

# Postcranial remains of *Knoetschkesuchus guimarotae* (Atoposauridae, Crocodylomorpha) from the Late Jurassic of Portugal and its locomotor behaviour

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## Abstract

Small bodied material of crocodylomorphs from the Late Jurassic of Portugal is rare and provenances are limited to just a few sites. Furthermore, most recovered material consists of single isolated skeletal elements. In this study a specimen comprising over fifty postcranial elements from the Porto de Barcas Member of the Lourinhã Formation near Baleal, Peniche, Portugal, is discussed. Micro CT-scans were performed in order to describe, measure and analyse the fragile specimen. Based on osteoderm morphology and comparisons to referred material of *Knoetschkesuchus guimarotae*, the specimen was ascribed to this taxon. Linear measurements of this specimen and referred material were used in a morphometric analysis to infer the locomotor behaviour of *K. guimarotae*. This quantitative approach indicates a semi-aquatic lifestyle, like present-day crocodylians. Due to the consistent postcranial osteology within Atoposauridae, this conclusion might extend to the entire family. Further research on this specimen could potentially reveal more about its lifestyle within the deltaic environment of the Lusitanian Basin during the Late Jurassic.

**Keywords:** Crocodylomorpha; Atoposauridae; *Knoetschkesuchus*; Portugal; Lusitanian Basin; Late Jurassic; locomotor behaviour.

# 1. Introduction

## 1.1 Crocodylomorpha from the Portuguese Upper Jurassic

The Late Jurassic of Portugal is known for its dinosaur fossils and ichnofossils. The material found throughout the Lusitanian Basin has been well studied and documented (e.g. Pérez-Moreno et al., 1999; Malafaia et al., 2012; Mateus et al., 2013; Mocho et al., 2017). Other groups such as the crocodylomorphs are less well-studied and information regarding these archosaurs comes from specimens concentrated in just a few sites, primarily the Guimarota Mine, near Leira in the northern sector of the basin (Martin and Krebs, 2000). Six Crocodylomorpha taxa have been described on a generic and/or specific level in the Late Jurassic-Early Cretaceous of Portugal: *Machimosaurus hugii* von Meyer (1837), *Lisboasaurus estesi* Seiffert (1973), *Bernissartia* sp. Brinkmann (1989), *Goniopholis baryglyphaeus* Schwarz (2002), *Knoetschkesuchus guimarotae* Schwarz & Salisbury (2005) and *Lusitanisuchus mitracostatus*, Seiffert (1973). The wide variety in morphological adaptations (e.g. *M. hugii* was adapted for marine life (Young et al., 2014) while *G. baryglyphaeus* was semi-aquatic (Schwarz, 2002)) and size (e.g. *M. hugii* got over 9m long (Young et al., 2014) while *K. guimarotae* was about 55cm long (Schwarz and Salisbury, 2005)) point to the different niches these crocodylomorphs occupied within the ecosystems. Furthermore, their coexistence along with other reptiles and early mammals illustrates the rich diversity of life in the Lusitanian Basin during the Late Jurassic (e.g. Martin and Krebs, 2000).

Diagnostics of crocodylomorphs generally focus on cranial features, due to the relatively rapid evolution and development of skulls. Teeth are among the most commonly preserved elements. They can provide insight into the feeding habits of these different taxa and show the diversity within a paleoecosystem (e.g. Guillaume et al., 2019). However, they are of limited use in the taxonomy and phylogenetics of crocodylomorphs, especially when found isolated. Postcranial material is also often of limited use in taxonomy due to their conservative nature. Rarely more than a few associated postcranial elements are recovered and by far most postcranial material consists of single isolated elements (e.g. Schwarz and Salisbury, 2005). When enough postcranial elements are preserved however, it could provide new insights into the taxonomy of the given taxon. Also, a relatively complete specimen can potentially merge less well-known taxa by matching loose material. The focus of this study is specimen SHN.014 (see *Figures 3-8*), housed at the Sociedade de História Natural (SHN), Torres Vedras, Portugal. It consists of over fifty posterior postcranial elements and its implications on the taxonomy and local paleodiversity are discussed.

## 1.2 Locomotor behaviour

Apart from their added value to taxonomy, postcranial material has the potential to give more insight into other aspects as well. Through morphometrics, the dimensions of postcranial bones can be informative about the locomotor behaviour and thus the lifestyle of a species (e.g. Losos 1990; Wainwright 2007; Samuels et al. 2013; Chen and Wilson 2015). Rooney (2018) studied this potential in extant Crocodylia and Lepidosauria and applied it to a number of extinct Crocodylomorpha taxa as well. Although all modern crocodylians have a semi-aquatic lifestyle, extinct species show a wider range in occupation of ecological niches. Basal, fully terrestrial crocodylomorphs diversified into semi-aquatic and fully marine lineages multiple times throughout their evolution (e.g. Wilberg et al., 2019). Although no modern fully aquatic or fully terrestrial crocodylomorphs exist, lepidosaurs that occupy those niches might be indicative as modern analogues. Despite being far removed in an evolutionary sense, a correlation in locomotor behaviour would point to convergent evolution between clades incorporating similar ecological niches (Rooney, 2018). Similarly, correlations in locomotor behaviour based on linear morphological measurements among a wide variety of mammals were found (e.g. Van Valkenburgh 1987; Samuels and Van Valkenburgh 2008; Rose et al. 2014; Tulli et al. 2015).

Only in more recent years has postcranial material been studied quantitatively to interpret locomotor behaviour in extinct crocodylomorphs and other archosaurs. Musculature of the hindlimbs and the pelvis (e.g. Schachner, 2011; Stein et al., 2017) and the joint stiffness in the vertebrae and osteoderms (e.g. Hua, 2003; Molnar et al., 2015) were studied to explain variations in locomotion. Crocodylomorpha and close relatives differ from mammals with regards to aquatic locomotion. Instead of using their hindlimbs, (semi-)aquatic taxa use their tail by undulating it mediolaterally. Doing so requires a more muscular tail which needs the appropriate attachment surfaces on the caudal vertebrae and pelvis. In turn, the hindlimbs proportionally are bigger than the forelimbs in order to support the heavy tail (e.g. Stein et al., 2017). By quantifying the differences between extant crocodylians and lepidosaurs with a different locomotion, the underlying principles become apparent. These principles in turn can be applied to extinct taxa to reveal more about their paleobiology (Rooney, 2018). Along with dietary information from the skull and dentition this creates a more complete picture.

One obvious problem is that in most cases only a very limited amount of postcranial material is preserved. Especially with smaller taxa the material is often fragmentary and isolated (e.g. Schwarz and Salisbury, 2005). The uniquely complete specimen SHN.014, along with measurements from material which is ascribed to *Knoetschkesuchus guimarotae* (previously *Theriosuchus guimarotae*) at the Museu Geológico (LNEG) in Lisbon, Portugal, could provide sufficient information to perform a reliable morphometric analysis.

## 2. Geological setting and palaeoenvironment

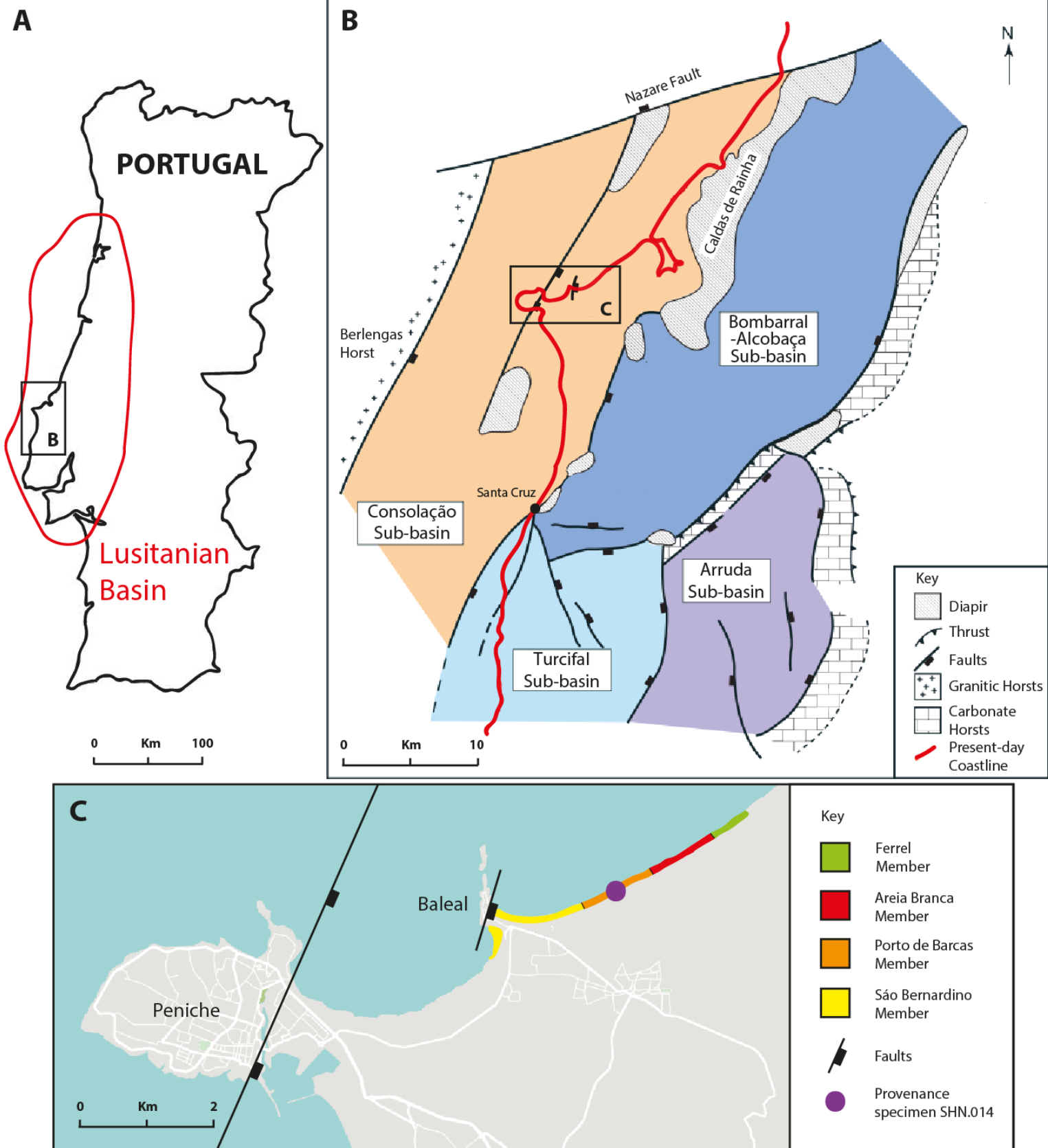
### 2.1 Lusitanian Basin

The Lusitanian Basin is located in western-central Portugal, extending offshore (*see Figure 1A*). Its preserved lithologies have an approximate surface of 22.000 km<sup>2</sup> (Alves et al., 2003) and are up to 6 km thick (Wilson et al., 1989). The formation and subsequent evolution of the Lusitanian Basin took place during four rifting- and subsidence phases between the Late Triassic and the Early Cretaceous (*see Figure 2A*) that led to the formation of the North Atlantic Ocean (e.g. Wilson, 1975; Wilson et al., 1989; Alves et al., 2003a,b, 2006). The boundaries and internal development of this extensional setting have been dictated by faults such as the Nazare Fault and Berlengas Horst and Triassic halite such as the Caldas de Rainha (*see Figure 1B*) (Taylor et al., 2013). The interplay between the basement faults and salts created fault- and diapir-bound sub-basins in the western part of the Lusitanian basin, namely the Arruda, Turcifal, Bombarral-Alcobaça and Consolação sub-basins (*see Figure 1B*) (e.g. Wilson et al. 1989; Alves et al., 2003a).

The infill of these sub-basins dates back to the Oxfordian-Tithonian (~ 163.5-145.0 Ma; Cohen et al., 2013) and comprises the Montejunto Formation, the Abadia Formation and the Lourinhã Formation (*see Figure 2A*). These respectively consisted of platform carbonates, mixed clastic and carbonate basin/shelf and terrigenous, largely continental deposits (Leinfelder and Wilson, 1989; Leinfelder, 1993). The main sources of this siliciclastic material of which the Lourinhã Formation consists are an igneous and metamorphic basement lying to the NE and the Berlengas Horst lying west of the Lusitanian Basin (Martinius and Gowland, 2010). The studied crocodylomorpha specimen originates from the Lourinhã Formation, which was deposited after the third rifting phase during the thermal subsidence of the Late Kimmeridgian to earliest Early Tithonian (*see Figure 2A*) (Taylor et al., 2013). The age was determined by Taylor et al. (2013) through micropalaeontological and palynological analyses.

### 2.2 Lourinhã Formation

Despite numerous studies on the Upper Jurassic lithologies of the Lusitanian Basin, there is a lack of consensus surrounding the stratigraphical nomenclature between the different sub-basins. Schneider et al. (2009) argue that this is due to the absence of consistent (bio)stratigraphic markers within the complex depositional environment created by the faults and diapirs. Mateus et al. (2017) provide a clear overview of different proposed models (*their Figure 3*). Specimen SHN.014 originates from the Consolação sub-basin (*see Figure 1B*). The sedimentological (Martinius and Gowland, 2010) and stratigraphical (Taylor et al., 2013) infill of this sub-basin have been studied in detail. In this sub-basin the Lourinhã Formation is interpreted as a broadly deltaic setting, dominated by coastal plain alluvial deposits (Leinfelder & Wilson, 1998; Alves et al., 2003b). The Lourinhã Formation in the Consolação sub-basin is subdivided in four members:



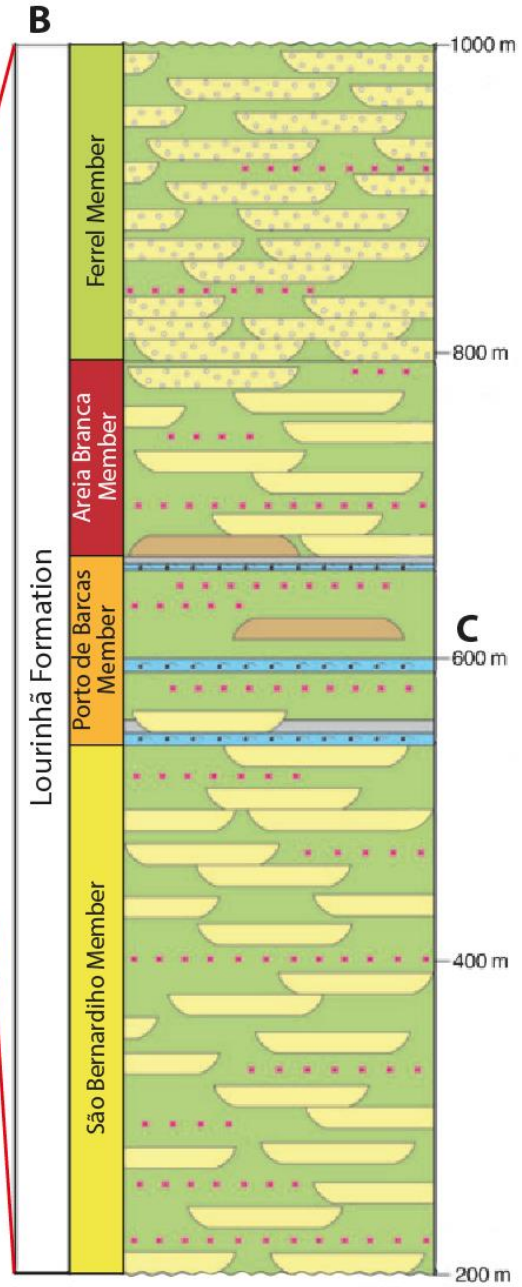
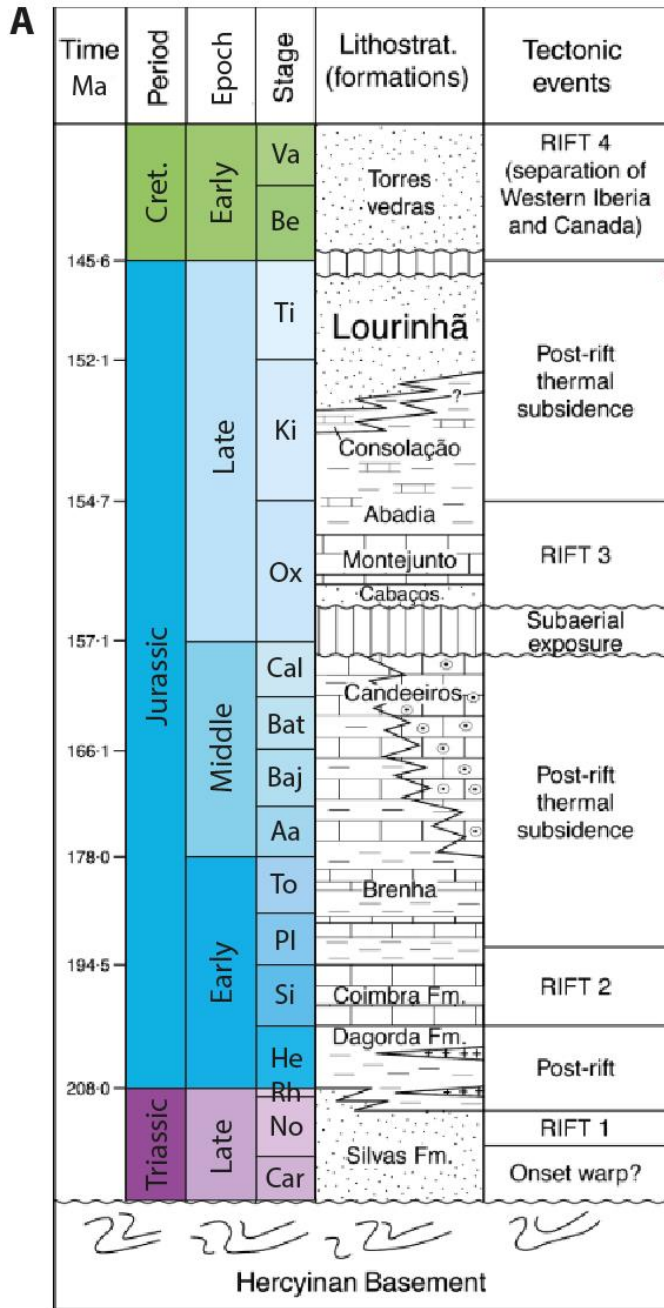
*Figure 1 (previous page): (A) outline Lusitanian Basin; (B) overview geological setting sub-basins in the central part of the basin (adapted from Taylor et al. (2013), who compiled it from Carmarate et al. (1960), Wilson (1979), GPEP (1993), Roche et al. (1996), Manupella (1996), Alves (2002), Alves et al. (2002, 2003) and DGGE (2007)); (C) provenance of the studied specimen SHN.014 with outcropping members (sensu Martinius and Gowland (2010) and Taylor et al. (2013)).*

the São Bernardino Member, Porto de Barcas Member, Areia Branca Member and Ferrel Member (*see Figures 1C, 2B*) (sensu Martinius and Gowland, 2010; Taylor et al., 2013). The studied material originates from the Porto de Barcas Member.

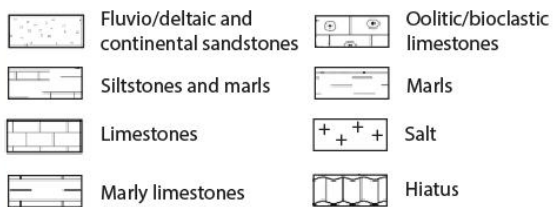
### 2.3 Locality and horizon

Both Martinius and Gowland (2010) and Taylor et al. (2013) incorporated detailed descriptions of the successions from which specimen SHN.014 originates (*see Figure 1C*). From Baleal, the Lourinhã Formation stretches for 3 km to the NE and is about 700 m thick with a general dip of 10° to the East (Taylor et al., 2013). In other outcrops along the coast in the Consolação sub-basin south of Baleal, the Porto de Barcas Member is characterised by three shell beds. These are laterally traceable and positioned at the base, halfway through and at the top of the member (Martinius and Gowland, 2010). NE of Baleal these shell beds are absent however. In this case Taylor et al. (2013) used the base of the first thick palaeosol bed. In general the member is characterised by a low sand percentage, whereas both adjacent members have a relatively high sand percentage. Martinius and Gowland (2010) interpreted the Porto de Barcas Member as a lower coastal plain alluvium with occasional fluvial channel mouth bars and sandy bay shoreline development. The outcrop in which specimen SHN.014 was found consists of a grey and reddish mudrock with pebble sized clasts throughout and is overgrown with seaweed, limpets and mussels (*see Figure 2C*). It is located in the present-day foreshore and floods during high tide.

Paleoclimatic models show that changing wind directions caused seasonal wet-dry fluctuations with wet winters and dry summers. This caused large fluctuations in water supply and therefore growing conditions for the local flora, which is reflected in tree growth patterns and caliche horizons in floodplain deposits (Martinius and Gowland, 2010). Furthermore the models show that insolation and temperature would not have caused limitations in growth patterns. Little is known about the ecological diversity at this specific locality. The known vertebrate assemblage consists of crocodylomorphs (e.g. Goniophoridae), turtles (Pleurosternidae), theropods (e.g. tooth material), pterosaurs (e.g. Dsungaripteroidea) and a relatively complete specimen of cf. *Eousdryosaurus* (pers. comm. Camilo da Silva). In time equivalent strata elsewhere in the basin with similar paleoenvironments a similar or greater diversity is found. Overview studies (e.g. Martin and Krebs, 2000; Mateus, 2008) show that many different Testudines, Squamata, Crocodylomorpha, Dinosauria, Pterosauria and Mammalia coexisted in these environments.



**Key (A)**



**Key (B)**

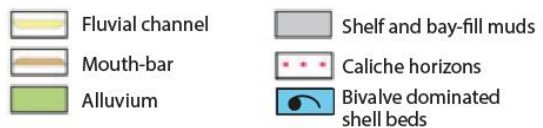


Figure 2 (previous page): (A) Lithostratigraphy and corresponding tectonic events of the Central Lusitanian Basin (adapted from Martinius and Gowland (2010), who incorporated data from Leinfelder and Wilson (1998), Alves et al. (2003b), GPEP (1993)); (B) Generalised lithostratigraphy of the Lourinhã Formation throughout the Central Lusitanian Basin (adapted from Martinius and Gowland (2010)); (C) provenance of specimen SHN.014, a mudrock outcrop on the present-day foreshore (floods during high tide).

### 3. Institutional abbreviations

**DFMMh/FV**, Dinosaurier-Freilichtmuseum Münchehagen/Verein zur Förderung der Niedersächsischen Paläontologie (e.V.), Rehburg-Loccum, Germany; **IPFUB**, Department of Palaeontology, Institute for Geological Sciences, Freie Universität Berlin, Berlin, Germany; **LNEG**, Laboratório Nacional de Energia e Geologia, Museu Geológico, Lisbon, Portugal; **SHN**, Sociedade de História Natural, Torres Vedras, Portugal;

### 4. Material and methods

The specimen SHN.014 was cleaned with an ultrasound bath, but further physical preparation of the specimen was not conducted due to its size and fragile state. Micro-CT scans of each of the (partially articulated) elements were made at the Micronsence facilities (Leiria, Portugal). The resulting DICOM files were processed and segmented using 3D Slicer v. 4.10.2, 2019 (Fedorov et al., 2012). Images of each element were made using CloudCompare v. 2.10.2 (2019) for detailed descriptions. MeshMixer v. 3.5.474 (2017) was used to decimate the 3D-file sizes and to articulate the bones in their original, anatomically correct positions. Several linear measurements were made for the inference of locomotive behaviour through a morphometric analysis. IBM SPSS statistics 26 (George and Mallery, 2019), a statistical software package, was used to analyse the data. This was executed along the same lines as done by Rooney (2018) and incorporated in her dataset in order to discuss possible inferences.

### 5. Systematic palaeontology

CROCODYLOMORPHA Walker, 1968.

CROCODYLIFORMES Hay, 1930.

MESOEUCROCODYLIA Whetstone and Whybrow, 1983.

NEOSUCHIA Benton and Clark, 1988.

Family ATOPOSAURIDAE Gervais, 1971.

Genus *Knoetschkesuchus* Schwarz et al., 2017.

Type species: *Knoetschkesuchus langenbergensis* Schwarz et al. (2017), from the Kimmeridgian of Lower Saxony, northwestern Germany.

*Knoetschkesuchus guimarotae* Schwarz and Salisbury, 2005



Holotype: “IPFUB Gui Croc 7308, partial skull and mandible, part of an isolated surangular, a second sacral vertebra and two partial osteoderms” (Schwarz and Salisbury, 2005). Type locality: “The coal mine of Guimarota, a suburb of Leiria in north-western Portugal” (Schwarz and Salisbury, 2005). See Schwarz and Salisbury (2005) for a full list of referred material and species diagnosis.

## 6. Description

### 6.1 Preservation

Specimen SHN.014 consists of a partial postcranial skeleton consisting of over fifty (partial) elements. These all belong to the posterior half of the postcranial skeleton. It consists of eight dorsal vertebrae, the first sacral vertebra, thirteen caudal vertebrae, partial ribs, osteoderms and material of the pelvis and hindlimbs (fragments of the femora, tibiae, fibulae, astragalus, calcaneum, intermedium and three metatarsals). Most elements underwent some deformation, although the original shapes have been largely preserved. The dorsal vertebrae show, if any, some dorsoventral deformation, whereas the caudal vertebrae mainly show mediolateral deformation. Extremities (e.g. the dorsal end of neural spines and lateral ends of transverse processes) are broken off in most cases. Most ribs, osteoderms and appendicular elements are fragmentary or show breaks and cracks.

### 6.2 Osteology

#### 6.2.1 Axial Skeleton

##### 6.2.1.1 Dorsal (thoracic and lumbar) vertebrae

Eight dorsal vertebrae from the posterior half of the dorsal chain were preserved (*see Figure 3*). The last dorsal vertebra is articulated with the first sacral vertebra, an osteoderm and a partial rib. Of the anteriormost preserved dorsal vertebra, only the posterior half is preserved. The two anteriormost preserved dorsal vertebrae show a suture between the centrum and the neural arch that is less well fused compared to the more posterior dorsal vertebrae. In most cases, the extremities of the neural spines and different processes are absent. The centrum of the dorsal vertebrae has a craniocaudal length about twice the dorsoventral height. The lateral and ventral surfaces of the centrum are concave (diameter in the middle of the centrum is about 20-25% smaller relative to the extremities). The articular surfaces of the centrum are amphicoelous. The articular surfaces on the most posterior dorsal vertebra are dorsoventrally compressed whereas the articular surfaces on more anterior dorsal vertebrae are rounded. In the posteriormost dorsal vertebra, the mediolateral diameter of the posterior articular surface of the centrum is about 1.4 times the dorsoventral diameter. The neural arches show a comparable development, with the more posterior dorsal vertebrae showing a dorsoventral compression. The dorsoventral height of the neural arches is slightly less than that of the centra. The transverse processes are positioned

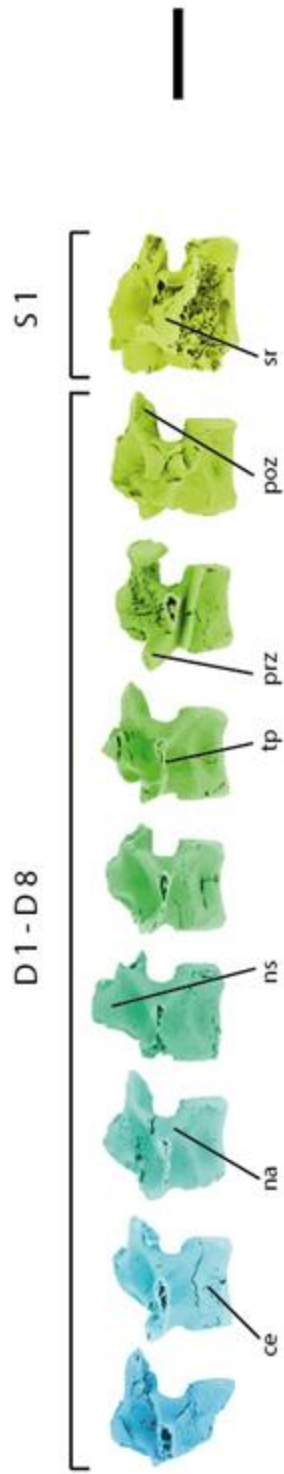
slightly to the anterior in dorsal view, with the extremities pointing slightly posterior. The pre- and postzygapophyses on the dorsal vertebrae widen towards the extremities and the articular surfaces are at an angle with the medial plane of about 65 degrees. The neural spine is situated on the posterior two thirds of the neural arch and has the same height as the centrum. It has a straight dorsal margin with an anteroposterior orientation and a sloping margin on both of these sides.

#### 6.2.1.2 Sacral vertebra

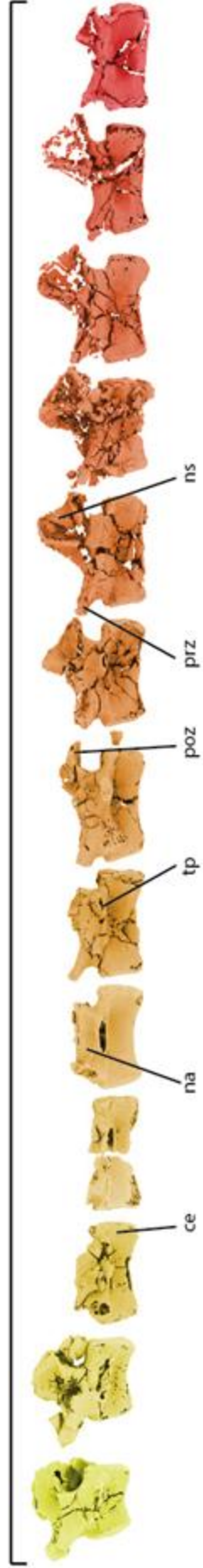
In this specimen only the first sacral vertebra is preserved, articulated with the posteriormost dorsal vertebra, an osteoderm and a rib (*see Figure 3*). The centrum is slightly longer than twice its height. The lateral and ventral surfaces are somewhat concave (diameter in the middle of the centrum is about 20% smaller relative to the extremities), as well as the articular surfaces, making it amphicoelous. The mediolateral diameter of these surfaces is approximately 1.4 times the dorsoventral diameter. The neural arch has slightly collapsed dorsoventrally, making the oval vertebral foramen somewhat skewed. The pre- and postzygapophyses widen towards the extremities and the articular surfaces are at an angle with the medial plane of about 60 degrees. Compared to the dorsal vertebrae, in lateral view the neural spine of the sacral vertebrae is longer along its anteroposterior axis.

#### 6.2.1.3 Caudal vertebrae

A total of thirteen caudal vertebrae have been preserved (*see Figure 3*). The first and second caudal vertebrae show a transitional morphology between the sacral vertebra and the more terminal caudal vertebrae. The ratio between the anteroposterior length and the dorsoventral height of the centrum transitions from 1.6 (1st caudal) and 1.8 (2nd caudal) to 2.4 (7th caudal) and 2.5 (13th caudal). Similar to the other vertebrae, the centra of the caudal vertebrae have a concave surface in lateral and ventral aspect. An accurate measure of the degree of concavity is not possible due to the strong mediolateral deformation most caudals endured. The articular surfaces of the centra again are amphicoelous and transform from more square in the anteriormost caudal vertebrae to more rounded in the more posterior caudal vertebrae. The neural arch is not as tall as the centrum and encompasses a rounded vertebral foramen. The transverse processes are prominent in the first few caudal vertebrae and are positioned lateral to the dorsal third of the centrum. They become less prominent and move slightly up to just above the centrum (7th caudal) and completely disappear in the more distal caudals. The pre- and postzygapophyses become less prominent towards the more distal caudals. They also slightly shift from being more mediolaterally orientated to being more anteroposteriorly orientated. The neural spine shifts from the posterior two third to the posterior one third of the neural arch. The dorsoventral height of the neural spine remains similar throughout the caudal vertebrae preserved here. In lateral view the anterior edge of the spine is steep, whereas the posterior side slopes down more gently. Of the two most distally preserved caudal vertebrae (12th and 13th), the (partial) haemapophysis has been preserved as well (*see Figure 4E,F*).

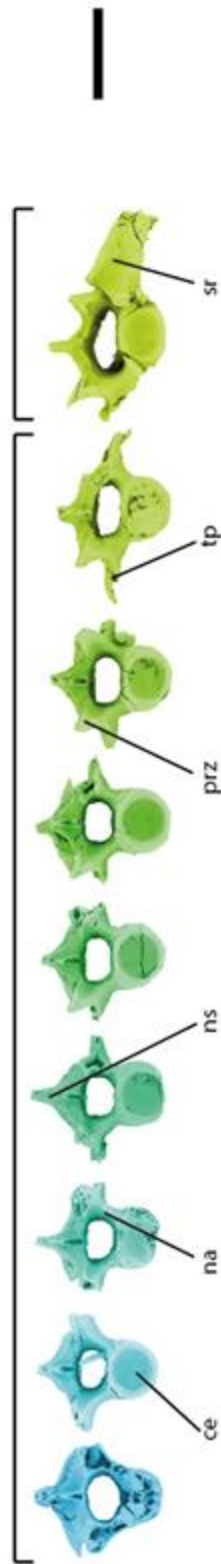


C1-C13

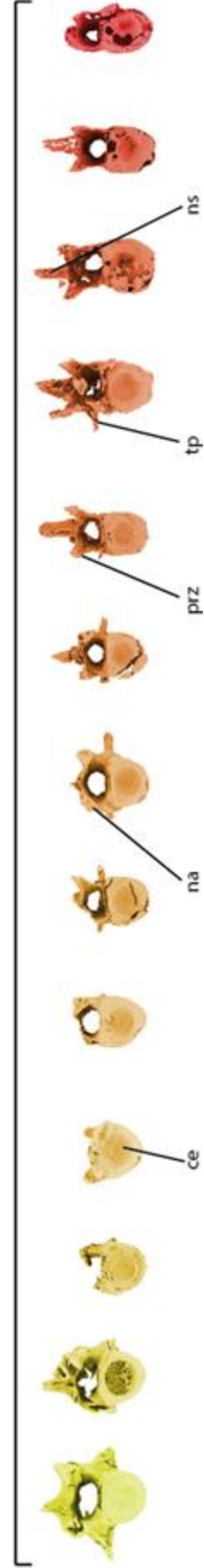


D1-D8

S1

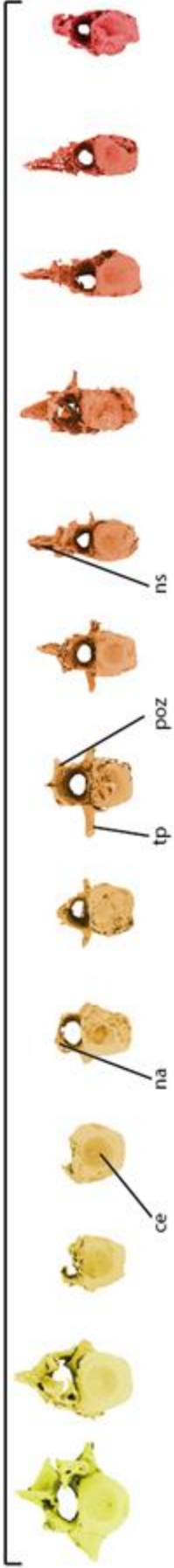
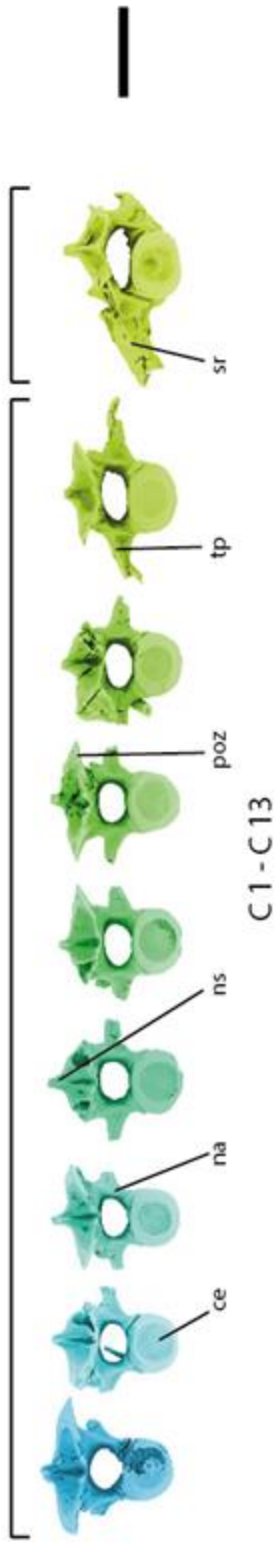


C1-C13



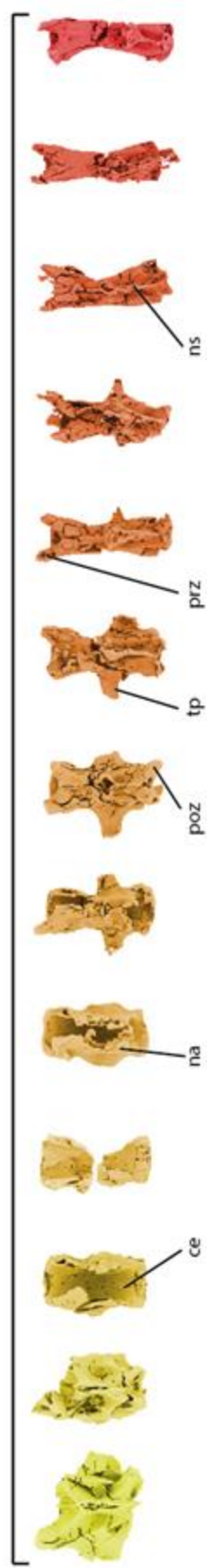
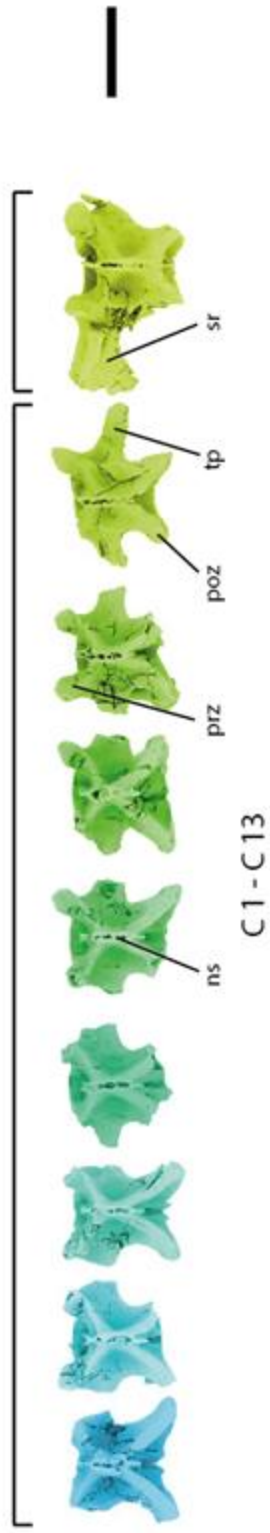
D1-D8

S1



D1-D8

S1



*Figure 3 (previous two pages):* dorsal (D1-D8), sacral (S1) and caudal (C1-13) vertebrae of specimen SHN.014. Respectively in left lateral, anterior, posterior and dorsal view. Abbreviations: ce: centrum; na: neural arc; ns: neural spine; tp: transverse process; prz: prezygapophysis; poz: postzygapophysis; sr: sacral rib. Scale bars are 10 mm.

#### 6.2.1.4 Thoracic ribs

Two partial thoracic ribs have been preserved in association with the two most posterior dorsal vertebrae (*see Figure 4A,B*). Both are fragments of the corpus of the ribs and are similar in length. This is most likely the result of both being preserved parallel to the centrum of their respective associated vertebrae, tucked under the transverse processes. The partial rib of the posteriormost dorsal vertebra is slightly curved, whereas the other is straight. The cross sections perpendicular to the rib are oval for both partial ribs.

#### 6.2.1.5 Sacral ribs

The left sacral rib of the first sacral vertebra is broken off but preserved in approximately the correct position. Both sacral ribs of the second sacral vertebra, which is missing, are (partially) preserved (*see Figure 4C,D*). These are roughly half the size of the first sacral rib. All consist of a short and broad corpus, which broadens further laterally in anteroposterior direction into the iliac articular surface. On the posterior side, the rib broadens slightly further. The iliac articular surface itself is rugose.

### 6.2.2 Appendicular skeleton

#### 6.2.2.1 Ischium and pubis

A fragment of the left (?) ischium (*see Figure 4G*) is preserved in association with a partial osteoderm. The fragment contains the pubic peduncle of the ischium and the anteriormost part of the ischium corpus. The corpus of the right pubis has been preserved (*see Figure 4H*). In dorsal view the corpus fans out in anterior direction, slightly more in medial direction relative to the lateral direction. In lateral view the corpus thins out slightly relative to the pubic shaft. The anterior edge of the pubis is rugose and has likely been exposed to some erosion.

#### 6.2.2.2 Femur

Both femora have been partially preserved (*see Figure 5A*). The remains of the right femur consist of the femoral head and the proximal half of the shaft and the distal end. Of the left femur part of the shaft has been preserved. The extrapolated total lengths in *Figure 5A* are based on referred material (*see section 5.3*). In the middle of the shaft the cross section of the femur is more circular, whereas towards both extremities the cross section is more oval in shape. The articular surface on the femoral head forms a ridge which protrudes cranially, forming a bulge on this side. The ridge continues along the dorsal and caudal edge of the femoral head, down the lateral side of the shaft where it fades away (caudolateral tuberosity). The lateral surface of the femoral head is practically flat, whereas the medial surface is slightly concave. Down the shaft, on the lateral surface, a proximal depression can be observed. The femoral trochanter on the medial side of the proximal shaft is only faintly visible as a gentle elevation. The

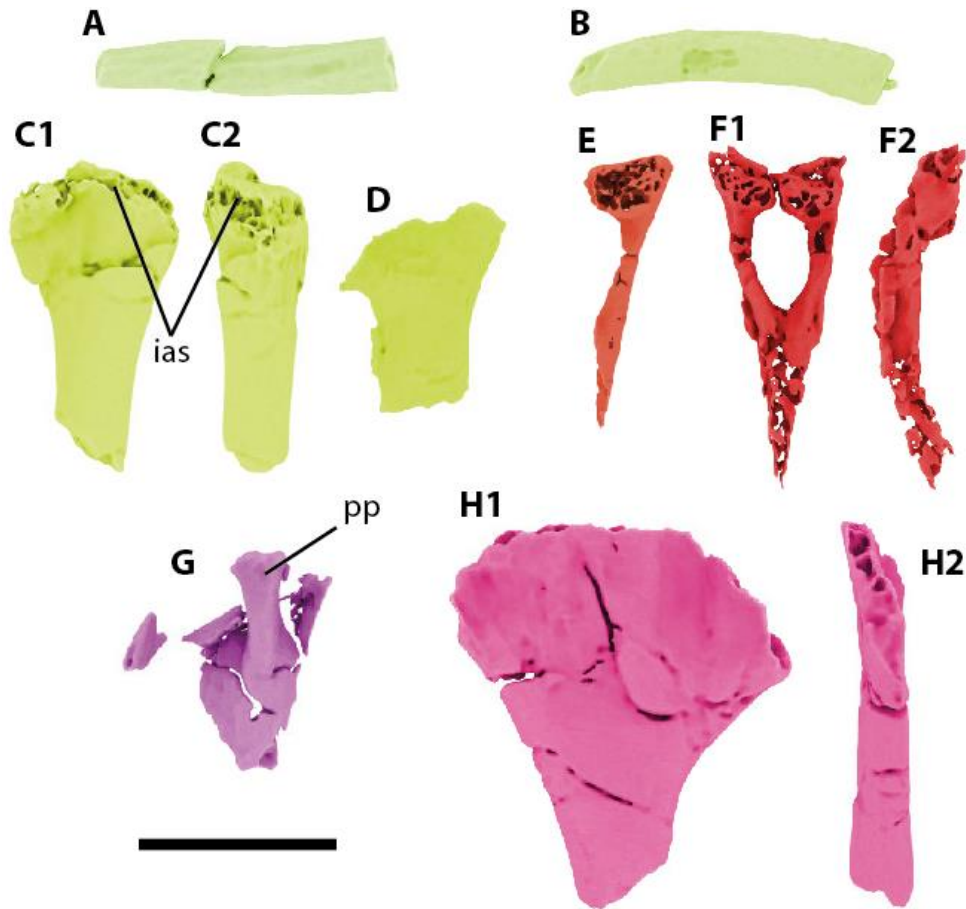
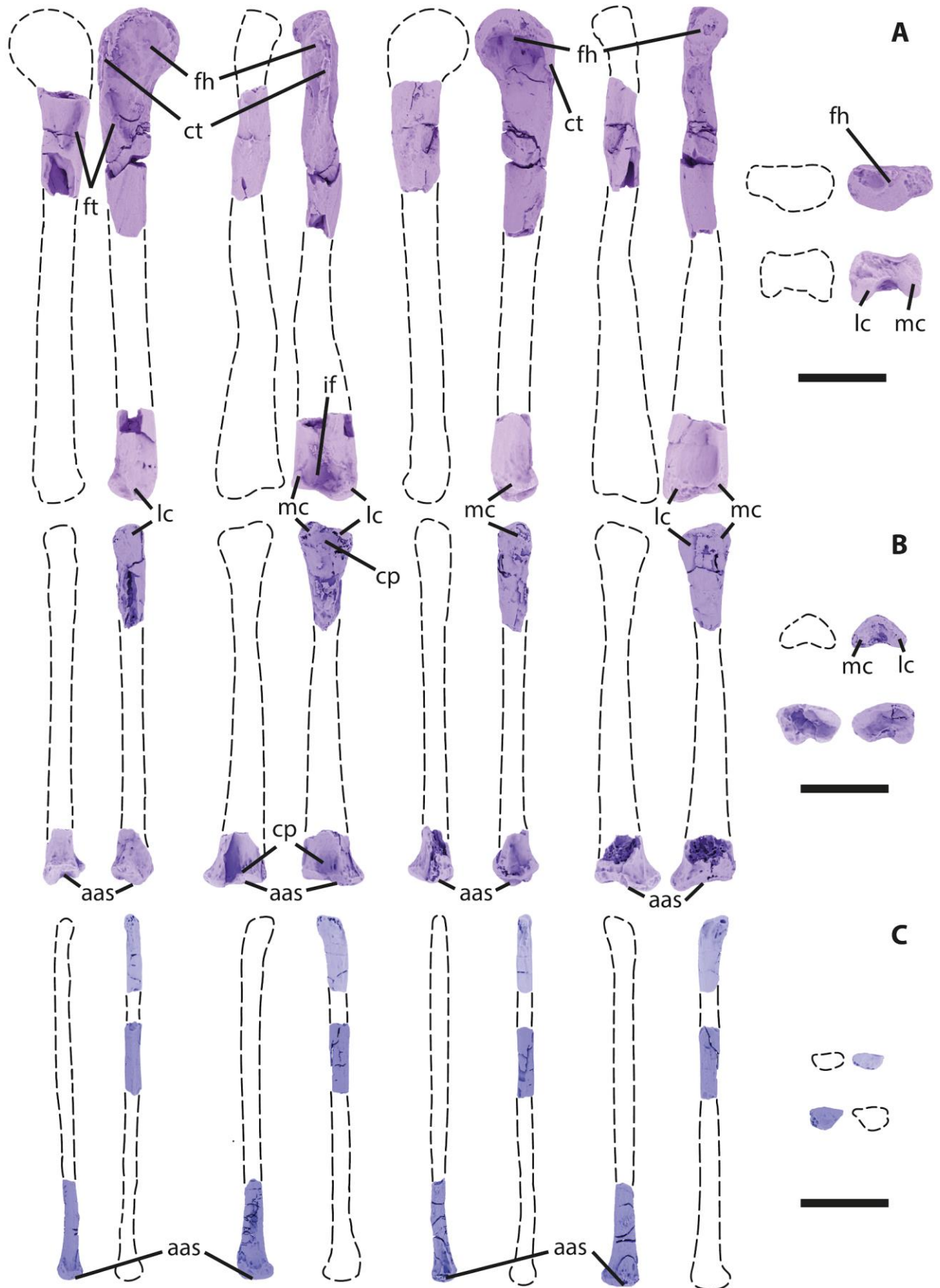


Figure 4: fragmentary dorsal (A, B) and sacral (C, D) ribs, chevrons (E, F) and partial ischium (G) and pubis (H) of specimen SHN.014. Colours of the ribs and chevrons match to the associated vertebrae. Abbreviations: ias: iliac articular surface; pp: pubic peduncle. Scale bar is 5 mm.

paratrochanteral fossa is not visible at all. The articular surface of the distal end of the femur consists of a lateral and a medial condyle, with the lateral condyle being more prominent. They are separated by the intercondylar fossa which is faint in craniocaudal view, but rather prominent in dorsoventral view due to the condyles extending caudally. Proximal to the condyles the surface is concave on both the cranial and caudal side.

### 6.2.2.3 Tibia

The distal ends of both tibiae and the head and proximal part of the shaft of the right tibia have been preserved (see Figure 5B). The extrapolated total lengths in Figure 5B are based on referred material (see section 5.3). Both the proximal and distal ends are broadened, whereas the shaft remains slender and circular in cross section. On the articular surface of the head the medial condyle is more prominent than the lateral condyle. They are separated on the proximocaudal side by a condylar pit. The distal end widens relative to the shaft, most prominently on the medial side. In distal view the extremity has a slightly convex cranial edge and a caudal edge



*Figure 5 (previous page):* fragmentary remains of (A) the left and right femora, (B) tibiae and (C) fibulae of specimen SHN.014. All respectively in lateral, posterior, medial, anterior, proximal and distal view. Abbreviations: fh: femoral head; ct: caudolateral tuberosity; ft: femoral trochanter; if: intercondylar fossa; lc: lateral condyle; mc: medial condyle; cp: condylar pit; aas: astragalar articular surface. Scale bars are 10 mm.

with two protruding condyles and a strongly concave pit in between. The astragalar articular surface is convex on the lateral side and concave on the medial side.

#### 6.2.2.4 Fibula

Of the right fibula the proximal part and a fragment of the shaft are preserved. The distal part of the left fibula is preserved (*see Figure 5C*). The extrapolated total lengths in *Figure 5C* are based on referred material (*see section 5.3*). The proximal articular surface of the fibula is flattened with the long side oriented in mediolateral direction and curves slightly laterally. The shaft is circular in cross section throughout. The distal end of the fibula widens in lateral direction, whereas the medial surface remains flat. In distal view the extremity is circular with a pointed extension in lateral direction.

#### 6.2.2.5 Astragalus, calcaneum and intermedium

The astragalus, calcaneum and intermedium of the left tarsus have been preserved with the calcaneum and intermedium fused/articulated (*see Figure 6A*). The arrangement of these ankle bones is typical for crurotarsi (Chatterjee, 1982), the lineage to which the crocodylomorpha belong. The astragalus articulates with the tibia and fibula and the calcaneum with the tarsals. The ankle joint is located between the two, where the lower peg of the astragalus fits inside the calcaneum socket and the upper hook slides over the saddle of the calcaneum (Chatterjee, 1982). The tibial and fibular articular surfaces are positioned dorsomedially and dorsolaterally respectively on the astragalus, separated by an anteroposterior crest. The tibial articular surface is mediolaterally longer than the fibular articular surface and both have a slight concave surface. In anterior view the astragalus has a slightly concave surface with two foramina visible. Medioventrally the astragalus has a large bulge while the lateral surface contains the articular surface with the saddle of the calcaneum. The calcaneal tuber protrudes posteriorly. The ventral surface of the calcaneum articulates with the dorsal surface of the intermedium. The intermedium bulges in both posterior and anterior direction. The ventral surface of the intermedium and the ventrolateral surface of the calcaneum form the articular surfaces of the preserved metatarsals.

#### 6.2.2.6 Metatarsals

The proximal portion of three metatarsals (I, II, III) have been preserved in association with one another (*see Figure 6B,C,D*). The total lengths in *Figure 6B,C,D* are estimated based on referred material. The heads of all three metatarsals extend anteroposteriorly to more than twice the width of the shaft, while the mediolateral width of the head only slightly extends. The elongated articular surfaces on the dorsal side of the heads are convex. The shaft is slightly oval in cross



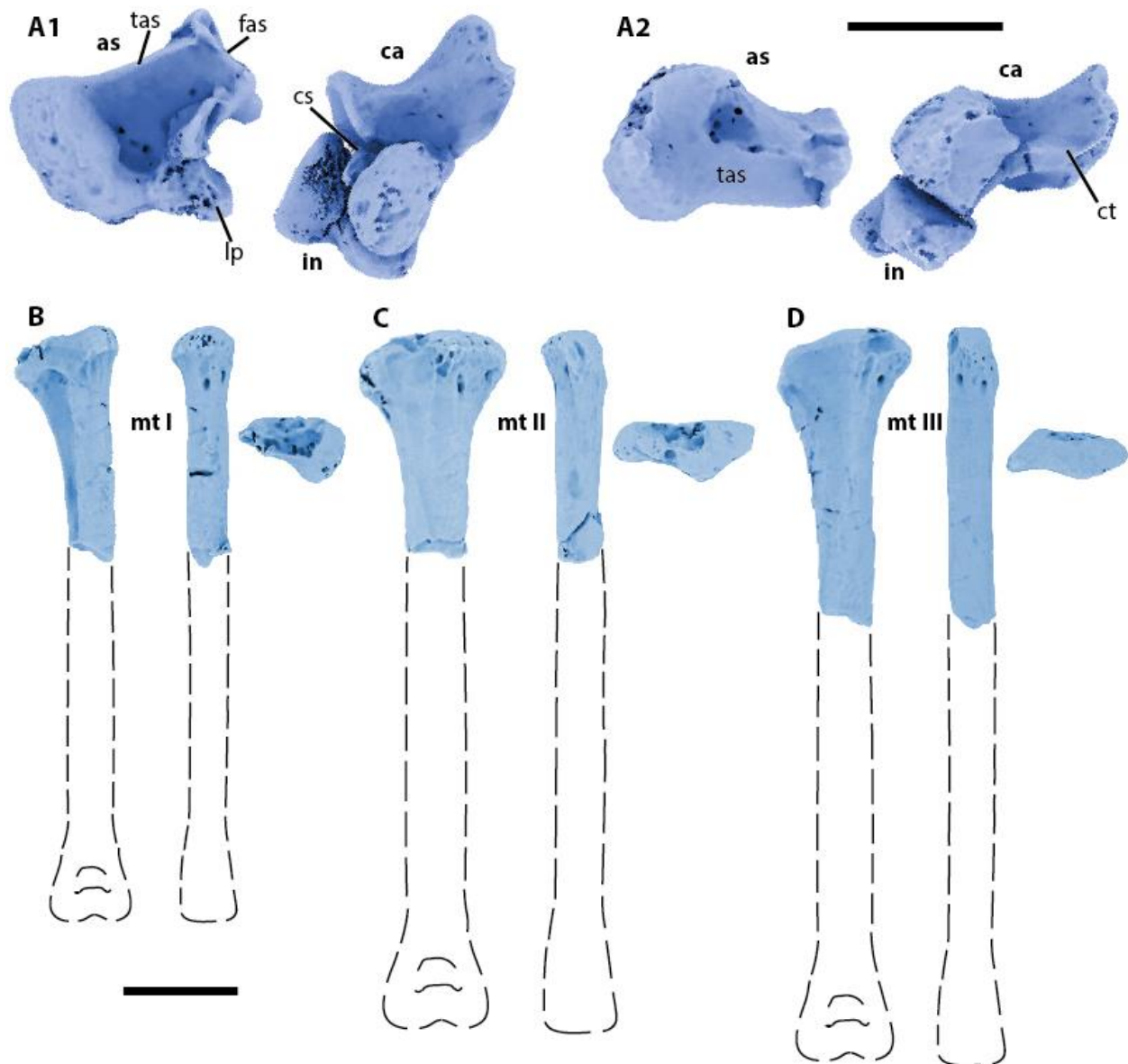


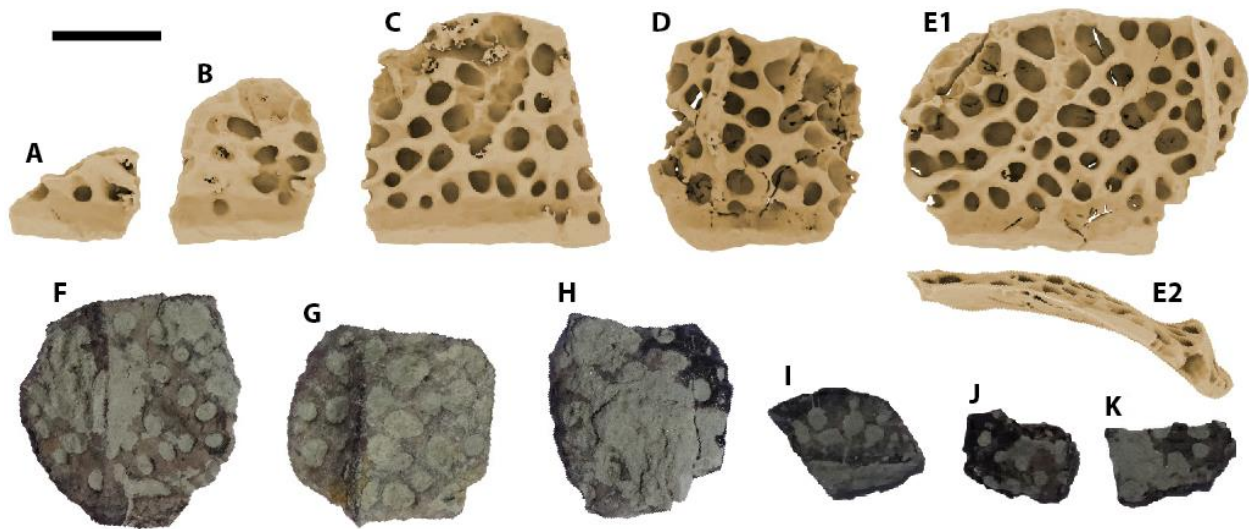
Figure 6 (previous page): left astragalus, calcaneum and intermedium and fragmentary remains of the left metatarsals I, II, III of specimen SHN.014. Abbreviations: as: astragalus; ca: calcaneum; in: intermedium; tas: tibial articular surface; fas: fibular articular surface; lp: lower peg; cs: calcaneal socket; ct: calcaneal tuber; mt: metatarsal. Scale bars are 5 mm.

section with the larger diameter being orientated anteroposteriorly. Metatarsal I has a smaller head and a more slender shaft compared to metatarsals II and III.

#### 6.2.2.7 Osteoderms

A number of (partial) dorsal osteoderms were preserved (see Figure 7). In dorsal view, the osteoderms are rectangular with slightly rounded edges. The mediolateral width is almost twice as large as the anteroposterior length. The dorsal, exterior surface is covered with circular, irregular pits. Only the anterior edge is smooth and straight. Towards the lateral edge of the

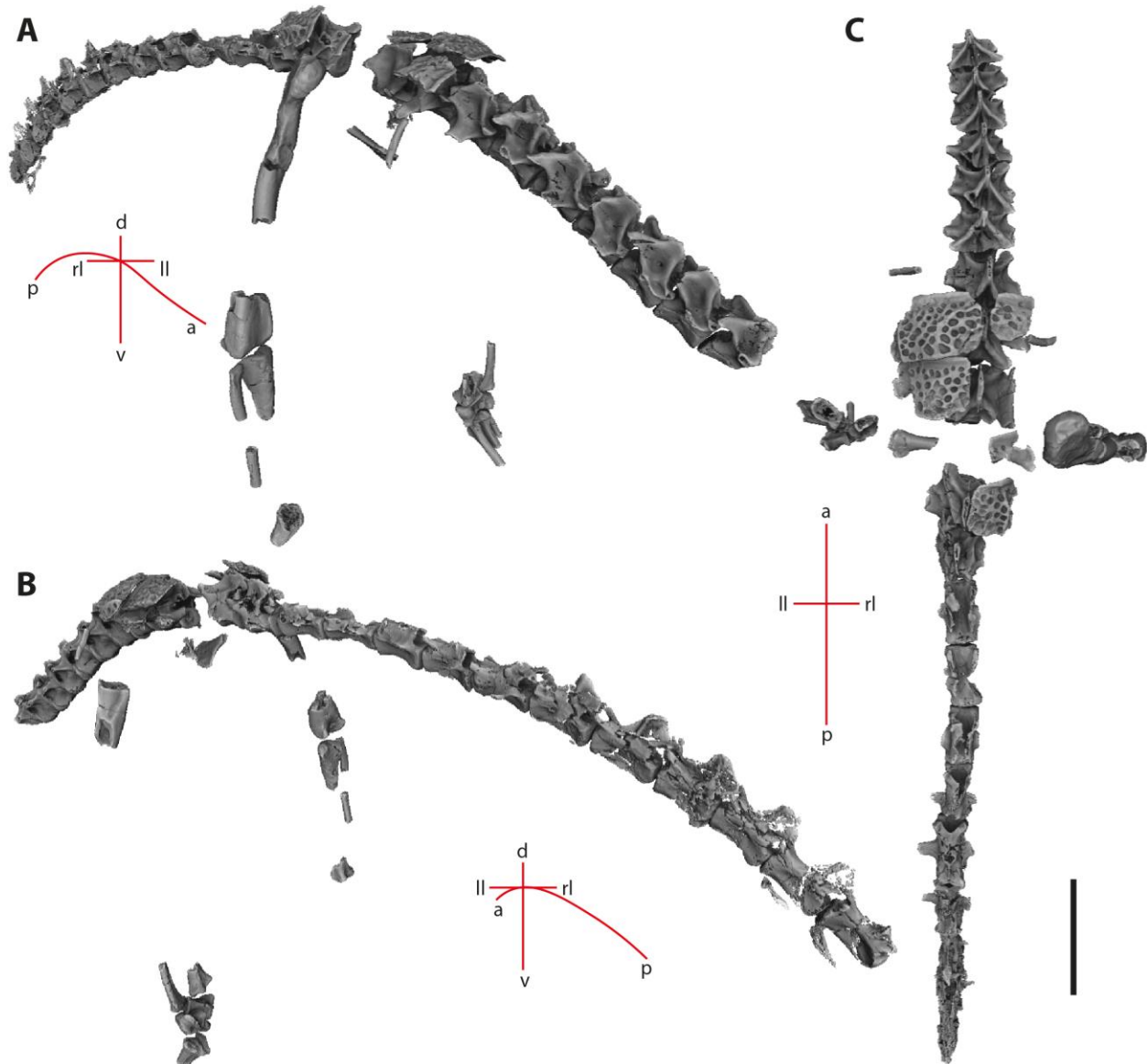
osteoderm an anteroposterior crest or keel is present. In anterior view the osteoderm shows an even convex curvature. The ventral, interior side of the osteoderm has a smooth surface. The anterolateral corner of none of the dorsal osteoderms has been preserved. Based on comparisons with referred material (Puértolas-Pascual and Mateus, 2019) a peg extending anteriorly was most likely present here. The (partial) caudal osteoderms are more square with strongly rounded corners in dorsal view. The dorsal, external surface is covered with circular, irregular pits. A anteroposterior crest or keel is present, just laterally of the middle of the osteoderm. The ventral, interior surface of the caudal osteoderms is smooth. In anterior view the osteoderm shows an even convex curvature.



*Figure 7:* fragmentary remains of the osteoderms of specimen SHN.014 in dorsal view (E2 in anterior view). A-E result from micro CT-scanning, F-K were photographed. Scale bar is 5 mm.

### 6.3 Anatomical reconstruction

Identification of all preserved elements confirmed that specimen SHN.014 consists of one partial individual. A 3-D, anatomically correct model of the specimen was reconstructed (*see Figure 8*).



*Figure 8*: 3D reconstruction of all preserved material of specimen SHN.014 in (A) right anterolateral view; (B) left posterolateral view and (C) dorsal view. Abbreviations: a: anterior; d: dorsal; ll: left lateral; p: posterior; rl: right lateral; v: ventral. Scale bar is 20 mm.

## 6.4 Linear measurements

In order to conduct a morphometric analysis, linear measurements were taken from specimen SHN.014 and several referred specimens of *Theriosuchus/Knoetschkesuchus guimarotae* housed at the Museu Geológico de Portugal (LNEG) in Lisbon (*see Table 1; Figure 9*). In all cases, measurements of material other than SHN.014 were scaled to fit this specimen. Isometric growth within the ontological development of the taxon and sexual monomorphism were assumed. Also, in cases in which no complete reference material was present for a certain bone, the measurement was extrapolated based on other material. For the lengths of the femur and tibia, complete referred specimens (*see Table 1*) were used to extrapolate both lengths based on the fragmentary proximal and distal remains of SHN.014. The length of the ischium was based on referred material of ischia with associated femora which were then scaled based on femora comparisons. The partial pubis of SHN.014 is the only known pubis of this taxon. Based on more generalised examples of pubes, the length was extrapolated. No scapular material is known from *K. quimarotae*. The scapular length was inferred from pictures of the holotype of *Knoetschkesuchus langenbergensis*, housed at the Dinosaurier-Freilichtmuseum Münchehagen/Verein zur Förderung der Niedersächsischen Paläontologie (e.V.) (catalogue numbers DFMMh/FV), in Rehburg-Loccum near Hannover in northern Germany (Schwarz et al., 2017). Currently *K. langenbergensis* is the only other species within the genus. Furthermore it was scaled based on the length of an associated tibia. The humeral proximal breadth and length are based on a referred humerus associated with a femur. Again, the measurements were extrapolated and scaled based on specimen SHN.014 (*see Table 1*).

*Table 1:* linear measurements of specimens used in the morphometric analysis.

<b>Measurement</b>	<b>(Extrapolated + scaled)</b>	<b>Based on specimen(s)</b>
Humerus proximal breadth (HPB)	5,8 mm	IPFUB Gui Croc 7661; IPFUB Gui Croc 7564; SHN.014
Humerus length (HL)	28,7 mm	IPFUB Gui Croc 7661; IPFUB Gui Croc 7564; SHN.014
Femur length (FL)	56,5 mm	IPFUB Gui Croc 73186; IPFUB Gui Croc 75127; SHN.014
Tibia length (TL)	42,0 mm	IPFUB Gui Croc 8053; SHN.014
Ischium length (IschL)	25,1 mm	IPFUB Gui Croc 73186; SHN.014
Pubis length (PubL)	16,2 mm	SHN.014
Scapula length (ScapL)	24,4 mm	DFMMh/FV200; SHN.014



*Figure 9:* linear measurements taken of specimen SHN.014 and various referred specimens from the Museu Geológico (LNEG), Lisbon, Portugal. (A) IPFUB Gui Croc 7564; (B) IPFUB Gui Croc 7661; (C) IPFUB Gui Croc 8053; (D) IPFUB Gui Croc 75127; (E) IPFUB Gui Croc 73186; (F) DFMMh/FV 200 (image from Schwarz et al., 2017). Scale bars are 5 mm (A-E) and 50 mm (F).

## 7. Discussion

### 7.1 Taxonomy

The taxonomic determination of a specimen solely consisting of postcranial material is generally limited. Diagnostic features often largely focus on cranial characters, as is the case in Crocodylomorpha and Atoposauridae more specifically. Schwarz et al. (2017) discussed the Crocodylomorpha phylogeny with a focus on Atoposauridae after the discovery of a new genus, *Knoetschkesuchus*, belonging to this family from the Upper Jurassic of Germany. The matrix used in their phylogenetic analysis was modified after Turner (2015), tweeking and leaving out some taxa that were not essential to a discussion on Atoposauridae and improving the matrix data of those that were. The variety in results of different attempts at tackling (1) the phylogenetic position of Atoposauridae within Crocodylomorpha (*see Figure 10*) and (2) which taxa are included in the family and which are positioned more basally (*see Figure 11*) illustrate the problems still present in the current approaches (e.g. Buscalioni and Sanz, 1988; Tennant et al., 2016; Schwarz et al., 2017).

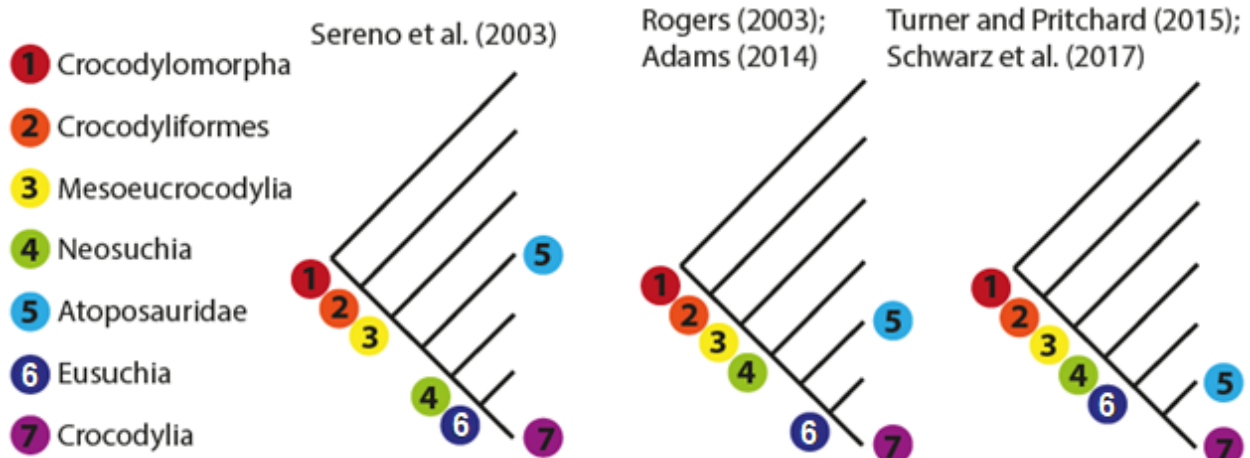


Figure 10: simplified trees with the different placements of Atoposauridae (5, light blue) within Crocodylomorpha.

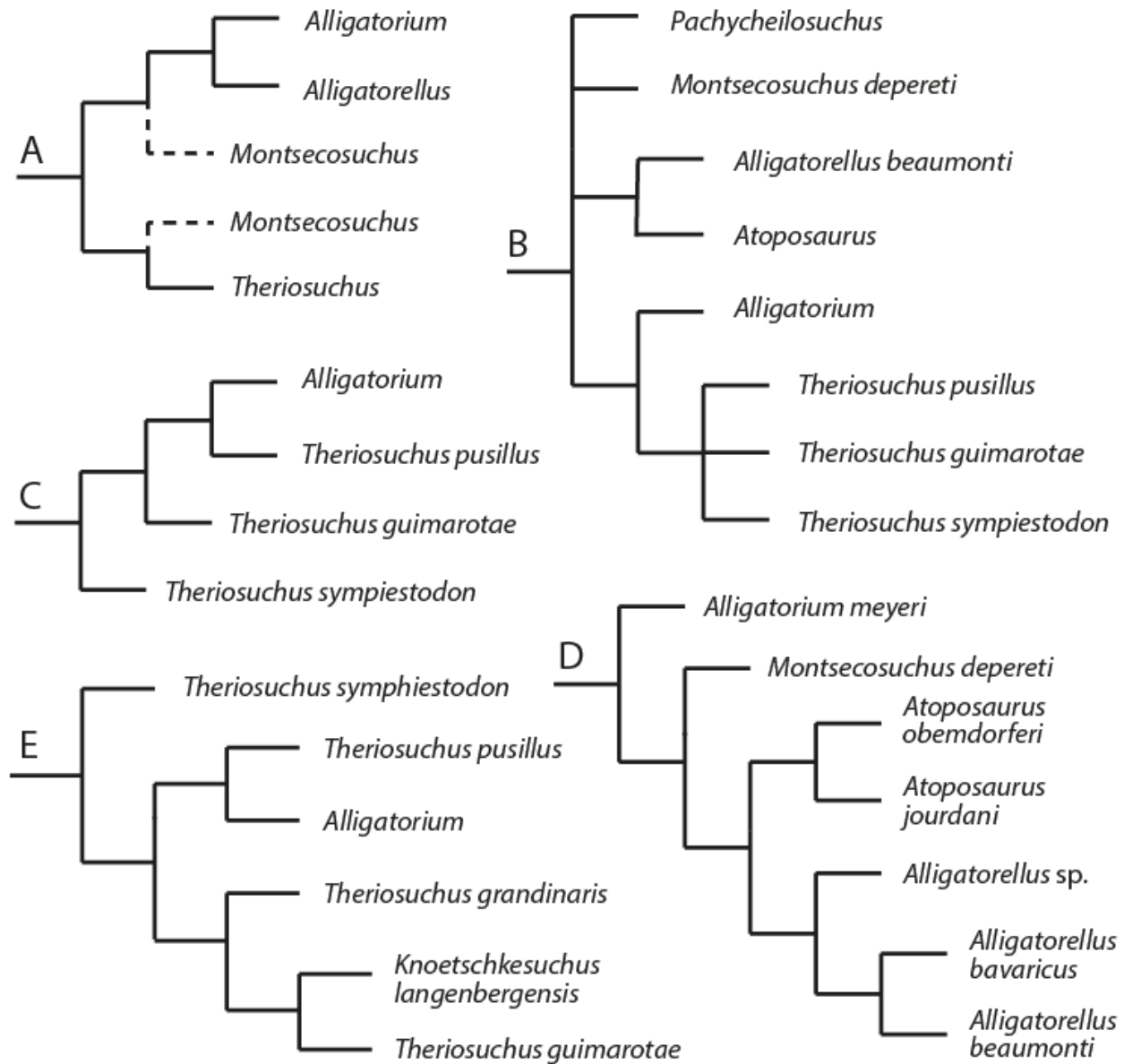


Figure 11: different arrangements and inclusions within the Atoposauridae family. (A) Buscalioni and Sanz, 1988; (B) Bronzati et al., 2012; (C) Turner, 2015; (D) Tennant et al., 2016; (E) Schwarz et al., 2017.

The possibilities of including specimen SHN.014 in the phylogenetic analysis of Schwarz et al. (2017) were explored. The same procedures described in Schwarz et al. (2017) were taken in TNT v. 1.5 (Goloboff et al., 2008). Upon addition of specimen SHN.014 to the matrix the stability of the resulting trees decreased and the appearance changed drastically. This result was to be expected since most of the characters in the matrix of Schwarz et al. (2017) were based on cranial features. However, this might not strictly point to the lack of diagnostic data in the postcranial material, but rather to the lack of using postcranial material. Also, there might be an overuse of cranial features, which strongly puts the emphasis on this material and takes away valid information from the remainder of the skeleton.

One postcranial feature that seemed fairly well represented in the matrix were the osteoderms. Indeed these have proven to be of use in determination within Neosuchia. Puértolas-Pascual and Mateus (2019) used a series of characters from osteoderms in their determination of postcranial remains of a Goniopholididae. Following the same determination, specimen SHN.014 falls within the Atoposauridae based on the following characteristics: the absence of (proof of) ventral osteoderms; two rows of dorsal osteoderms; rectangular shape of dorsal osteoderms; the presence of a dorsal crest; the absence of a ventral crest. Also, small anterolaterally positioned pegs are expected to have been present originally, which have broken off prior to discovery. Despite the unstable results of the phylogenetic analysis, the specimen indeed was placed among other Atoposauridae in the attempted phylogenetic analysis despite its disruption.

Ascribing specimen SHN.014 to a species was explored by comparing it to material from the only known Atoposauridae from the Upper Jurassic of Portugal, *Knoetschkesuchus guimarotae*. The holotype, IPFUB Gui Croc 7308, consists of ‘a partial skull and mandible, part of an isolated surangular, a second sacral vertebra and two partial osteoderms’ (Schwarz and Salisbury, 2005). Along with a long list of referred material (see Schwarz and Salisbury, 2005) it is stored in the Museu Geológico (LNEG) in Lisbon, Portugal. Observable traits from specimen SHN.014, especially the osteoderms, are considered synapomorphic within Atoposauridae. However, just like the referred material at LNEG, this specimen is ascribed to *Knoetschkesuchus guimarotae* on the premise that there is no evidence to suggest that it belongs to another species. Future research might provide a more conclusive argument to this discussion. Comparing the specimen with different material from the LNEG collection helps with determining its ontogenetic stage. Specimen SHN.014 falls around the upper limit of the size range observed in the referred material of *K. guimarotae* (see Figure 9). Based on comparisons with other Atoposauridae, Schwarz and Salisbury (2005) extrapolated the total adult size of *K. guimarotae* to be about 55 cm. Since specimen SHN.014 falls at the very upper size limit of the studied referred material, this specimen would also likely have been about 55 cm long.

## 7.2 Locomotion *Knoetschkesuchus guimarotae*

The inference of locomotion in terrestrial vs (semi-)aquatic reptiles largely comes from the strong hindlegs that carry a muscular tail which undulates mediolaterally in order to propel the body forward in the water (Webb and Blake, 1985). The presence of these large, well-developed muscles is reflected in the increased size, robustness and surface area of the bones in the hindlimbs, pelvis and caudal vertebrae. Efforts towards quantifying these qualitative, intuitive statements have been made over the past decades and are utilized here (e.g. Hua and Buffrenil, 1996; Hua, 2003; Schachner, 2011; Molnar et al., 2015; Stein et al., 2017; Rooney, 2018).



### 7.2.1 Osteological indices

In order to perform a morphometric analysis which is both meaningful and manageable with limited fossil material, the complex muscle system of the hindlimbs and tail was reduced to simple linear measurements (*see Table 1*). Rooney (2018) compiled a list of osteological indices based these linear measurements (*her Table 5*) which could potentially be meaningful in inferring locomotor behaviour. These indices were partially based on Samuels and Van Valkenburg (2008) and Samuels et al. (2013) who performed similar analyses on various mammal groups, but customised for extant crocodylians and lepidosaurs. An Univariate Analysis of Variance (ANOVA) was performed by Rooney (2018) to identify the indices most useful for distinguishing between the different locomotor groups. *Table 2* and *Figure 12* show these osteological indices and the calculated values for specimen SHN.014.

*Table 2:* osteological indices for specimen SHN.014. See *Table 1* for abbreviations of linear measurements.

Osteological indices	Calculation	Ratio
Proximal forelimb index (PFI)	ScapL / HL	0,850
Ischium-pubis index (Isch-Pub)	IschL / PubL	1,549
Crural index (CI)	TL / FL	0,743
Humeral proximal robustness index (HPRI)	HPB / HL	0,202

*Figure 12* shows the median, upper and lower quartiles, extreme values and outliers of the osteological indices for the different locomotor groups based on data from Rooney (2018), with the added values for specimen SHN.014 indicated by a red line. For both the PFI and the Isch-Pub osteological indices, specimen SHN.014 plots above the upper whiskers of all three locomotor groups. However, in both cases the semi-aquatic locomotor group shows the greater ratio value with a wider range. Both the PFI and Isch-Pub plots seem to clearly separate the semi-aquatic locomotor group from the terrestrial and arboreal locomotor groups. In the HPRI plot, the specimen is shown to fall just below the lower whiskers of the semi-aquatic and arboreal locomotor groups. In the CI plot, specimen SHN.014 falls within both the semi-aquatic and the terrestrial groups. Comparing the ranges of both groups, the specimen seems to fall more solidly within the semi-aquatic locomotor group.

### 7.2.2 Discriminant Function Analysis

The previously discussed Univariate ANOVA gives insight into which osteological indices are useful in distinguishing between different locomotor groups. A Discriminant Function Analysis (DFA) does the opposite. In the DFA the indices are a given and the discriminant functions determine how well these indices are able to determine the locomotor group of the extant species. *Figure 13* shows the DFA results and includes extant crocodylians and lepidosaurs as well as six extinct crocodylomorph taxa (five which were analysed by Rooney (2018) and *Knoetschkesuchus guimarotae*). Discriminant Function 1 (DF1) on the x-axis accounts for 81,9%

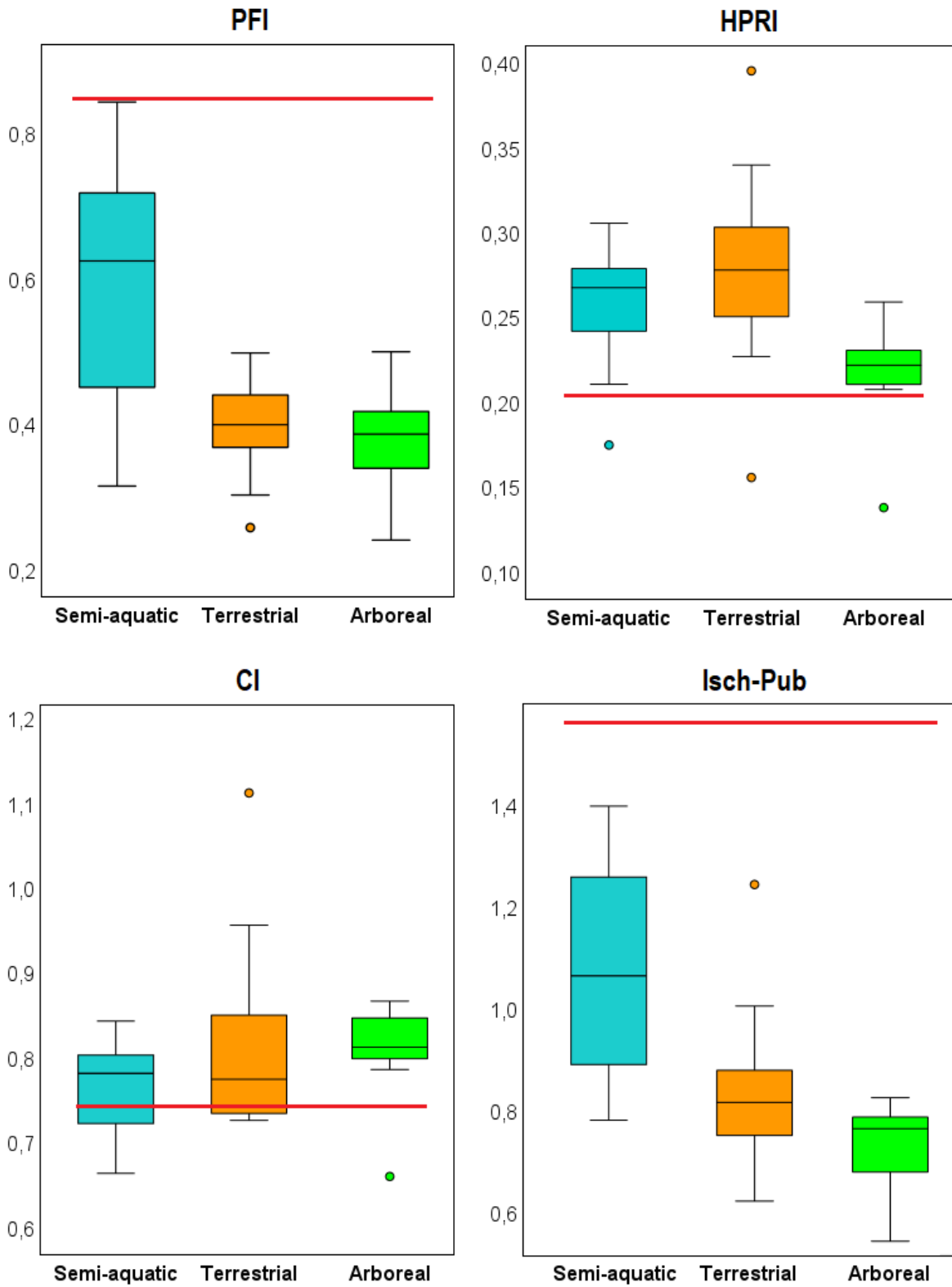


Figure 12: osteological indices that best separate the different locomotor groups. Data from Rooney (2018), with median (bar), upper and lower quartiles (boxes), extreme values (whiskers) and outliers (circles). Red line indicates index value for specimen SHN.014. See Table 2 for abbreviations.

of the variance and mainly separates the semi-aquatic locomotor group from the terrestrial and arboreal locomotor groups. Generally, the semi-aquatic taxa have a negative value for DF1 which correlates negatively with both the PFI and Isch-Pub indices and positively with the CI and HPRI indices (*see Table 3*). This quantifies the tendencies of semi-aquatic taxa to have (1) a long scapula relative to the humerus, (2) a long ischium relative to the pubis, (3) a short tibia relative to the femur and (4) a relatively slender proximal humerus respectively.

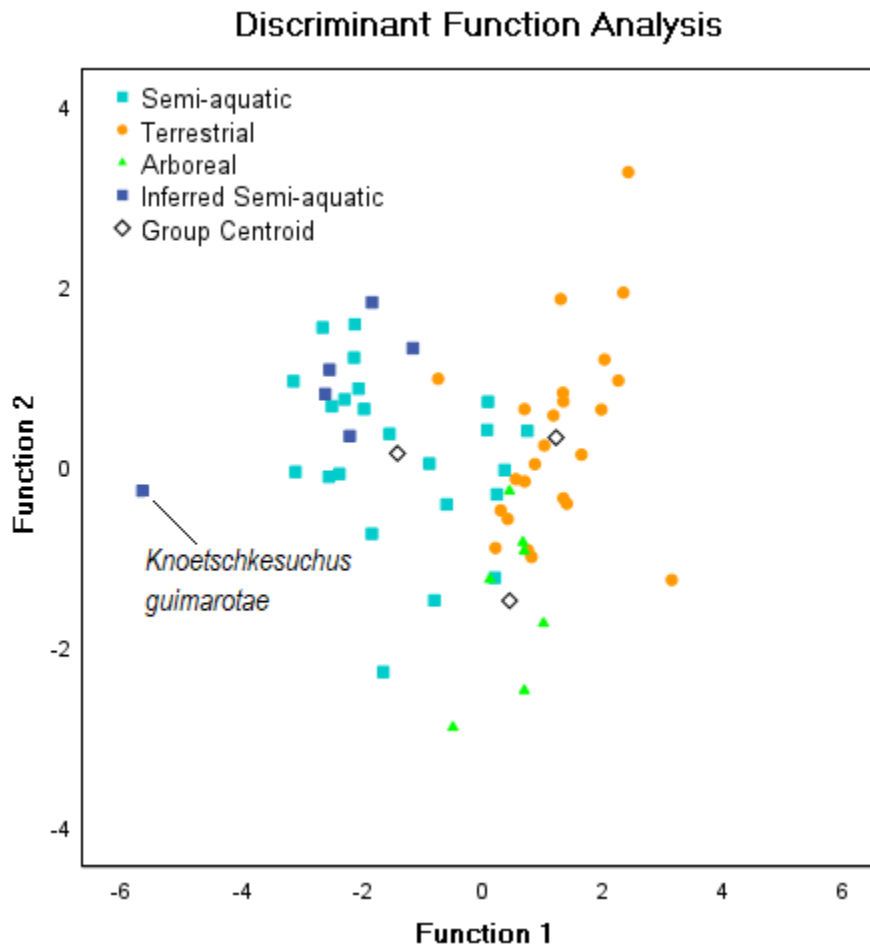


Figure 13: results from the indices DFA, based on data from Rooney (2018) and indices from SHN.014.

Discriminant Function 2 (DF2) on the y-axis accounts for 18,1% of the variance and mainly separates the arboreal locomotor group from both the semi-aquatic and terrestrial locomotor groups. Generally, the arboreal taxa have a more negative value for DF2 which correlates positively with the PFI, HPRI and Isch-Pub indices and slightly negatively with the Crural Index (*see Table 3*). This quantifies the tendencies of arboreal taxa to have (1) a long humerus relative to the scapula, (2) a relatively narrow proximal humerus, (3) a short ischium relative to the pubis and (4) a somewhat longer tibia relative to the femur respectively.

Table 3: structure matrix and summary statistics of the DFA, same results as Rooney (2018).

	<b>Discriminant Function 1</b>	<b>Discriminant Function 2</b>
PFI	-0,643	0,375
HPRI	0,117	0,820
CI	0,218	-0,051
Isch-Pub	-0,631	0,626
Eigenvalue	1,636	0,361
% variance	81,9	18,1
Wilks' lambda	0,279	0,735
Sig.	<0,001	0,002

Figure 13 also shows some overlap in the middle of the plot between taxa from different locomotor groups. Indeed, not all the extant taxa were correctly classified based on the four selected osteological indices. In general, 81,5% of the taxa were correctly classified. Of the semi-aquatic taxa 74% were correctly classified, of the terrestrial taxa 96% and of the arboreal 57%. The relatively low percentage of arboreal taxa being correctly classified may be attributed to the low number of taxa incorporated in the group.

The five extinct taxa incorporated in the DFA by Rooney (2018) plot fairly close to the semi-aquatic group's centroid and among extant semi-aquatic taxa. Applying Bayes' rule shows that all five have a significant  $P(D|G)$  score (see her Table 14), representing "the conditional probability of the observed canonical score, given membership in the most likely group" (Samuel et al., 2013). The  $P(G|D)$  score represents "the posterior probability that a case belongs in the predicted group, given the sample used to create the discriminant model" (Samuel et al., 2013) and is very high ( $>0,9$ ) for all five. *Knoetschkesuchus guimarotae* was predicted to fall within the semi-aquatic locomotor group as well, as reflected by a high  $P(G|D)$  score ( $>0,999$ ). However, it plots rather far from the group's centroid and other semi-aquatic taxa, as reflected by a low  $P(D|G)$  score ( $<0,001$ ). This later score indicates that the locomotor behaviour of *K. guimarotae* differs from those other semi-aquatic taxa incorporated in this analysis.

There are a few points to consider when trying to explain the plot position of *Knoetschkesuchus guimarotae*. Since this specimen is so small, the osteological adaptations it needs for a certain lifestyle might be less or more pronounced compared to bigger crocodylomorph taxa. Alternatively, its position away from the three incorporated locomotor modes might indicate different locomotor behaviour, or a more generalised approach. In order to draw conclusions about the locomotor behaviour of *K. guimarotae* (and to an extent that of other Atoposauridae) with more certainty, other locomotor modes and more small bodied taxa should be incorporated in the analysis. Based on this dataset and these chosen variables however, *K. guimarotae* most likely had a semi-aquatic lifestyle.

### 7.3 Implications paleobiology *Knoetschkesuchus guimarotae*

Based on its small body size and teeth, Schwarz and Salisbury (2005) suggest the diet of *K. guimarotae* most likely consisted of invertebrates and small amphibians and mammals based on dietary preferences of modern juvenile crocodylians. Since its dietary niche would have been so different from other, larger crocodylians from the Late Jurassic (such as *Goniopholis*), it is likely that they could have lived sympatrically within an ecosystem. Schwarz and Salisbury (2005) argue that the relatively long hindlimbs and interlinking osteoderms of *K. guimarotae* would be beneficial on land, creating a longer stride and reducing strain on its spine through rigidity. They also discuss the possibility of the taxon being more terrestrial leaning because of its paleobiogeographical distribution. From the relatively isolated landmasses of western Europe during the Late Jurassic (Ziegler, 1988), *Knoetschkesuchus* and the closely related *Theriosuchus* have been described from relatively isolated locations (both temporally and spatially). Furthermore, at each of the major discovery sites of these taxa, a different taxon was found. On the other hand the semi-aquatic *Goniopholis* has been described at many different sites in western Europe of the Late Jurassic (e.g. Salisbury et al., 1999). The morphometric analysis performed in this study suggests that *K. guimarotae* was semi-aquatic too. This would imply that, in order to explain the difference in occurrences, *K. guimarotae* was less common than *Goniopholis* rather than terrestrial. Perhaps its smaller size made it impossible for *K. guimarotae* to spread out amongst the different landmasses.

#### 7.3.1 Implications paleobiogeography

In this study specimen SHN.014 was ascribed to *Knoetschkesuchus guimarotae* Schwarz and Salisbury (2005), formerly known as *Theriosuchus guimarotae*. This taxon has previously only been described from the Upper Kimmeridgian strata of the Guimarota Mine near Leiria, Portugal (Schwarz and Salisbury, 2005). The provenance of this specimen is the Upper Kimmeridgian Porto de Barcas Member east of Baleal, Peniche, Portugal. The relatively well preserved material of SHN.014 suggests that the specimen was not transported over great distances, at most within the ecosystem in which it was found. Therefore the temporal occurrence of *K. guimarotae* is not altered. The two localities both lay within the Lusitanian Basin, about 60 km apart, and are part of two different sub-basins. The occurrence of this taxon throughout multiple sub-basins indicates that these did not form fully isolated environments, but had some interchange at least part of the time. This is in line with the occurrence of other lifeforms between sub-basins. The occurrence of the diverse Atoposauridae family throughout Europe in the Late Jurassic and Early Cretaceous indicates a high degree of allopatric speciation. The semi-aquatic lifestyle (and thus dependence on land) led to isolation in an environment dominated by relatively small landmasses and epicontinental seas (Ziegler, 1988).

#### 7.4 Further research specimen SHN.014

The uniquely complete specimen SHN.014 and the Micro CT-scans made in this study lend themselves well to further research. The Micro CT-scans, along with thinslices that could be made of some of the appendicular bones could be used for histological research to gain further insight in the ontogenetic stage of the specimen. Furthermore, the preservation of the spine material is well enough and the Micro CT-scans are detailed enough to study the neuroanatomy of the specimen. The non-destructive approach taken in this study with this fragile and small material could result in several different research outputs.

### 8. Conclusion

Through the use of Micro CT-scans, a small, fragile and uniquely complete crocodylomorph specimen from the Late Jurassic of Portugal was described. It consists of large parts of the posterior vertebral chain and the hindlimbs. Based on osteoderm morphology and comparisons with referred material it was ascribed to *Knoetschkesuchus guimarotae* (Atoposauridae, Crocodylomorpha). Measurements of the pelvic and hindlimb elements were used to infer locomotor behaviour of *K. guimarotae* through a morphometric analysis. The measurements of the forelimbs and pectoral girdle were taken from referred specimens and extrapolated to the size of specimen SHN.014. The analysis suggests that the species was semi-aquatic. The lower but more diverse occurrence of Atoposauridae relative to other semi-aquatic crocodylomorphs at the time suggests that they were less common and less-well adapt to swim large distances.

## References

- Adams, T. L. (2014). Small crocodyliform from the Lower Cretaceous (Late Aptian) of Central Texas and its systematic relationship to the evolution of Eusuchia. *Journal of Paleontology*, 88(5), 1031-1049.
- Alves, T. M., Gawthorpe, R. L., Hunt, D. W., & Monteiro, J. H. (2003a). Jurassic tectono-sedimentary evolution of the Northern Lusitanian Basin (offshore Portugal). *Marine and Petroleum Geology*, 19(6), 727-754.
- Alves, T. M., Manuppella, G., Gawthorpe, R. L., Hunt, D. W., & Monteiro, J. H. (2003b). The depositional evolution of diapir-and fault-bounded rift basins: examples from the Lusitanian Basin of West Iberia. *Sedimentary Geology*, 162(3-4), 273-303.
- Alves, T. M., Moita, C., Sandnes, F., Cunha, T., Monteiro, J. H., & Pinheiro, L. M. (2006). Mesozoic–Cenozoic evolution of North Atlantic continental-slope basins: The Peniche basin, western Iberian margin. *AAPG bulletin*, 90(1), 31-60.
- Benton, M. J., & Clark, J. M. (1988). Archosaur phylogeny and the relationships of the Crocodylia. *The phylogeny and classification of the tetrapods*, 1, 295-338.
- Brinkmann, W. (1989). Vorläufige Mitteilung über die Krokodilier-Faunen aus dem Ober-Jura (Kimmeridgium) der Kohlegrube Guimarota, bei Leiria (Portugal) und der Unter-Kreide (Barremium) von Uña (Provinz Cuenca, Spanien). *Documenta naturae*, 56, 1-28.
- Bronzati, M., Montefeltro, F. C., & Langer, M. C. (2012). A species-level supertree of Crocodyliformes. *Historical Biology*, 24(6), 598-606.
- Buscalioni, A. D., & Sanz, J. L. (1988). Phylogenetic relationships of the Atoposauridae (Archosauria, Crocodylomorpha). *Historical Biology*, 1(3), 233-250.
- Camarate Franca, J., Zbyszewski, G., Moitinho de Almeida, F. (1960). Carta geológica de Portugal 1/50000. Folha 26-C, Peniche. Departamento de Geologia e Minerio.
- Chatterjee, S. (1982). Significance of ankle structures in archosaur phylogeny (reply). *Nature*, 299(5884), 657-658.
- Chen, M., & Wilson, G. P. (2015). A multivariate approach to infer locomotor modes in Mesozoic mammals. *Paleobiology*, 41(2), 280-312.
- Cohen, K. M., Finney, S. C., Gibbard, P. L., & Fan, J. X. (2013). The ICS international chronostratigraphic chart (updated). *Episodes*, 36(3), 199-204.
- DGGE (Direcção Geral de Geologia e Energie). (2007). Archives (see [www.dgge.pt](http://www.dgge.pt)).
- Fedorov, A., Beichel, R., Kalpathy-Cramer, J., Finet, J., Fillion-Robin, J. C., Pujol, S., ... & Buatti, J. (2012). 3D Slicer as an image computing platform for the Quantitative Imaging Network. *Magnetic resonance imaging*, 30(9), 1323-1341.
- George, D., & Mallery, P. (2019). IBM SPSS Statistics 26 step by step: A simple guide and reference. Routledge.
- Gervais, P. (1871). Remarques au sujet des Reptiles provenant des calcaires lithographiques de Cerin, dans le Bugey, qui sont conservés au Musée de Lyon. *Comptes Rendus des séances de l'Academie de Sciences*, 73, 603-607.

- GPEP (Gabinete Para a Pesquisa e Exploração). (1993). The Petroleum Potential of Portugal. Data Package.
- Guillaume, A. R., Moreno-Azanza, M., Puértolas-Pascual, E., & Mateus, O. (2019). Palaeobiodiversity of crocodylomorphs from the Lourinhã Formation based on the tooth record: insights into the palaeoecology of the Late Jurassic of Portugal. *Zoological Journal of the Linnean Society*.
- Goloboff, P. A., Farris, J. S., & Nixon, K. C. (2008). TNT, a free program for phylogenetic analysis. *Cladistics*, 24(5), 774-786.
- Hay, O. P. (1930). *Second bibliography and catalogue of the fossil vertebrata of North America*.
- Hill, G. (1989). Distal alluvial fan sediments from the Upper Jurassic of Portugal: controls on their cyclicity and channel formation. *Journal of the Geological Society*, 146(3), 539-555.
- Hua, S. (2003). Locomotion in marine mesosuchians (Crocodylia): the contribution of the. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, 139-152.
- Hua, S., & De Buffrenil, V. (1996). Bone histology as a clue in the interpretation of functional adaptations in the Thalattosuchia (Reptilia, Crocodylia). *Journal of Vertebrate Paleontology*, 16(4), 703-717.
- Kullberg, J. C., da Rocha, R. B., Soares, A. F., Duarte, L. V., & Marques, J. F. (2014). Palaeogeographical evolution of the Lusitanian Basin (Portugal) during the Jurassic. Part I: The tectonic constraints and sedimentary response. In *STRATI 2013* (pp. 665-672). Springer, Cham.
- REINHOLD, R. (1993). A sequence stratigraphic approach to the Upper Jurassic mixed carbonate-siliciclastic succession of the central Lusitanian Basin, Portugal.
- Leinfelder, R. R., & Wilson, R. C. L. (1989). Seismic and sedimentologic features of Oxfordian-Kimmeridgian syn-rift sediments on the eastern margin of the Lusitanian Basin. *Geologische Rundschau*, 78(1), 81-104.
- Leinfelder, R. R., & Wilson, R. C. L. (1998). Third-Order Sequences in a Upper Jurassic Rift-Related Second Order Sequence, Central Lusitanian Basin, Portugal.
- Losos, J. B. (1990). The evolution of form and function: morphology and locomotor performance in West Indian Anolis lizards. *Evolution*, 44(5), 1189-1203.
- Malafaia, E., Ortega, F., Silva, B., & Escaso, F. (2012). Theropod dinosaurs from the Late Jurassic of the Lusitanian Basin (Portugal): analysis of diversity based on dental morphotypes. In *Royo-Torres, R., Gascó, F. and Alcalá, L., coord.(2012). 10th Annual Meeting of the European Association of Vertebrate Palaeontologists. 20: 1-290.* (p. 133).
- Manuppella, G. (1996). Carta geológica de Portugal 1/50000. Folha 30-A, Lourinhã. *Departamento de Geologico e Mineriro*.
- Manuppella, G., Antunes, M. T., Pais, J., Ramalho, M. M., & Rey, J. (1999). Notícia explicativa da folha 30-A (Lourinhã). *Carta Geológica de Portugal, escala, 1, 50000*.
- Martin, T., & Krebs, B. (2000). *Guimarota: a Jurassic ecosystem*. Verlag Dr. Friedrich Pfeil.



- Martinius, A. W., & Gowland, S. (2011). Tide-influenced fluvial bedforms and tidal bore deposits (late Jurassic Lourinhã Formation, Lusitanian Basin, Western Portugal). *Sedimentology*, 58(1), 285-324.
- Mateus, O. (2008). Checklist for Late Jurassic reptiles and amphibians from Portugal. In *Livro de Resumos do X Congresso Luso-Espanhol de Herpetologia*.
- Mateus, O., Dinis, J., & Cunha, P. P. (2013). Upper Jurassic to Lowermost Cretaceous of the Lusitanian Basin, Portugal-landscapes where dinosaurs walked. *Ciências da Terra special no VIII*.
- Mateus, O., Dinis, J., & Cunha, P. P. (2017). The Lourinhã Formation: the Upper Jurassic to lower most Cretaceous of the Lusitanian Basin, Portugal-landscapes where dinosaurs walked. *Ciências da Terra/Earth Sciences Journal*, 19(1), 75-97.
- von Meyer, H. (1837). Mittheilungen an Professor Bronn gerichtet. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde*, 1837, 557-562.
- Mocho, P., Royo-Torres, R., Malafaia, E., Escaso, F., & Ortega, F. (2017). Sauropod tooth morphotypes from the Upper Jurassic of the Lusitanian Basin (Portugal). *Papers in Palaeontology*, 3(2), 259-295.
- Molnar, J. L., Pierce, S. E., Bhullar, B. A. S., Turner, A. H., & Hutchinson, J. R. (2015). Morphological and functional changes in the vertebral column with increasing aquatic adaptation in crocodylomorphs. *Royal Society Open Science*, 2(11), 150439.
- Pérez-Moreno, B. P., Chure, D. J., Pires, C., Da Silva, C. M., Dos Santos, V., Dantas, P., ... & De Carvalho, A. G. (1999). On the presence of *Allosaurus fragilis* (Theropoda: Carnosauria) in the Upper Jurassic of Portugal: first evidence of an intercontinental dinosaur species. *Journal of the Geological Society*, 156(3), 449-452.
- Puértolas-Pascual, E., & Mateus, O. (2019). A three-dimensional skeleton of Goniopholididae from the Late Jurassic of Portugal: implications for the Crocodylomorpha bracing system. *Zoological Journal of the Linnean Society*, 189(2), 521-548. Roche et al. (1996),
- Rogers, J. V. (2003). *Pachycheilosuchus trinquei*, a new procoelous crocodyliform from the Lower Cretaceous (Albian) Glen Rose Formation of Texas. *Journal of Vertebrate Paleontology*, 23(1), 128-145.
- Rooney, L. (2018). Postcranial morphology and the locomotor adaptations of extant and extinct crocodylomorphs and lepidosaurs. (Published Master's Thesis, East Tennessee State University)
- Rose, J. A., Moore Crisp, L., Russell, A., Butcher, M. (2014). Functional osteology of the forelimb digging apparatus of badgers. *Journal of Mammalogy*. 95. 543- 558.
- Salisbury, S. W., Willis, P. M., Peitz, S., & Sander, P. M. (1999). The crocodylian *Goniopholis simus* from the Lower Cretaceous of north-western Germany. *Special Papers in Palaeontology*, 60, 121-148.
- Samuels, J. X., & Van Valkenburgh, B. (2008). Skeletal indicators of locomotor adaptations in living and extinct rodents. *Journal of morphology*, 269(11), 1387-1411.
- Samuels, J. X., Meachen, J. A., & Sakai, S. A. (2013). Postcranial morphology and the locomotor habits of living and extinct carnivorans. *Journal of morphology*, 274(2), 121-146.

- Schachner, E. R. (2011). Anatomical reconstructions of respiratory morphology and hindlimb musculature in *Poposaurus gracilis* (Archosauria: Poposauroida) and related dinosauriformes.
- Schneider, S., Fürsich, F. T., & Werner, W. (2009). Sr-isotope stratigraphy of the Upper Jurassic of central Portugal (Lusitanian Basin) based on oyster shells. *International Journal of Earth Sciences*, 98(8), 1949-1970.
- Schwarz, D. (2002). A new species of *Goniopholis* from the Upper Jurassic of Portugal. *Palaeontology*, 45(1), 185-208.
- Schwarz, D., & Salisbury, S. W. (2005). A new species of *Theriosuchus* (Atoposauridae, Crocodylomorpha) from the late Jurassic (Kimmeridgian) of Guimarota, Portugal. *Geobios*, 38(6), 779-802.
- Schwarz, D., Raddatz, M., & Wings, O. (2017). *Knoetschkesuchus langenbergensis* gen. nov. sp. nov., a new atoposaurid crocodyliform from the Upper Jurassic Langenberg Quarry (Lower Saxony, northwestern Germany), and its relationships to *Theriosuchus*. *PLoS One*, 12(2), e0160617.
- Seiffert, J. (1973). Upper Jurassic lizards from central Portugal.
- Sereno, P. C., Sidor, C. A., Larsson, H. C. E., & Gado, B. (2003). A new notosuchian from the Early Cretaceous of Niger. *Journal of Vertebrate Paleontology*, 23(2), 477-482.
- Stein, M. D., Yates, A., Hand, S. J., & Archer, M. (2017). Variation in the pelvic and pectoral girdles of Australian Oligo–Miocene mekosuchine crocodiles with implications for locomotion and habitus. *PeerJ*, 5, e3501.
- Taylor, A. M., Gowland, S., Leary, S., Keogh, K. J., & Martinius, A. W. (2013). Stratigraphical correlation of the Late Jurassic Lourinhã Formation in the Consolação Sub-basin (Lusitanian Basin), Portugal. *Geological Journal*, 49(2), 143-162.
- Tennant, J. P., Mannion, P. D., & Upchurch, P. (2016). Evolutionary relationships and systematics of Atoposauridae (Crocodylomorpha: Neosuchia): implications for the rise of Eusuchia. *Zoological Journal of the Linnean Society*, 177(4), 854-936.
- Tulli, M. J., Carrizo, L. V., & Samuels, J. X. (2015). Morphological variation of the forelimb and claw in Neotropical sigmodontine rodents (Rodentia: Cricetidae). *Journal of Mammalian Evolution*, 23(1), 81-91.
- Turner, A. H. (2015). A review of *Shamosuchus* and *Paralligator* (Crocodyliformes, Neosuchia) from the Cretaceous of Asia. *PLoS One*, 10(2), e0118116.
- Turner, A. H., & Pritchard, A. C. (2015). The monophyly of *Susisuchidae* (Crocodyliformes) and its phylogenetic placement in Neosuchia. *PeerJ*, 3, e759.
- Van Valkenburgh, B. (1987). Skeletal indicators of locomotor behavior in living and extinct carnivores. *Journal of Vertebrate Paleontology*, 7(2), 162-182.
- Wainwright, P. C. (2007). Functional versus morphological diversity in macroevolution. *Annual Review of Ecology, Evolution, and Systematics*, 38.
- Walker, A. D. (1968). *Protosuchus*, *Proterochampsia*, and the origin of phytosaurs and crocodiles. *Geological Magazine*, 105(1), 1-14.

Webb, P.W., Blake, R.W. (1985). Swimming. In: Hildebrand M, Bramble DM, Liem KF, Wake DB, editors. Functional vertebrate morphology. Cambridge, MA: Harvard University Press. pp. 111–128.

Whetstone, K. N., & Whybrow, P. J. (1983). *A "cursorial" crocodilian from the Triassic of Lesotho (Basutoland), southern Africa*. Museum of Natural History, University of Kansas.

Wilberg, E. W., Turner, A. H., & Brochu, C. A. (2019). Evolutionary structure and timing of major habitat shifts in Crocodylomorpha. *Scientific Reports*, 9(1), 1-10.

Wilson, R. C. L. (1975). Atlantic opening and Mesozoic continental margin basins of Iberia. *Earth and Planetary Science Letters*, 25(1), 33-43.

Wilson, R. C. L. (1979). A reconnaissance study of Upper Jurassic sediments of the Lusitanian Basin. *Ciências da Terra* 5, 53–84.

Wilson, R. C. L., Hiscott, R. N., Willis, M. G., & Gradstein, F. M. (1989). The Lusitanian Basin of West-Central Portugal: Mesozoic and Tertiary Tectonic, Stratigraphic, and Subsidence History: Chapter 22: European-African Margins.

Young, M. T., Hua, S., Steel, L., Foffa, D., Brusatte, S. L., Thüring, S., ... & De Andrade, M. B. (2014). Revision of the late Jurassic teleosaurid genus *Machimosaurus* (Crocodylomorpha, Thalattosuchia). *Royal Society Open Science*, 1(2), 140222.

Ziegler, P. A. (1988). Evolution of the Arctic-North Atlantic and the Western Tethys: A visual presentation of a series of Paleogeographic-Paleotectonic maps. *AAPG memoir*, 43, 164-196.