

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

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ABSTRACT

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

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1. Introduction

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

This is the first Cretaceous scorpion to have been investigated by computed microtomography, and is only the second scorpion fossil ever investigated this way (the first was a Carboniferous fossil in sideritic matrix; Legg et al., 2012). It is also the first scorpion fossil

in limestone matrix to be analyzed microtomographically, highlighting the usefulness of this procedure for study of small fossil arthropods in carbonate matrix.

Cretaceous scorpions are important because of their close evolutionary relationships to modern forms. In the case of *Araripescorpius* and *Protoschinurus*, de Carvalho and Lourenço (2001) observed that these taxa “could be classified together with some extant families within the Superfamily Scorpionoidea”. Subsequently, Baptista et al. (2006) considered that *Protoischnurus* is a stem scorpionoid and that *Araripescorpius* is a stem chactoid, both contained within the Parvorder lurida Soleglad and Fet, 2003a. Menon (2007) assigned *Protoischnurus* to the scorpionoid family Hemiscorpiidae Pocock, 1893, and *Araripescorpius* to the chactoid family Chactidae Pocock, 1893; i.e., among crown (rather than stem) scorpionoids and chactoids. However, the criteria currently used to assign fossil scorpions to groups, living or extinct, are mostly unsatisfactory, and an assessment of their interrelationships will only become possible within an acceptable theory of relationships of extant scorpions.

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

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2. Geological context of the material

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

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

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

3. Material and methods

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

Like many fossil insects from the Crato Formation (Barling et al., 2015), the scorpion fossil is preserved as an orange to brown amorphous material, probably representing goethite (limonite)

replacement of the original cuticle. The main body of the fossil has split horizontally, exposing the internal surfaces of the carapace and mesosoma in UFRJ-DG 101-Ac-a, and the internal surface of the sternal region in the counterpart. The metasomal segments are contained almost completely in UFRJ-DG 101-Ac-a, with only an external mold of the metasoma ventral surface in the counterpart. The external features of the fossil are largely 'face-down' in matrix and most cannot be observed directly, even under a microscope. The pedipalp chelae are both well preserved (Figs. 2, 3). The legs are also well preserved but were fractured through the patellae when the rock matrix was opened, so some parts of these appendages are preserved on the part and others on the counterpart (Fig. 2). The complete appendages are shown in the merged reconstitution of the part and counterpart (Fig. 3). The coxapophyses of the first paired legs are incomplete, but those of the second pair are almost complete. The sternites are better preserved on the left side and towards the midline of the fossil; the right parts of these elements are mostly missing, exposing the inner surfaces of the tergites in ventral view (Fig. 3B). All five metasomal segments and the telson with its vesicle and aculeus are preserved, but the dorsal surfaces of the metasomal segments in the study specimen have caved in and are cracked longitudinally (Fig. 3A). The telson is very well preserved but is completely enclosed by matrix and cannot be seen in the fossil, only in the scan (Figs. 2,3).

3.1. Taphonomy

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

3.2. Microtomography

The specimen was subjected to computed microtomography (CT) at the Nuclear Instrumentation Laboratory in the Department of Nuclear Engineering (COPPE), at the Universidade Federal do Rio de Janeiro (UFRJ). Prior to scanning, the fossil was trimmed using a conventional rock saw to reduce the amount of matrix, and the part and counterpart were scanned separately to improve scan quality. Both pieces were scanned using identical parameters (180 kV, resolution 0.5 μm). The scans were processed in Mimics© Version 18.0 x64, on a Dell© Precision 7710 Mobile Workstation. Separate reconstitutions of the part and counterpart pieces were created, as well as a merged reconstitution of the part and counterpart scans, which were aligned using Meshlab© Version 2022.02. Additionally, the carapace and elements of the pedipalps were reconstituted separately. Scan images were captured in Meshlab© Version

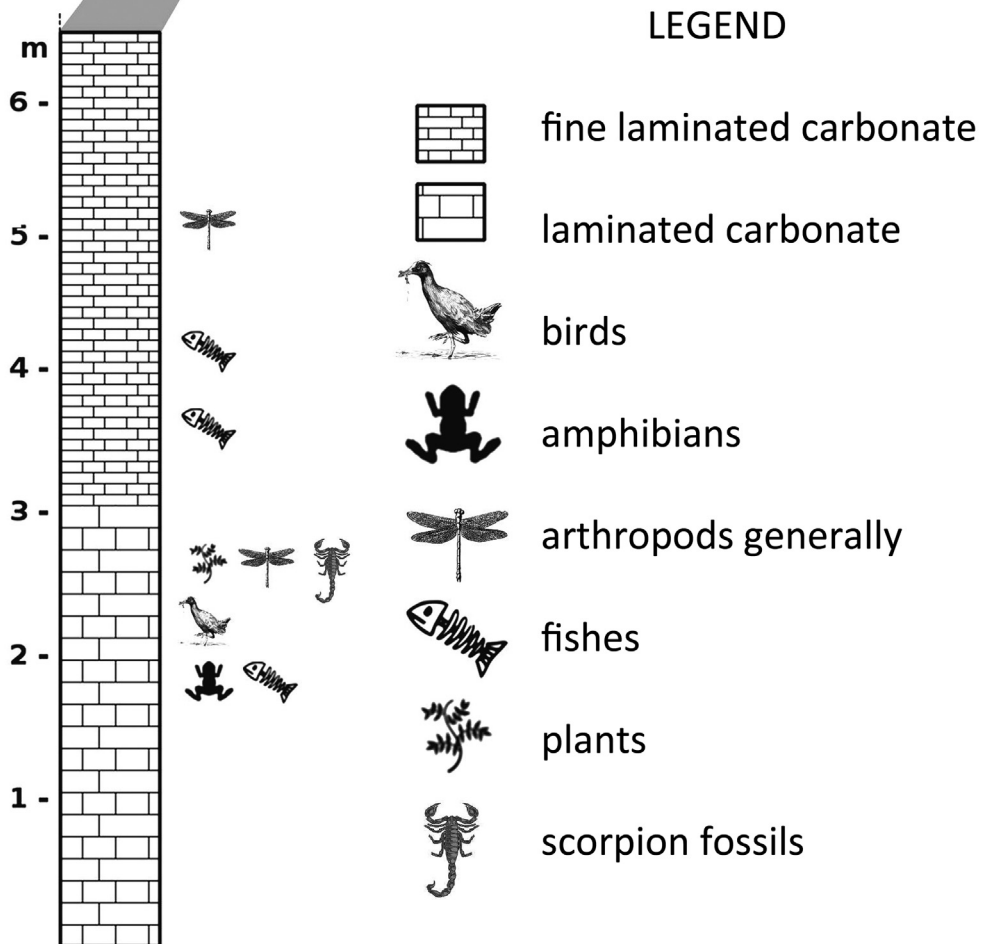
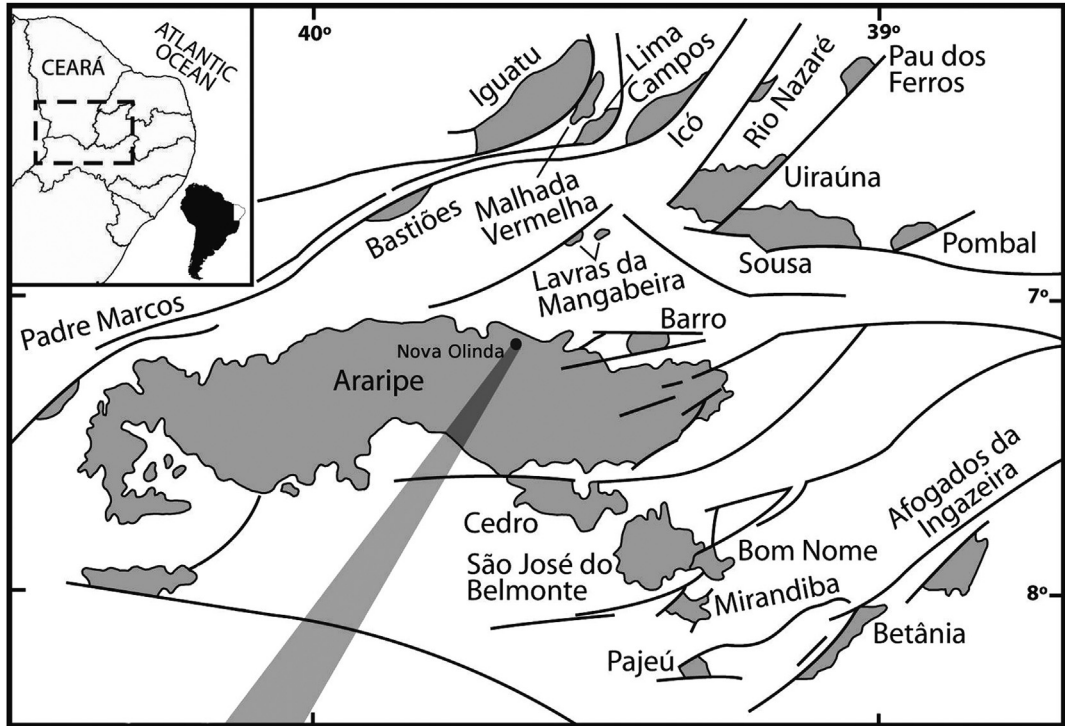


Fig. 1. Sketch map of the Araripe Basin (northeastern Brazil) and a simplified stratigraphic chart of the Crato Formation carbonate sequence, showing the principal fossiliferous layers, including the level where scorpion fossils occur. No scale.



A



B

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

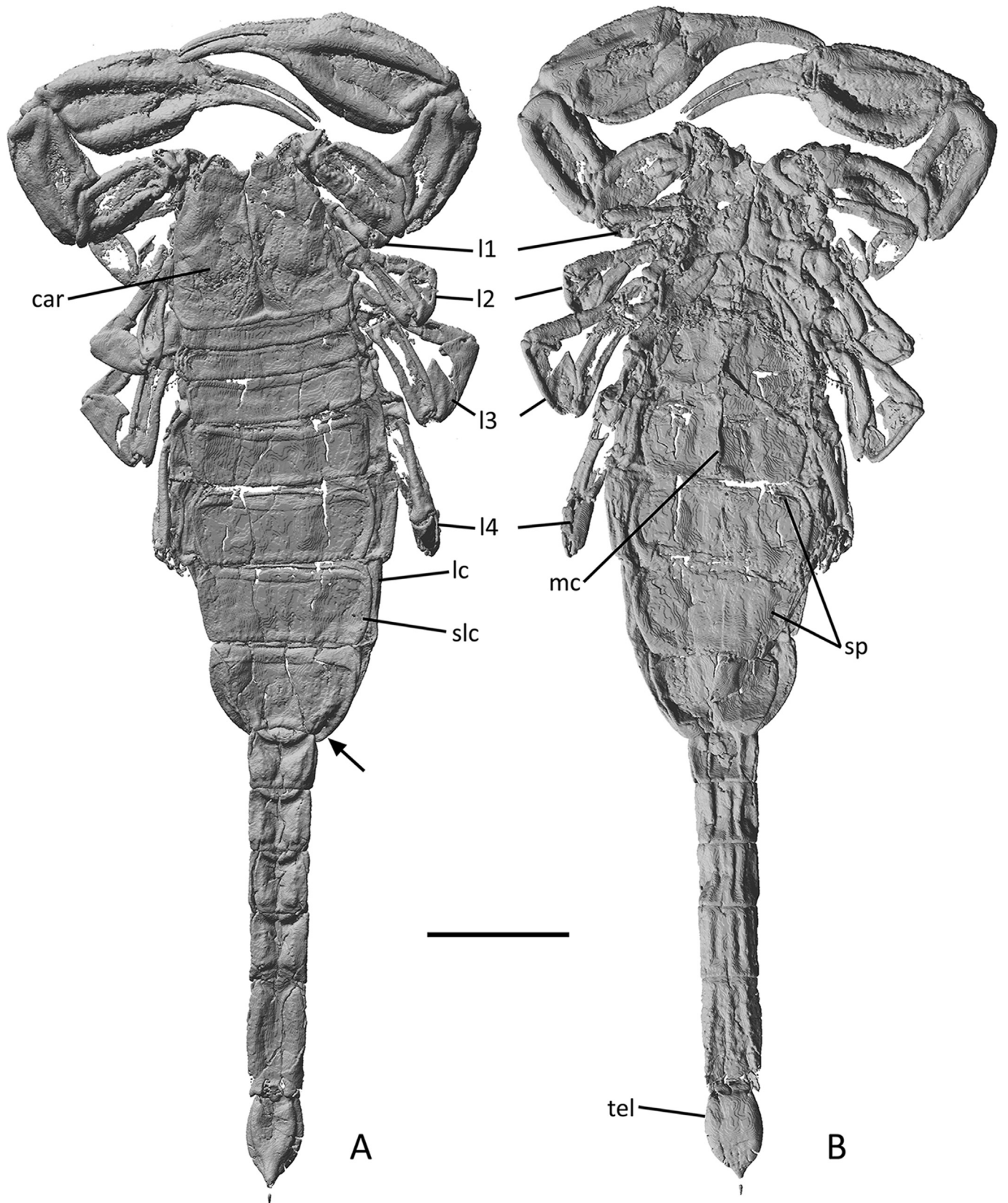


Fig. 3. UFRJ-DG 101-Ac; digital reconstitution of the entire specimen in (A) dorsal view and (B) ventral view. Arrow in Fig. 3A indicates where sublateral carina of last mesosomal tergite slopes ventrally towards the anterior margin of metasoma sternite I. Abbreviations: car, carapace; lc, lateral carina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

2022.02, using the program's orthographic view option, and illustrations were prepared in Adobe Photoshop® Elements Version 10.

3.3. Photography and measurement

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

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

4. Systematic paleontology

Order Scorpiones Koch, 1837

Parvorder Iurida Sologlad and Fet, 2003

Superfamily Scorpionoidea Latreille, 1802

Family Protoischnuridae de Carvalho and Lourenço, 2001

Genus *Protoischnurus* de Carvalho and Lourenço, 2001

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

Emended diagnosis (based mostly on the new specimen UFRJ-DG 101-Ac): scorpion of medium size; robust pedipalp with the chela, patella and femur bounded by thick, prominent carinae ornamented with several tubercles; chela with two robust tubercles proximally, adjacent to patella; carinae of pedipalp femur ornamented with thick tubercles; chela fixed and free finger each with a single row of denticles; tibial spurs absent from legs; trichobothrial pattern of basic type "C" sensu Vachon (1974); spiracles slit-like; pectines moderately large, with 14–15 teeth; sublateral carinae of tergite VII extend obliquely downward posteriorly to

meet the anterolateral border of metasoma segment I; no subaculear tooth on telson.

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

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

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

Emended diagnosis. As for genus.

Referred material. UFRJ-DG 101-Ac-a and -b, from the Macrofossil Collection, Department of Geology, Universidade Federal do Rio de Janeiro; a complete adult individual of *Protoischnurus axelrodorum* de Carvalho and Lourenço, 2001.

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

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

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

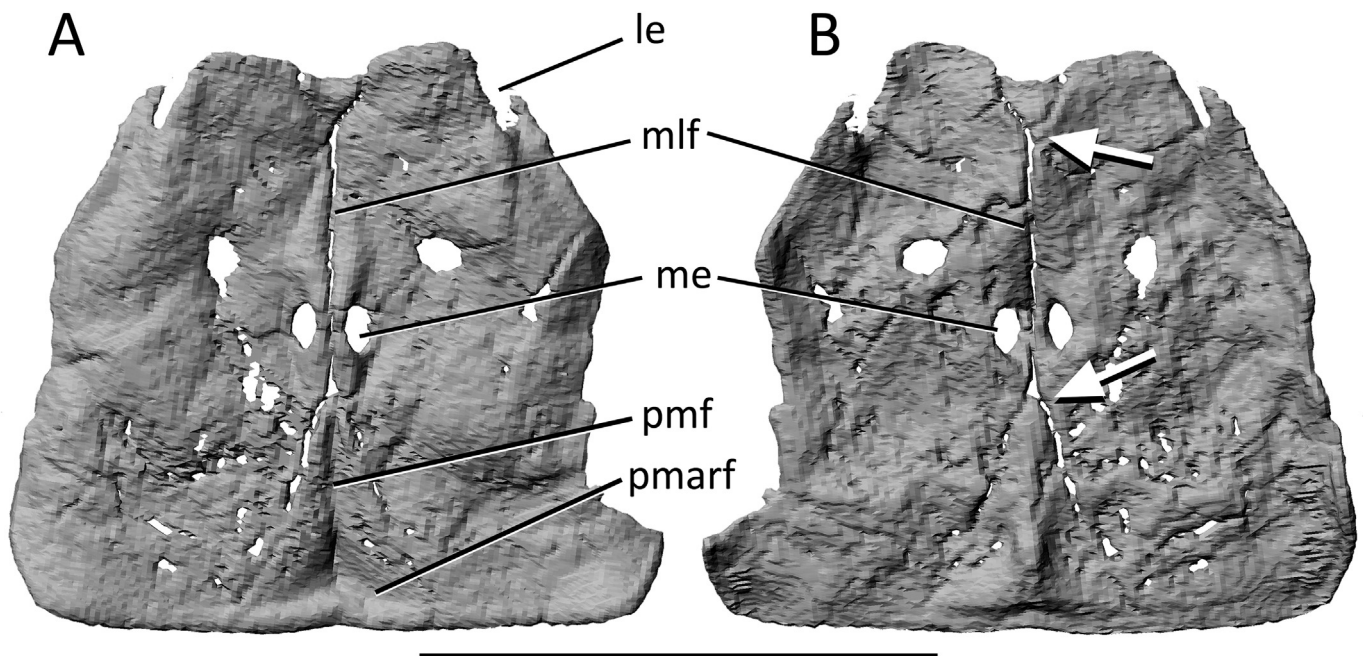


Fig. 4. A, B, UFRJ-DG 101-Ac-a, dorsal (A) and ventral (B) reconstructions of the carapace. Abbreviations: le, recess for lateral eyes; me, openings for median eyes; mlf, median longitudinal furrow; pmarf, posterior marginal furrow; pmf, posterior median furrow. Scale bar = 5 mm.

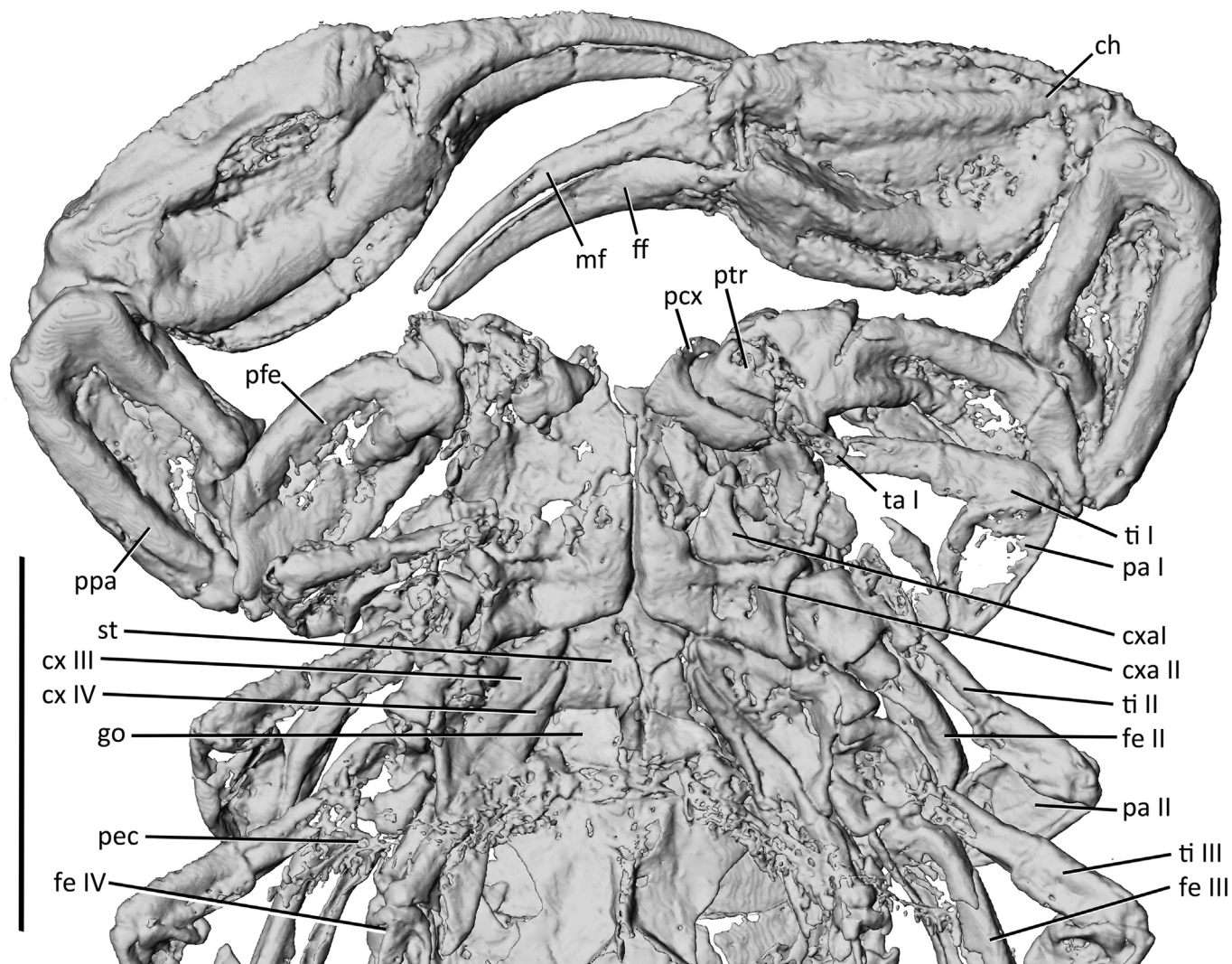


Fig. 5. Ventral view of specimen UFRJ-DG 101-Ac, made from combined reconstructions of part and counterpart. Abbreviations: cxa I, II, coxapophysis of first two legs; fe II–IV, femur of legs; ff, fixed finger of chela; go, genital operculum; mc, median carina of sternite 3; mf, movable finger of chela; pa I,II, patella of legs; pcx, pedipalp coxa; pec, pectines; pfe, pedipalp femur; ppa, pedipalp patella; ptr, pedipalp trochanter; st, sternum; ta I, tarsus of first leg; ti I,II,III, tibia of legs. Scale bar = 5 mm.

Carapace: The dorsal surface of the carapace is smooth, with total length of 5.2 mm, anterior width 5.08 mm, and posterior width of 6.29 mm (Fig. 4A, B). The carapace is strongly emarginated anteriorly and has paired notches anterolaterally, presumably for the lateral eyes (which are not preserved in the study specimen). Paired openings for the median eyes are located slightly anterior to the center of the carapace. A suturiform median longitudinal furrow is present, with anterior and posterior bifurcations (arrowed in Fig. 4B). Many Recent scorpionoid genera possess a similar suturiform median longitudinal furrow with Y-shaped branches at either end (Stockwell, 1989; Prendini, 2000). In *Protoischnurus*, the anterior longitudinal furrow extends posteriorly between the median eyes and then divides, forming an inverted Y-shape that terminates before reaching the posterior margin of the carapace. A wide, somewhat deep posterior longitudinal furrow is also present between the Y-shaped posterior branches, becoming broader posteriorly to form paired posterior marginal furrows like those found in many recent scorpions. A shallow paired furrow extends from the anterolateral border of each median eye towards a pair of large symmetrical openings located approximately half-way between the median and lateral eyes. These openings may represent scan or

image processing artifacts in thin or poorly mineralized regions of the carapace.

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

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

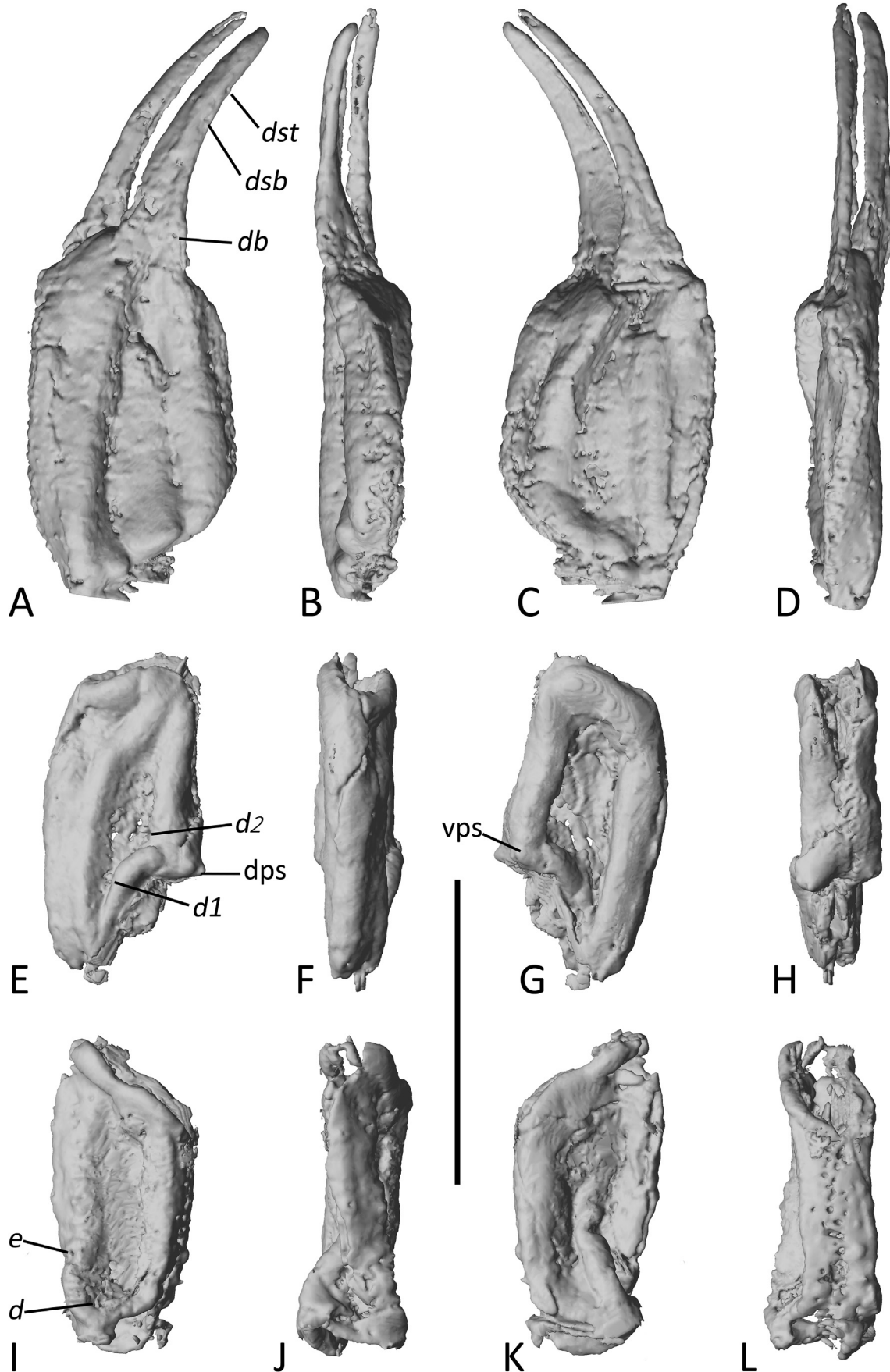


Fig. 6. UFRJ-DG 101-Ac. Left pedipalp elements; A-D, chela and movable finger; E-H, patella; I-L, femur. From left to right, views show dorsal, retrolateral, ventral, and prolateral aspects of each element. Abbreviations; dps, dorsal patella spur; vps, ventral patellar spur. Trichobothrial abbreviations;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

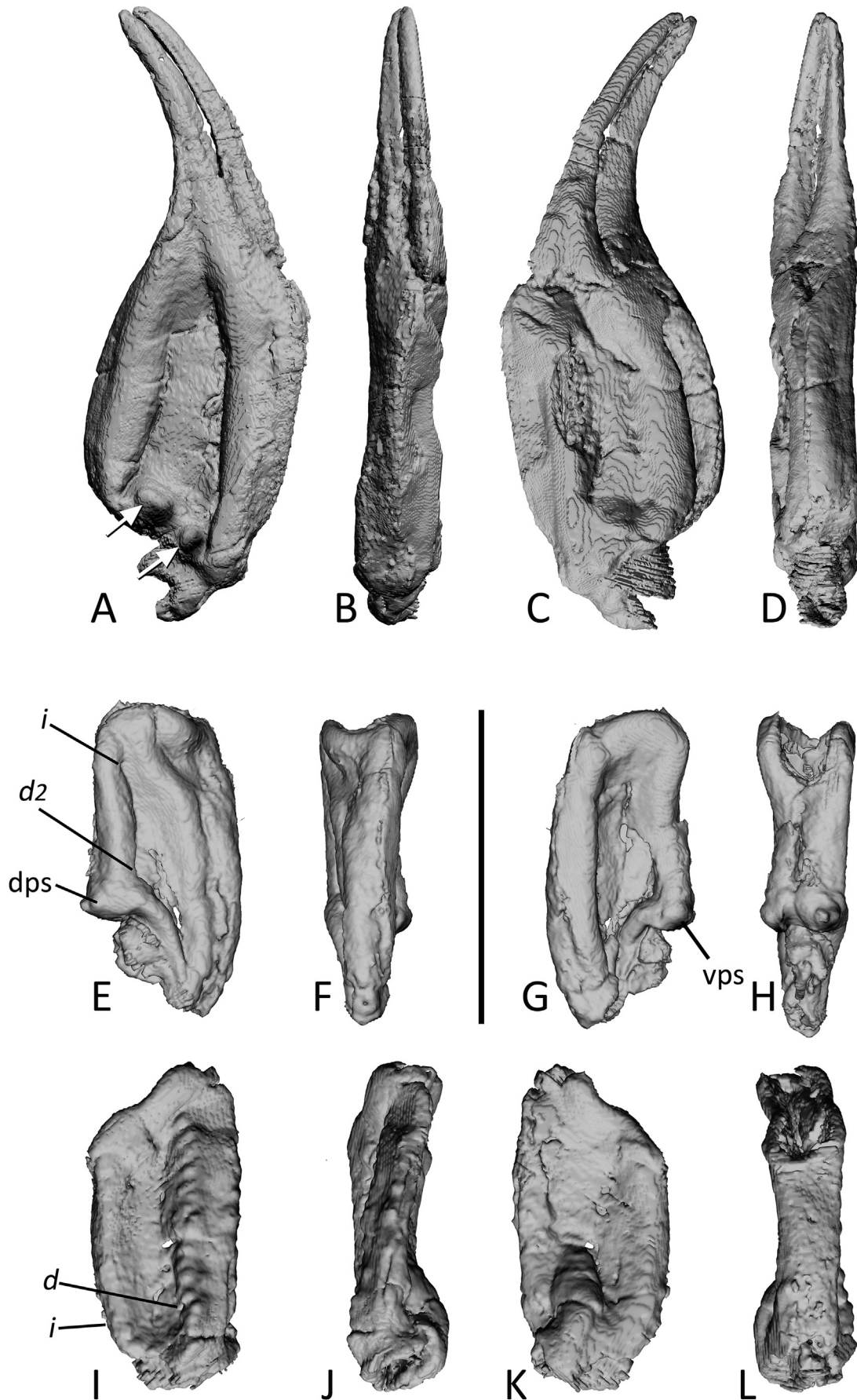


Fig. 7. UFRJ-DG 101-Ac. Right pedipalp elements. Arrangement and abbreviations as in Fig. 6. Robust dorsal tubercles of the chela are arrowed in A. Scale bar = 5 mm.

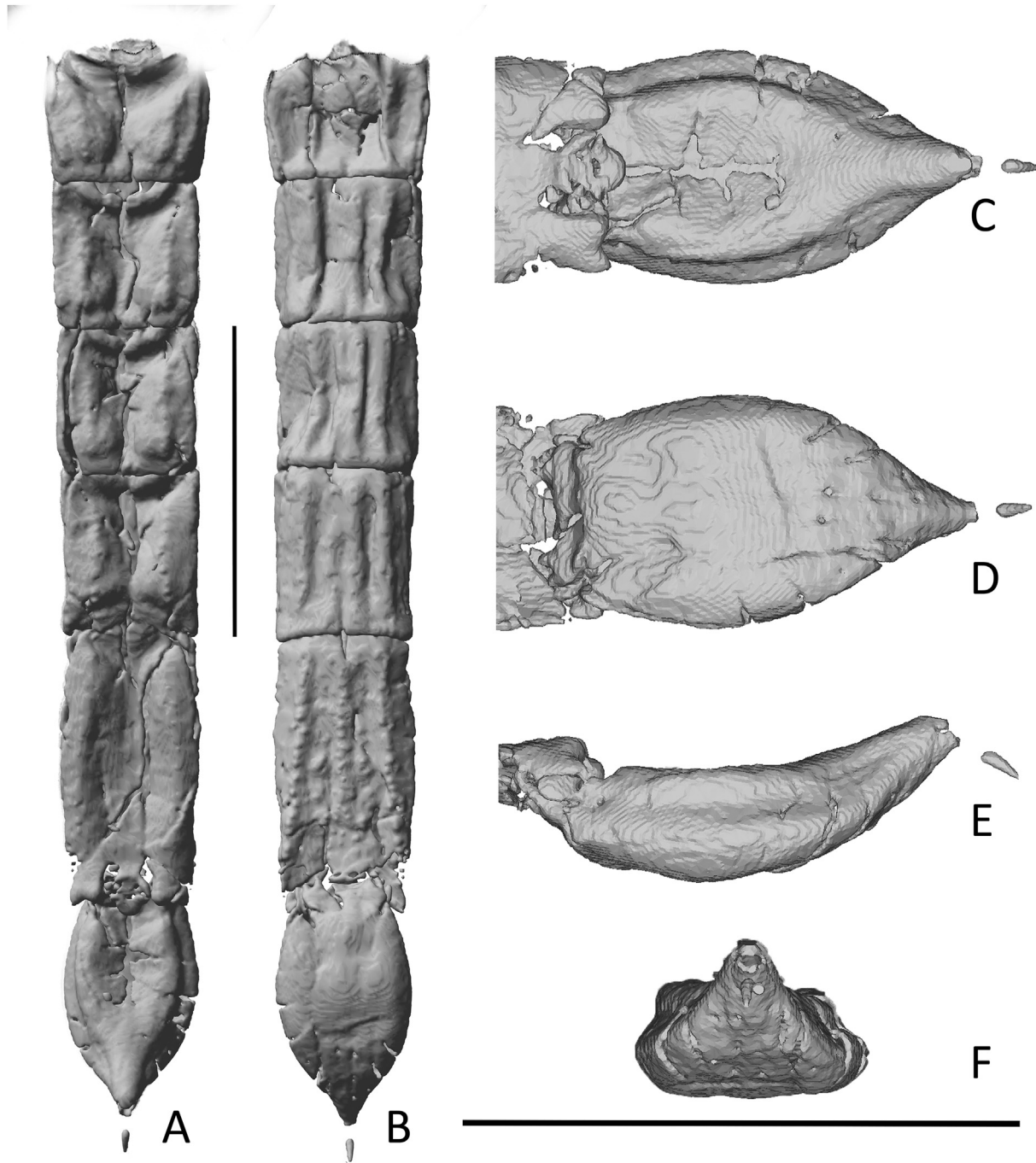


Fig. 8. UFRJ-DG 101-Ac; metasoma: A, B, metasomal segments I–V plus telson, with vesicle and part of aculeus in dorsal (A) and ventral (B) views; C–F, details of telson; C, dorsal view; D, ventral view; E, lateral view, left side; F, posterior view. Scale bars = 5 mm (vertical bar for A, B; horizontal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

originally present. Presence of a posterior emargination on the sternum has been considered a synapomorphy of the *lurida* (Soleglad and Fet, 2003a,b). The genital operculum is wider than long, with a slightly elevated anterior margin. A gap between the left and right parts of the genital operculum in the study specimen may represent a posterior emargination. A narrow median longitudinal carina is present on the anterior sternites, becoming indistinct on sternite V and absent on sternites VI and VII (Fig. 3B). This unusual feature is not present in the holotype of *Protoischnurus axelrodorum*, which, like some modern scorpions, has smooth and unkeeled sternites (de Carvalho and Lourenço, 2001). It is unclear whether this keel represents a morphological feature, or is an

artifact of preservation in the study specimen, so we refrained from including it in the emended diagnosis. Openings near the external margins of the sternites in the study specimen are interpreted as spiracular pores, although their shape was difficult to determine; they are slit-like in the holotype of *Protoischnurus axelrodorum*. The pectines are poorly resolved in the scan and the number of pectine teeth could not be accurately determined, although it appears to be greater than 10 (Fig. 3B).

Pedipalps: Individual elements of both pedipalps are illustrated here in dorsal, retrolateral, ventral, and prolateral views (Figs. 6, 7). The chela, patella, and femur are all bounded by thick and prominent carinae dorsally. The pedipalp coxa is covered dorsally by the

carapace, but can be observed in ventral view (Fig. 5). The chelicerae ought to be located close to the coxa, but these were not observed. Adjacent to the femur, the articular rim of the trochanter is raised and bears several low tubercles (Fig. 5). The femur is 6.32 mm long and 2.26 mm maximum width. The retrolateral surface of the femur bears rows of numerous dense tubercles along its dorsal and ventral margins (the dorsal row can be seen in Fig. 6I and the ventral row in 6J). The patella is 4.94 mm long and 2.67 mm maximum width. It bears somewhat prominent, rounded dorsal and ventral patellar spurs proximally (Figs. 6, 7E, G). The chela (including the fixed finger) is 8.65 mm long and 3.51 mm maximum width. The chela has two robust tubercles located proximally on its dorsal surface (arrowed in Figs. 6A, 7A), which represent vestigial subdigital and dorsal secondary carinae (for details, see Prendini, 2000). The fixed and movable fingers are of almost equal size, and both have sharp, weakly tuberculated cutting margins. The movable finger is narrow and elongated, with no basal or accessory teeth.

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

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

Metasoma: Successive metasomal segments become progressively longer posteriorly, but the metasomal width is consistent, with a very slight taper posteriorly (the width of metasoma segment I is approx. $0.2\times$ the length of the metasoma (excluding the telson); the width of segment V is approx. $0.15\times$). The last segment (V) is much longer than the previous ones, comprising approx. 34% of the metasoma total length (again excluding the telson). By contrast, segment I represents approx. 13%, segments II and III each form approx. 17%, and segment V represents approx. 19%. Paired longitudinal dorso-lateral carinae are present on each segment, bearing scattered low tubercles. Two apodemes are preserved at the end of the segment V and can be observed in dorsal view (Fig. 8A). On the ventral surface, metasomal segments I–IV have two pairs of longitudinal carinae (these are less distinct on segment I), including ventrosulmedian carinae close to the midline (Fig. 8B). No tubercles are evident on the carinae of segment I and II; one or two tubercles are present on the ventrolateral carinae in segment III and three or four in segment IV. By contrast, the ventrolateral carinae on segment V are divergent posteriorly and are densely ornamented with numerous small tubercles. No median ventral carina was observed except on segment V, which has a low median carina ornamented with small tubercles. The telson has a distinct peduncle, vesicle, and sting. The telson vesicle is elongated and laterally flattened (Fig. 8C–F). The sting is short (its tip appears to be separated from the rest of the telson in the reconstitution, possibly because the intervening region was poorly mineralized). A subaculear tubercle is absent.

5. Discussion

Morphological characters of extant and fossil organisms are crucial to establishing their systematic position, ecological role and evolutionary trends. Unfortunately, some kinds of data utilized in

phylogenetic analyses of modern scorpions are unavailable in fossils (e.g., 'soft' morphology such as reproductive organs, and molecular sequence data), while others can be problematic to observe (e.g., trichobothrial positions). Nevertheless, Legg et al. (2012) demonstrated that computed microtomography and 3-D imaging could provide greatly improved morphological resolution of Carboniferous scorpion fossils in sideritic matrix. The present study demonstrates the utility of computed microtomography in studying scorpion fossils preserved in limestones, and adds considerably to our understanding of the preservation and morphology of *Protoischnurus* from the Crato Formation of Brazil. Our observations support Schwermann et al.'s (2016) statement that mineralized fossils, even those with macroscopically poor preservation, can constitute a rich source of anatomical data for fossil arthropods when investigated using microtomographic methods. Our results also support McCoy and Brandt's (2009) proposal that fossil scorpion taphonomy can help distinguish between carcasses and molts.

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

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

Baptista et al. (2006, fig. 35) positioned *Protoischnurus* on the scorpionoid stem within Lurida, for which orthobothriotaxy Type C and a posterior emargination of the sternum were considered apomorphic (Soleglad and Fet, 2003a; characters 1[5], 63[1]). Both of these features seem to be present in *Protoischnurus*. Given that an extinct taxon can be placed definitively within a crown group only if it exhibits synapomorphies of one of its subtended groups (Friedman and Brazeau, 2010), both *Araripescorpius* and *Protoischnurus* can be considered members of the Lurida crown group,

apparently within different subtended groups (Hormuridae and Chactidae respectively), and *Protoischnurus* could be regarded as a stem hormurid.

6. Concluding remarks

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

Data availability

Data will be made available on request.

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