



# Revised anatomy, taxonomy and biostratigraphy of *Notochampsia istedana* Broom, 1904, a Lower Jurassic crocodyliform from the Clarens Formation (Stormberg Group), and its implications for early crocodyliform phylogeny

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The early-branching crocodylomorph species *Notochampsia istedana* is known from a single South African specimen collected more than 100 years ago. This species is potentially important for understanding early crocodylomorph evolution, but it is of uncertain taxonomic status and its stratigraphic position is poorly constrained. Here we reinvestigate the anatomy, taxonomy, systematics and biostratigraphy of the holotype specimen, SAM-PK-4013. SAM-PK-4013 has a unique suite of features that distinguish it from the closely related taxa *Orthosuchus* and *Protosuchus*. These features include the length and shape of the dentary symphysis, the number and shape of dentary teeth, and the number of dorsal ribs with expanded intercostal ridges. *Notochampsia* is therefore a valid taxon, and our phylogenetic analysis recovers it as sister to *Orthosuchus*, in a monophyletic Notochampsidae. *Notochampsia* and *Orthosuchus* share a ventrally expanded squamosal flange and expanded intercostal ridges on the dorsal ribs. Notochampsidae is in turn sister to Protosuchidae, forming the monophyletic group Notochampsioidea. Fieldwork and stratigraphic revisions show definitively that SAM-PK-4013 is from the Clarens Formation, approximately ~65 m above the Elliot contact, ageing *Notochampsia* to the Pliensbachian stage, a period of vertebrate body fossil scarcity. Thus, *Notochampsia istedana* is the youngest known occurrence of a crocodylomorph (and vertebrate body fossil) from the Karoo Basin of South Africa.

**Keywords:** Crocodylomorpha; phylogenetics; Clarens Formation; systematics; South Africa; Notochampsidae

## Introduction

*Notochampsia istedana* is the first described extinct crocodylomorph species from South Africa. It was named and briefly described by Broom (1904) over a century ago in a paper that also named a second species within the genus, *Notochampsia longipes*. There are at least four short publications that describe the anatomy of the two *Notochampsia* species (Broom 1904, 1927; Haughton 1924; von Huene 1925) but their anatomical interpretations differ, particularly with regards to skull morphology, in part due to poor preservation. Although *Notochampsia* was considered to be an early-branching member of the Crocodylomorpha (i.e. a ‘protosuchian’), these differing observations have called into question the taxonomic validity and phylogenetic position of the genus *Notochampsia* almost since its initial description.

Haughton (1924) agreed that *Notochampsia istedana* was a valid taxon, but that *Notochampsia istedana* and *Notochampsia longipes* could not be congeneric because *Notochampsia longipes* possessed ‘truer’ crocodylian

features (e.g. the exclusion of the pubis from the acetabulum), whereas *Notochampsia istedana* exhibited features which were not congruent with what was generally understood as ‘crocodylian’, e.g. paired, laterally facing external nares. Therefore, Haughton (1924) assigned *Notochampsia longipes* to a new genus *Erythrochampsia*. Haughton (1924) went on to hypothesize that *Notochampsia istedana* was closely related to *Pedeticosaurus* van Hoepen, 1915, and grouped them in the clade Notochampsidae.

Subsequent authors have hypothesized several, sometimes confusing, taxonomic affinities for *Notochampsia istedana*, assigning it to different clades, including: Watson (1917) to Aetosauridae; Nopcsa (1928) to Erpetosuchidae (along with *Erythrochampsia* and *Pedeticosaurus*); and Ellenberger (1970) to Notochampsidae. Sill (1967) placed *Notochampsia* with *Proterochampsia* in the Notochampsidae, but the similarities were later disputed (Walker 1968) and *Proterochampsia* is now recognized to be outside of Archosauria (Benton & Clark 1988; Nesbitt 2011; Irmis

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*et al.* 2013). Walker (1968) discussed the similarities between *Notochamps*, *Protosuchus* and *Stegomosuchus*, drawing them together into one family he termed Stegomosuchidae (according to the priority of the family named by von Huene [1922]). These taxonomic affinities are generally pre-cladistic hypotheses that are not supported by any character optimizations (as implemented in this study). Nash (1975) also compared *Orthosuchus* to *Notochamps* and described them as closely related, but with noticeable differences, including the shape of the supratemporal fenestra and the pattern of the quadrate fenestrae. However, Nash (1975) noted the latter difference was between the holotype of *Orthosuchus* and NHMUK PV R8503, which she considered to be *Notochamps* but that was later named *Lesothosuchus charigi* Whetstone & Whybrow, 1983. Whetstone & Whybrow (1983) designated *Notochamps istedana* as a *nomen dubium* based on the lack of preservation of diagnostic features in the type specimen (SAM-PK-4013). Clark (1986) in his PhD dissertation described the notable similarities between *Notochamps* and *Orthosuchus*, which includes the extended posterolateral process of the squamosal and absence of ventral osteoderms, and tentatively considered *Notochamps istedana* to be a *nomen dubium*. Carroll (1988) also refers to *Notochamps* as a senior synonym of *Orthosuchus*, although not citing any feature between the specimens.

The loosely bracketed term ‘early-branching crocodylomorphs’ blankets an extended period in crocodylomorph evolution and includes any taxa in either the paraphyletic evolutionary grade of ‘Sphenosuchia’ (non-crocodyliform crocodylomorphs) and ‘Protosuchia’ (non-mesoeucrocodylian crocodyliforms). The number of documented early-branching crocodylomorph taxa has grown greatly since *Notochamps* was last revised, and with it our understanding of their anatomy, ecology and diversity has progressed, thanks to detailed work on their anatomy and systematics (e.g. Walker 1990; Wu & Chatterjee 1993; Clark & Sues 2002; Clark *et al.* 2004; Pol *et al.* 2013). Early-branching crocodylomorphs have small- to medium-sized body ranges, e.g. *Shartegosuchus* and *Sphenosuchus*, although *Carnufex* is currently the only early crocodylomorph known to possess a large body size. Some forms possess very complex dental cusp morphology, such as *Edentosuchus* and UCMP 97638, and are hypothesized to be herbivorous (Ösi 2014; Melstrom & Irmis 2019), and other forms are inferred to be hypercarnivores, e.g. *Sphenosuchus* and *Junggarsuchus*. Body shapes also vary greatly, with taxa such as *Terrestriusuchus* and *Litargosuchus* having long, gracile limbs, and other taxa like *Shantungosuchus* possessing stouter limb proportions. Early-branching

crocodylomorphs were numerous and likely inhabited a range of ecological niches considering their morphological diversity. Within the context of southern Africa, currently recognized crocodylomorph taxa include the non-crocodylomorph crocodyliforms *Litargosuchus* and *Sphenosuchus*, and the ‘protosuchian’ protosuchids *Protosuchus* and *Orthosuchus* (Dollman *et al.* 2018), now with the addition of *Notochamps*.

Our understanding of the biostratigraphic context of southern African fossils from the Stormberg Group has also grown (e.g. Bordy *et al.* 2004, 2020a; Bordy & Eriksson 2015; Dollman *et al.* 2017; McPhee *et al.* 2017; Chapelle *et al.* 2019; Smith *et al.* 2020). The Elliot Formation has produced abundant vertebrate body and trace fossil remains, which include dinosaurs, pseudosuchians, lepidosaurs, stem-group turtles, therapsids and crocodylomorphs. More recent studies on sedimentary facies and intercontinental faunal correlations indicate that the Elliot Formation is divided into lower (IEF) and upper (uEF) sedimentary units, and that the IEF and uEF represent the Late Triassic and Early Jurassic, respectively.

The Clarens Formation, the stratigraphic unit overlying the Elliot Formation in the Stormberg Group and the uppermost sedimentary rock unit in the Karoo Supergroup, is comparatively depauperate in vertebrate body fossil remains, but is known for numerous trace fossils. Bordy *et al.*'s (2020a) recent work on the chronostratigraphy of the Elliot and Clarens Formations indicates that the Elliot Formation is middle Norian–Sinemurian in age, and that the Clarens Formation is mostly Pliensbachian.

Vertebrate fossil occurrences from the Pliensbachian are rare compared to the Sinemurian (e.g. Close *et al.* 2020). Any vertebrate fossil recovered and identified from the Clarens Formation provides insight into the fauna present during this period, and may provide insight into the palaeoenvironmental changes that occurred through the Sinemurian–Pliensbachian stages. The Clarens Formation contains aeolianites which suggest that the palaeoenvironment was more arid than during the earlier times when *Protosuchus* and *Orthosuchus* lived during deposition of the underlying uEF (Bordy & Head 2018). However, aeolian, fluvial and lacustrine depositional conditions are also present in the Clarens Formation (Eriksson 1981, 1986; Bordy & Head 2018; Bordy *et al.* 2020a, b, 2021).

Improved knowledge of early crocodylomorphs and advances in the chronostratigraphy and the biostratigraphy of the Elliot Formation, combined with the importance of early-branching taxa for deciphering relationships, makes this an opportune moment to reinvestigate *Notochamps istedana* in order to assess its

validity, phylogenetic affinities and stratigraphic position. Here, the holotype of *Notochamps istedana* is reinvestigated using CT-scanning technology to uncover previously unknown anatomical data which are then used to clarify its phylogenetic affinities. Furthermore, the anatomy of the SAM-PK-4013 is reconsidered and compared to other South African specimens. Additionally, the type locality of *Notochamps istedana* was revisited and it is now confirmed that SAM-PK-4013 is the youngest known crocodylomorph (and indeed, currently, the youngest occurring vertebrate known) from the Karoo Supergroup of South Africa.

## Materials and methods

### Institutional abbreviations

**BP**, Evolutionary Studies Institute, Johannesburg, South Africa; **NHMUK PV R**, Natural History Museum, London, UK; **QG**, Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe; **QR**, National Museum, Bloemfontein, South Africa; **SAM**, Iziko South African Museum, Cape Town, South Africa; **UCMP**, University of California Museum of Paleontology, Berkeley, USA.

### Computed tomography scan

SAM-PK-4013 was scanned at the CT Scan Facility at Stellenbosch University (du Plessis *et al.* 2016) at a voxel size of 50  $\mu\text{m}$  (100 kV, 240  $\mu\text{A}$ , 1 fps, no filter). BP/1/4242 was CT scanned at the Wits Micro CT scan Facility at the Evolutionary Studies Institute, University of Witwatersrand at a voxel size of 79.9  $\mu\text{m}$  (130 kV, 190  $\mu\text{A}$ , 1 fps, 1.2 Cu). The dentary symphysis and rib of SAM-PK-4013, and a comparative dorsal rib of BP/1/4242 were digitally segmented and visualized in VG Studio Max v. 3.2 using the region growing tool.

### Phylogenetic analysis

The phylogenetic relationships of *Notochamps istedana* to other crocodylomorphs were tested by scoring SAM-PK-4013 into a phylogenetic data matrix adapted from Dollman *et al.* (2018) (see [Supplementary material](#)). The resulting matrix has 64 terminal taxa and 262 discrete characters, 32 of which are ordered. The trees are rooted on *Gracilisuchus stipanicorum* and include *Postosuchus kirkpatricki* as a second outgroup taxon. The data matrix was managed using Mesquite v. 3.5 (Maddison & Maddison 2018), and was analysed heuristically for shortest tree topologies using equally weighted parsimony as the optimality criterion in the software package TNT v. 1.5 (Goloboff & Catalano 2016). The data matrix was analysed with the

following parameters: tree bisection and reconnection (TBR) as a heuristic search strategy; 1000 Wagner builds with a random seed of 1; keeping two trees per replication; and replacing existing trees when more optimal trees were discovered. An additional round of branch swapping on shortest-length topologies was then performed using the trees in memory and holding up to 10,000 trees of shortest length.

Support for MPTs was assessed using Bremer support, jackknife and bootstrap (Goloboff & Nixon 2008). Bremer support was calculated in TNT by a round of TBR swapping on the optimal topologies, saving trees up to 10 steps longer than the MPTs and stopping when the tree buffer contained 10,000 total topologies of any length. Jackknife and bootstrap support measures were calculated in TNT using GC frequencies. Jackknife analysis used 36 removal probability and 100 replicates. Bootstrap analysis used a standard resampling strategy (with replacement) and 100 replicates. An additional analysis with the same parameters was performed with *Thalattosuchia* constrained outside of *Crocodyliformes* to evaluate how the position of *Thalattosuchia* affects 'protosuchian' ingroup relationships. *Thalattosuchia* has been found in multiple different positions in the crocodylomorph tree: as a sister clade to *Tethysuchidae* in a mostly pelagic clade of later-branching neosuchians; as sister clade to *Crocodyliformes*; and as an early-branching clade in *Mesoeucrocodylia* (e.g. Benton & Clark 1988; Sereno *et al.* 2001; Pol & Gasparini 2009; Wilberg 2015). The latter is not included in our analysis because it is only found when 'protosuchians' are selected as the outgroup (Larsson & Sues 2007; Sereno *et al.* 2001, 2003; Sereno & Larsson 2009), which excludes the possibility of *Thalattosuchia* as a sister clade to *Crocodyliformes*. Finally, a series of implied weighting analyses with a range of *k* values (12, 6 and 3) were performed with the same parameters as outlined above on the data matrix as a sensitivity analysis to investigate how down-weighting characters of worse fit affected resulting tree topologies.

## Systematic palaeontology

Superclass **Reptilia** Laurenti, 1768 *sensu* Modesto & Anderson (2004)

Class **Pseudosuchia** Zittel, 1887–1890 *sensu* Sereno (2005)

Cohort **Loricata** Merrem, 1820 *sensu* Nesbitt (2011)  
Subcohort **Paracrocodylomorpha** Parrish, 1993 *sensu* Nesbitt (2011)

Superorder **Crocodylomorpha** Hay, 1930 *sensu* Walker (1970)

Order **Crocodyliformes** Hay, 1930 *sensu* Clark, in Benton & Clark (1988)  
 Superfamily **Notochampsoidae**

**Diagnosis.** Small-bodied crocodyliforms (less than 1 m in anteroposterior length) with the following unique combination of features that are diagnostic for the group: otoccipital has a large ventrolateral surface ventral to the paroccipital process; the quadrate has three or more fenestrae; the basisphenoid contribution to the ventral surface of the braincase is larger than that of the basioccipital; the anterior dentary tooth opposite the premaxilla–maxilla suture is more than twice the apicobasal length of other dentary teeth.

**Definition.** Notochampsoidae is defined here as the least inclusive clade including *Notochampsia*, *Protosuchus* and all descendants of their most recent common ancestor.

Family **Notochampsidae** Haughton, 1924

**Diagnosis.** Diagnosed by the following unique combination of features: an elongated process extending posterovertrally from the posterolateral edge of the squamosal; broad intercostal ridges expanding the anterior and posterior margins of the dorsal ribs.

**Definition.** Notochampsidae is defined here as the least inclusive clade including both *Notochampsia* and *Orthosuchus* and all descendants of their most recent common ancestor.

**Remarks.** Following the results of this phylogenetic analysis (below), *Orthosuchus* and *Notochampsia* are placed as the only two currently known members of Notochampsidae.

*Notochampsia* Broom, 1904

**Diagnosis.** As for type and only valid species, *Notochampsia istedana*.

*Notochampsia istedana* Broom, 1904

**Type species.** *Notochampsia istedana*. Broom (1904) did not designate a type species and we are not aware of any subsequent designation, but we support the designation of *Notochampsia istedana* as the type species of the genus *Notochampsia* considering that: (1) it was the first species described in the original publication; (2) *Notochampsia longipes* was later separated into the genus *Erythrochampsia* (Haughton, 1924); and (3) the

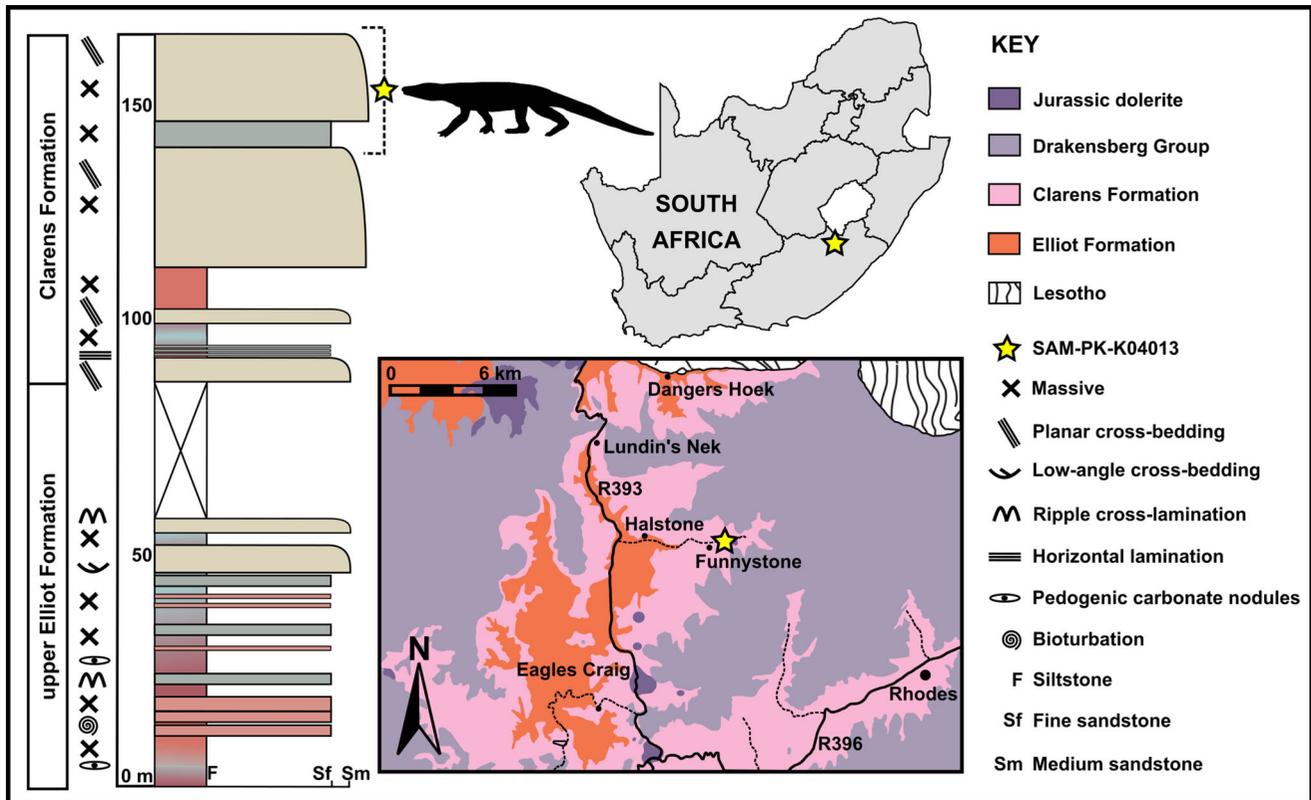
holotype of *Erythrochampsia longipes* apparently lacks diagnostic features.

**Revised species diagnosis.** Anterior and posterior expansions of the dorsal ribs are restricted to the first four elements in the series.

**Material.** The holotype and currently only known specimen of *Notochampsia istedana* is SAM-PK-4013. It is an articulated specimen preserved in a very fine-grained, pale olive (10Y 6/2) sandstone block and includes: a partial skull exposed in dorsal view; right hemimandible; right scapula; both coracoids; interclavicle; the proximal end of the right humerus; left forelimb (humerus, radius, carpus, metacarpus); partial left femur; left tibia; left fibula; dorsal osteoderms; and associated ribs.

**Type locality and stratigraphy.** SAM-PK-4013 was discovered on Funnystone farm (Farm number 35, referring to the municipal plot number) near the town of Rhodes in the Eastern Cape Province of South Africa (S –30.72113; E 27.81452) in the early 1900s by Mr Art Isted. It was later described by Dr Robert Broom (1904). Funnystone farm is located stratigraphically within the *Massospondylus* Assemblage Zone, Clarens Formation (Viglietti *et al.* 2020). According to the current land owner (Mr Bob Viedge, Mr Isted’s grandson) there is limited outcrop on the land, except for a small outcrop area exposed immediately across the road from the entrance of the homestead, which consists of fine-grained, pale olive sandstone that is similar to the matrix of SAM-PK-4013.

Our stratigraphic measurements of this site place SAM-PK-4013 approximately 65 m above the Elliot/Clarens formation contact (Fig. 1). The total thickness of the Clarens Formation in the area is estimated to be ~277 m based on Bordy & Head (2018), which places *Notochampsia istedana* in the lower to middle part of the Clarens Formation. Currently, this makes *Notochampsia* the stratigraphically highest-occurring (and thus youngest) vertebrate body fossil recovered from the Karoo Supergroup of South Africa. Other vertebrate body fossil taxa have been described from the Clarens Formation (e.g. *Tritylodontoides*, *Pachygenelus*, *Diarthrognathus*, *Massospondylus*, *Ngwevu*, *Lycorhinus*), but these were discovered much lower in the section, close to the Elliot/Clarens formation contact (Owen 1854; Watson 1913; Crompton 1958; Crompton & Charig 1962; Fourie 1962; Weishampel & Witmer 1990; Chapelle *et al.* 2019; Bordy *et al.* 2020a, b; Viglietti *et al.* 2020). Many ichnites are much higher occurring than *Notochampsia istedana* in the Clarens Formation, and continue into the lower Drakensburg Group (Bordy *et al.* 2020b). The overlying Drakensburg



**Figure 1.** Geological context for the holotype of *Notochampsia istedana* (SAM-PK-4013). It shows the inferred stratigraphic position, where the specimen was discovered, and site of the type locality. The vertical section represents a composite section measured at Eagles Craig (upper Elliot Formation), Halstone and Funnystone farms (Clarendon Formation). The stratigraphic position for *N. istedana* is approximate; however, the dotted line represents the exposure of Clarendon Formation on Funnystone farm, which is at least 65 m above the base of the Elliot/Clarendon contact. A section of the stratigraphy is not exposed which is marked by the crossed box; only the thickness, but not the lithology, could be documented.

Group extrusive igneous rocks are dated to between  $180.1 \pm 1.4$  and  $182.8 \pm 2.6$  Ma (Moulin *et al.* 2017), and recent chronostratigraphic work suggests the Clarendon Formation is latest Sinemurian–Pliensbachian in age. The stratigraphic position of *Notochampsia* therefore places it within the Pliensbachian (Bordy *et al.* 2020a, b).

**Differential diagnosis between *Notochampsia* and other notochoampsoids.** *Notochampsia* can be distinguished from *Edentosuchus* by its lack of bicuspid dentition. *Notochampsia* can be distinguished from *Protosuchus* and *Hemiprotosuchus*, but is similar to *Orthosuchus*, by possessing an elongated process of the squamosal that extends posterolaterally from the posterolateral corner of the squamosal. The anterior process of the frontal of *Notochampsia* separates the posterior processes of the nasals, which is similar to *Orthosuchus* but differs from *Protosuchus* and *Hemiprotosuchus*. *Notochampsia* and *Orthosuchus* can be distinguished from *Protosuchus* by possessing broadly expanded anterior and posterior intercostal ridges of the dorsal ribs. *Notochampsia* can be further distinguished from

*Orthosuchus* by having broadly expanded anterior and posterior intercostal ridges of at least two dorsal ribs, whereas *Orthosuchus* has expanded intercostal ridges on all dorsal ribs. The dentary symphyses of *Notochampsia*, *Protosuchus*, *Hemiprotosuchus* and *Orthosuchus* are different from *Edentosuchus* because the dentary symphysis of *Edentosuchus* is extremely anteroposteriorly extensive and continues posteriorly to the level between the seventh and eighth alveolus. The dentary symphysis of *Notochampsia* is anteroposteriorly extensive and tapers anteriorly in medial view, which is similar to *Protosuchus* and *Hemiprotosuchus* but differs from *Orthosuchus*, in which the symphysis has a reniform shape in medial view and does not taper anteriorly. The symphysis of *Notochampsia* continues until the level of the sixth dentary alveolus, whereas the dentary symphysis of *Orthosuchus* is relatively short anteroposteriorly and continues until between the third and fourth dentary alveolus. The ventral surface of the coracoid of *Notochampsia* is similar to *Protosuchus* but different from *Orthosuchus* because it has an elongate posterior process that is lacking in *Orthosuchus*. *Notochampsia*

has large, paired, labiolingually compressed dentary caniniforms in alveoli three and four that are followed by much smaller (less than half the size), labiolingually compressed post-caniniform dentary teeth. This differs from *Orthosuchus*, which has large dentary caniniforms in alveoli three and four that are sub-circular in cross section, followed by post-caniniform teeth that are sub-circular in cross-section and gradually decrease in apico-basal height posteriorly. The dentary caniniform of *Notochampsia* also differs from *Protosuchus*, which has dentary caniniforms that are sub-circular in cross-section. Finally, *Notochampsia* has at least four maxillary teeth, whereas *Orthosuchus* has only three maxillary teeth.

## Description

Portions of SAM-PK-4013 exposed on the surface are preserved as fossil bone, including the anterior and posterior surface of the right mandible, the partial right quadrate (visible in CT scan data but with insufficient definition to segment digitally), the left coracoid, radius, ulna, radiale, carpals and metacarpals, the left femur and associated tibia and fibula (Figs 2, 3). Several other cranial regions are preserved as surface impressions on the matrix, but contain sub-surface cortical bone surface that is visible in CT scan data. These include the rostral region, the intertemporal fenestral region, a small portion of the occipital surface of the skull and the posterior end of the left mandible. Several postcranial bones are preserved as impressions on the surface of the matrix, including: the right scapula, the right coracoid, the interclavicle, the left humerus and a row of paired osteoderms. The osteoderms are preserved as impressions, but there is fossilized bone preserved along their lateral-most edges. Several ribs are preserved as bone impressions on the surface of the matrix (right ribs ?2–?9), and a complete rib is preserved in the matrix, which has been digitally reconstructed and described. The rib count is imprecise because of the state of preservation: it is likely that the cervical ribs have not been preserved, perhaps together with the first few dorsal ribs. Many of the bones or bone impressions are too poorly preserved to discern any meaningful anatomical data, such as the interclavicle, the preserved surfaces of both right and left humeri, the radius, ulna, carpals, metacarpals of the left forelimb and the femur, tibia and fibula of the left hind limb.

The fossilized bone and the remaining bone impressions are brown or white, and are easily discernible from the surrounding pale sandstone matrix. Impressions of bone uniformly preserve only the natural mould of

the ventral surface of that bone, i.e. what is visible of the squamosal is the ventral surface of the squamosal. A CT scan of the cranial and anterior portion of SAM-PK-4013 reveals that there is additional bone enclosed within the matrix. The contrast between bone and rock matrix is poor, effectively preventing segmentation of the remaining mandibular region, the braincase region, vertebral column and any limb material present. However, the dentary symphyseal region and associated teeth has sufficient density separation to digitally reconstruct, as does an isolated dorsal rib.

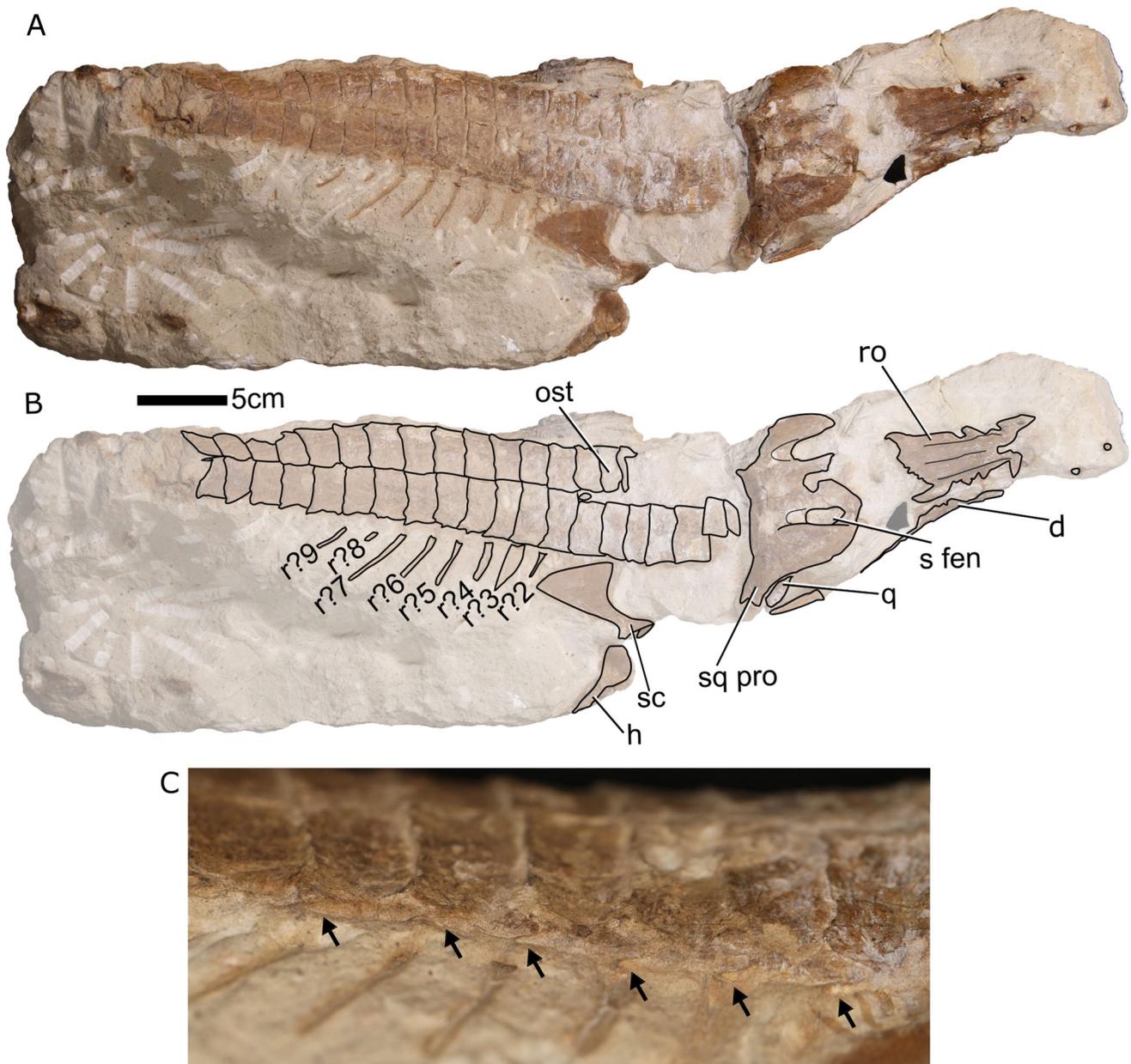
## Skull and mandible

The skull resembles other notochampsoids with a narrow oreinorostral snout, combined with a broad and flat posterior skull roof (Fig. 4). The anterior-most region of the rostrum, together with the orbital region of the skull, have not been preserved. However, a portion of both postorbitals, frontal, parietal, both squamosals, supraoccipital and otoccipital can be observed.

The supratemporal fenestrae are preserved as oval, matrix-filled gaps between dermal impressions of roofing bones. In right lateral view of the skull, the lateral-most surface of the right hemimandible can be observed, together with the surface of the right maxilla and a few remaining teeth. In ventral view of the skull, only the dentary symphysis and the partial remains of the mandible can be discerned.

**Maxilla.** The maxilla is observable in dorsal and right lateral views. There is bone from the maxilla along the lateral surface of the rostrum, above the maxillary tooth row. The maxilla forms a small portion of the lateral edge of the dorsal surface of the rostrum. The antorbital fenestrae have not been preserved, and the region where the premaxilla/maxilla contact would have been is missing. However, the presence of a premaxillary/maxillary notch of some kind is indicated by the enlarged dentary caniniforms in the position that would have been opposite the notch. The presence of a premaxillary/maxillary notch is observable in most early-branching crocodyli-forms, excluding *Gobiosuchus* which has a maxillary foramen to host the large caniniform. In lateral view, two large teeth that are possibly premaxillary teeth and four maxillary teeth are observable.

**Nasals.** The nasals are paired elements that form the dorsal surface of the rostrum. The anterior portion of the paired nasals, together with the internarial bar and premaxilla have not been preserved (Fig. 4A, B). The remaining body of the paired nasals converge anteriorly, so that the posterior edge of the nasal, along the margin of the nasal–maxilla contact, is laterally broader than the anterior portion of the nasal. Each nasal bone tapers

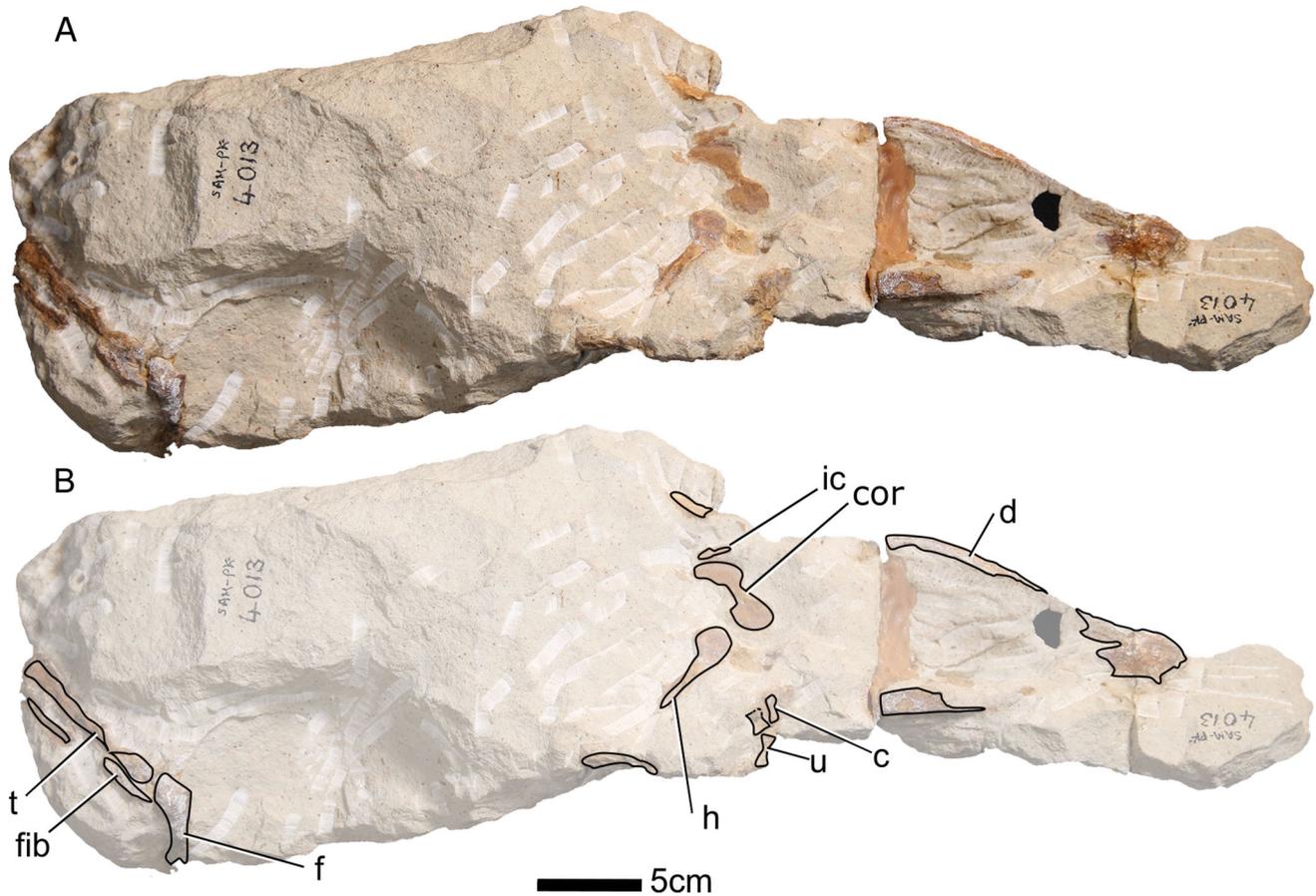


**Figure 2.** The holotype of *Notochampsia istedana* (SAM-PK-4013): **A**, dorsal view; **B**, semi-transparent with the fossil outlined in black; **C**, right lateral view of cervical osteoderms with arrows indicating the position of the anterolateral process. **Abbreviations:** **d**, dentary; **h**, humerus; **ost**, osteoderm; **q**, quadrate; **r**, rib; **ro**, rostrum; **s fen**, supratemporal fenestra; **sc**, scapula; **sq pro**, squamosal process.

to point posteriorly. Together, the posterior edges of the paired nasals are separated by the frontal (Fig. 4A, B), a condition more closely resembling *Sphenosuchus* (Walker 1990), *Litargosuchus* (Clark & Sues 2002) and *Orthosuchus* (Nash 1975) than *Protosuchus* (Gow 2000), and is also observed broadly in neosuchians (e.g. Pritchard *et al.* 2013; Turner & Pritchard 2015).

**Postorbital.** The contact between the postorbital and squamosal is a point of difference between von Huene

(1925) and Broom (1904, 1927). Von Huene (1925) described the postorbital as extending posteriorly along the skull roof and medial to the squamosal to contact the quadrate within the supratemporal fenestra. Broom (1904, 1927) described the postorbital as being restricted to the anterolateral corner of the squamosal, with no contact with the quadrate and not involved in the supratemporal fenestra. We regard Broom's (1904, 1927) interpretation as correct, with the postorbital contacting the anteromedial surface of the squamosal. This is made

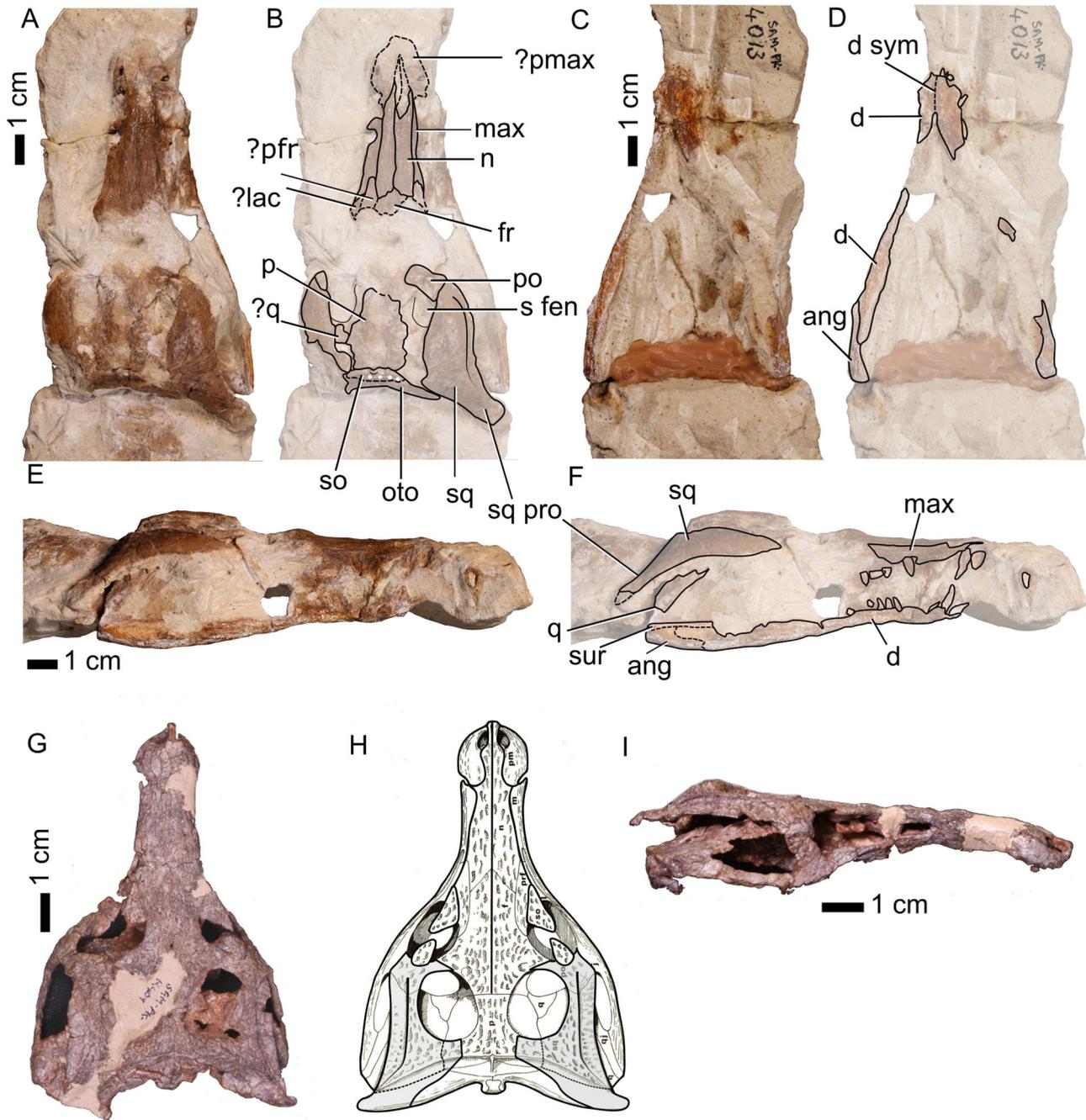


**Figure 3.** The holotype of *Notochampsia istedana* (SAM-PK-4013): **A**, ventral view; **B**, semi-transparent with the fossil outlined in black. **Abbreviations:** c, carpals; cor, coracoid; d, dentary; f, femur; fib, fibula; h, humerus; ic, interclavicle; t, tibia; u, ulnae.

evident by the presence of a suture at the anterolateral corner of the supratemporal fenestra (Fig. 4A). The position of the postorbital of *Notochampsia* resembles other early-branching crocodyliforms (where it is preserved: *Protosuchus*, *Hemiprotosuchus*, *Orthosuchus*, *Gobiosuchus* and *Zaraasuchus*) as restricted to the anterolateral corner of the squamosal. In earlier-branching crocodylomorphs (e.g. *Sphenosuchus*) and later branching taxa (e.g. *Araripesuchus*, *Simosuchus*, *Hylaeochampsia*, *Crocodylus*, *etc.*) the postorbital extends posteriorly and forms a margin of the supratemporal fenestra.

**Squamosal.** The shape of the ventral surface of the squamosal is broad and flat and forms the majority of the posterior dorsal surface of the skull roof as preserved. It is evident from CT scan cross-sections that there is bone remaining of the original squamosal. However, the bone is very fine, and it is likely that it is only a thin layer of the ventral surface. Nevertheless, it is sufficient to determine that the outline of the bone remaining is actually a true reflection of the shape of

the squamosal. The squamosal of *Notochampsia* has an elongated process extending ventrally from the posterolateral edge towards the articular region (Fig. 4E, F). On closer inspection of the *Orthosuchus* holotype skull (SAM-PK-K409), it appears that *Orthosuchus* shares with *Notochampsia* a large ventral process of the squamosal, and that Nash's (1975) original interpretation of the squamosal should be reconsidered. Rather, the region Nash (1975) had described as a large paroccipital process of the otoccipital includes a lateral part belonging to the squamosal (Clark 1986). The ventral process of the squamosal in *Orthosuchus* resembles *Notochampsia* but does differ marginally in its construction, in *Notochampsia* it is a distinct element that diverges away from the otoccipital surface as it extends ventrally away from the dorsal skull roof. However, in *Orthosuchus* it is more confluent with the otoccipital surface (Fig. 4G, H). However, given the poor state of preservation of this region, it should be considered, that the condition of the otoccipital and squamosal contact could more closely resemble *Orthosuchus*. The crushing



**Figure 4.** A–F, the skull of *Notochampsia istedana* (SAM-PK-4013): **A**, dorsal view; **B**, semi-transparent with the fossil outlined in black; **C**, ventral view; **D**, semi-transparent with the fossil outlined in black; **E**, right lateral view; **F**, semi-transparent with the fossil outlined in black. **G–I**, the skull of the holotype of *Orthosuchus stormbergi* (SAM-PK-K410): **G**, dorsal view; **H**, line drawing (taken from Nash 1975); **I**, lateral view. Greyed area on *Orthosuchus* shows reinterpretation of the squamosal over Nash's (1975) original reconstruction. Dashed black lines in line drawings indicate unclear sutural contacts. Dashed white lines and dots indicate the possible passage of the transverse intertympanic canal in the supraoccipital. **Abbreviations:** ang, angular; d, dentary; d sym, dentary symphysis; fr, frontal; lac, lacrimal; max, maxilla; n, nasal; oto, otoccipital; p, parietal; pfr, prefrontal; pmax, premaxilla; po, postorbital; q, quadrate; s fen, supratemporal fenestra; so, supraoccipital; sq, squamosal; sq pro, squamosal process; sur, surangular.

of the holotype of *Orthosuchus* (SAM-PK-K409) makes it difficult to determine if the squamosal process would have descended as far ventrally as observed in *Notochampsia* (Fig. 4I).

**Occipital.** The occipital surface of the skull is in a condition similar to the squamosal, in that there is little of the original bone preserved. Distinguishing between the supraoccipital and otoccipital is impossible given the lack of preservation of the surface. A crack along the posterior region of the parietal may indicate the parietal/supraoccipital contact.

There is a distinct notch along the dorsal edge of the supraoccipital. A series of small foramina ventral to the supraoccipital notch potentially indicate the passage of the transverse intertympanic canal within the supraoccipital, but without further clarity on this region this observation cannot be confirmed (Fig. 4B).

**Angular.** Only the right hemimandible is exposed enough for a partial description (Fig. 4E, F). Sutural contacts are only partially observable along the posterolateral-most corner of the hemimandible, where the dentary, angular and surangular meet. The angular forms the posterior-most surface of the mandible, contacting the surangular dorsally, the dentary anteriorly and, presumably, the articular posteriorly (although this element is not exposed and not distinguishable in CT scan data). The angular contacts the medial surface of the dentary anteriorly along the ventral edge of the hemimandible. Posteriorly, the angular becomes more exposed on the lateral surface of the hemimandible, excluding the dentary from the region of the surangular/angular contact (Fig. 4F).

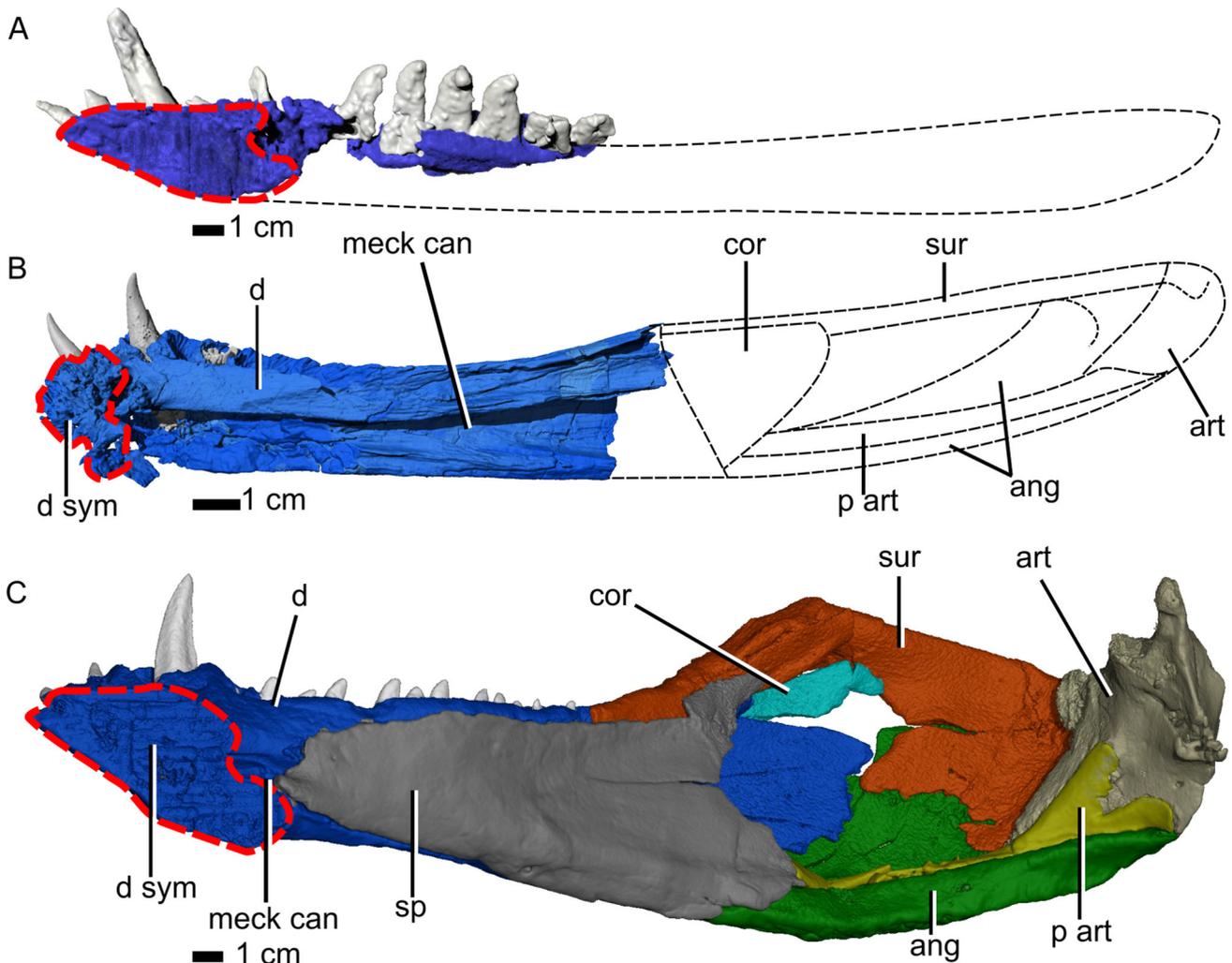
**Surangular.** Only the posterior-most surface of the surangular is preserved (Fig. 4F). The anterior contact between the surangular and dentary is not preserved. The poorly preserved section of the surangular that is visible is observable as a dorsoventrally narrow bar of bone that extends over the dentary and angular (Fig. 4E, F).

**Dentary symphysis.** The dentary symphysis of *Notochampsia* is exposed in ventral view (Fig. 3) and has been digitally reconstructed in medial view (Fig. 5A). The symphysis resembles other non-mesoeucrocodylian crocodyliforms, in that it is anteroposteriorly expansive and has a shallow anterodorsal slope (Fig. 5A). The anterior edge of the symphyseal region is angled anteromedially, resembling the symphyseal shape described in *Protosuchus* (Dollman *et al.* 2017). Partially exposed along the lateral region of the symphysis are four teeth on the right hemimandible and one exposed on the left. In medial view, the symphyseal region of *Notochampsia* resembles *Protosuchus* (Fig. 5C)

but is distinct from *Orthosuchus* (Fig. 5B). The symphyseal region of *Notochampsia* is anteroposteriorly broad, gently tapering dorsally, with a small indentation on the posterior surface for the Meckelian canal. The symphyseal region of *Orthosuchus* (BP/1/7979, SAM-PK-K409) is an anteroposteriorly short, reniform structure. The symphyseal region of *Notochampsia* extends until the fifth or sixth alveolus, as in *Protosuchus*, but unlike *Orthosuchus* which only extends until between the third and fourth alveolus (Fig. 5B).

**Dentition.** Although the dentition is poorly preserved, a few dentary teeth are visible in CT cross sections, and we were able to digitally segment them (Fig. 6A–C). Anteriorly on the rostrum and observable in right lateral view are two large, upper caniniforms near the anterior edge of the maxilla (Fig. 4E, F). Although the bone is not preserved, given their anterior position on the rostrum and their location relative to the dentary symphysis, it is likely these two large teeth are posterior premaxillary teeth. Visible in right lateral view are also four maxillary teeth, three of which are positioned within their separate alveoli, and one has dislocated and is orientated parallel to the ventral margin of the maxilla (Fig. 4E, F). There is an additional isolated, partial tooth preserved anterior to the skull on the surface of the specimen (Fig. 4E, F). The posterior premaxillary teeth of *Notochampsia* are much larger than the preserved maxillary teeth. The number of observable maxillary teeth of *Notochampsia* (four) are distinct from *Orthosuchus* which has only three small maxillary teeth. The apices of the premaxillary teeth are slightly recurved posteriorly and are much larger than any of the maxillary teeth but are similar in size to the corresponding dentary teeth. The maxillary teeth lack any curvature, with the apices orientated ventrally.

The CT scans show that there are 11 right and six left dentary teeth preserved. The first two dentary teeth are procumbent and sub-circular in cross-section (Fig. 6A–C). The two anterior dentary teeth are followed by two large dentary caniniforms in alveoli three and four. The large caniniforms are labiolingually compressed, and with the apices recurved posteriorly to a small degree. The dentary tooth immediately posterior to the large caniniforms (the fifth alveolus) is significantly smaller than the large dentary caniniforms and is sub-circular in cross-section. The remaining dentary teeth are highly labiolingually compressed and sub-oval in cross-section. No further detail on the presence of serrations could be determined because of the poor preservation. The presence of recurved apices on teeth, together with strongly procumbent anterior dentary teeth, resembles the condition described for *Orthosuchus*. However, the posterior dentary teeth of *Notochampsia* differ distinctly from *Orthosuchus* in that they are tightly



**Figure 5.** Medial views of the right dentaries of **A**, *Notochampsia istedana* (SAM-PK-4013), **B**, *Orthosuchus stormbergi* (BP/1/7979), and **C**, *Protosuchus haughtoni* (BP/1/4770) with the dentary symphysis outlined by red dashed lines. Black dashed lines outline unpreserved regions. **Abbreviations:** ang, angular; art, articular; cor, coronoid; d, dentary; d sym, dentary symphysis; meck can, Meckelian canal; p art, prearticular; sur, surangular; sp, splenial.

compressed labiolingually, whereas in *Orthosuchus*, the teeth are broader labiolingually. Measurements taken from the CT scan data of *Notochampsia* (SAM-PK-4013) and from the dentary of the *Orthosuchus* holotype (SAM-PK-K409) show the abrupt reduction in tooth size and the labiolingual compression described for *Notochampsia*, contrasting with the gradual reduction in tooth size and the lack of labiolingual compression observed in *Orthosuchus* (Table 1).

### Postcrania

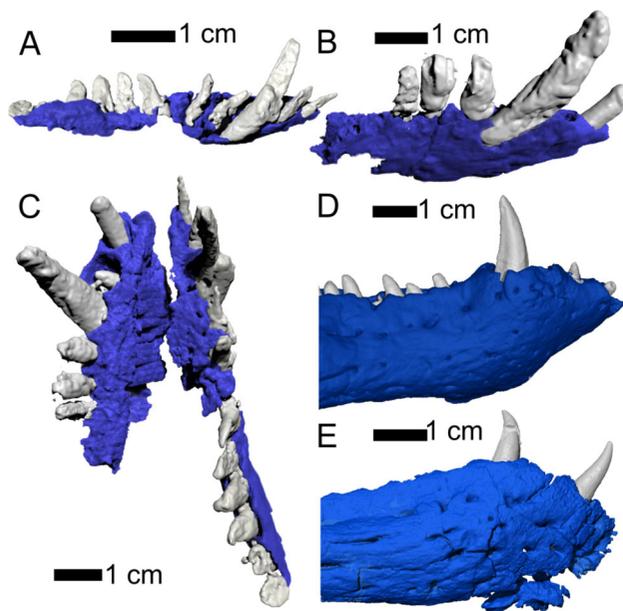
The postcranial remains include the impression of the right scapula, both coracoids, the interclavicle and the proximal surfaces of the left and right humeri, together with the poorly preserved fossilized bone remains of the radius,

ulna, carpus and metacarpus, and the partial right femur, tibia and fibula. Additionally, SAM-PK-4013 preserves the impressions of an articulated set of dorsal osteoderms, extending from the cervical to the sacral region. Preserved on the right lateral side of the dorsal osteoderms are the impressions of eight dorsal ribs on the surface of the matrix, together with at least an additional two dorsal ribs preserved within the matrix (one of which has been digitally reconstructed for comparison). Of the aforementioned postcranial bones, only the scapula, coracoid, osteoderms and the reconstructed dorsal rib are preserved in sufficient detail to be described further (Figs 2, 3).

**Scapula.** The right scapula of *Notochampsia* is observable in dorsal and dorsolateral views (Fig. 7A, B). CT scan data show that the remaining dorsal surface of the scapula is preserved as a layer of thin cortical bone.

There is a dorsoventrally thicker portion of the bone of the scapula preserved closer to the glenoid region, medial to the right humeral head, but insufficient for any digital reconstruction of the anatomy. The reconstruction presented is based on the imprint of the remaining surface of the scapula (Fig. 7B). The scapula blade is anteroposteriorly broad with the dorsal margin convex. As the anterior-most edge of the scapula of *Notochampsia* has preserved poorly, it cannot be confirmed whether the scapula has a prominent lip, the posterodorsal projection, which is present in both *Orthosuchus* (SAM-PK-K409; Fig. 7C, D) and *Protosuchus* (SAM-PK-8026, referred specimen of *Protosuchus haughtoni*: Fig. 7E, F).

The anterior margin of the scapula of *Notochampsia* is strongly concave. In comparison, Clark's (1986)



**Figure 6.** The digital segmentation and 3D visualizations of the dentary of *Notochampsia istedana* (SAM-PK-4013) shown in A, right, lateral B, left lateral and C, dorsal views. D, anterior portion of the dentary of *Protosuchus haughtoni* (BP/1/4770). E, *Orthosuchus stormbergi* (BP/1/7979) in lateral view for comparison.

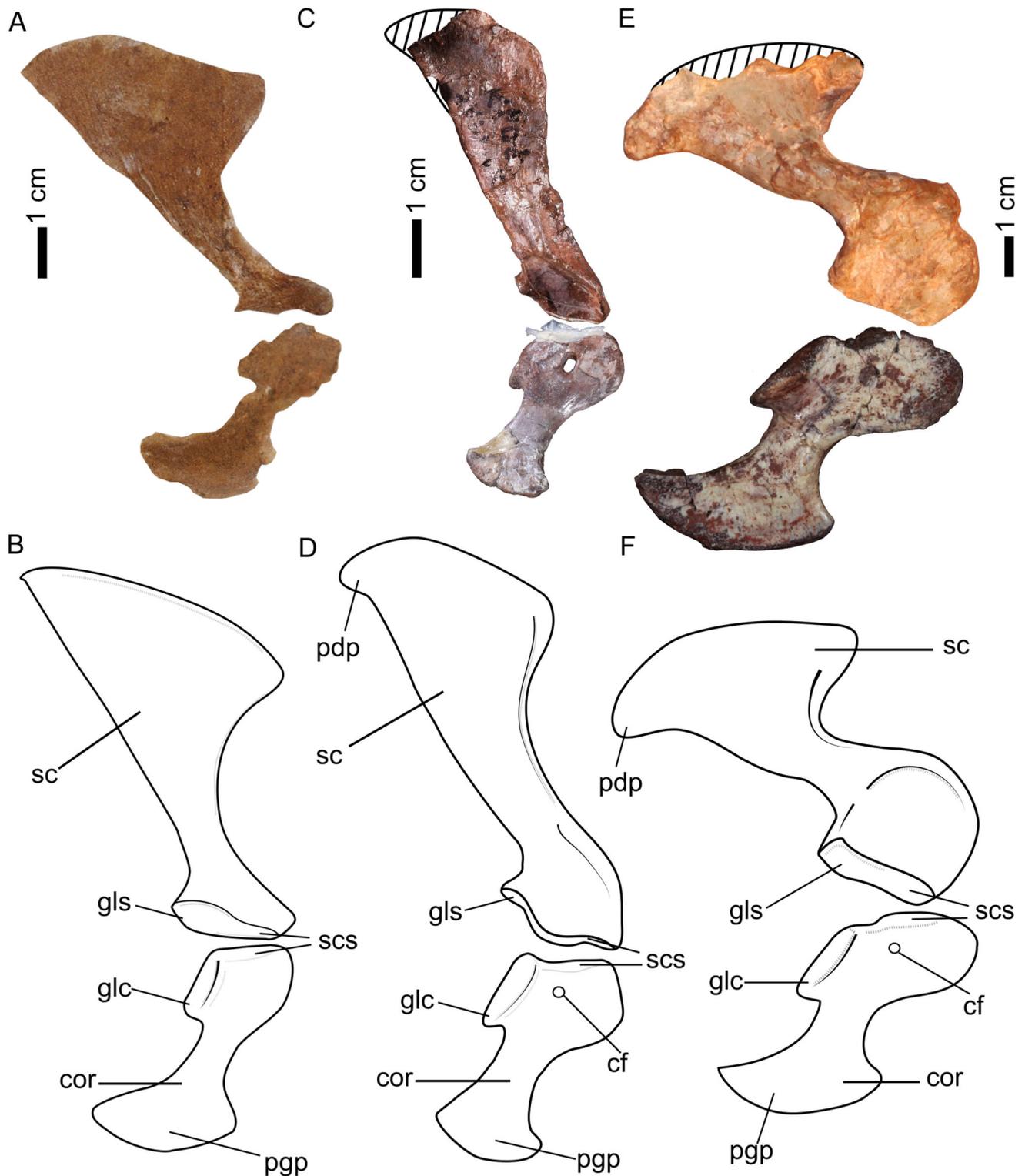
personal observation of the more complete left scapula of *Orthosuchus* (SAM-PK-K409, which unfortunately now only has the glenoid region remaining) showed the anterior edge to be much more convex than in Nash's (1975) original reconstruction. The illustration presented in this research (Fig. 7D) of the scapula of *Orthosuchus* is based on personal observation of the right scapula of SAM-PK-K409 combined with notes taken by JMC. Therefore, the broad, convex anterior edge of the scapular blade of *Notochampsia* resembles the condition described here for *Orthosuchus*, more than the acute, convex anterior edge of the scapula of *Protosuchus* (Fig. 7F). The preserved impression of the glenoid and scapulocoracoid synchondrosis region of the scapula of *Notochampsia* is much smaller than that of *Orthosuchus*, which in turn is smaller than that of *Protosuchus* (SAM-PK-8026) (Fig. 7). The outline of the lip separating the glenoid region and the scapulocoracoid synchondrosis is outlined, and it can be discerned that the scapular contribution to the glenoid is directed posteroventrally.

The overall shape of the scapula of *Notochampsia* and *Orthosuchus* resembles *Sichuanosuchus*, but can be distinguished from non-crocodyliform crocodylomorphs which have a more robust glenoid region and lack a narrow neck between the glenoid region and a broad scapular blade (i.e. *Junggarsuchus*, *Dibothrosuchus* and *Sphenosuchus*). Extant crocodylians have a more robust scapula with a large glenoid region and lack an anteroposteriorly broad scapular blade. Mesoeucrocodylians have a variety of scapular shapes, which include a morphology similar to non-crocodyliform crocodylomorphs (e.g. *Araripesuchus*), or have very stout scapula with a rounded scapular blade that is not distinguished from the glenoid region by a narrowed neck (i.e. *Baurusuchus*).

**Coracoid.** The right coracoid of *Notochampsia* is preserved as a rough impression (Figs 3, 7A), and the left coracoid is preserved as very crushed bone in articulation with the left scapula: therefore, we can present only a cursory description of this bone. The outline of the left coracoid has an expanded proximal surface with a

**Table 1.** Measurements taken of alveolar dimensions from the left and right dentaries of *Notochampsia istedana* (SAM-PK-4013) and *Orthosuchus stormbergi* (SAM-PK-K409) to show differences in tooth geometry between the two taxa.

Measurements (mm)	<i>Notochampsia istedana</i> (SAM-PK-4013)	<i>Orthosuchus stormbergi</i> (SAM-PK-K409)
Third alveolus labiolingual length	3.84 mm (left dentary)	2.49 mm (left dentary)
Third alveolus anteroposterior length	4.83 mm (left dentary)	2.21 mm (left dentary)
Fourth alveolus labiolingual length	3.34 mm (left dentary)	2.45 mm (left dentary)
Fourth alveolus anteroposterior length	4.39 mm (left dentary)	2.68 mm (left dentary)
Fifth alveolus labiolingual length	2.95 mm (left dentary)	2.10 mm (right dentary)
Fifth alveolus anteroposterior length	2.46 mm (left dentary)	1.75 mm (right dentary)
Seventh alveolus labiolingual length	1.55 mm (right dentary)	2.02 mm (right dentary)
Seventh alveolus anteroposterior length	3.29 mm (right dentary)	2.18 mm (right dentary)



**Figure 7.** The right scapula and coracoid and reconstructions in lateral view of **A, B**, *Notochamps* *istedana* (SAM-PK-4013), **C, D**, *Orthosuchus* *stormbergi* (SAM-PK-K409) and **E, F**, *Protosuchus* *haughtoni* (based on scapula SAM-PK-8026 and coracoid NHMUK PV R8503). Hatched lines indicate sections of the bone that are fractured or unexposed. **Abbreviations:** **cf**, coracoid foramen; **cor**, coracoid; **glc**, coracoid contribution to glenoid; **gls**, scapular contribution to glenoid; **pdp**, posterodorsal projection of scapula; **pgp**, postglenoid process; **sc**, scapula; **scs**, scapulocoracoid synchondrosis.

broad surface for the coracoid contribution to the glenoid and scapulocoracoid synchondrosis. The proximal surface of the coracoid is distinguished by a narrow waist from an expanded distal end, or postglenoid process (Fig. 7A, B). The coracoid of *Notochampsia* closely resembles the coracoid of *Protosuchus* (NHMUK PV R8503; Fig. 7E, F), and both can be distinguished from the coracoid of *Orthosuchus* (SAM-PK-K409; Fig. 7C, D). The scapulocoracoid synchondrosis of the coracoid of *Notochampsia* is preserved as an outline. The glenoid contribution of the coracoid is orientated posterodorsally with a lip leading onto the narrow 'waist'. The postglenoid process of *Notochampsia* and *Protosuchus* are anteroposteriorly broad and its distal margin has a crescentic outline in lateral view. The postglenoid process of the coracoid of *Orthosuchus* is smaller, lacking the long posterior process present in both *Notochampsia* and *Protosuchus*.

The general shape of the coracoid of *Notochampsia* agrees with crocodyliforms, which share a broad proximal surface that is separated by a narrow neck from an expanded, crescentic postglenoid process. The coracoid of crocodyliforms can be distinguished from non-crocodyliform crocodylomorphs which have a posteriorly directed rod-like postglenoid process (e.g. *Dibothrosuchus*, *Sphenosuchus*).

**Dorsal osteoderms.** The dorsal osteoderms (cervical, thoracic, sacral and caudal) of *Notochampsia* are paired and rectangular. The paired, rectangular dorsal osteoderms resemble those of other early-branching noto-champsoids (i.e. *Orthosuchus*, *Protosuchus*, *Hemiprotosuchus*); however, gobiosuchids are noted for having rectangular but highly ornamented osteoderms (e.g. *Zaraasuchus*). There is also no evidence preserved of lateral, ventral and appendicular osteoderms in *Notochampsia*. However, it has to be considered, given the poor preservation of the specimen, that *Notochampsia* had additional armour. CT scan cross-sections of *Notochampsia* show that there is only a thin layer of the cortical bone of the ventral surface of the osteoderms preserved. Measured against the cross-sectional depth of the osteoderms of *Orthosuchus* (SAM-PK-K409, BP/1/4242), the portions preserved on *Notochampsia* are much thinner, suggesting that weathering has removed all traces of sculpturing if it was present. Observable on the 8th–13th right osteoderms is a well-developed anterolateral process that extends towards the preceding osteoderm. On SAM-PK-4013 the process is positioned beside the lateral-most margin of the osteoderm (indicated by small arrows in Fig. 2C). However, in life this process would have extended beneath the preceding osteoderm.

**Ribs.** Eight right dorsal ribs are preserved as impressions on the surface of the matrix of the holotype (ribs ?2–?9; Fig. 2). There is also a right dorsal rib that is enclosed within the matrix has been digitally segmented from the CT scan data (rib ?1; Fig. 8A–C). The preserved ribs can be identified as dorsal ribs based on their position. The dorsal ribs exposed on the surface are natural casts with no preservation of the original bone. The digitally segmented dorsal rib of *Notochampsia* was modelled on actual bone that is preserved within the matrix, and is positioned beneath the scapula blade, anterior to the dorsal ribs which are preserved as only impressions (Fig. 8A). A dorsal rib from a similar position was digitally segmented from *Orthosuchus* (BP/1/4242, referred specimen) for comparison (Fig. 8D–F).

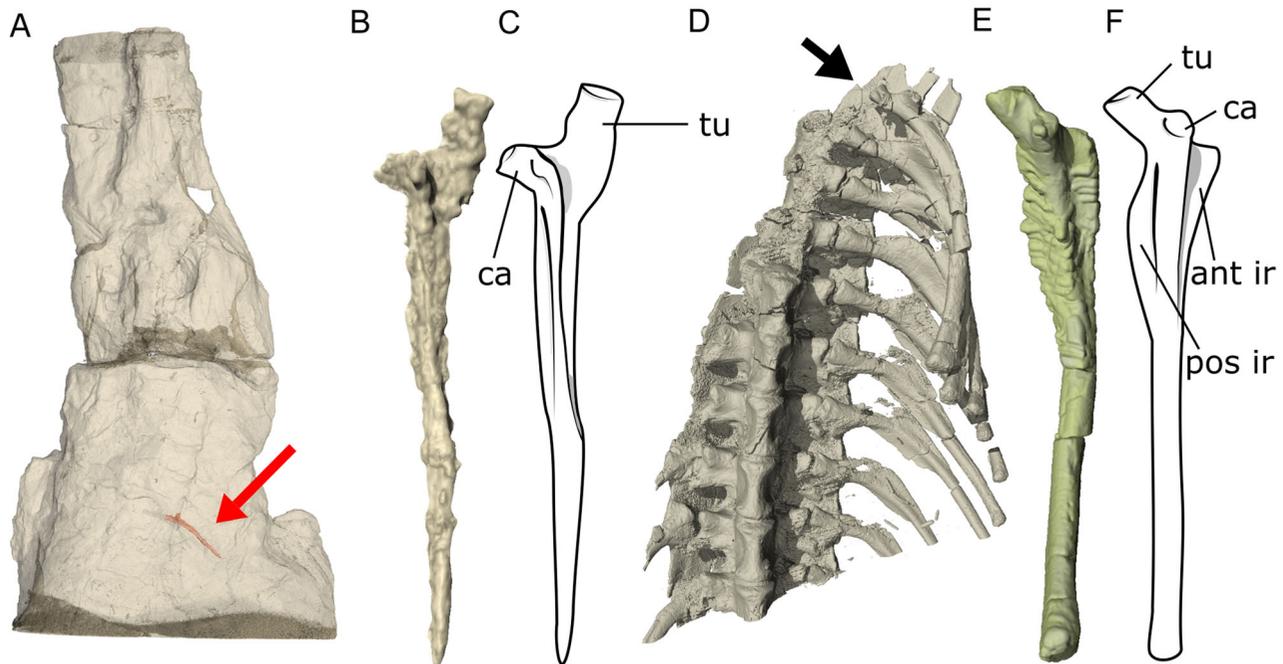
Dorsal rib ?3 is markedly distinct from the remaining ribs because the lateral edge of the shaft of the rib is anteroposteriorly broad (Fig. 2). The shaft of the next dorsal rib (rib ?4) in the row is anteroposteriorly narrower than rib ?3, but is still broader than the remaining dorsal ribs. Dorsal rib ?1 (Fig. 8B, C) lacks any anteroposterior expansion along the shaft. Nash (1975) describes *Orthosuchus* as bearing prominent 'anteroventral and posterodorsal flanges' on the dorsal ribs. The digitally segmented dorsal rib of *Orthosuchus* shows that even the first few dorsal ribs in the row of *Orthosuchus* exhibit broad anteroventral and posterodorsal flanges (Fig. 8D–F), but that only rib ?3 and rib ?4 of *Notochampsia* have these processes (Fig. 2). These broad flanges found both in *Notochampsia* and *Orthosuchus* are homologous to the intercostal ridge present in extant crocodylians (Brocklehurst *et al.* 2017).

The capitulum and tuberculum of *Notochampsia* are only describable from dorsal rib ?1 (Fig. 8B, C). The tuberculum of rib ?1 has a longer neck than the capitulum, extending further medially to articulate with the costal facet of the vertebra. The capitulum is a much shorter process extending only a short distance to articulate with the demi-facet, and it is angled at approximately 90° from the tuberculum. The capitulum of *Orthosuchus*, unlike *Notochampsia*, lacks any significant neck, instead being separated from the tuberculum by only a small groove (Fig. 8E, F).

## Phylogenetic relationships

### Unweighted and unconstrained analysis

Our unweighted and unconstrained parsimony analysis found eight most parsimonious tree (MPT) topologies, with lengths of 895 steps, consistency index (CI) = 0.358 and retention index (RI) = 0.716 (strict consensus of these MPTs is shown in Fig. 9). In all MPTs 'Protosuchia' is paraphyletic, and is instead represented



**Figure 8.** **A**, Highlighted position with red arrow pointing to the reconstructed right dorsal rib ?1 in *Notochampsia istedana* (SAM-PK-4013) with the rest of the skeleton made transparent. **B**, digitally segmented dorsal rib ?1. **C**, reconstruction of dorsal rib ?1 of *Notochampsia istedana* (SAM-PK-4013) in medial view. **D**, *Orthosuchus stormbergi* (referred specimen BP/1/4242) with arrow indicating reconstructed rib. **E**, digitally segmented dorsal rib 1. **F**, reconstruction of dorsal rib 1 of *Orthosuchus stormbergi* (referred specimen BP/1/4242) in medial view. **Abbreviations:** **ant ir**, anterior intercostal ridge; **ca**, capitulum; **pos ir**, posterior intercostal ridge; **tu**, tuberculum.

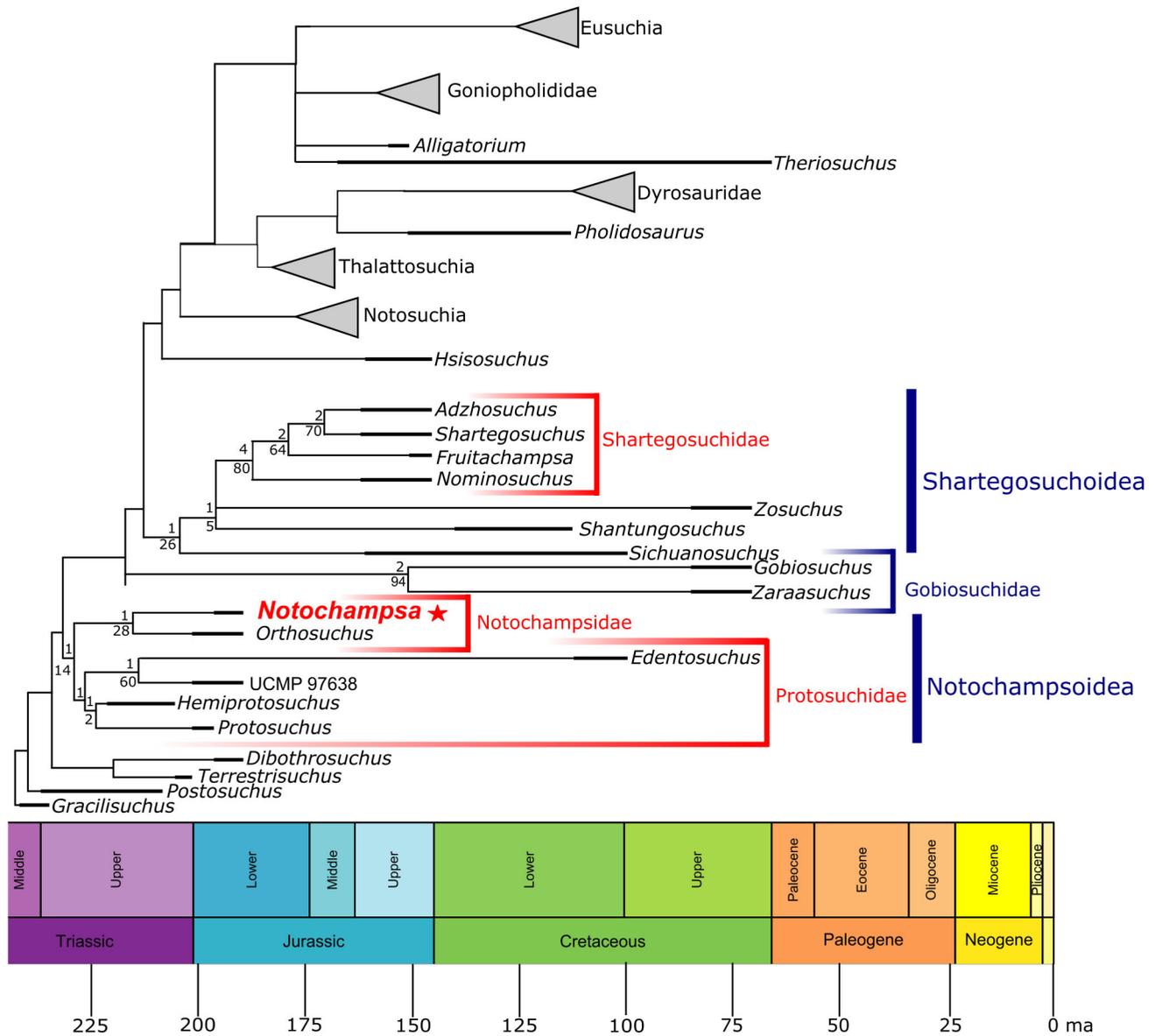
by three smaller monophyletic clades, Notochampsioidea, Shartegosuchoidea and Gobiosuchidae, which in turn form nested sister-taxon relationships with Mesoeucrocodylia.

*Notochampsia* and *Orthosuchus* are recovered as sister-taxa within Notochampsidae in all MPTs. Features that notochampsids share include the abrupt expansion of the skull along the orbital margin (character [char.] 2, state 1), a feature that is homoplastically shared with *Protosuchus* and more distantly related crocodyliforms, such as *Hsisosuchus* and *Gavialis*. Additionally, the caudal tips of the nasals are separated by an anterior projection of the frontals in both *Notochampsia* and *Orthosuchus* (char. 165, state 1).

Protosuchidae includes *Edentosuchus*, UCMP 97638, *Hemiprotosuchus* and *Protosuchus*. Protosuchidae is supported by a broad contact between the ventrolateral edge of the otoccipital and the quadrate (char. 48, state 0; unknown in *Edentosuchus*). The pterygoid ramus of the quadrate of protosuchids UCMP 97638 and *Protosuchus* has a deep groove along the ventral edge (char. 50, state 1; unknown in *Edentosuchus* and *Hemiprotosuchus*), which is also present in the crocodylian *Borealosuchus*. The surangular is arched dorsally in protosuchids (char.

74, state 1), which is independently present in several shartegosuchoids (*Nominosuchus*, *Fruitachampsia* and *Shartegosuchus*) and in many later-branching mesoeucrocodylians. The openings to the lateral eustachian tubes of UCMP 97638 and *Protosuchus* are aligned anteroposteriorly and dorsoventrally to the medial eustachian tube opening (char. 132, state 1), but this feature is unknown in the remaining protosuchids *Edentosuchus* and *Hemiprotosuchus*, and is also present in mesoeucrocodylians *Mariliasuchus* and *Sphagesaurus*. The shape of the dentary symphysis in ventral view tapers anteriorly (char. 154, state 0), which is observed in all protosuchids except *Hemiprotosuchus* where it is unknown, and is also observed homoplastically throughout Crocodyliformes.

We find Notochampsidae and Protosuchidae as sister taxa in the monophyletic clade Notochampsioidea. Features that support Notochampsioidea are an expanded otoccipital ventrolateral to the paroccipital process (char. 60, state 1), which is also independently present in thalattosuchians. The jugal of notochampsoids does not exceed the anterior margin of the orbit (char. 122, state 0), a feature that is independently evolved within shartegosuchoids (excluding *Sichuanosuchus*) and in the mesoeucrocodylians *Malawisuchus* and *Mariliasuchus*.



**Figure 9.** Time calibrated strict consensus of the eight MPTs obtained from the unweighted unconstrained analyses (tree length = 895 steps, CI = 0.358, RI = 0.716). Bremer supports are listed above and GC Jackknife values are listed below each node.

Notochampsoids also share a laterally concave nasal border posterior to the external nares (char. 127, state 0), a feature that is also homoplastically distributed throughout the tree. All notochampsoids except *Edentosuchus* share a postorbital process of the jugal that is anteriorly placed (char. 143, state 0), whereas *Edentosuchus* has a postorbital process of the jugal that is medially placed to the postorbital. Support for Notochampoidea is weak with a Bremer support of 1 and a jackknife value of 10.

Interrelationships of the clade Shartegosuchoidea are similar to those described in Dollman *et al.* (2018) and

Clark (2011). The clade includes *Sichuanosuchus*, *Zosuchus*, *Shantungosuchus*, *Nominosuchus*, *Fruitachampsia*, *Adzhosuchus* and *Shartegosuchus*. Features that support Shartegosuchoidea include an antorbital fenestra that is much smaller than the orbit (char. 67, state 2), which is also present homoplastically throughout the crocodyliform tree. Furthermore, synapomorphic of shartegosuchoids is a small palatine that is excluded from the margin of the suborbital fenestra by the pterygoid and maxilla (char. 199, state 1).

Shartegosuchidae, the clade that includes *Nominosuchus*, *Fruitachampsia*, *Adzhosuchus* and

*Shartegosuchus*, is a monophyletic group in all trees. Characters that support Shartegosuchidae include: the lacrimal contacting the nasal along the medial and anterior edges (char. 12, state 1); the palatal surface of their pterygoids are sculptured (char. 40, state 1); the ventral surface of their basisphenoid is shorter than the basioccipital (char. 55, state 0); no mandibular fenestra (char. 75, state 1); the lateral border of their nasal is straight posterior to the external nares (char. 127, state 0); and their posterior maxillary teeth and post-caniniform dentary teeth have an anteroposteriorly long horizontal cusp with vertical crenulations extending ventrally from it (char. 261, state 1). Of these aforementioned characters, only character 261 is synapomorphic for Shartegosuchidae. Support for Shartegosuchoidea is weak with a Bremer support of 1 and a jackknife value of 23; however, there is stronger support for Shartegosuchidae with a Bremer support value of 4 and a jackknife value of 81.

### Implied weighting analysis

With an implied weighting concavity function of six ( $k=6$ ), our analysis finds two MPTs (tree length = 60.36356, CI = 0.356, RI = 0.714), in which 'Protosuchia' is found to be paraphyletic with the same branching structures as found with equal weights.

Analyses using more stringent concavity functions ( $k=3$ ) found four MPTs (tree length = 90.40678, CI = 0.355, RI = 0.713). 'Protosuchia' is found to be a paraphyletic clade with the same branching structures as described with an implied weighting concavity of six ( $k=6$ ).

When the analysis is completed with less stringent concavity function of  $k=12$ , as preferred by Goloboff *et al.* (2018), we found two MPTs (tree length = 36.71398, CI = 0.357, RI = 0.715) with a similar tree topology as equal weighting, a paraphyletic Protosuchia with early-branching crocodyliforms grouping into three monophyletic clades: Notochampsoida, Gobiosuchidae and Shartegosuchoidea.

### Constrained analysis

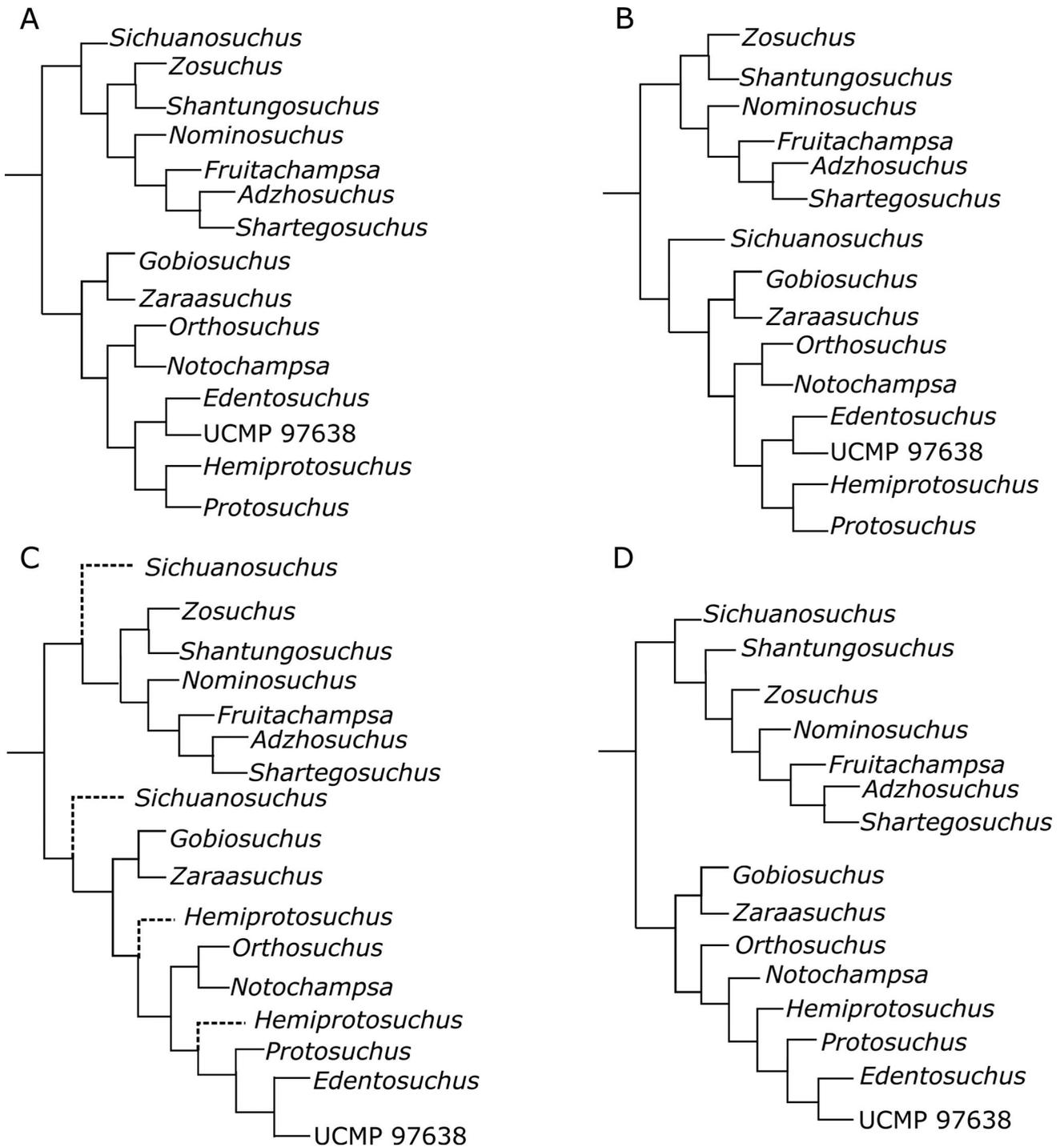
Thalattosuchia has previously been found in three different positions: as a sister to Crocodyliformes (e.g. Jouve 2009; Pol & Gasparini 2009; Wilberg 2015); as an early-branching clade within Mesoeucrocodylia (Larsson & Sues 2007; Sereno *et al.* 2001, 2003; Sereno & Larsson 2009); or as a sister clade to Tethysuchia (Clark 1994; Wu *et al.* 1997; Pol & Norell 2004a, b; Jouve *et al.* 2006; Turner & Sertich 2010; de Andrade *et al.* 2011; Pritchard *et al.* 2013). Thalattosuchia is only found as an early-branching clade within Mesoeucrocodylia when the phylogenetic analyses are

rooted on an early-branching crocodyliform (e.g. *Protosuchus*), which excludes the potential of finding Thalattosuchia as a sister group to Crocodyliformes. However, this research evaluates the possibility of Thalattosuchia as a sister clade to Crocodyliformes by specifying that Crocodyliformes must be monophyletic to the exclusion of Thalattosuchia.

When Thalattosuchia is constrained outside of Crocodyliformes, 28 MPTs are found with lengths of 901 steps (CI = 0.355, RI = 0.713), i.e. six steps longer than the MPTs from the unconstrained, equally weighted analyses. Protosuchia is returned as a monophyletic group.

The monophyletic Protosuchia includes the groups Shartegosuchoidea, Gobiosuchidae and Notochampsoida (Fig. 10). The interrelationships of Shartegosuchoidea are mostly as found in prior analyses (Clark 2011; Dollman *et al.* 2018), with the exception that in four MPTs *Sichuanosuchus* is found to be more closely related to Gobiosuchidae and Notochampsoida than to Shartegosuchidae (Fig. 10B, C). Characters that support this relationship are palatines that have developed palatal shelves, but the palatal shelves do not meet along the midline of the palate below the narial passage (char. 37, state 1); the lateral surfaces of the dentaries below the alveolar margin in the mid- to posterior region of the toothrow are flat with a ridge that separates it from the remaining lateral surface of the dentary (char. 192, state 1); and the presence of a longitudinal ridge on the lateral surface the jugal beneath the infratemporal fenestra (char. 215, state 1). Character 37 (state 1) is only known to be present in *Sichuanosuchus* and UCMP 97638. Notochampsoids and gobiosuchids have the plesiomorphic condition of palatines that do not form palatal shelves (char. 37, state 0). Shartegosuchoids share with mesoeucrocodylians palatines that meet on the midline of the palate (char. 37, state 2). Character 97 (state 1) is homoplastically present throughout the tree, and is observed in many mesoeucrocodylians, e.g. *Simosuchus* and *Malawisuchus*. The presence of a longitudinal ridge on the jugal is observed only in *Sichuanosuchus*, *Nominosuchus*, *Gobiosuchus*, *Zaraasuchus* and *Hemiprotosuchus*. However, the synonymy of this character cannot be fully tested because the presence or absence of this feature is still unknown in many early-branching crocodyliforms, e.g. *Shantungosuchus*, *Orthosuchus* and *Adzhosuchus*.

Gobiosuchidae is found to be a sister group to Notochampsoida and several characters support this association (Fig. 10). These include a sculptured postorbital bar (char. 25, state 0), which is observed in Notochampsoida and the gobiosuchid *Zaraasuchus*. Outside of Notochampsoida and Gobiosuchidae, this feature is only observed in *Fruitachamps* and *Pelagosaurus*. Furthermore, *Gobiosuchus* shares with notochampsoids the choanal groove being continuous with the pterygoid except



**Figure 10.** Tree topologies with Thalattosuchia constrained outside of Crocodyliformes (28 MPTs, CI = 0.355, RI = 0.713) with a monophyletic Protosuchia. The four main branching structures for non-mesoeucrocodylian crocodyliforms returned are shown as: **A**, *Sichuanosuchus* more closely related to Shartegosuchoidea; **B**, *Sichuanosuchus* more closely related to Notochampoidea; **C**, both potential relationships of *Sichuanosuchus* and *Hemiprotosuchus* (dashed lines indicate potential position); and **D**, Notochampoidea as a paraphyletic grade leading up to *Edentosuchus* (UCMP 97638).

for the anterolateral and lateral borders (char. 39, state 0); the pterygoids are separated posterior to the choanal opening (char. 41, state 0); and an absence of a posterolateral

process of the premaxilla (char. 125, state 0). Gobiosuchids also share with *Protosuchus* the presence of a ridge along the quadrate/quadratojugal contact (char. 217, state 1):

however, this feature is also observed in the shartegosuchoid *Zosuchus*, and this feature is mostly unknown amongst early-branching crocodyliforms. A feature that is potentially synapomorphic of Gobiosuchidae + Notochampsoida is the presence of a medial process of the articular that contacts the braincase (char. 73, state 2). This feature is observed in *Gobiosuchus*, UCMP 97638, *Hemiprotosuchus* and *Protosuchus*, but is unknown in the remaining gobiosuchids and notochampsoids.

With *Thalattosuchia* constrained to lie outside of Crocodyliformes, relationships within Notochampsoida are unresolved. *Hemiprotosuchus* is either sister to the early-branching protosuchid *Protosuchus* or alternatively the earliest-branching notochampsoid (Fig. 10C). Multiple most-parsimonious positions are possible for notochampsoids, including *Notochamps* and *Orthosuchus* as sister taxa, with *Orthosuchus* as the earliest-branching notochampsoid, or with *Orthosuchus* and *Notochamps* as part of a paraphyletic grade of protosuchians leading to the sister group of *Edentosuchus* and UCMP 97638 (Fig. 10D).

In this constrained analysis, Protosuchia is supported by three features with little homoplasy: a quadrate that has three or more fenestrae (char. 45, state 2), which is only otherwise observed in *Notosuchus* and *Mariliasuchus*; a basisphenoid that is similar in length or longer than the basioccipital (char. 55, state 1); and an articular with a medial process extending towards or contacting the braincase (char. 73, state 1), although a medial process of the articular is also observed in *Dibothrosuchus* and *Terrestriisuchus* (but does not contact the braincase). Other features supporting a monophyletic Protosuchia have much broader distributions across the crocodylomorph tree, including: the quadratojugal broadly contacting the post-orbital (char. 19, state 1); an enlarged dentary caniniform opposite the premaxilla/maxilla contact (char. 80, state 1); the palatines overlie the pterygoids along their contact (char. 193, state 0); the pterygoid flanges are dorsoventrally thick with pneumatic spaces (char. 197, state 1); the postorbital is excluded from the infratemporal fenestra (char. 198, state 0); the quadrate ramus of the pterygoid in ventral view is broad (char. 202, state 1); and an anterior palatal fenestra (char. 207, state 1). The presence of an anterior palatal fenestra is only found to be supportive of a monophyletic Protosuchia when *Sichuanosuchus* is found to be more closely related to gobiosuchids and notochampsoids than shartegosuchoids.

## Discussion

### Taxonomy of *Notochamps istedana*

*Notochamps istedana* is a valid species with close affinities to *Orthosuchus*. *Notochamps* and

*Orthosuchus* share an elongated process extending posteroventrally from the posterolateral edge of the squamosal and broad intercostal ridges expanding the anterior and posterior margins of the dorsal ribs. Features that distinguish *Notochamps* from *Orthosuchus* include the shape and length of the dentary symphysis, the number of maxillary teeth and the shape and size of the dentary teeth, the number of and position of ribs with expanded intercostal ridges, and the shape of the ventral edge of the coracoid.

The large anterior and posterior flanges of the ribs in *Notochamps* and *Orthosuchus* are most likely homologous to the anterior and posterior intercostal ridges present in extant crocodylians and also present in some basal pseudosuchian archosaurs, e.g. *Euscolosuchus olseni* (Scheyer & Sues 2017). In extant crocodylians, the intercostal ridges are only present on the anterior dorsal ribs (i.e. the first six in *Alligator*), diminishing in size from the anterior to the posterior dorsal rib (Brocklehurst *et al.* 2017). Nash (1975) equates the posterior expansion of *Orthosuchus* to be functionally homologous to the cartilaginous uncinat processes of extant crocodylians; however, this is unlikely as the ridges are positioned too far dorsally and lack the tab-like shape present in extant crocodylians. The presence of broad intercostal ridges is unique to *Notochamps* and *Orthosuchus* amongst notochampsoids.

*Erythrochamps longipes* (Broom, 1904) was originally referred to the genus *Notochamps* (Broom 1904) and then considered a *nomen dubium* by Whetstone & Whybrow (1983). The type specimen of *Erythrochamps* (SAM-PK-K445) consists of a partial postcranial skeleton, including dorsal and ventral osteoderms, dorsal vertebrae, a pubis, an ischium, proximal femur and fragmentary metatarsals. None of the observable elements, except the dorsal osteoderms, preserved in SAM-PK-K455, are present in the *Notochamps istedana* holotype (SAM-PK-4013), making it impossible to ascertain whether SAM-PK-K455 can be referred to the genus *Notochamps*. The exposed portion of SAM-PK-K455 currently lacks any other diagnostic features, and so until further analysis is done (with either digital or manual preparation), we continue to consider *Erythrosuchus longipes* a *nomen dubium*.

Raath (1981) suggested that a crocodylomorph specimen (QG 49) recovered from the Lower Jurassic Forest Sandstone of Zimbabwe could possibly be ascribed to *Notochamps*, identifying it as 'cf. *Notochamps*'. Raath (1981) further suggested that *Notochamps* may be congeneric with *Orthosuchus* based on strong similarities between QG 49 and the *Orthosuchus* holotype (SAM-PK-K409). He referred particularly to the sculpturing on the dorsal osteoderms, an elongated coracoid, the

transverse processes of the dorsal vertebra, the mediolateral expansions on the proximal end of the dorsal vertebrae, and the similarity in size. Our examination of QG 49 show that it lacks obvious synapomorphies of either *Notochampsia* and *Orthosuchus*, or indeed Notochampsidae.

### Biostratigraphy and palaeoenvironment of *Notochampsia istedana*

The validity of *Notochampsia* has a broad impact on biostratigraphic and macroevolutionary hypotheses for Crocodylomorpha. Crocodylomorph fossils are globally scarce in the earliest Jurassic when compared to many other Mesozoic intervals, mirroring the situation in vertebrates generally. This is especially true during the Pliensbachian, where *Notochampsia* is perhaps the only non-volant vertebrate fossil from the southern hemisphere (Close *et al.* 2020). Nonetheless, this time period is important for crocodylomorph evolution because it documents the transition from early-branching crocodylomorph to mesoeucrocodylian-dominated ecosystems. Formations that bear crocodylomorph fossils and that are potentially coeval with the Clarens Formation are the Navajo Sandstone (Lower Jurassic, Sinemurian–Pliensbachian: Clark & Fastovsky 1986) and the Kayenta Formation (Lower Jurassic, Pliensbachian–Toarcian: Marsh *et al.* 2014) from the Glen Canyon Group in North America (Sues *et al.* 1994), the Zhanjia’ao Member of the Lufeng Formation (Lower Jurassic, Sinemurian: Bien 1941; Luo & Wu 1994) and the Forest Sandstone Formation (Lower Jurassic, Sinemurian–Pliensbachian: Sciscio *et al.* 2020) in Zimbabwe (Raath 1981).

Crocodylomorphs from the Kayenta Formation include *Calsoyasuchus*, *Eopneumatosuchus*, an *Edentosuchus*-like form (UCMP 97638) and *Kayentasuchus*. *Calsoyasuchus* is a goniopholidid (Tykoski *et al.* 2002), and both *Eopneumatosuchus* (taxonomically uncertain) and UCMP 97638 are early-branching crocodyliforms (Crompton & Smith 1980; Clark 1986), and *Kayentasuchus* is a non-crocodyliform crocodylomorph (Clark & Sues 2002). Crocodylomorphs recovered from the Lufeng Formation are the non-crocodyliform crocodylomorphs *Dibothrosuchus* and *Phyllodontosuchus* and the early-branching crocodyliforms *Platyognathus* (Wu & Sues 1996) and *Dianosuchus* (Young 1982). Thalattosuchian fossils have also been reported from the Lower Lias of Chile (Lower Jurassic, Sinemurian: Gasparini *et al.* 2000) but remain taxonomically unspecific.

However, these stratigraphic units cannot be directly correlated to the same age as the Clarens Formation, or they remain imprecisely dated, such as the Zhanjia’ao

Member of the Lufeng Formation. Uranium-lead (U-Pb) analyses of carbonate deposits in the Navajo Sandstone date the formation between  $200.5 \pm 1.5$  Ma (Hettangian) and  $195.0 \pm 7.7$  Ma (Hettangian–Sinemurian: Parrish *et al.* 2019), which is older than the Clarens Formation. Radiometric dating from the Kayenta Formation in northern Arizona places it as no older than  $183.7 \pm 2.7$  Ma (Marsh *et al.* 2014), which is latest Pliensbachian and younger than the Clarens Formation. U-Pb ages of detrital zircons from the Kayenta Formation are dated as  $\sim 12$  Ma older than that (Dickinson & Gehrels 2009), which would make the Kayenta Formation (or at least areas of the formation) Sinemurian in age. Detrital grains give the maximum age, and so could be potentially much older than the formation. The U-Pb dating of carbonates of the Navajo Sandstone date it 20 million years older than the radiometric dating of the underlying Kayenta Formation. The Navajo Sandstone was sampled in Utah and the Kayenta Formation from Arizona, so both samples are geographically broadly separated. The possibility should be considered that the beds in Arizona are not correlated with the beds in Utah. Indeed, Steiner & Tanner (2014) report that the Kayenta Formation in the Moab region, Utah, was not correlative with the Kayenta Formation near Kanab, Utah. Furthermore, Steiner & Helsen (1974) indicate that the Kayenta Formation in the Moab region is Late Triassic. For the purpose of this research we will agree with the dates presented by Marsh *et al.* (2014) for the Kayenta Formation ( $183.7 \pm 2.7$  Ma, Early Jurassic, late Pliensbachian–Toarcian), because these dates are also supported by biostratigraphy. The vertebrate fossils recovered from the Kayenta Formation include relatives of later-branching crocodyliforms (e.g. *Calsoyasuchus*), and the underlying Moenave Formation is potentially coeval with the upper Elliot Formation, based on the co-occurrence of *Protosuchus* (Colbert & Mook 1951; Gow 2000; Lucas *et al.* 2011; Viglietti *et al.* 2020).

The Lower Lias of Chile is correlated with the Sinemurian (Gasparini *et al.* 2000). The Forest Sandstone Formation (Zimbabwe) is correlated most closely with the upper Elliot Formation (Sciscio *et al.* 2020), which is also Sinemurian. The Forest Sandstone Formation is thus older than the Clarens Formation (Sinemurian–Pliensbachian), which potentially supports a hypothesis of southerly progressing aridification in southern Africa through time (Visser 1984). Furthermore, given the temporal difference between the Forest Sandstone and Clarens formations, it is unlikely that QG 49 (the Zimbabwean crocodylomorph) is the same species as *Notochampsia istedana* (see above).

The only other potential crocodylomorph from the Clarens Formation is QR 606 (*Pedeticosaurus*, a likely *nomen dubium*: Clark & Sues 2002). However, the provenance data for *Pedeticosaurus* is vague and it cannot be confirmed if it is from the Clarens Formation without further investigation. Therefore, *Notochampsia* is the only confirmed crocodylomorph fossil from the Clarens Formation. However, there is evidence for more vertebrate taxa in the Clarens Formation, with the presence of many trace fossils (Bordy *et al.* 2020b). Discovery of more body fossils from the Clarens is likely in the future, especially with more collecting effort and the identification of additional suitable outcrops.

The Clarens Formation is generally considered to be an aeolian deposit with large to massive cross-bedded sandstones (Beukes 1970; Eriksson 1986; Visser 1984; Bordy & Head 2018). However, it contains interbedded fluvial-lacustrine deposits that indicate flash-flooding and standing pools of water. These fluvial sandstone deposits occasionally interbed with the flood basalts of the Drakensburg Group (Bordy *et al.* 2020b, 2021). These deposits record vertebrate trace fossil remains and show that the Karoo Basin was still inhabited during the initial period of the Karoo-Ferrar basalt outpourings that led up to the Pliensbachian–Toarcian extinction event (Marsh & Eales 1984; Moulin *et al.* 2011, 2017; Jay *et al.* 2018).

The presence of *Notochampsia* in the Clarens Formation shows that crocodylomorph taxa were still living in drier, more aeolian environments (as also supported by the presence of QG 49 in the Forest Sandstone Formation). *Notochampsia* was a small, terrestrial predator and/or scavenger that would have existed in a dry to wet desert palaeoenvironment, with periods of seasonal flooding and pooling of water. This occurrence suggests it is possible that *Notochampsia* had more specialized adaptations to an arid environment than its precursors (e.g. *Protosuchus*).

## Conclusions

*Notochampsia istedana* is a valid genus of early-branching crocodylomorph distinguishable from, but closely related to, *Orthosuchus*. *Notochampsia* and *Orthosuchus* present unique morphologies which distinguish them from other closely related crocodylomorphs, including a ventrally expanded squamosal flange and expanded intercostal ridges on the dorsal ribs. The name Notochampsidae is given for the least inclusive group that includes *Notochampsia* and *Orthosuchus*. Additionally, the name Notochampsioidea is given for the monophyletic group that includes *Notochampsia*, *Protosuchus*, their most recent common ancestor and all of its descendants.

*Notochampsia* is currently the youngest-known vertebrate body fossil occurrence from the Karoo Basin. Furthermore, it is one of only a very few crocodylomorph fossils described from the Pliensbachian, which is a period in which vertebrate body fossils are scarce globally. *Notochampsia* was recovered from the lower to middle Clarens Formation (approximately 65 m above the Elliot/Clarens contact), which is the last sedimentary stratum before the large basalt flows of the Drakensburg Group that cap the Karoo Supergroup. *Notochampsia* would have inhabited a ‘wet desert’ palaeoenvironment in southern Africa. It is interesting to describe a crocodylomorph existing in an increasingly arid environment, which hints at the potential ecological diversity and adaptability present in the very earliest members of this large clade.

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## Supplemental material

Supplementary material for this article can be accessed at: <https://doi.org/10.1080/14772019.2021.1948926>.

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