula-Freitas, A.B.L, Carvalho, I.S., Regali, M.P.S., Borghi,  
601 L.,Freitas, F.I., 2012a. Formalização estratigráfica do Membro Fundão, Formação Rio  
602 da Batateira, Cretáceo Inferior da Bacia do Araripe, Nordeste do Brasil. *Revista*  
603 *Brasileira de Geociências* 42(2), 281-292.

604

605 Rios-Netto, A.M., Regali, M.S.P., Carvalho, I.S., Freitas, F.I., 2012b. Palinoestratigrafia  
606 do intervalo Alagoas da Bacia do Araripe, Nordeste do Brasil. *Revista Brasileira de*  
607 *Geociências* 42 (2), 331-342.

608

- 609 Scherer, C.M.S., Jardim de Sá, E.F., Córdoba, V.C., Sousa, D.C., Aquino, M.M.,  
610 Cardoso, F.M.C., 2014. Tectono-stratigraphic evolution of the Upper Jurassic-  
611 Neocomian rift succession, Araripe Basin, Northeast Brazil. *Journal of South*  
612 *American Earth Sciences* 49, 106-122.
- 613
- 614 Schwermann, A.H., dos Santos Rolo, T., Caterino M.S., Bechly, G., Schmied, H., Tilo  
615 Baumbach, T., van de Kamp, T. 2016. Preservation of three-dimensional anatomy in  
616 phosphatized fossil arthropods enriches evolutionary inference. *eLife* 5:e12129.  
617 <https://doi.org/10.7554/eLife.12129>
- 618
- 619 Sissom, W.D., 1990. Systematics, Biogeography, and Paleontology. In: Polis G.A. (Ed.), *The*  
620 *Biology of Scorpions*, Stanford University Press, 64-75.
- 621
- 622 Soleglad, M.E., Fet, V. 2003a. High-level systematics and phylogeny of the extant scorpions  
623 (Scorpiones: Orthosterni). *Euscorpius* 11, 1-175.
- 624
- 625 Soleglad, M.E., Fet, V. 2003b. The scorpion sternum: structure and phylogeny  
626 (Scorpiones: Orthosterni). *Euscorpius* 4, 1-34.
- 627
- 628 Stahnke, H.L. 1970. Scorpion nomenclature and mensuration. *Entomological News* 81, 297-316.
- 629
- 630 Stockwell, S.A. 1989. Revision of the phylogeny and higher classification of scorpions  
631 (Chelicerata). PhD thesis, University of California, Berkeley, CA, 413pp.

632

633 Vachon, M., 1974. Études des caractères utilisés pour classer les familles et les genres de  
634 Scorpions (Arachnides). 1. La trichobothriotaxie en arachnologie. Sigles trichobothriax et types  
635 des trichobothriotaxie chez les Scorpions. Bulletin du Muséum National d'Historie Naturelle  
636 104, 857-958.

637

638 Varejão, F.G., Silva, V.R., Assine, M.L., Warren, L.V., Matos, S.A., Rodrigues, M.G.,  
639 Fürsich, F.T., Simões, M.G., 2021a. Marine or freshwater? Accessing the  
640 paleoenvironmental parameters of the Caldas Bed, a key marker bed in the Crato  
641 Formation (Araripe Basin, NE Brazil). Brazilian Journal of Geology 51(1), e2020009.

642

643 Varejão, F.G., Warren, L.V., Simões, M.G., Fürsich, F.T., Matos, S.A., Assine, M.L.,  
644 2019. Exceptional preservation of soft tissues by microbial entombment: insights into  
645 the taphonomy of the Crato Konservat-Lagerstätte. Palaios 34(7), 331-348.

646

647 Varejão, F.G., Warren, L.V., Simões, M.G., Buatois, L.A., Manganó, M.A., Bahniuk,  
648 A.M.R., Assine, M.L., 2021b. Mixed siliciclastic-carbonate sedimentation in an  
649 evolving epicontinental sea: Aptian record of marginal marine settings in the interior  
650 basins of north-eastern Brazil. Sedimentology 68 (5), 2125-2164.

651

652 Wolfe, J.M., Daley, A.C., Legg, D.A., Edgecombe, G.D. 2016. Fossil calibrations for the  
653 arthropod tree of life. Earth Science Reviews 160, 43-110.

654

655 Xuan, Q., Cai, C., Huang, D., 2022. A new Palaeoburmesebuthidae scorpion from mid-  
656 Cretaceous Burmese amber (Arachnida: Scorpiones: Buthoidea). *Cretaceous Research* 134,  
657 105165.

658

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659 Figure captions

660

661 Fig. 1. Sketch map of the Araripe Basin (northeastern Brazil) and a simplified stratigraphic chart  
662 of the Crato Formation carbonate sequence, showing the principal fossiliferous layers, including  
663 the level where scorpion fossils occur. No scale.

664

665 Fig. 2. *Protoischnurus axelrodorum* UFRJ-DG 101-Ac; part (UFRJ-DG 101-Ac-a) and  
666 counterpart (UFRJ-DG 101-Ac-b); photos of the studied specimen. Scale bar = 5 mm.

667

668 Fig. 3. UFRJ-DG 101-Ac; digital reconstitution of the entire specimen in (A) dorsal view and (B)  
669 ventral view. Arrow in Fig. 3A indicates where sublateral carina of last mesosomal tergite slopes  
670 ventrally towards the anterior margin of metasoma sternite I. Abbreviations: car, carapace; lc,  
671 lateral carina of tergite; mc, median carina of sternite; sp, spiracles; st3,7, first and last sternites;  
672 t1, t7, first and last tergites; tslc, tergite sublateral carina; l1-4, legs. Arrow in (A) indicates  
673 where sublateral carina of tergite 7 meets the articulation of the metasoma. Scale bar = 5 mm.

674

675 Fig. 4. A, B, UFRJ-DG 101-Ac-a, dorsal (A) and ventral (B) reconstitutions of the carapace.  
676 Abbreviations: le, recess for lateral eyes; me, openings for median eyes; mlf, median longitudinal  
677 furrow; pmarf, posterior marginal furrow; pmf, posterior median furrow. Scale bar = 5 mm.

678

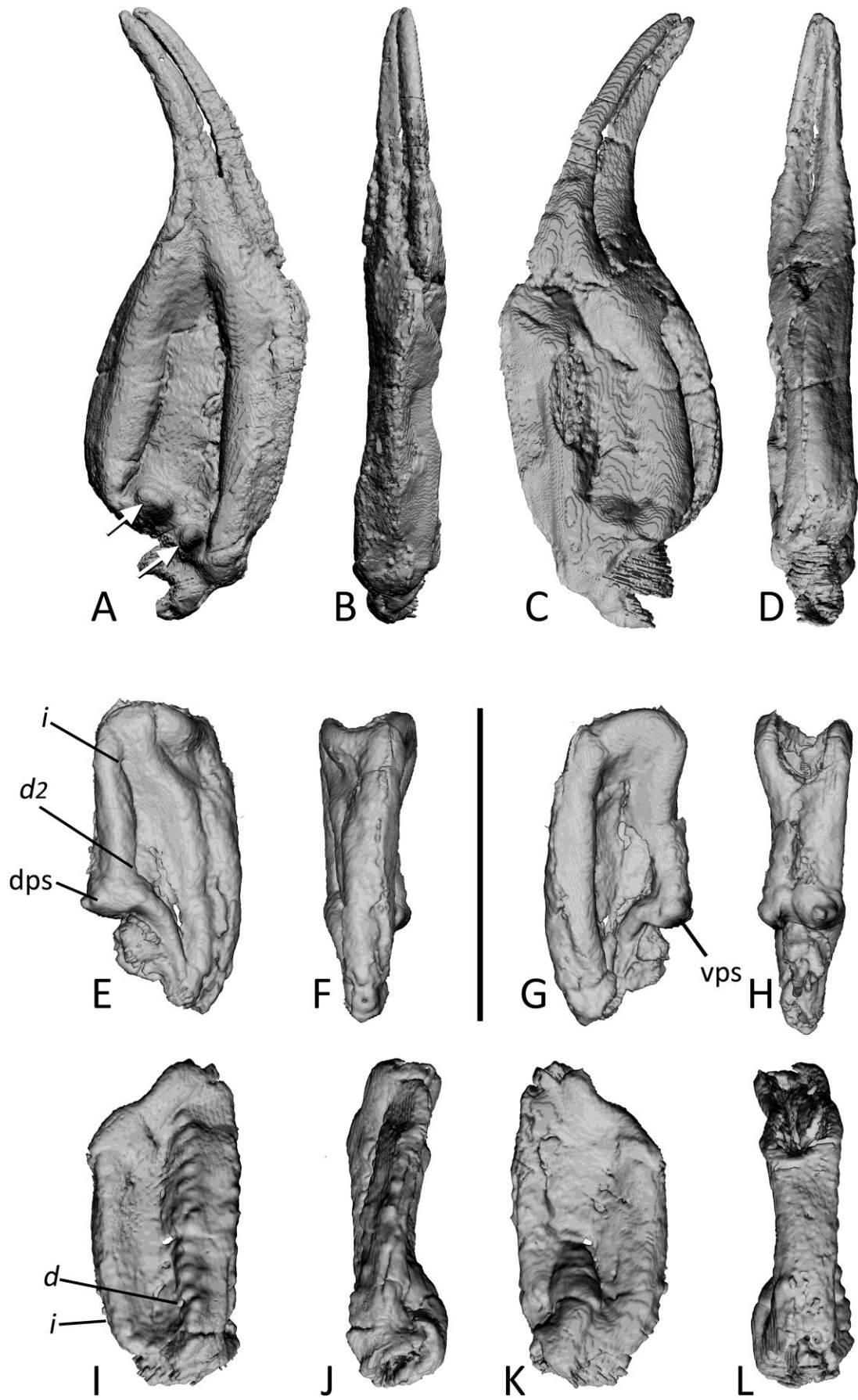
679 Fig. 5. Ventral view of specimen UFRJ-DG 101-Ac, made from combined reconstitutions of part  
680 and counterpart. Abbreviations: cxa I, II, coxapophysis of first two legs; fe II-IV, femur of legs;  
681 ff, fixed finger of chela; go, genital operculum; mc, median carina of sternite 3; mf, movable

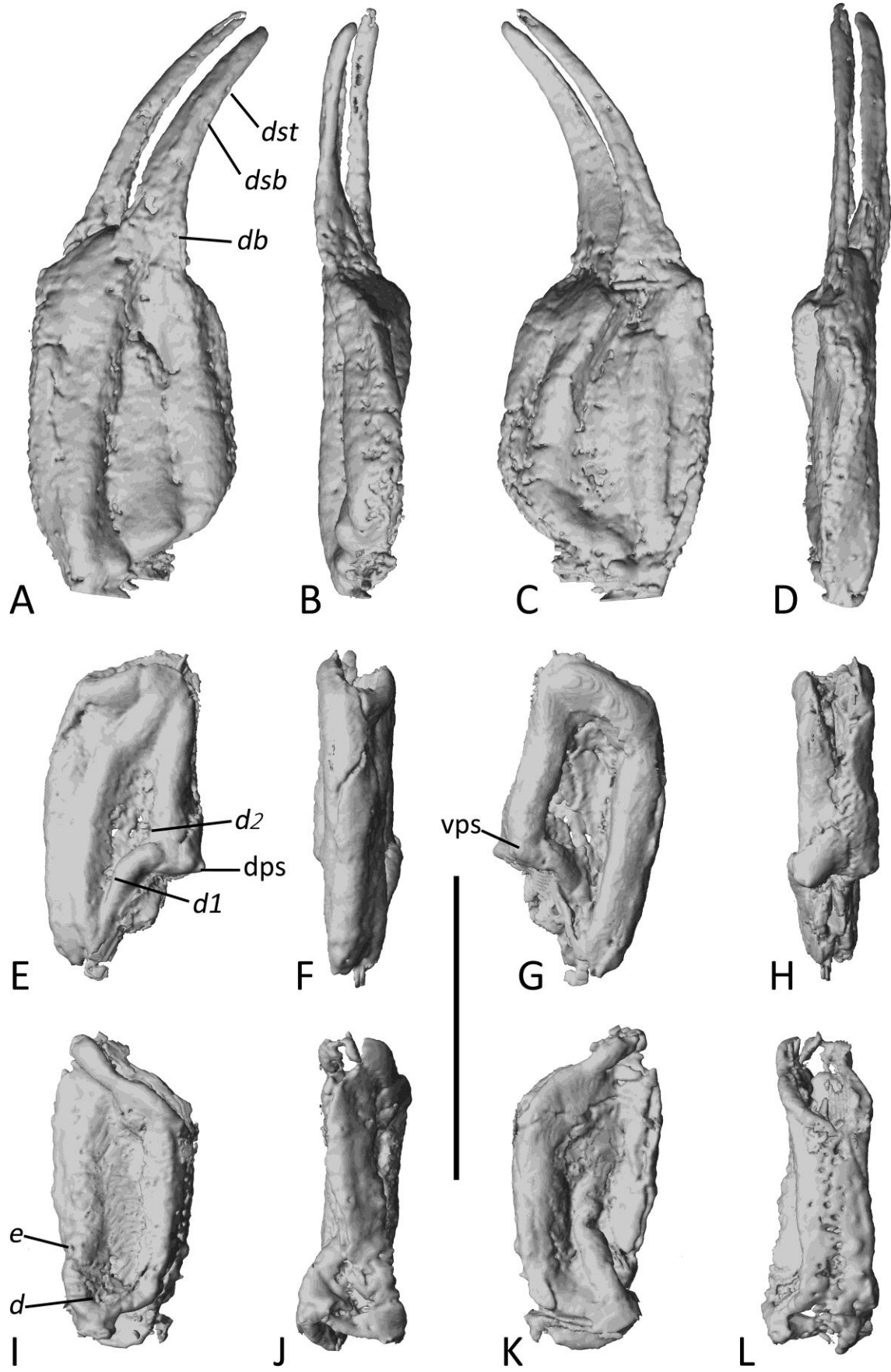
682 finger of chela; pa I,II, patella of legs; pcx, pedipalp coxa; pec, pectines; pfe, pedipalp femur;  
683 ppa, pedipalp patella; ptr, pedipalp trochanter; st, sternum; ta I, tarsus of first leg; ti I,II,III, tibia  
684 of legs. Scale bar = 5 mm.

685  
686 Fig. 6. UFRJ-DG 101-Ac. Left pedipalp elements; A-D, chela and movable finger; E-H, patella;  
687 I-L, femur. From left to right, views show dorsal, retrolateral, ventral, and prolateral aspects of  
688 each element. Abbreviations; dps, dorsal patella spur; vps, ventral patellar spur. Trichobothrial  
689 abbreviations; *d*, dorsal; *db*, dorsal basal; *dsb*, dorsal suprabasal; *dst*, dorsal subterminal; *e*,  
690 external (retrolateral), *v* = ventral. Robust dorsal tubercles of the tibia are arrowed in A. Scale bar  
691 = 5 mm.

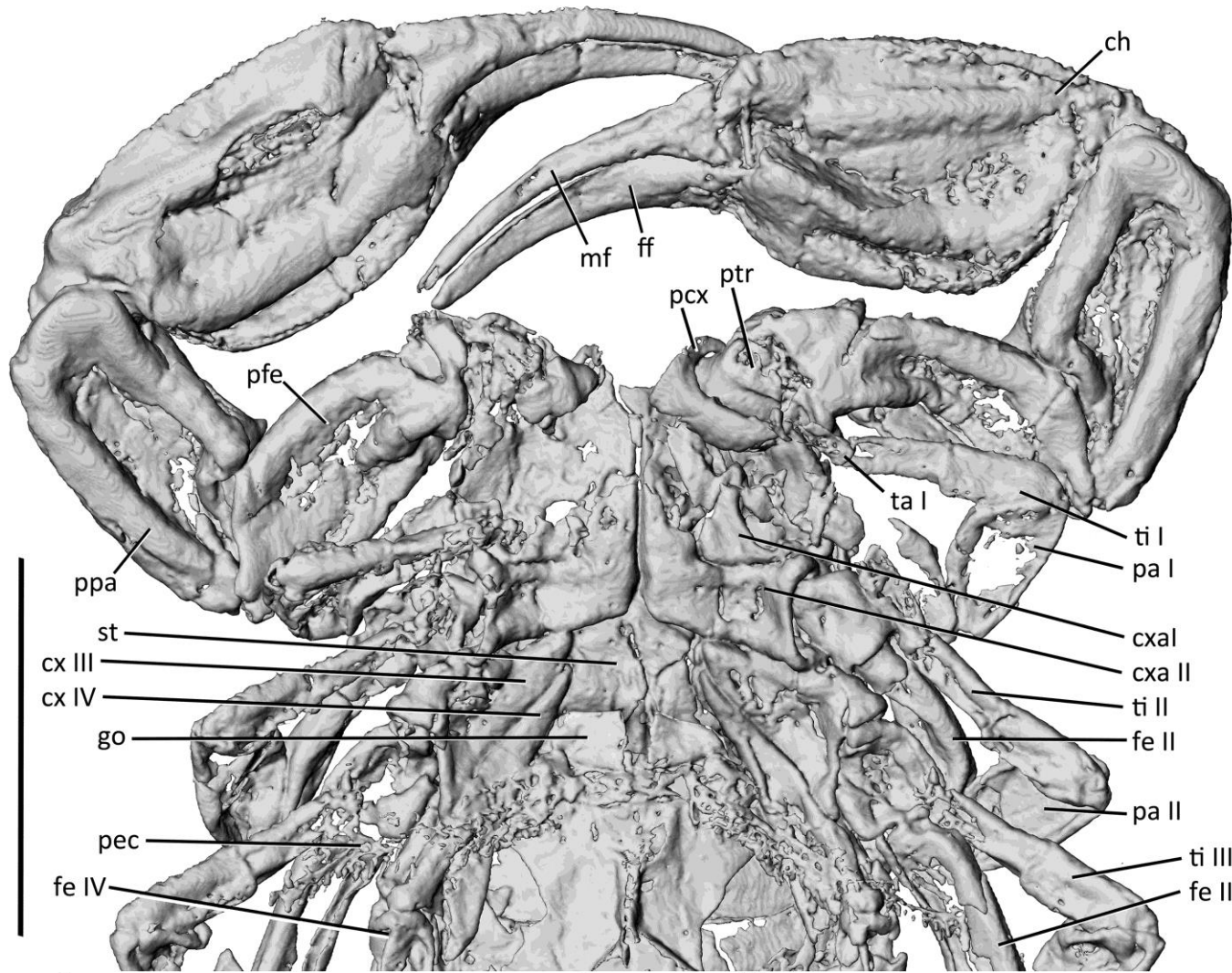
692  
693 Fig. 7. UFRJ-DG 101-Ac. Right pedipalp elements. Arrangement and abbreviations as in Fig. 6.  
694 Robust dorsal tubercles of the chela are arrowed in A. Scale bar = 5 mm.

695  
696 Fig. 8. UFRJ-DG 101-Ac; metasoma: A, B, metasomal segments I-V plus telson, with vesicle  
697 and part of aculeus in dorsal (A) and ventral (B) views; C-F, details of telson; C, dorsal view; D,  
698 ventral view; E, lateral view, left side; F, posterior view. Scale bars = 5 mm (vertical bar for A,  
699 B; horizontal bar for C-F).



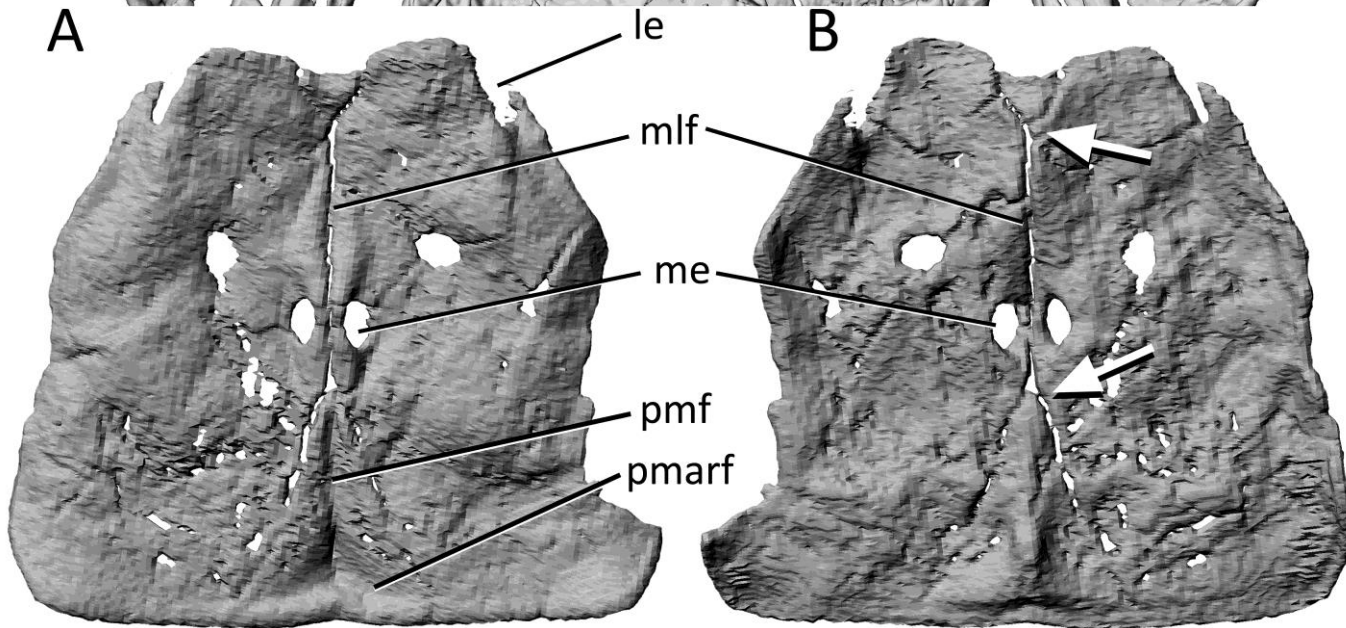


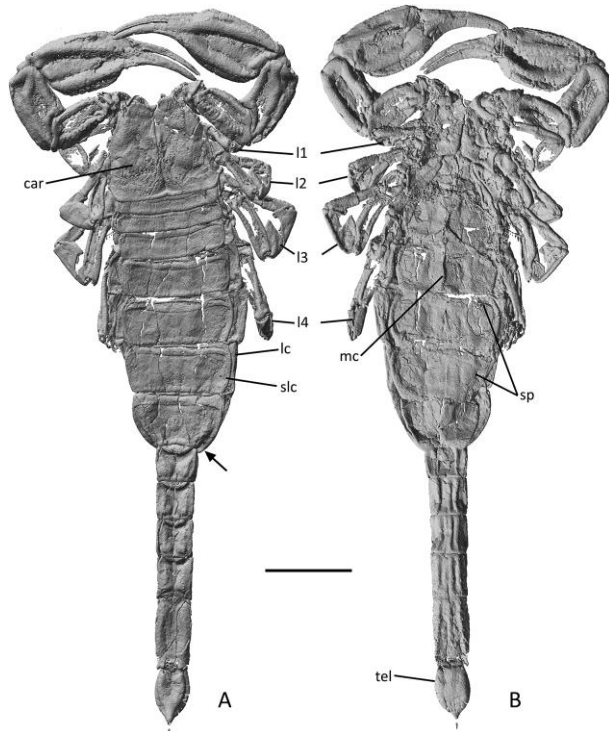




**A**

**B**

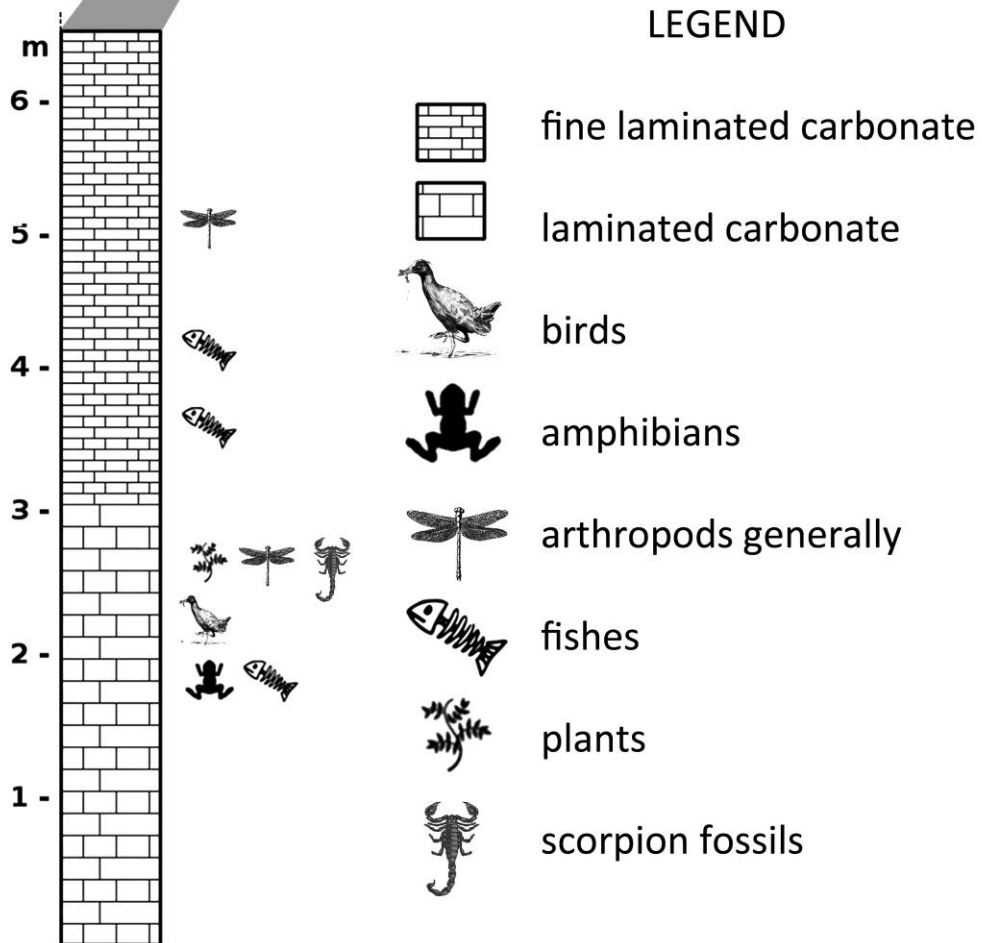
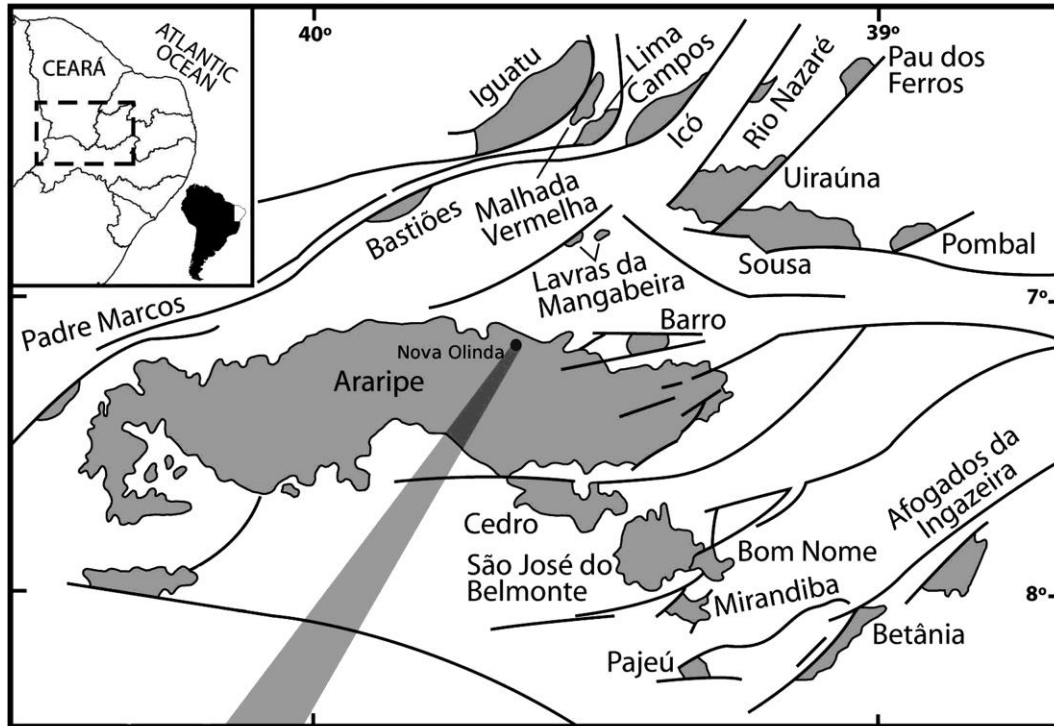


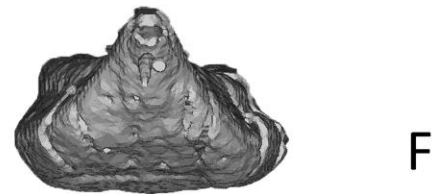
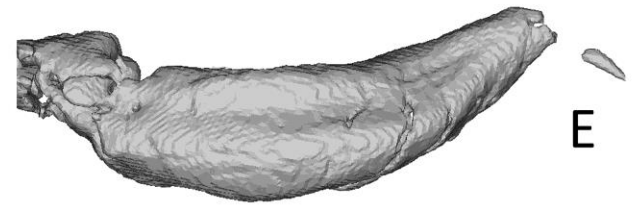
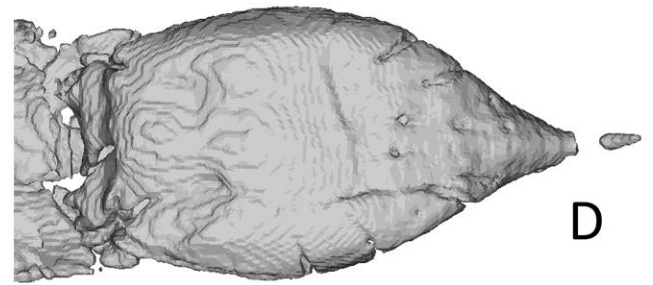
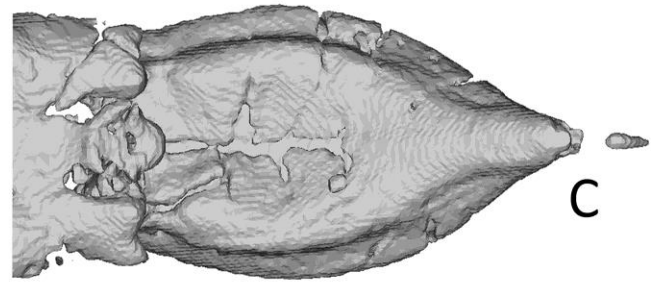
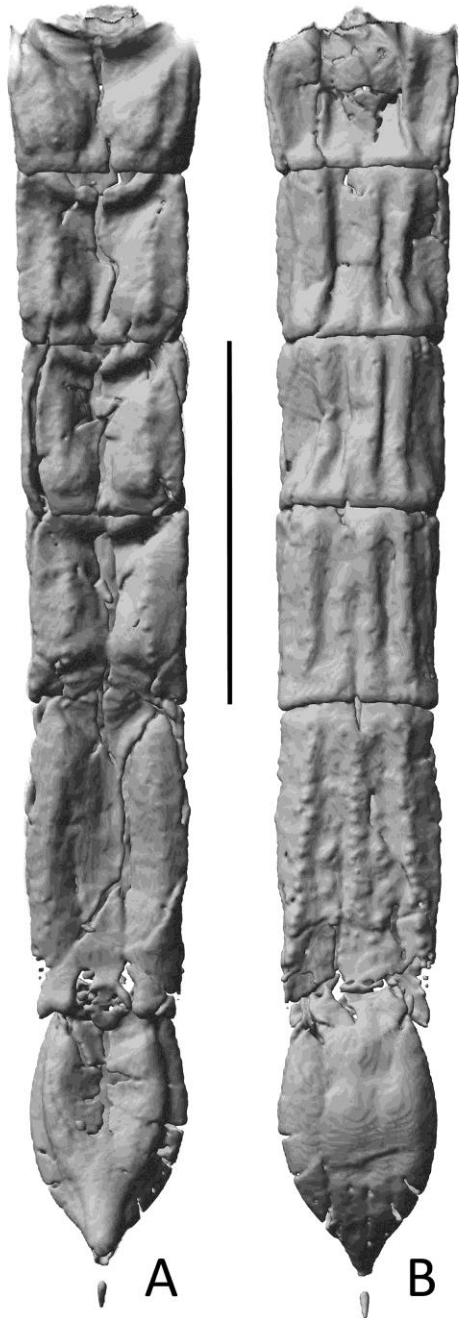


A

B









Micro-tomographic analysis of a scorpion fossil from the Aptian Crato Formation of North-  
Eastern Brazil

Maria G. P. de Carvalho, John G. Maisey, Ighor Dienes Mendes, Ismar de Souza Carvalho

**Highlights**

One of only two non-amber Cretaceous scorpion taxa known.

From the Lower Cretaceous Crato Formation (Aptian, northeastern Brazil).

Taphonomic evidence suggests that the fossil represents a corpse, not a molted exoskeleton.

The first Cretaceous scorpion to be studied using computerized microtomography.

The most complete and detailed morphological account of any Cretaceous scorpion.

An early member of the Lurida crown group, falling evolutionarily either within the scorpionoid crown or on its stem.

Author statement

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The authors' respective contributions to this work are as follows:

Maria de Carvalho: Investigation, Supervision, Validation, Writing- Original draft preparation. John

Maisey: Methodology, Visualization software, Writing-, Reviewing and Editing. Ighor Mendes:

Visualization, Investigation. Ismar Carvalho: Conceptualization, Project administration.

**Declaration of interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Corresponding author John Maisey currently serves in an editorial capacity for Cretaceous Research, and also reports equipment and supplies were provided by American Museum of Natural History (retired from American Museum of Natural History, therefore not employed but currently Curator Emeritus and Senior Scientist in Residence)

JGM