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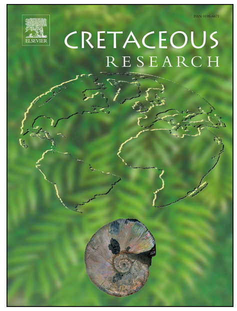

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Unusual soft tissue preservation in the Early Cretaceous (Aptian) crocodile cf. *Susisuchus* from the Crato Formation of north east Brazil

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A B S T R A C T

A new specimen of the neosuchian crocodylomorph, *Susisuchus* sp. from the Lower Cretaceous (Aptian) Crato Formation of Ceará, North East Brazil is remarkable for extensive preservation of the epidermis and limb musculature. The specimen comprises incomplete post-cranial remains, including an articulated sequence of thirteen thoracic vertebrae, a disarticulated pair of lumbar vertebrae and all four limbs articulated in varying degrees of completeness but divorced from the axial skeleton. Soft tissues are preserved in two distinct modes, in close association with the skeletal remains. An external mould of the dorsolateral scales of the trunk extends over a bedding plane surface while mineralisation of soft tissues preserving the musculature surrounds the left forelimb. Soft tissue preservation is extremely rare in crocodylomorphs and this is only the second report of soft tissue preservation in a crocodilian from the Crato Formation.

Keywords:

Crato Formation
Cretaceous
Crocodylomorpha
Neosuchia
Susisuchus
Soft tissue preservation

1. Introduction

A new specimen (UERJ-PMB R07) comprising the partial skeleton of a susisuchid crocodilian from the Crato Formation of north east Brazil is remarkable for the extensive soft tissue preservation intimately associated with the skeletal remains. Crocodilian remains are extremely rare in the Crato Formation (Salisbury et al., 2003, Frey and Salisbury, 2007, Figueredo and Kellner, 2009, Figueredo et al., 2011), which is otherwise better known for the abundance of its invertebrates (primarily insects, but also arachnids and decapod crustaceans (Bechly, 2007, Dunlop et al., 2007, Schweigert et al., 2007 respectively)). Vertebrates in the Crato Formation are diverse, including osteichthyans (Brito, 2007), amphibians (Baéz et al., 2009), turtles (Naish, 2007), lizards (Martill, 2007), pterosaurs (Unwin and Martill, 2007) and an ancestral snake (Martill et al., 2015). A wide variety of flora are also preserved including many early angiosperms (Mohr et al., 2007).

Soft tissue preservation has previously been reported in Crato Formation vertebrates, having been described for the head crests and wing membranes of the pterosaurs *Tapejara* (Frey et al., 2003a, b) and *Tupandactylus* (Kellner and Campos, 2007) and the limbs of the turtle *Araripemys* (Fielding et al., 2005). Soft tissues were found in the holotype of the neosuchian crocodile *Susisuchus anatoceps* as amorphous goethite stains, a result of weathering of low-fidelity mineralisation most likely by iron sulphides (Salisbury et al., 2003). Here we describe another example of cf. *Susisuchus* sp., in which soft tissues are preserved associated with the thoracic and appendicular skeleton. For a more detailed account of the palaeontology of the Crato Formation the reader is referred to Martill et al. (2007).

Abbreviations used

The specimen described here is deposited in the collection of the Departamento do Zoologia of the Universidade Estadual de Rio de Janeiro, R.J., Brazil, accession number UERJ-PMB R07. SMNK; Staatlisches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany. UFRGS; Laboratory of Vertebrate Palaeontology, Universidade Federal do Rio Grande do Sul, Porto Alegre, RGS, Brazil.

2. Locality and Geology

2.1 Locality

The new specimen was obtained by one of the authors (DMM) while on field work in the Araripe Basin in 2006. It was given by a quarry worker, who was digging limestone between the small towns of Nova Olinda and Santana do Cariri in the South of Ceará, north east Brazil. This area has been extensively exploited for laminated limestone and has proven to be one of the most productive sites worldwide for Lower Cretaceous non-marine fossils. The stone quarries are located on the flanks of the Chapada do Araripe, a large tableland dominated by Upper Cretaceous strata (Fig. 1 and 2). It outcrops around the Chapada do Araripe in both southern Ceará and Pernambuco, with possible equivalents in Piauí. It is missing in some places due to overlapping by younger strata. The formation can be traced extensively around the chapada, but is only excavated for paving stone in the area between Tatajuba, Santana do Cariri and Nova Olinda, and at one site near the town of Crato, but the vast majority of fossils are found in the Nova Olinda-Santana do Cariri region of Ceará. A large excavation in the Crato Formation at Barbalha for cement production does not yield abundant fossils.

(Fig. 1. Locality map)

2.2 Geological Setting and Stratigraphy

The Crato Formation is a heterolithic clastic/carbonate sequence of lacustrine, lagoonal and possibly deltaic facies. Extensive and labour intensive, manual quarrying of the Nova Olinda Member limestone at the base of the formation results in very many fossils collected by the quarrymen. Ever since the late 1980s these numerous quarries have been the source of many spectacular fossils (for a summary see Martill et al., 2007). These strata are dated as late Aptian by Batten (2007) on the basis of the palynoflora. For details on the stratigraphy of this unit and its areal extent see Martill and Heimhofer (2007).

The Crato Formation rests either unconformably on Neoproterozoic basement or conformably on strata of the Batateiras Formation (names vary depending on authors, e.g. Missao Velha Formation of Beurlen, 1962). Where it sits with stratigraphic conformity on older strata there appears to be a transition from mudstones and siltstones of the Batateiras Formation into laminated limestones. Such conformable sequences are best seen in the region around the town of Crato and near Nova Olinda. In many places, however, a topographic unconformity is present, representing a submerged palaeo-landscape of some considerable relief. This ancient terrain is composed of low grade metamorphic rocks with granitic intrusions and coarse, immature sandstones of the Cariri Formation that may have represented islands within the Crato Formation lagoon/lake system (Martill and Heimhofer, 2007).

The fossiliferous, laminated limestones of the Nova Olinda Member that form the fossil Lagerstätte are well exposed around Nova Olinda in many quarries and natural bluffs. It is also quarried near Crato, but elsewhere, although well developed, the limestones appear to be largely devoid of fossils.

(Fig. 2. Strat log)

3. Materials and Methods

3.1 Material

The new specimen, preserved on a typical (for the Nova Olinda Member) slab of cream coloured, laminated limestone has contrasting preservational styles (Fig. 3 and 4). The slab has a sub-triangular outline, with the specimen extending over the majority of its surface. Numerous pellet-like structures are scattered over the bedding plane surface, which is also typical, and distinctive for this unit. The specimen is remarkable for the exquisite preservation of epidermal scales of the body flank and dorsal surface as well as an intriguing preservation of soft tissues of the limbs. The scales of the trunk have been preserved as a soft tissue impression while the soft tissues of the right forelimb have been mineralised. Material similar to that around the right forelimb is preserved around the left femur however much of it appears to have been removed during preparation in the quarry with little material remaining. The epidermal scales are not, as might be supposed, moulds of the inferior surface of osteoderms, as in places overlapping sediment shows no bone material between the overlying and underlying lamina.

There are just two osteoderms preserved, both detached from the body. One displays its upper surface of small pits, while the other its lower surface which is smooth. All four limbs are preserved, with the forelimbs articulated and nearly complete with both manus. The hind limbs are less complete but include the femur, tibia and fibula, as well as fragments of the pelvis in the left hind limb. The right hind limb includes the tibia, fibula, metatarsals and disarticulated elements of the pes. The appendicular skeleton is detached from the axial skeleton however remains close to life position. The vertebral column is articulated for a length of thirteen thoracic vertebrae exposed in ventral view. There are two detached lumbar vertebrae lying to one side at the posterior end of the sequence.

There has been damage to the specimen caused by splitting of the slab during the excavation and in preparation, which has been poorly repaired with what appears to be an adhesive past. A gritty material has been used to fill in some damaged areas of the specimen and slab on both sides and several chisel marks have damaged part of the exposed soft tissues of the trunk. Some bones have been repaired and glued into place as they appear to have dropped from the slab during preparation.

3.2 Methods

The specimen has been examined under UV light and by light and scanning electron microscopy. No additional preparation was performed on the specimen in order not to further damage the surface with soft tissues, but small samples of the soft tissue of the forelimb were removed for analysis by scanning electron microscopy and energy dispersive x-ray spectroscopy. Samples examined by electron microscopy were mounted on flat aluminium stubs, sputter coated with a gold-palladium alloy and examined using a JEOL JSM 6100 machine. The specimen was photographed using an Olympus E-420 DSLR camera and images were processed using Adobe Photoshop CC 2015.

(Fig. 3. Specimen photo)

(Fig. 4. Schematic)

4. Description

4.1 Systematic Palaeontology

Crocodyliformes Hay, 1930

Mesoeucrocodylia Whetstone and Whybrow, 1983

Neosuchia Benton and Clark, 1988

Susisuchidae Salisbury et al., 2003

cf. *Susisuchus* Salisbury et al., 2003

Specimen: Partial skeleton of a neosuchian including axial and appendicular elements of both girdles and areas of extensive soft tissue preservation referred to cf. *Susisuchus* sp. Accession number UERJ-PMB R07 (Universidade do Estado do Rio de Janeiro).

UERJ-PMB R07 is identified as a crocodyliform due to the presence of typical crocodilian osteoderms with smooth basal surface and pitted epidermal surface shown, and a crocodilian type squamation of the trunk integument. The amphicoelous vertebrae show that it belongs in Mesoeucrocodylia. The clade Neosuchia is diagnosed on cranial features and features of the neural spines (Benton and Clarke, 1988), both elements that are not visible in the specimen. A neosuchian affinity is assumed based on its identification and hinted at by the neosuchian-like proportions of the limbs with a forelimb-hind limb ratio of approximately 0.85.

Its familial placement within Susisuchidae is based upon the same features used to diagnose the specimen as cf. *Susisuchus*. In comparing the specimen with the two crocodilian genera reportedly previously from the Crato Formation by Salisbury et al. (2003) and Frey and Salisbury (2007) UERJ-PMB R07 appears closer to *Susisuchus* than *Araripesuchus*. Both taxa are diagnosed primarily on cranial features not visible in the specimen. Nevertheless, other diagnostic features are present in the forelimbs of UERJ-PMB R07; the presence of unguals only on manual digits I and II, and the maximum width of the proximal extremity of the ulna is approximately twice the minimum width of the ulna shaft, the distal extremity cannot be confidently compared due to damage. Furthermore, the limb proportions of UERJ-PMB R07 are more closely allied to those of *Susisuchus* and so we here refer the specimen to cf. *Susisuchus* sp. A palaeohistological study on *Susisuchus* has identified the animal as a dwarf taxon, markedly smaller than other crocodylomorphs from the Cretaceous (Sayão et al., 2016), and consequently the new specimen is considered a sub-adult due to its size.

4.2 Description

Axial skeleton

Lumbar vertebrae. Two lumbar vertebrae are articulated and preserved in ventral view (Fig. 5), detached from the axial skeleton but still in close association with the thoracic vertebrae. One lumbar vertebra is preserved as a broad, flat shelf, the transverse processes extending from the ventral surface of the centrum and broadening distally with an aspect ratio of 24:9 for the total width: length. The second lumbar vertebra appears more typical of other centra however matrix exposure obscures other details.

Thoracic vertebrae. An articulate sequence of thirteen thoracic vertebrae are preserved, exposed in ventral view. These are considered thoracic vertebrae based on their position relative to the limbs of the animal and the presence of articular facets for the ribs present on the anterior edge of the transverse processes of several vertebrae. The centra of the eight posterior-most thoracic vertebrae are preserved but the ninth centrum has been damaged, lacking the anterior half. The centra of the four anterior vertebrae are not present, likely in the missing counter slab, exposing the mineralised neural canal parallel to the bedding surface.

Several of the posterior thoracic vertebrae are damaged revealing detail of the articulatory surfaces. They are amphicoelous indicating mesoeucrocodylian affinities (Frey and Salisbury, 2007). The transverse processes become shorter and thinner towards the cranial end of the preserved sequence. Further anterior vertebrae may be preserved in the sequence but preserved on the counter slab.

(Fig. 5. Vertebrae photo and schematic)

Appendicular skeleton

Pectoral girdle. A thin, sheet-like fragment of bone overlies the proximal right humerus and is considered to be part of the pectoral girdle. Although it lacks landmarks and cannot be confidently identified, it is likely a portion of the right scapula due to the arrangement of the bones. Other fragments of bone are also present between the forelimbs but are similarly unidentifiable and may be part of the proximal right humerus, the pectoral girdle or osteoderms.

Forelimb

Humerus. Both humeri are preserved and exposed in posterior view (Fig. 6). They are almost complete missing just the proximal end in the left humerus, which is damaged and is obscured by matrix. Despite fragments of the pectoral girdle obscuring much of the proximal third of the right humerus, the point at which it terminates appears visible before it extends beneath the soft tissue impressions. Using the visible range, the humerus measures at 45 mm, here used as an approximate total length for the humerus.

The corpus is slender, smooth and round in cross-section with a diameter of 4 mm, roughly one third the width of the distal end. In the right forelimb, where much of the corpus is broken and absent, a cross-section reveals the interior of the bone and a mineral filled medullar cavity. The distal end of the humerus appears typical of *Susisuchus anatoceps* with two distinct ridges on the medial and lateral side extending from both distal condyles (Salisbury et al. 2003), more pronounced in the left humerus than in the right. These extend for 12.5 mm, approximately one quarter the length of the humerus, forming a concave facies.

Ulna. Both ulnae are damaged due to prior preparation with the right ulna lacking its distal third and a section of the proximal corpus, but an impression of the bone remains. The corpus of the right ulna has been broken off and glued back in place but appears displaced at the distal end. The proximodistal length of the right ulna is 29 mm, with an ulna-humeral ratio of 0.66 and a corpus minimum width of 2mm. Both the proximal and distal ends are broad compared to the shaft, the proximal being the broader end twice the width of the corpus, the distal extremity damaged but similar in width. Both heads have convex facies but are otherwise featureless.

Radius. As with the ulnae the radii have been damaged. The distal end of the right radius has broken off and been glued back into place, deep scratches extend along the length of the corpus. Similar to the right humerus, a broken cross-section exposes the mineral filled medullar cavity and the solid nature of the bone wall. In the left radius the corpus has been broken off and glued back into place, a gritty material has been added to the glue around the distal end displacing the bone.

The radius is slightly shorter than the respective ulna, approximately 95% its proximodistal length but the corpus is also 2mm thick. Both heads are smaller than in the ulna, the distal head 2mm thick and the proximal 4mm thick. The articular ends of both radii are flat and the proximal end of the left radius is inflected dorsally. This is not present in the right radius and may be an artefact of damage to the rock, where it has been repaired, or to the bone where it has been broken and glued.

Carpals. Both the radiale and ulnare are preserved in the right forelimb but are absent in the left. Both are small elements, the radiale measuring 7.5 mm in length, the ulnare measures 5 mm in length. The radiale is a flat, hourglass-shaped element with a minimum thickness of 1.5 mm. The proximal end is wider than the distal end at 3.5 mm compared to 3 mm. The ulnare is also hourglass-shaped with a less pronounced distal end, just 1.5 mm wide compared to the minimum width of 1 mm and the proximal end measuring 2.5 mm wide.

Manus. Both manus are preserved in association with their respective limbs and are largely articulated and almost complete but the left manus is detached from the forelimb but still closely associated with it. In the left manus, metacarpals II-V are present, and in the right metacarpals I-III and V are present. Metacarpal IV may also be present in the right manus but is obscured by sediment and other metacarpals and so cannot be confidently described as either a metacarpal or a phalanx. The metacarpals are typically long and slender with lengths of 3.5 mm to 8 mm and thicknesses of 0.5 – 1.5 mm. Metacarpal I is both the shortest and thickest metacarpal.

In the right manus all digits are preserved but in varying completeness. Digits I and II are the only two complete digits comprising of two and three elements respectively. The ungual of digit I is a blunt, thick element compared to the other unguals with a very gentle curvature whereas digit II's ungual is partially obscured by sediment. Digit III comprises three phalanges but lacks an ungual as is diagnostic of *Susisuchus*. Digit IV consists of two medial phalanges adjacent to digit III, digit V is preserved as phalanx 1 and a mould of phalanx 2. In the left manus digits I-III and V are preserved but no elements from digit IV are identified. Both phalanges are again preserved of digit I, however phalanx 1 is preserved only as the distal portion. Three phalanges are preserved in digit II with a less obscured view of the ungual, which is more strongly curved than in digit I and is significantly sharper. Three phalanges are preserved in digit III and two from digit V.

(Fig. 6. Forelimb photo and schematic)

Pelvic girdle. A broken piece of sheet-like bone is preserved adjacent to the right femur, pressed against the proximal end. It is considered to most likely be a portion of the pubis based on the general morphology but it lacks useful landmarks as is typical of the cranial end of the pubis. A cross-section of bone is visible in an adjacent surface of the rock and is likely a fragment of the ischium, but it cannot be confidently identified.

Hind limb

Femur. The left femur is preserved and is complete in length however the proximal end is both obscured in part by a fragment of the pelvic girdle and has been damaged, the femoral head split along the bedding plane. It appears to still be in association with the pubis. The femur is similar in length to the humerus, measuring slightly shorter proximodistally at 44.5 mm long. The corpus is smooth and round in cross-section and as thick as the humeral corpus at 4 mm, but is curved posteriorly. The distal end is broad, almost three times the thickness of the corpus, with distinct medial and lateral ridges extending for 11 mm.

Tibia. The tibia is a long, straight bone, approximately 90% the proximodistal length of the femur at 39.5 mm long. It is preserved in both limbs but is significantly damaged in the right hind limb, the proximal third having been broken off and repaired. The corpus is slender a 2.5 mm thick with a broad, robust and curved proximal head and a broad, flat distal head, both almost three times as wide as the corpus is thick. The surface is smooth except for at the proximal head of the right tibia where striations extend lengthways, parts of the head have a fibrous texture, however, this may be a result of degradation. Damage at the distal end of the left tibia reveals a hollow interior.

Fibula. The fibula is present in both hind limbs, complete in the left, although the distal end is damaged where the rock has been cut, and heavily damaged along the corpus in the right, the distal head broken off lying adjacent to the corpus. The fibula is slightly shorter than the tibia at 39 mm long and is slender, the corpus 2 mm thick and the distal head 4 mm thick. The proximal head is obscured by the tibia in the left hind limb but is visible in the right measuring 2.5 mm thick.

Tarsals. Tarsals are only preserved in the right hind limb. They are small, smooth, round bones, the lateral tarsal is the smaller of the two. The medial tarsal is a rounded square bone, 7.5 mm long and 5 mm thick. The lateral tarsal is semi-circular with a flattened lateral face, only 4.5 mm long and 3 mm thick.

Metatarsals and pes. Three metatarsals are preserved in the right hind limb. They are long, slender bones, all measuring at least 22 mm in length and between 1.5 mm and 2 mm thick. The proximal end is very broad in metatarsal I, three times as thick as the corpus and twice as thick as metatarsal III, the proximal head of metatarsal II obscured by metatarsal I. The distal ends of metatarsal II and III are damaged and incomplete while metatarsal I has a broad distal end, 4 mm wide, with a pit in the centre of the head. Damage to metatarsal III at the distal end reveals a cavity. Phalanges from the right pes are preserved but disarticulated and overlapping each other at the distal end of the metatarsals. A single ungual is identifiable disassociated from the pes, it is a heavily curved, sharp bone 7 mm in length.

(Fig. 7. Hind limbs photo and schematic)

Osteodermal skeleton

Two osteoderms are identified in association with the specimen, one located near the left hind limb but is relatively distant from other skeletal elements except for unidentifiable bone fragments, potentially other osteoderms. This osteoderm has a rounded margin as well as typically crocodilian pitting of the dorsal surface. The rounded margin suggests that this osteoderm was probably an accessory osteoderm of the dorsal body shield (Salisbury et al., 2003). The osteoderm appears to be broken during preparation.

A second osteoderm is located adjacent to the distal left humerus and is exposed in ventral view. It is identified as an osteoderm despite the unfavourable view based upon the uneven margin consistent with the pitting of osteoderms. The surface exposed is smooth and rectangular in shape, however, the osteoderm may extend further beneath the humerus too. It cannot be confidently identified based upon the lack of landmarks present on the ventral view.

5. Results

5.1 Light microscopy

Microscopic analysis was utilised to examine the enigmatic nature of the soft tissues surrounding the right forelimb. The material is a mixture of rounded to sub-angular grains ranging from 0.5 mm to 2.0 mm in diameter. Microscopic analysis of this mineralised material alleviated concerns that it may have been an artificial cement, these concerns were disproved by the relationship of the grains with the skeletal elements and the surrounding limestone. The mineralogy is seen growing around the skeletal elements, around both sides and underneath, where the humeral corpus and the distal corpus and head of the ulna is missing the same granular mineralogy is observed on the underside (Fig. 8A). Individual grains are also observed grown into the surrounding rock (Fig. 8B). The grains appear to consist of calcite, silicified material and fragments of bone. The granular material is a mix of brown, orange and black grains of calcite and grey siliceous grains.

(Fig. 8 Microscopy photos)

5.2 SEM Analysis

An SEM analysis was carried out on the mineralogy of the soft tissues surrounding the right forelimb. The grains analysed were a mixture of rounded grains and irregularly shaped grains (Fig. 9). All of the grains studied appear to have a similar structure despite variation in shape. The surface of the grains is typically smooth and undulating forming a shell-like structure, some of these surfaces also include small holes only a few micrometres across covering the surface (Fig. 9). Orthogenic calcite crystals are also noted, growing on these grains (Fig. 9).

(Fig. 9 SEM plate)

5.3 EDX spectrometry

Further compositional analysis was carried out using EDX spectrometry. The specimen was prepared using a gold-palladium coating and as such associated peaks are ignored in readings. The primary composition of the sample was found to be calcium, carbon, oxygen and iron (Fig. 10A, B), attributed to calcite and iron oxides. Silicon is identified as the next most common element, likely a result of the silicification noted around some areas of the slab, including around several elements of the fossil. Other elements found in smaller quantities include manganese, zinc, chlorine, barium, lead, potassium and copper (Fig. 10C, D), all associated with other minerals found at lower strata within the Crato Formation.

(Fig. 10 EDX spectrometry)

5.4 Ultra-Violet Imaging

Ultra-violet imaging of the specimen was undertaken to aid in the identification and observation of skeletal elements and to identify if any mineralised tissues were present in association with the soft tissue impressions of the trunk. Skeletal elements fluoresced under ultra-violet lights, allowing easier analysis of elements difficult to observe under normal lighting (Fig. 11A, B). The soft tissue impressions however, did not fluoresce, nor did the mineralised material around the right forelimb (Fig. 11B). The similar mineralised material around the right hind limb does fluoresce however (Fig. 11A). Silicified sediment fluoresced around the right manus, closely following the soft tissue outline, and in the area surrounding the right hind limb.

(Fig. 11 UV images)

6. Taphonomy

6.1 Preservation

All of the skeletal elements present in the specimen are preserved as three-dimensional brown biominerals. Elements are situated relatively parallel to the bedding plane except for the proximal and distal vertebral elements, which penetrate into the sediment. The preserved bones are typically smooth and solid with the exception of the right tibia and fibula in which the proximal and distal heads have a fibrous texture. Where the femoral head has been damaged in the right hind limb, the interior appears crystalline with dendrites inside the bone. Where the humerus and radius of the left forelimb are damaged, however, the bone appears consistent with the exterior with a mineralised medullar cavity. The neural canal of the anterior thoracic vertebrae appears to have been infilled with calcium carbonate and is slightly more orange than the surrounding limestone.

Soft tissue preservation is reported in two modes in this specimen. An impression of the dorsolateral integument of the trunk has been preserved on a bedding plane extending from around the eighth preserved thoracic vertebra to the left forelimb (Fig. 3 and 12). The impression shows detail of the specimen’s scale arrangement. Ultra-violet imaging reveals that there are no traces of mineralised soft tissues in association with the integument. The other form of soft tissue preservation, unique to this specimen in the Crato Formation, is the enigmatic mineralised material surrounding the right forelimb from the proximal head of the humerus to the wrist (Fig. 3 and 6). Similar mineralisation is observed around the femur of the right hind limb but notably less is preserved, largely as orange-brown staining, possibly removed during preparation (Fig. 7). The mineralogy is described as primarily calcium carbonate (Fig. 10 A-B) however the variety of minerals seen in some samples (Fig. 10 C-D) is likely the result of material from lower strata being eroded out and remineralised here. This material is described here as mineralised musculature due to a consistent texture observed in the grains resembling the striations of muscles.

(Fig. 12 soft tissue impression photos)

6.2 Taphonomy

The cause of death of the animal is unknown, as they are only partial remains without any indicative features it is impossible to determine. However, given the condition of the specimen it is probable the animal was dead prior to its arrival in the lagoon. *Susisuchus anatoceps* has been described as a semi-aquatic crocodilian, probably inhabiting a fluvial setting relatively near to the lagoon (Salisbury et al. 2003) where the animal died and was subsequently washed into the lagoon. It is possible that the transportation and deposition of the specimen could be sufficiently traumatic to result in the damage and disarticulation observed in the dermal skeleton and axial skeleton. Given the relative good condition of the specimen it is unlikely that the carcass was scavenged or predated upon. Whatever the cause and mode of transport, the damaged carcass must have been held together by skin and sinew. As the counter slab is missing it is unknown as to how complete the specimen could be.

Presumably the specimen arrived at the lagoon in a condition similar to that seen fossilised. Anoxia in the lagoonal bottom waters would have inhibited macroscavengers, and may also have delayed bacterial degradation. Despite some damage and disarticulation of the specimen soft tissues did still remain on at least the left forelimb and on the flank of the torso. The soft tissue of the torso, however, was damaged and torn from the skeletal component, hanging from it as a sheet of flesh or skin or both. This could potentially have occurred when the dermal skeleton disassociated from the specimen. The forelimbs of the animal, however, were in good condition, fully articulated and with the musculature untouched in the left forelimb at least. In order to preserve these soft tissues, it is necessary that the specimen would have been buried rapidly after transportation. This is due to the rapid disarticulation and decay crocodilians undergo if not prevented from floating (Syme and Salisbury, 2014).

Reduced decay in the anoxic bottom waters of the Cretaceous lagoon permitted the mineralisation of soft tissues (Heimhofer and Martill, 2007). As the sediments lithified an impression (external mould) of the torso integument was left in the rock, possibly with mineralised tissues too, however if these were present that have since been eroded away. At the same time the soft tissues of the left forelimb were mineralised, possibly as a result of anaerobic, microbial activity, preserving the musculature and sequestering minerals and elements present in the lagoon as available resources. During this time the slowly decaying organism acted as a nucleus for silicification around the manus of the left forelimb and the left hind limb.

7. Discussion

Presently two crocodilian species in two genera have been reported in the Crato Formation: *Susisuchus anatoceps* (Salisbury et al., 2003) and *Araripesuchus* sp. (Frey and Salisbury, 2007). As previously mentioned, the Crato Formation has not yielded many crocodilians in the past, besides the specimen described here there are three other specimens of *Susisuchus anatoceps* reported (Salisbury et al., 2003, Figueiredo and Kellner, 2009, Figueiredo et al., 2011) and only one specimen of *Araripesuchus* sp. (Frey and Salisbury, 2007). This scarcity in specimens is likely a result of the animals avoiding the lagoon due to their inferred lifestyles, *Susisuchus anatoceps* as a fluvial semi-aquatic animal and *Araripesuchus* sp. as a terrestrial hunter or forager (Frey and Salisbury, 2007).

Despite the scarcity of crocodilian remains in the Crato formation soft tissues have previously been reported in the holotype specimen of *Susisuchus anatoceps* (SMNK-PAL 3804) and could potentially be present in *Araripesuchus* sp. (SMNK-PAL 6404). SMNK-PAL 3804 is described as having orange-brown stains, restricted to the forelimbs, the right manus and cranium, which are considered to be the result of goethitic weathering of pyritised soft tissues (Salisbury et al., 2003). SMNK-PAL 6404 however is noted by the authors as having a partial outline of the belly region preserved as a dark stain which may be preserved soft tissues.

Unlike either of these specimens, this specimen (UERJ-PMB R07) is preserved with two different modes of soft tissue preservation and is far more extensive in the amount preserved. The first mode of soft tissue preservation, the mould of the dorsolateral integument of the skin (Fig. 12), is a typical form of preservation and is noted in other specimens from the Crato Formation and other localities (Martill et al., 2007). The second mode of soft tissue preservation, the mineralisation of the soft tissues around the right forelimb (Fig. 6), proves far more enigmatic. This kind of mineralisation is not recognised in any other specimen described from the Crato Formation and is believed to be the first account of its occurrence.

The cause of this mineralisation is currently unknown but we hypothesise that it is still likely a result of anaerobic bacterial decay in the anoxic bottom waters of the lagoon.

This resulted in minerals in the water, eroded from lower strata in the formation, being used in the mineralisation process. No other fossils looked at from the Crato Formation appear to demonstrate this mode of soft tissue preservation, as such it is considered a rare occurrence for the formation suggesting that the conditions that generate this mineralisation were similarly rare in the lagoon or that such conditions are not conducive to fossilisation. It is important to further investigate the occurrence of this mode of preservation in the Crato Formation and other formations to better understand the taphonomic pathway in effect.

8. Conclusions

UERJ-PMB R07 is considered here to be the fourth specimen of *Susisuchus* from the Crato Formation diagnosed using features of the forelimb. The specimen is relatively intact and provides new details on the anatomy and morphology of *Susisuchus*. This is the first specimen of *Susisuchus* to be reported with hind limbs in association with diagnostic material, the only other instance of a hind limb being described as a single, isolated limb (Figueiredo and Kellner, 2009). This specimen also demonstrates exquisite soft tissue preservation with the most extensive amount preserved in a crocodile from the Crato Formation. It is preserved as both a mould of the dorsolateral integument of the torso and as enigmatic mineralised soft tissues around the right forelimb. The mineralised material represents a previously unseen type of preservation for the formation and has been examined using light microscopy, UV imaging, scanning electron microscopy and energy dispersive X-ray spectrometry. This has elucidated the composition and relationship of the material with the specimen but its origin remains poorly understood.

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FIGURE CAPTIONS

Fig. 1. Locality map of the aerial extent of the Araripe Basin of North East Brazil. The new specimen was collected from a quarry between Crato and Nova Olinda.

Fig. 2. A stratigraphic log of the Crato Formation as exposed approximately 4 km south of Nova Olinda, Ceará, Brazil. The exposure comprises the lower three Crato Formation member: the Nova Olinda Member, a homogenous laminated limestone; the Caldas Member, heterolithic strata of mudstone, silts and siltstone; and the Jamacaru Member, a sequence of alternating laminated limestones and mudstone. (Heimhofer et al., 2010)

Fig. 3. The new specimen of crocodylomorph UERJ-PMB R07, here referred to *Susisuchus* sp. (Scale bar: 10 mm).

Fig. 4. A schematic representation of UERJ-PMB R07; *Susisuchus* sp. (Scale bar: 10 mm). *Abbreviations used: Adhes.:* Adhesive. *Ost.*: Osteoderm. *Fem.*: Femur. *Fib.*: Fibula. *Hum.*: Humerus. *M. Tars.*: Metatarsals. *Neur. Can.*: Neural Canal. *Pec. Girdle*: Pectoral Girdle. *Pub.*: Pubis *Tars.*: Tarsals. *Trans. Proc.*: Transverse Process. *Vert.*: Vertebra. *L.*: Left. *R.*: Right.

Fig. 5. A: Thoracic and disarticulated paired lumbar vertebrae of UERJ-PMB R07 preserved in ventral view. **B**: A schematic diagram of the vertebral elements of UERJ-PMB R07. (Scale bar: 10 mm).

Fig. 6. The forelimbs of UERJ-PMB R07. **A**, The right forelimb surrounded by preserved soft tissues with a fragment of the pectoral girdle covering the proximal humerus. **B**, A schematic diagram of the right forelimb. **C**, The left forelimb with an isolated, disarticulated osteoderm. **D**, A schematic diagram of the left forelimb. (Scale bar: 10 mm).

Fig. 7. The hind limbs of UERJ-PMB R07. **A**, The left hind limb. Elements of the pelvic girdle are preserved around the proximal femur and soft tissue mineralisation is noted around the femur. **B**, A schematic diagram of the left hind limb. **C**, The right hind limb with surrounding silicification. **D**, A schematic diagram of the right hind limb. (Scale bar: 10 mm).

Fig. 8. A, The mineralised soft tissue of the right forelimb extending beneath the bone, as exposed beneath the broken humerus. (Scale bar: 5 mm) **B**: Individual grains in the mineralised soft tissue growing into the surrounding mineral matrix. (Scale bar: 2 mm).

Fig. 9. SEM images of the soft tissue material surrounding the right forelimb. **A-C,** Grains of mineralised material showing a rounded, irregular morphology. (Scale bar: **A**, 200 µm **B**, 600 µm **C**, 600 µm) **D**, Detail of the crust of the grains showing the porous surface. (Scale bar: 200 µm) **E-F**, Orthogenic calcite growths observed on grains, typically on broken surfaces. (**E**, Scale bar: 60µm **F**, 100 µm).

Fig. 10. A-B, Results of EDX analysis of the mineralised material surrounding the right forelimb showing the primary composition of grains as calcium carbonate and iron oxides. **C-D,** Results of EDX analysis demonstrating the variety in elemental composition that occur less frequently in the mineralised material surrounding the left forelimb, typically found on the surface of grains.

Fig. 11. UV imaging using a green filter. **A,** The right hind limb, with surrounding possible soft tissue and adjacent thoracic vertebrae. (Scale bar: 10 mm) **B,** The right forelimb, surrounding soft tissue and silicified sediment. (Scale bar: 10 mm).

Fig. 12. A, The soft tissue impression of the scales of the dorsolateral surface of the trunk. (Scale bar: 10 mm) **B,** The soft tissue impression of the trunk scales under high angle lighting highlighting its topography. (Scale bar: 10 mm).


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Crato
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BASIN
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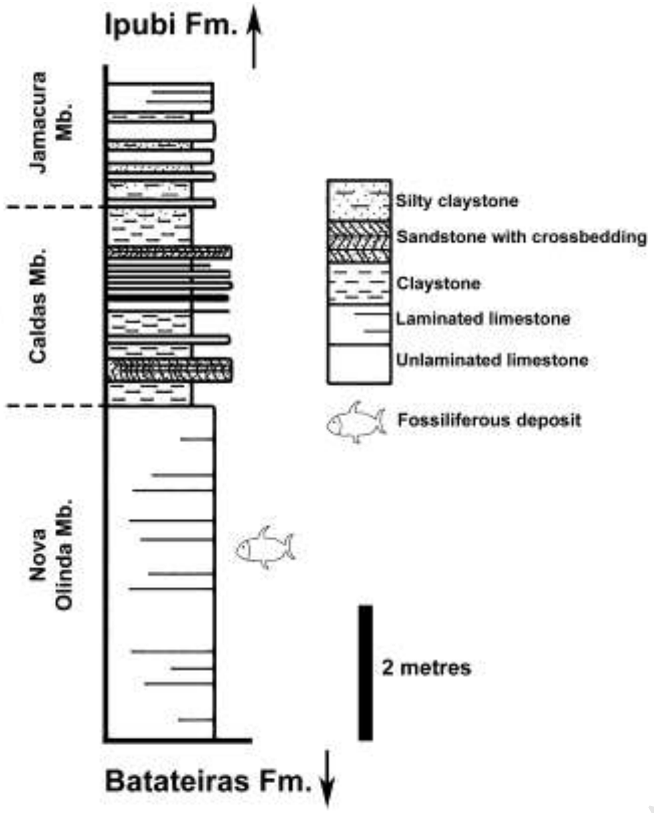

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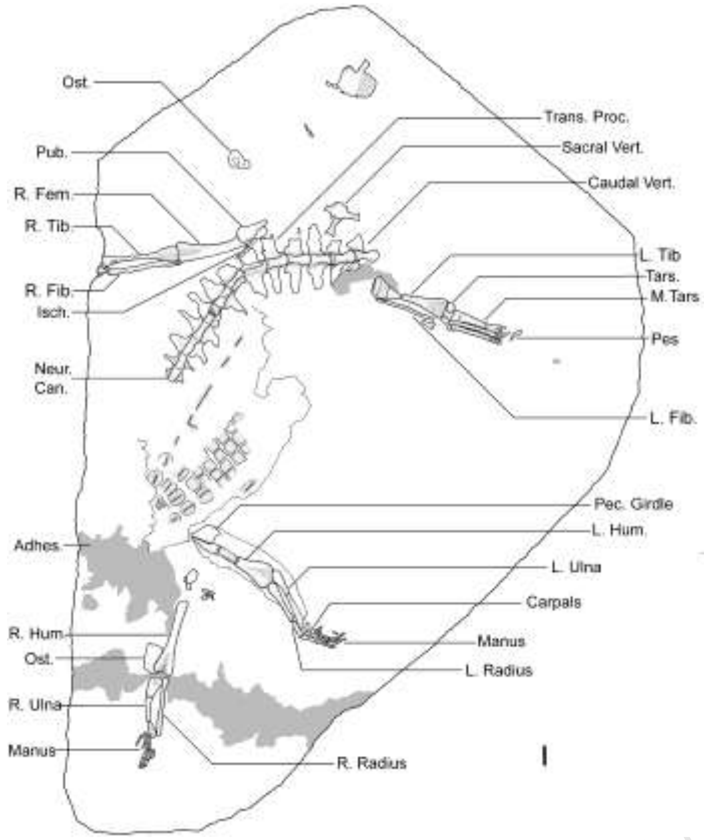
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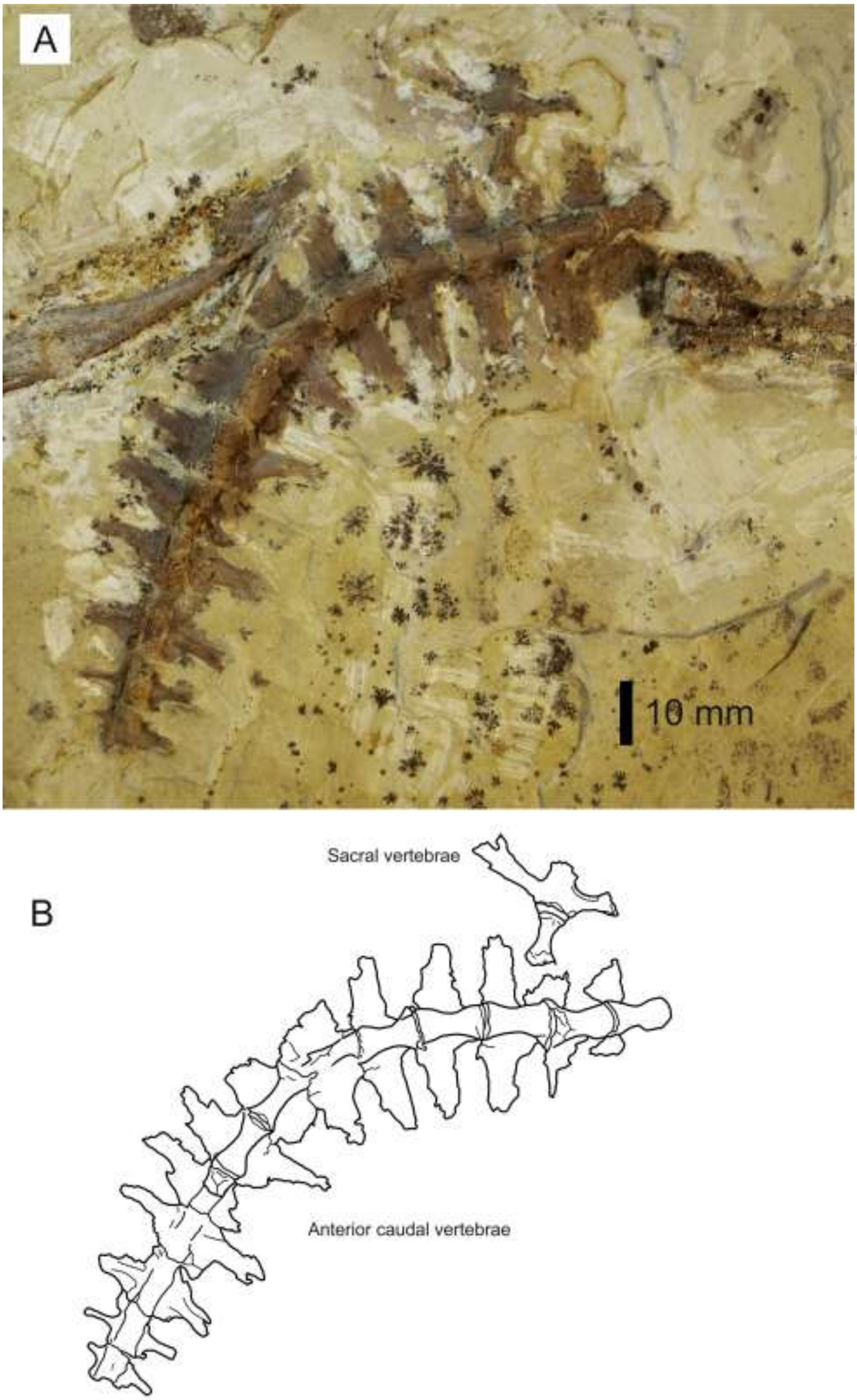
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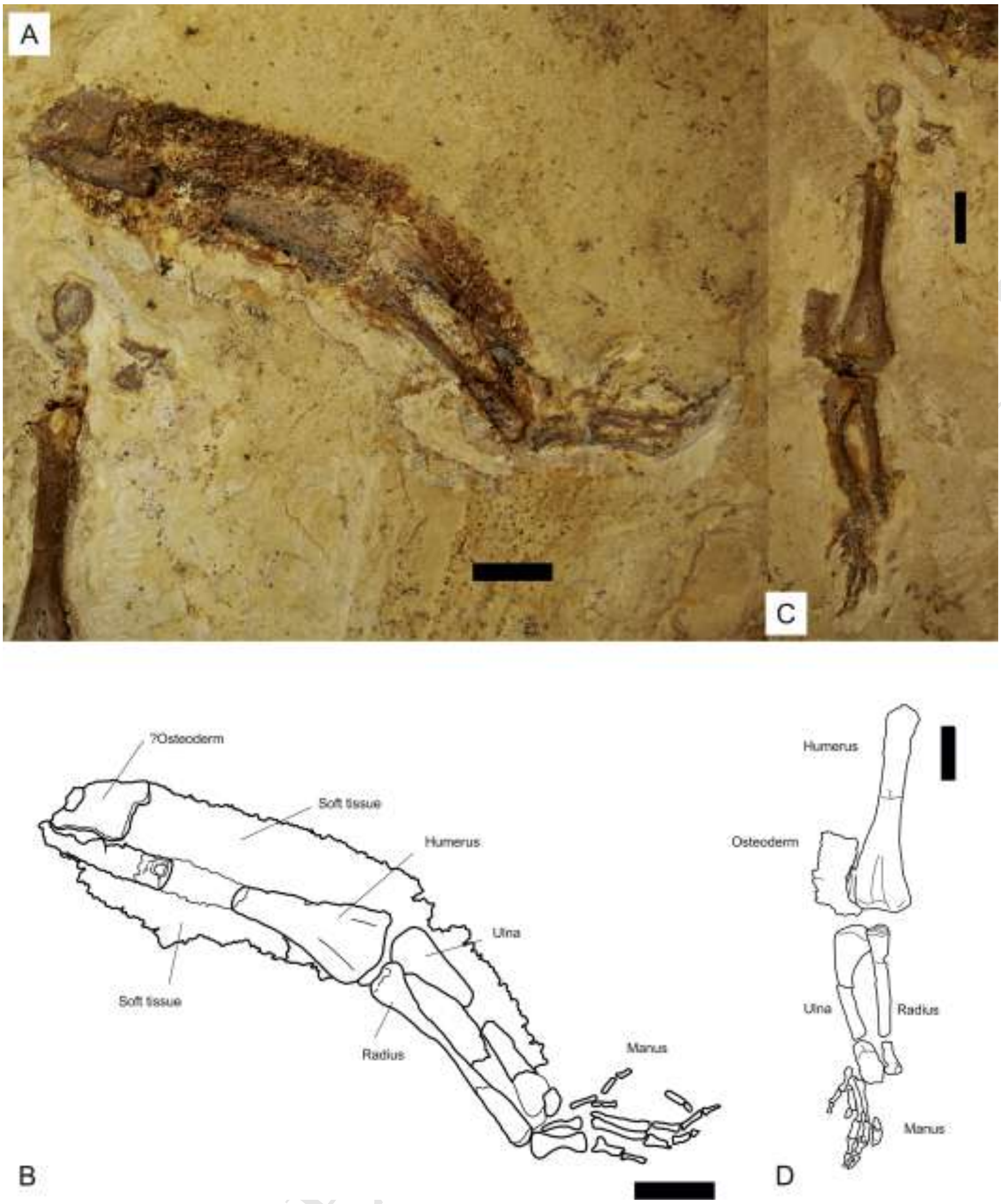
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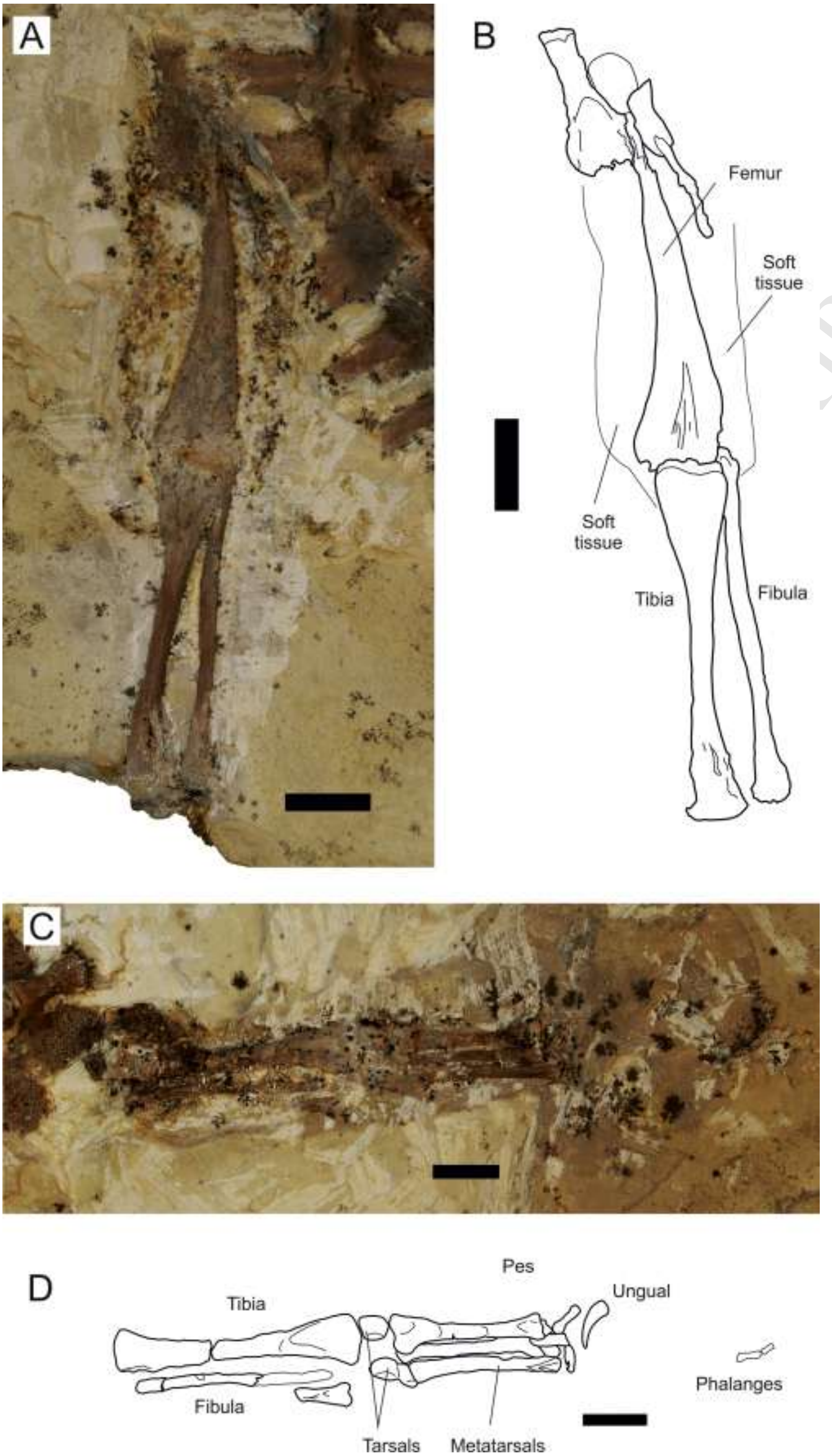
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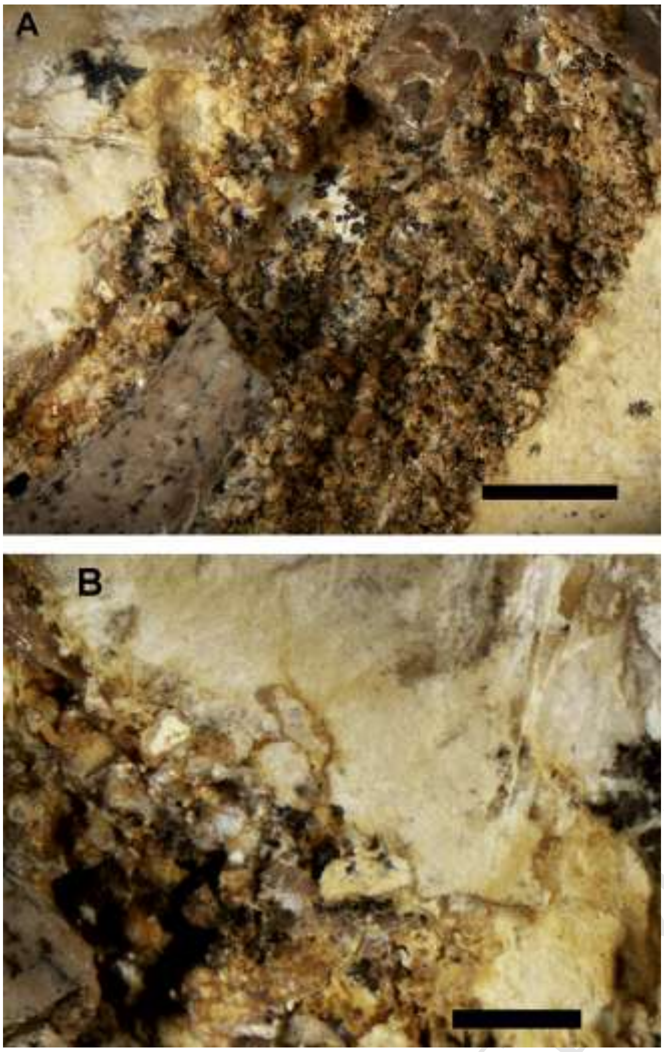
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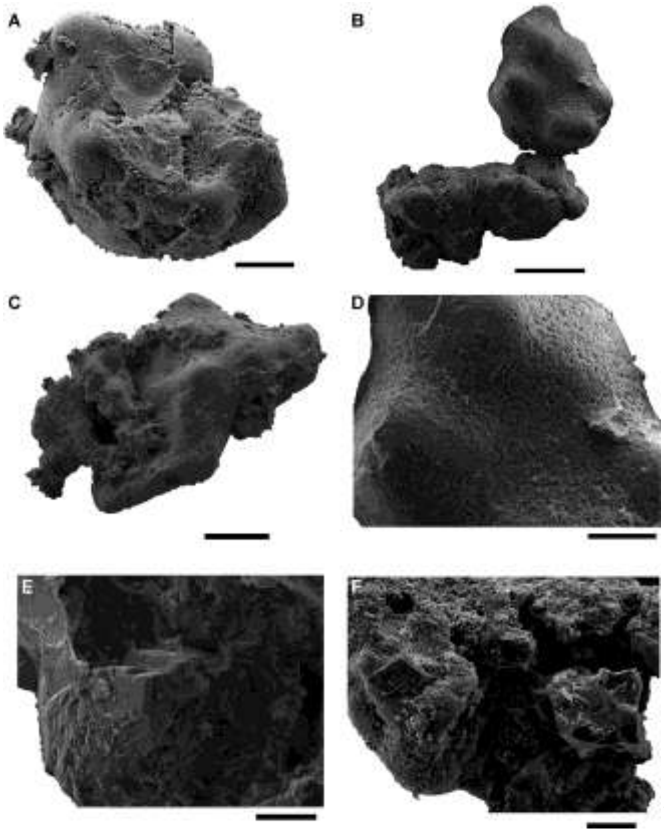
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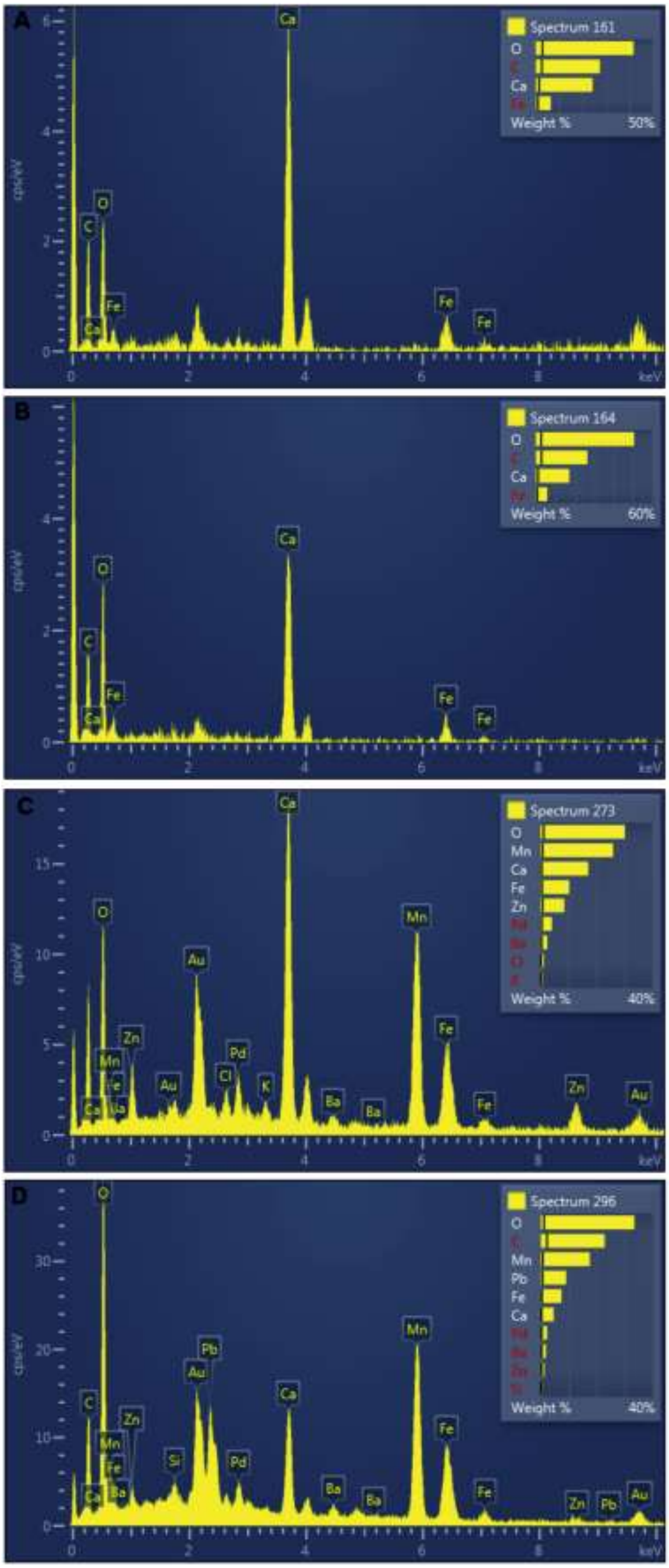
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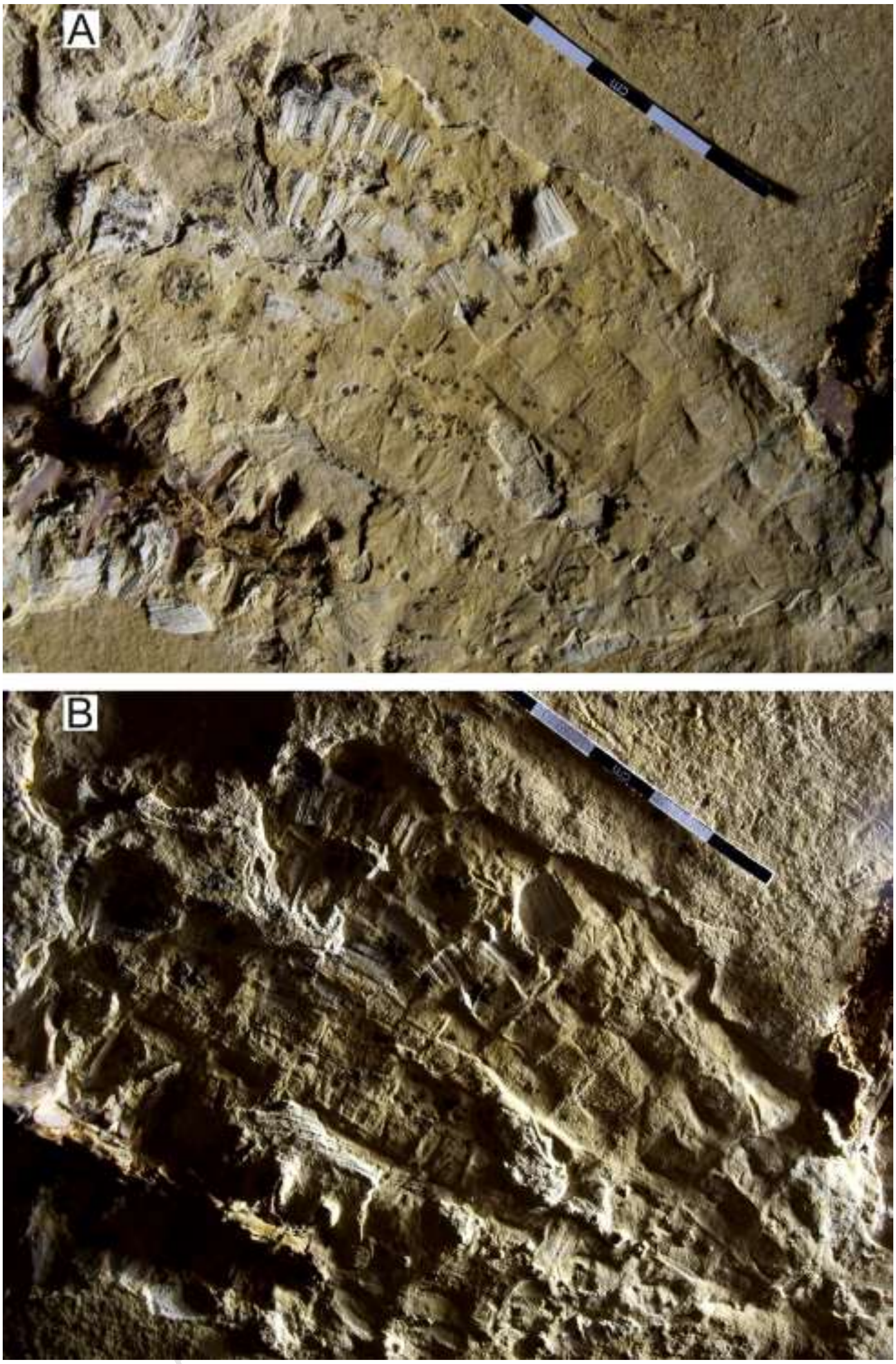
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