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A second peirosaurid crocodyliform from the mid-Cretaceous Kem Kem Group of Morocco and the diversity of Gondwanan notosuchians outside South America

Journal:	*Royal Society Open Science*
Manuscript ID	RSOS-211254.R1
Article Type:	Research
Date Submitted by the Author:	08-Sep-2021
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Subject:	Palaeontology < EARTH SCIENCES, palaeontology < BIOLOGY
Keywords:	Notosuchia, Crocodylomorpha, Gondwana, Kem Kem, Mesozoic, Africa
Subject Category:	Organismal and Evolutionary Biology

Author-supplied statements

Relevant information will appear here if provided.

Ethics

Does your article include research that required ethical approval or permits?:
This article does not present research with ethical considerations

Statement (if applicable):
CUST_IF_YES_ETHICS :No data available.

Data

It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:
Yes

Statement (if applicable):
The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Conflict of interest

I/We declare we have no competing interests

Statement (if applicable):
CUST_STATE_CONFLICT :No data available.

Authors' contributions

This paper has multiple authors and our individual contributions were as below

Statement (if applicable):
C.S.C.N and P.D.M. conceived of the study and interpreted the results. All authors contributed to the design of the study and to the drafting of the manuscript. Analyses were conducted by C.S.C.N. Figures were produced by C.S.C.N. and E.S.E.H. All authors approved the final version of the manuscript.

Response to Reviewer Comments for Manuscript

Reviewer 1:

1) Perhaps the most important issue that I raise is related to the α-taxonomy of the peirosaurids from the Kem Kem beds. One of the main goals of the MS is to diagnose the new taxon *Antaeusuchus* and differentiate it from *Hamadasuchus*. However, it is not clear for me which specimens referred to *Hamadasuchus* the authors considered for their analysis. If I understood correctly, the OTU *Hamadasuchus* in their phylogenetic analysis is composed by the fragmentary holotype (MDE C001) and the skull (ROM 52620) described by Larsson & Sues (2007), while in along the comparison section, the authors also compare to a broader sampling of specimens (e.g. BSPG 2005 I 83, ROM 49282, etc). In general, I would be ok with such strategy, in fact, I used a similar *Hamadasuchus* OTU in my own phylogenetic analyses. The problem is that the preserved parts of the holotype of the taxon *Hamadasuchus* and the referred specimen ROM 52620 do not overlap. Also, Ibrahim et al. (2020) suggests that several specimens referred to *Hamadasuchus* present a morphological variation with possible taxonomical implications. The new taxon Antaeusuchus can be differentiated from the holotype of *Hamadasuchus* but both cannot be differentiated from the specimen ROM 52620. I would say that the best strategy at this point is to restrict the *Hamadasuchus* OTU to only the holotype of the taxon awaiting further revision of the remaining specimens.

We had already noted in our “Detailed comparisons with *Hamadasuchus rebouli*” section that the OTU for *Hamadasuchus rebouli* is composed of the holotype mandibular fragment (MDEC001) plus the cranial material (ROM 52620) referred by Larsson & Sues (2007), but we have now also clarified this in our Phylogenetic methods section. Although we have changed a few scores from previous studies, this combined OTU has been used in all analyses which include *Hamadasuchus* since the publication of Larsson & Sues (2007). Given the need for a full revision of material assigned to *Hamadasuchus* (beyond the scope of our study) and the focus of our paper (i.e. the description and phylogenetic placement of *Antaeusuchus*), we would prefer to retain *Hamadasuchus* as a combined OTU. Finally, the holotype specimen of *Hamadasuchus* is very incomplete: including it as a separate OTU in a preliminary set of analyses results in far less phylogenetic resolution across our topology. As such, we think that the best solution for this MS is to retain the current *Hamadasuchus* OTU pending revision of that taxon.

2) I detected the lack of explicit definitions of most clades used in the MS, for example figure 7. Which definition of Notosuchia and Ziphosuchia were used? In addition, which definition for Metasuchia was used? I was not able to find any definition in recent papers.

The primary aim of the manuscript is to describe a new specimen and place it into a phylogenetic analysis. We therefore don’t agree that it is necessary to provide explicit clade definitions, as it is not the intention of the paper to deal with broader notosuchian taxonomy. Where appropriate, and to discuss the phylogenetic positioning of the new specimen, we provide the definition we have used for Peirosauridae, within which *Antaeusuchus* is recovered. We believe that the specific clades used throughout the manuscript are standard, widely used terminology used by authors working on this topic, and are not especially pertinent to the key focus of the paper. It is our understanding that explicit clade definitions are not usually required for work such as this. Furthermore, there is only currently a single proposed phylogenetic definition for Notosuchia, Ziphosuchia, and Metasuchia, and these have been in usage for most of the last two decades.

3) Although it is not particularly relevant, the revised phylogeny presented by the MS is not the largest notosuchian-focused character-taxon matrices yet to be compiled.

The text states that the matrix is “one of the largest” rather than “the largest” which we believe to be true given the high degree of character and taxon sampling, and our particular focus on including more peirosaurid taxa. As such, we have made no changes in response to this comment.

4) We have proposed a phylogenetic definition for Notosuchia in our paper (Ruiz, et al. 2021), perhaps include it on the Systematic Palaeontology section.

As mentioned above, the aim of this paper is to present a new crocodylomorph specimen, not to review broader notosuchian taxonomy. We do not believe the inclusion of phylogenetic definitions of all clades relating to notosuchians to be standard procedure in work such as this. Furthermore, the definition of Notosuchia in that paper is identical to the original phylogenetic definition provided by Sereno et al. (2001).

5) In relation to the anatomy of *Antaeusuchus*, I suggest the authors to take a look on Pinheiro’s et al. (2020, Plos One) description of the enamel of *Roxochampsa*.

The paper suggested by the reviewer describes a Late Cretaceous Brazilian notosuchian, which was recovered outside of Peirosauridae. In our manuscript, detailed comparisons with other crocodylomorphs are restricted to Peirosauridae given the position recovered by *Antaeusuchus* in our phylogenetic analyses. As such, we feel it is unnecessary to include text regarding *Roxochampsa* within the manuscript based on its recovery in a different clade and lack of spatiotemporal overlap. If the reviewer is suggesting potential similarities between the two taxa, we note that the enamel in *Roxochampsa* differs from that of *Antaeusuchus* in several aspects, most notably in that the apicobasal enamel ridges are themselves crenulated along their length. As such, we have not added in comparisons to this taxon.

6) Which are the parameters used during sectorial searches, drift and tree fusing?

We have modified the text to confirm the exact parameters used during our analyses. These sections have been highlighted in the marked-up draft.

7) I did not understand what the authors mean when they say that *Uberabasuchus* can be used as a proxy for *Peirosaurus*?

We described in the preceding sentence how *Uberabasuchus terrificus* has been consistently recovered as a close relative of *Peirosaurus torminni*, with some authors regarding the latter as a junior synonym of the former (e.g. Larsson & Sues 2007; Martinelli et al. 2012). As such, we think the existing text is clear and explicit in terms of what we mean, i.e. “Although *Peirosaurus torminni* is not included in our data matrix, *Uberabasuchus terrificus* has been consistently recovered as a close relative, with some authors regarding the latter as a junior synonym of the former (e.g. Larsson & Sues 2007; Martinelli et al. 2012). As such, we regard the *Uberabasuchus* OTU as a proxy for *Peirosaurus* in terms of identifying Peirosauridae.”

8) In the discussion about the multicusped teeth described by Larsson & Sidor (1999), I suggest the authors to also take a look on the papers by Montefeltro et al. (2009) and Pinheiro et al. (2021, *Coronelsuchus*).

The paper by Montefeltro et al. (2009) describes six multicuspid teeth from the Upper Cretaceous of Brazil. Though similar in broad morphology to those described from Morocco, the authors note that they are “not related to two unnamed forms” from the Kem Kem beds. Pinheiro et al. (2021) also describe a notosuchian with heterodont, multicuspid dentition from the Bauru Basin of Brazil. Although both papers describe multicuspid teeth, this is not a particularly unusual morphology amongst notosuchians. The condition is more widespread than the papers mentioned by the reviewer and so it is unclear why these two precisely have been chosen. We refrain from including these specific examples in this work as our review focuses on the Gondwanan record outside of South America.

9) The reference Evans et al. 2014 cited in the text is not listed. There is a reference cited as Montefeltro et al. (2019). I guess it is Montefeltro (2019, JVP) or Montefeltro et al. (2020, J. Anato).

We have added the appropriate citations to the manuscript. The latter has been corrected to Montefeltro et al. (2020) in the References.

Reviewer 2:

1) The authors used two different protocols for their phylogenetic analyses, one employing equally weighting of characters, and the other employed the extend implied weighting protocol. I do think it is interesting to see the results using two alternative methods. However, if two alternative methods are used in the paper, I think that the authors should then explain if they prefer any of the methods employed. If they do prefer one of the two methods, justify. If no, just mention that you are using different methods because there is no study so far that says that we should ‘definitely’ opt for one instead of

the other. In this context, sentence like "we applied extend implied weighting to notosuchians for the first time' are not very relevant, especially when the authors use the phylogeny obtained from their analysis using equal weighting in their Figure 11. In this case, I think there should be a justification for the reason why you selected the equal weighting analysis for this figure.

We are pleased to hear that the reviewer is interested to see the results of the alternative methods in this paper. Goloboff (2014; 2017) described the potential benefits of using extended implied weighting on morphological datasets, and several recent neosuchian-focused studies (e.g. Groh et al. 2020; Rio et al. 2020; Rio and Mannion 2021) also show that analyses run using extended implied weighting (EIW) score higher in measures of phylogenetic accuracy. We do not "prefer" any particular method, nor do we analyse the benefits and pitfalls of each as it is beyond the remit of this paper. We do, however, think that it is important to mention that the method has not yet been used on notosuchians given the discrepancies seen in tree topologies between both methods. Given that we do not have a preferred analysis, the method used to illustrate the tree in Figure 11 is not important: given that our analyses had broadly congruent results we merely chose to represent one tree as a time calibrated figure given that both are already figured as cladograms.

2. The authors did a good job in providing comparisons between the new species with other peirosaurids. Also, by the end of this section, they list the differences the differences between Antaeusuchus and the other peirosaurids from the Kem Kem, Hamadasuchus. The authors mention that one of the differences is that specimens assigned to Antaeusuchus are much larger than species assigned to Hamadasuchus. Thus, I think that an interesting addition to their study would be to try ruling out the possibilities that the differences between Antaeusuchus and Hamadasuchus are not related to ontogeny – i.e. that individuals of Antaeusuchus do not correspond to larger individuals of Hamadasuchus. I'm not sure it is possible to check this for all the different characteristics they mentioned based on the differences observed in extant crocodylians – but anyway, this might strength their argument to separate the two species.

We agree with the reviewer that this would be an interesting aspect to include in the study. Griffin et al. (2020) suggested that the best measure of ontogeny in crocodylomorphs can be ascertained from long bone histology and neurocentral fusion in vertebrae, neither of which are applicable in this paper given the preserved material. The sister taxon to *Antaeusuchus*, and therefore potentially the best proxy for evaluating ontogenetic changes in the new specimens, *Hamadasuchus rebouli* is known from several specimens that are described by Larsson & Sues (2007) as representing an ontogenetic series. Within the paper they refer to several morphological differences that are evident between the various growth stages. These almost entirely relate to the cranium (e.g. the reduction of a sagittal crest on the frontoparietal suture, the reduction of medial rims of the supratemporal fenestra, and the reduction of a crest on the posterodorsal surface of the quadrate), and thus are not helpful in assessing the growth stage of the *Antaeusuchus* mandible. The final morphological feature mentioned by Larsson & Sues (2007) relates to shape changes in the posterior dentary teeth, and describes a change from more gracile, labiolingually compressed morphology to more robust, wider teeth in relatively mature individuals. The teeth in *Antaeusuchus* are actually closer in diameter to the less mature specimens of *Hamadasuchus*, going some way to ruling out that the former is a more mature than the latter. Though we understand the reviewer's concerns about using size as a justification for the erection of a new species, A*ntaeusuchus* is significantly larger than even the largest of all known specimens referred to *Hamadasuchus*, which is already known from an ontogenetic series Larsson & Sues (2007). We agree that as a sole comparison, size would be an insufficient reason to justify a new species, but as part of a large, unique combination of morphological features, we believe it to be a valid difference. A paragraph explaining this has been added to the text.

3. I have mixed feelings about the last section of the discussion, which brings a revision of the notosuchians outside South America. Whereas I think it is interesting to see this kind of information compiled in a single study, I do not think that the authors used the information already available in the literature in order to provide any new insight on the evolution of African notosuchians. For example, the section dealing with the presence of *Razanandrongobe* in the Middle Jurassic of Madagascar brings no novel information that is worth being included in the discussion section of this manuscript. In sum, there is not much of new insights or new perspectives in all the sections of this part of the discussion that would justify the inclusion of this part of the manuscript together with the description of the new taxon and discussions on the phylogenetic analysis of peirosaurids. For example, section 6.3.5 would better fit as part of an introduction of a manuscript on the fossil record of notosuchians.

We believe that a revision of Gondwanan notosuchians outside of South America is an integral part of this manuscript. We provide the first ever comprehensive overview of all notosuchians from this region, several of which we reidentify. Our reappraisal deals with multiple putative remains, the assignment of which will significantly affect the outcome of macroevolutionary studies for notosuchians outside of South America. In terms of biogeography, the notosuchian record from the Arabian Peninsula is removed. Furthermore, the review provides updated stratigraphic information which is often missed by many authors. As such, we strongly disagree with the reviewer and have retained this section.

Comments from Reviewer 2 provided in the attached PDF:

1. Please add dates in millions of years - this will facilitate readers to locate themselves in geologic time.

We have included all relevant dates within the abstract as well as at their first mention in the main body of text.

2. In the way that it is written, it seems that an analysis of the fossil record is what indicates that Miadanasuchus might be a peirosaurid. Is that really what is intended to be said here? My view is that only a phylogenetic analysis can indicate the phylogenetic affinities of a taxon.

The wording has been altered to reflect the role of phylogenetic analyses in the designation of *Miadanosuchus* as a peirosaurid as opposed to solely the reappraisal of the non-South American notosuchian record.

3. Usually, I like to see a final sentence wrapping up the main point of the manuscript, and also bringing some directions for future studies. The authors might want to consider to include something like this to the abstract.

We feel that the abstract as a whole does a sufficient job of summarising the main points of the manuscript and so we refrain from adding a further sentence, especially given that we were already at the word limit in our original submission. Furthermore, our entire abstract summarises our study – having a final sentence that summarises the abstract seems somewhat redundant. A future studies section is not needed and we have already noted several things that need doing in the existing text (e.g. revision of Hamadasuchus).

4. You can also cite Ruiz et al. 2020 here.

Requested citation has been added to the text.

5. What do you mean by apparent diversity here? Number of known species? Please specify.

Text has been clarified to indicate that we are referring to the raw number of species.

6. Could you indicate where each wave starts and ends?

Information regarding the positioning of the waves has been added.

7. Is it possible that the suture extends further posteriorly? Are the splenials overlapping the dentaries in this region?

We have not amended this section as it simply describes the dentary suture visible in dorsal view. The suture is seen to extend to the 8th tooth in specimen PV R36829, and its shape can also be inferred in PV R36874. On the ventral surface the dentary extends to the 7th/8th teeth. The exposure of the suture in medial view in PV R36874 indicates that the suture did not extend further posteriorly due to intrusion of the splenials between the dentaries.

8. These two processes, the one forming the dorsal margin of the mandibular fenestra and the one dorsal to it, are they really processes or is it just the case that the surangular is overlapping the dentary in this region?

Although the surangular does marginally overlap the dentary as scored in character 366, an oblique suture can be seen in both lateral and medial view indicating that these are distinct, separate processes rather than superficial ones formed just by a surangular process overlapping the dentary.

9. It would be great to have these processes labelled in the figure.

As requested, the posterior processes have been labelled in figures 2 and 3.

10. However, shouldn't it be three processes, as you consider as the process ventral to the mandibular fenestra as a posterior process as well?

The addition of this text clarifies the specific processes we are referring to. The “third” process is described later in the text and is not referred to here as it cannot be considered “major”, forming only a short protrusion.

11. I suggest changing to: and occupy approximately 38% of the anteroposterior symphyseal length on the dorsal surface of the mandible.

The text has been changed as requested.

12. On the ventral surface.

The text has been changed as requested.

13. It is better to cite the work of Iordanksy, cited in Larsson & Sues, than to cite the latter. Should then change the sentence slightly - likely homologous the foramen intermandibularis oralis of living crocodylians.

We have cited Iordansky (1973), and have changed the text as requested.

14. I couldn't see it on the figures.

A label has been added to figures 2 and 3.

15. For the angular and some of the other bones previously described, I missed a more general description of each bone, detailing the general shape of the bone and indicating the bones that it contacts.

We have added in several additional descriptions of general morphology; however, we feel that we have already been fairly consistent with describing the contact between bones.

16. I **think that if you are using a whole new section for the description of the mandibular fenestra, you could provide some more details, even if it is incomplete. For example, is it possible to add some relative measurements to the description of this structure?**

We have added in an additional comment although refrain from too many descriptions given the fragmentary nature of the fenestra.

17. Which are the parameters used during sectorial searches, drift and tree fusing?

Precise parameters have been included.

18. Not necessary to include this. Just cite Goloboff.

We have kept this text as we feel that it provides an overview of the benefits of using extended implied weighting on a dataset, especially as the method has not previously been applied to notosuchian crocodylomorphs. We do not believe that the inclusion of the text detracts from the manuscript in any way.

19. A better approach would be to try different values of 'k' instead of adopting the values from previous studies.

We selected these specific values as previous studies (e.g. Goloboff et al. 2017) have indicated that lower values of *k* can be excessive in downweighting putative homoplastic characters. Despite extended implied weighting never having been used before in a notosuchian-focused matrix, such effects can be seen in datasets for neosuchian crocodylomorphs (e.g. Rio & Mannion 2021) in which low *k*-values consistently produce trees that score poorly in measures of phylogenetic accuracy. Whilst attempting to avoid lower values of *k*, we still undertake multiple analyses to determine the possible impact of different *k*-values.

20. If a taxon is included in the matrix, I think that it also should be included in the analyses. So, you should either show the topology of the strict consensus with these unstable taxa, or simply generate a reduced consensus tree using the prunnelsen command (Goloboff & Szumik, 2015 or 2016). I think that the last option is more appropriate because it shows where these problematic taxa are floating on your tree.

We refrain from changing the analysis on the basis that if these taxa were not included within the matrix at all then the issue would not have been raised. We are unaware of a similar paper which includes all described species of notosuchian. We therefore follow the recommendations of Pol et al. (2014) to exclude this taxa.

21. Which are the parameters used during sectorial searches, drift and tree fusing?

Precise parameters have been included.

22. This should be tree length - not branch length.

Changed as requested.

23. I think it will be easier to follow the results if you already mention the phylogenetic definition here.

The definition is written out later on in a separate section of text relating to peirosaurids, and therefore we refrain from including it here. We feel that writing the full definition of clades in this section of the manuscript would potentially make the text harder to follow, especially given that these are generally widely used clade terms in notosuchian-focused literature.

24. How did you recover this? You used the prunnelsen command or you removed *Gasparinisuchus* and ran a new analysis? Please indicate that.

Gasparinisuchus was removed from the analysis in the agreement subtree.

25. I'm not very convinced that you can use this characteristic for comparisons between *Antaeusuchus* and other taxa, because it is not entirely preserved in the former.

We still include this morphology in our comparisons, as despite the fenestra being incomplete in either single specimen, the majority of its border is preserved across both NHMUK PV R36829 and R36874. In both specimens the preserved margins indicate that the opening is clearly larger than in *Barrosasuchus* with which it is compared.

26. I think that in this case, you should score your taxon with '?' rather than 1 and 2.

We have chosen not to alter the score to ‘?’ as the splenial is clearly elongate and would be scored for either state 1 or 2 if complete. We feel in this instance it is better to score for either scenario rather than to exclude morphological information. Furthermore, the character construction needs to be addressed given the large gap between states 1 and 2, however, this is beyond the scope of this paper.

27. Don't you think that this polymorphism could also exist in specimens assigned to *Hamadasuchus*?

There is definitely variation amongst taxa referred to *Hamadasuchus*, as discussed in our comparisons section. Given the character state boundaries for character 77, we felt it best to provide a detailed account of the measurements in each specimen. A comprehensive review of notosuchian characters would help to produce definite scores for many taxa with polymorphic scoring; However, this is not the aim of the paper.

28. That is not necessarily true - you should remove this sentence.

We have removed the sentence as requested.

A second peirosaurid crocodyliform from the mid-Cretaceous Kem Kem Group of Morocco and the diversity of Gondwanan notosuchians outside South America

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RRH: SECOND MOROCCAN PEIROSAURID
LRH: NICHOLL, HUNT, OUARHACHE & MANNION

Abstract

Notosuchians are an extinct clade of terrestrial crocodyliforms with a particularly rich record in the late Early to Late Cretaceous (~130–66 Ma) of Gondwana. Although much of this diversity comes from South America, Africa and Indo-Madagascar have also yielded numerous notosuchian remains. Three notosuchian species are currently recognised from the early Late Cretaceous (~100 Ma) Kem Kem Group of Morocco, including the peirosaurid *Hamadasuchus rebouli*. Here, we describe two new specimens that demonstrate the presence of at least a fourth notosuchian species in this fauna. *Antaeusuchus taouzensis* n. gen. n. sp. is incorporated into one of the largest notosuchian-focused character-taxon matrices yet to be compiled, comprising 443 characters scored for 63 notosuchian species, with increased sampling of African and peirosaurid species. Parsimony analyses run under equal and extended implied weighting consistently recover *Antaeusuchus* as a peirosaurid notosuchian, supported by the presence of two distinct waves on the dorsal dentary surface, a surangular which laterally overlaps the dentary above the mandibular fenestra, and a relatively broad mandibular symphysis. Within Peirosauridae, *Antaeusuchus* is recovered as the sister taxon of *Hamadasuchus*. However, it differs from *Hamadasuchus* with respect to several features, including the ornamentation of the lateral surface of the mandible, the angle of divergence of the mandibular rami, the texture of tooth enamel, and the shape of the teeth, supporting their generic distinction. We present a critical reappraisal of the non-South American Gondwanan notosuchian record, which spans the Middle Jurassic–late Eocene. This review, as well as our phylogenetic analyses, indicate the existence of at least three approximately contemporaneous peirosaurid lineages within the Kem Kem Group, alongside other notosuchians, and support the peirosaurid affinities of the 'trematochampsid' *Miadanasuchus oblita* from the Maastrichtian of Madagascar. Furthermore, the Cretaceous record demonstrates the presence of multiple lineages of approximately contemporaneous notosuchians in several African and Madagascan faunas, and supports previous suggestions regarding an undocumented pre-Aptian radiation of Notosuchia. By contrast, the post-Cretaceous record is depauperate, comprising rare occurrences of sebecosuchians in north Africa prior to their extirpation.

Keywords: Notosuchia, Crocodylomorpha, Gondwana, Kem Kem, Mesozoic, Africa

1. Introduction

Today's crocodylians are the remnants of a once much more diverse and widespread clade, Crocodyliformes (Brochu 2003; Carvalho et al. 2010; Mannion et al. 2015; Wilberg et al. 2019; Stubbs et al. 2021). One extinct group, Notosuchia, comprises a morphologically diverse, speciose clade of terrestrial crocodyliforms (Carvalho et al. 2010; Pol et al. 2014; Pol & Leardi, 2015). Often noted to exhibit bizarre bauplans relative to other crocodyliforms, notosuchians include species characterised by features such as 'pug-nosed' and 'duck'-like snouts (e.g. Buckley et al. 2000; Sereno et al. 2003; Kley et al. 2010), elongate limbs indicative of a parasagittal posture (e.g. Gasparini 1971; Pol 2005; Riff and Kellner 2011; Godoy et al. 2016), mammal-like heterodont dentition (e.g. Carvalho 1994; Wu et al. 1995; Buckley et al. 2000; Ősi 2014), and even herbivory (e.g. O'Connor et al. 2010; Melstrom & Irmis 2019). Notosuchians have predominantly been recovered from Gondwanan landmasses, especially South America (e.g. Carvalho et al. 2010; Pol et al. 2014; Ruiz et al. 2021), from which more than 70% of species have been discovered (Pol & Leardi 2015). Although the group had its highest apparent (i.e. 'raw number of') species diversity in the middle–Late Cretaceous (~120–66 Ma) (Riff et al., 2012; Pol & Leardi, 2015), notosuchians survived until the middle Miocene (~12 Ma) (Langston 1965; Langston & Gasparini 1997; Paolillo & Linares 2007), with putative remains extending their record back to the Middle Jurassic (~168 Ma) (Dal Sasso et al. 2017).

Despite severe and pervasive under-sampling of fossiliferous localities relative to most other continents (Mannion et al. 2019), diverse assemblages of extinct crocodyliforms have been discovered from several spatiotemporal intervals in Africa (e.g. Jouve 2007; Sereno & Larsson 2009; Brochu & Storrs 2012; Stefanic et al. 2020), including those yielding notosuchians. One such interval is represented by the 'middle' Cretaceous Kem Kem Group, a series of highly fossiliferous continental strata exposed in the east of Morocco along its border with Algeria, forming the northwestern edge of the Sahara Desert (Lavocat 1948; Russell 1996; Sereno et al. 1996; Bardet et al. 2010; Cavin et al. 2010; Ibrahim et al. 2020) (Fig. 1). The Kem

Kem Group is generally considered to be either late Albian or Cenomanian (~105–94 Ma) (e.g. Martin and Lapparent de Broin 2016), with the most recent stratigraphic reappraisal favouring this younger age (Ibrahim et al. 2020). A diverse vertebrate fauna has been recovered from the Kem Kem Group, including sharks, bony fishes, lissamphibians, turtles, squamates, pterosaurs, non-avian dinosaurs, and crocodyliforms (Sereno et al. 1996; Rage & Dutheil 2008; Sereno & Larsson 2009; Bardet et al. 2010; Cavin et al., 2010; Ibrahim et al. 2020).

The Kem Kem crocodyliforms comprise the neosuchians *Aegisuchus witmeri* (Holliday & Gardner 2012), *Elosuchus cherifiensis* (Lavocat 1955; Lapparent de Broin 2002), and *Laganosuchus maghrebensis* (Sereno & Larsson 2009), as well as three notosuchians (Ibrahim et al. 2020). The first of these notosuchians to be named, the peirosaurid *Hamadasuchus rebouli* (Buffetaut 1994), was erected based on a fragmentary dentary. Several specimens have since been referred to this taxon, including a nearly complete cranium and lower jaws (Larsson & Sidor 1999; Rauhut & López-Arbarello 2006; Larsson & Sues 2007; Ibrahim et al. 2020). Sereno & Larsson (2009) described a second Kem Kem notosuchian species, the small-bodied uruguaysuchid *Araripesuchus rattoides*, which is currently known from several dentaries (Ibrahim et al. 2020). The third notosuchian species to be described, the candidodontid *Lavocatchampsa sigogneaurussellae* (Martin & Lapparent de Broin 2016), is known from a small partial skull with unusual mammal-like multicuspid teeth. Ibrahim et al. (2020) suggested that multicuspid crocodyliform teeth described by Larsson & Sidor (1999) might represent additional notosuchian taxa. Finally, Ibrahim et al. (2020) also noted anatomical differences between the type and referred material of *Hamadasuchus* that could indicate yet higher crocodyliform diversity in the Kem Kem Group.

Here, we describe new notosuchian remains from the Kem Kem Group of Morocco that support Ibrahim et al.’s (2020) suggestion of higher crocodyliform diversity in this fauna. We test the phylogenetic position of these new specimens in an expanded version of an existing data set. Finally, we provide a critical reappraisal of the Gondwanan record of non-South American notosuchians, in which we reassess the group’s diversity through time and space.

1.1. Institutional abbreviations — **BSPG**, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **CMN (formerly NMC)**, Canadian Museum of Nature, Ottawa, Canada; **MDE**, Musée des Dinosaures, Espéraza, France; **MNHM**, Muséum national d'Histoire naturelle, Paris, France; **NHMUK**, Natural History Museum, London, UK; **ROM**, Royal Ontario Museum, Toronto, Canada.

2. Systematic Palaeontology

Crocodylomorpha Walker, 1970

Crocodyliformes Hay, 1930 (sensu Clark in Benton and Clark, 1988)

Mesoeucrocodylia Whetstone and Whybrow, 1983

Notosuchia Gasparini, 1971

Peirosauridae Gasparini, 1982

Antaeusuchus taouzensis gen. et sp. nov.

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Etymology—Genus name after the giant *Antaeus* from Berber and Greek mythology, who is said to be buried at Msoura in northern Morocco, and *suchus*, from the Greek *souchos*, meaning crocodile. Species name after the township *Taouz* from where the holotype and paratype specimens were recovered.

Holotype—NHMUK PV R36829: paired mandibles, comprising an essentially complete left dentary and splenial, along with a partial angular and surangular, in articulation with the anterior portion of the right dentary and splenial.

Paratype—NHMUK PV R36874: a partial right mandible, comprising an incomplete dentary, surangular, and angular.

Locality and horizon—Near to Jebel Beg'aa, Taouz township, Errachidia Province, eastern Morocco. The specimens were commercially collected and recovered from unspecified beds within the Cenomanian (lower Upper Cretaceous) Kem Kem Group.

Diagnosis—A crocodyliform characterized by the following unique combination of features: (1) wide divergence angle (40–45°) of the mandibular rami; (2) dorsal margin of dentary sinusoidal with two distinct waves; (3) relatively unornamented surface texture of dentary adorned with narrow, shallow ridges; (4) ventrolateral dentary surface anterior to mandibular fenestra transversely compressed and vertical; (5) dentary extends posteriorly beneath the mandibular fenestra; (6) anterior alveoli of dentary strongly procumbent; (7) concavity for the reception of the enlarged maxillary tooth lateral to the 7th alveolus of the dentary; (8) splenial forming approximately 40% of the total mandibular anteroposterior length; (9) surangular overlaps dentary above the mandibular fenestra; (10) rugose tooth enamel formed by anastomosing grooves and ridges; (11) enlarged 4th and 13th dentary teeth; (12) tooth margins in posterior region of the dentary toothrow with denticulate carinae formed by homogeneous and symmetrical denticles with a sharp cutting edge; and (13) sub-triangular dentary tooth crowns (in lateral view) with a gently curved apex.

3. Description

After detailed description and comparison of the two specimens, we consider both NHMUK PV R36874 and R36829 to belong to the new species, *Antaeusuchus taouzensis*, and as such they are described together. In instances where the feature being described is preserved in only one specimen, the relevant museum accession number is provided.

3.1. Preservation

The preserved parts of both specimens are undistorted and in good condition, such that small-scale morphological details are still visible. Damage is restricted mainly to the teeth, several of which are missing.

3.2. General Shape

The anterior region of the mandible is characterised by a broad, ’U’-shaped symphysis that forms at least one quarter of the total anteroposterior mandibular length. Each mandibular ramus diverges at an angle of approximately 22° from the sagittal midline. The ramus remains approximately straight along the majority of its preserved length, curving very slightly medially close to its posterior margin (visible on the left side of NHMUK PV R36829). The anterior half of the mandibular dorsal margin is characterized by two distinct ‘waves’, whereas the strongly sloping posterior half is largely straight, with the dentary increasing in dorsoventral height towards the surangular.

3.3. Dentary

The dentary is anteroposteriorly elongate, and its lateral, ventral, and dorsal surfaces are sculpted by neurovascular foramina and vermiform grooves. On the lateral surface, the foramina are largest and most numerous in the anterodorsal region of the snout. In the middle region of the snout, a series of short grooves run anteroposteriorly along the lateral surface, ~10 mm ventral to the toothrow. These grooves meet an anteroposteriorly elongate groove that extends to the dorsal suture of the dentary and surangular process (Figs 2 & 3). Another prominent, anteroposteriorly elongate vascular groove runs from the anterior-most point of the mandibular fenestra to the level of the posterior tip of the toothrow.

In lateral view, the dentary has a sinusoidal dorsal margin composed of two distinct waves. The most anterior wave spans teeth 1–6, whereas the most posterior wave is dorsally raised between teeth 9–15. The dorsoventrally tallest region of each wave corresponds with the position of dentary teeth 4 and 13, the posteriormost of which is more dorsally elevated than the anterior (Figs 2 & 3). The dentary forms the anterior region of a relatively wide mandibular symphysis (Fig. 4), the dorsal surface of which is very mildly concave. In dorsal view, the midline dentary suture extends posteriorly to the level of the 8th tooth (Fig. 4). The bone in this region is relatively unornamented, with the exception of a series of foramina immediately adjacent to the toothrow. On the ventral surface of the mandibular symphysis, the medial dentary suture extends posteriorly to a level between the 7th–8th teeth. A concavity is situated lateral to the 5th–10th teeth, most likely for the reception of an enlarged maxillary tooth. The posterior region of the lateral dentary surface dorsal to the mandibular fenestra is divided into two major acute posterior processes, separated by an anterior process of the surangular (Fig. 2). The ventral-most dentary extension forms the anterodorsal margin of the external mandibular fenestra and is dorsoventrally wide, forming approximately three quarters of the dorsoventral height of the mandible at the same level. The dorsal-most process is much narrower; its dorsal and ventral margins converge posteriorly to form an acute angle. An anteroposteriorly short dentary process is situated ventral to the external mandibular fenestra, although this does not contact the fenestral border. In NHMUK PV R36874, the splenial is not preserved, exposing the dentary's medial surface (Fig. 3).

The dentary has 18 tooth positions. On the left side of NHMUK PV R36829, whole or partial teeth are preserved in alveoli 1–16, whereas 17–18 are empty. On the right side of the specimen, 10 alveoli are preserved, with whole or partial teeth preserved in all but one (alveolus 9). Although the anterior region of NHMUK PV R36874 has broken away, the first preserved alveolus is large, and is assumed to be the fourth in the series. Whole or partial teeth are present in alveoli 5–6, 8, and 10–16 in NHMUK PV R36874. The largest tooth is the 13th, followed closely by the 4th, 11th, and 12th, which are approximately equidimensional in their circumference. In dorsal view, the tooth row is slightly sinusoidal, with lateral waves corresponding to the position of the 4th and 13th teeth (Fig. 4). Although not fully preserved in either specimen, the anteriormost two teeth appear to be procumbent. Dentary teeth 3–10 project slightly anterolaterally. All of the dentary teeth are closely arranged, without the presence of diastemas.

3.4. Splenial

The splenials are only preserved in NHMUK PV R36829. They participate in a relatively wide mandibular symphysis (Table 1) and occupy approximately 38% of the anteroposterior symphyseal length on the dorsal surface of the mandible, extending anteromedially to the position of the 8th alveolus (Fig. 4). On the dorsal surface of the symphysis, the splenial-dentary suture diverges gradually from the sagittal midline. This suture is slightly concave until the 11th tooth, from which point it is parallel to the tooth row. A line of small foramina run parallel to the toothrow along the lateral margin of the dorsal surface of the splenial. On the ventral surface of the mandible, the splenial occupies approximately 31% of the anteroposterior length of the symphysis, and it extends anteriorly to the position of the 9th tooth. The ventromedial splenial surface of the mandibular symphysis is dorsally displaced relative to the lateral margin. A posterior peg is located on the ventromedial surface of the symphysis (Fig. 4). The splenial is transversely thin and dorsoventrally tall, covering the inner surface of the mandibular ramus from the ventral margin of the dentary to the lingual alveolar groove. Positioned just posterior to the mandibular symphysis, on the medial surface of the splenial, is an opening, likely homologous to the intermandibularis oralis of living crocodylians (Iordansky 1973). This is elliptical, such that its anteroposterior length is approximately twice that of its dorsoventral height.

3.5. Surangular

The surangular is more completely preserved in NHMUK PV R36829, extending from the posterior margin of the toothrow to its broken posterior margin at the dorsal-most region of the mandibular fenestra. Its lateral surface is covered with interconnected shallow grooves. Of the surangular’s two acute anterior processes, the most anteroposteriorly elongate is located on the dorsal and medial surfaces of the mandible and extends to the posterior margin of the toothrow (Fig. 4). A second anterior process is present on the dorsal region of the lateral mandibular surface (Figs 2 & 3). Approximately halfway between the anterior margin of the mandibular fenestra and the posterior margin of the toothrow, the dorsal and ventral margins of this second anterior process meet anteriorly to form a subtriangular tip. An anteroposteriorly elongate dorsal coronoid tuberosity protrudes from the dorsomedial surangular surface, running anteroposteriorly for a distance of approximately 30 mm; its anterior margin is at the same level as the posterior-most point of the posterodorsal dentary process. The surangular forms the dorsal-most margin of the mandibular fenestra.

3.6. Angular

Albeit highly incomplete, the angular is best preserved in NHMUK PV R36874. The angular has an elongate anterior process that extends along the ventromedial surface of the mandible to the level of the 14th dentary tooth (Fig. 5). A second, smaller anterior process is present on the lateral surface of the skull (Fig. 3). This extends to the anterior margin of the mandibular fenestra, such that the angular forms the latter’s entire ventral margin. The posteriormost preserved region of the angular projects laterally, forming a prominent ventrolateral ridge beneath the mandibular fenestra.

3.7. Mandibular Fenestra

Although not fully preserved in either specimen, the mandibular fenestra can be inferred to be large and anteroventrally–posterodorsally elongate, as indicated by its extensive, straight anterodorsal margin in NHMUK PV R36874 (Figs 2 & 3). Its anteriormost margin is positioned at approximately the same level as the posteriormost extension of the dorsal-most dentary process; however, the posterior fenestral margin is not preserved in either specimen.

3.8. Dentition

In the anterior region of the snout, the approximately circular alveoli suggest that the teeth are essentially conical; however, those towards the posterior of the toothrow (from the tenth tooth posteriorly) become more labiolingually compressed (Table 2). More extreme labiolingual flattening is present on the anterior and posterior margins of all preserved teeth (Fig. 6). These labiolingually flattened margins are adorned with denticulated carinae forming the anteriormost and posteriormost cutting edges of the teeth. The denticles are small and subtle, showing no significant size variation along the carinae (Fig. 6). There are approximately 35–40 denticles per 10 mm. All preserved teeth are covered by a layer of red-brown enamel upon which apicobasal striations are evident around the whole circumference of the tooth. There are approximately 3–4 bifurcating striations per 1 mm, giving the enamel a wrinkled appearance.

4. Phylogenetic analysis and results

4.1. Dataset and analytical approach

Specimens NHMUK PV R36829 and R36874 were combined as one operational taxonomic unit (OTU), *Antaeusuchus taouzensis*, into a character-taxon matrix (CTM) sampling a large number of crocodyliforms, with particular emphasis on notosuchians. This matrix was originally published by Pol et al. (2014) and has since formed the underlying dataset for phylogenetic analysis in a number of studies, with each one making minor additions and/or revisions to taxa and/or characters. Unfortunately, many of these iterations have occurred in parallel, rather than representing a continuous series of revisions to one dataset, meaning that there is no single dataset incorporating all of these changes to the original Pol et al. (2014) data matrix. Here, we united many of these ‘daughter’ matrices, using that of Martínez et al. (2018) as a starting point. The latter is a successive iteration of the data matrices of Leardi et al. (2015) and Fiorelli et al. (2016), which emanated from that of Pol at al. (2014). We included two additional characters, following Leardi et al. (2018), and revised 20 existing character scores based on observations from recent studies (Stromer 1914; Gomani 1997; Larsson & Gado 2000; Carvalho et al. 2005; Carvalho et al. 2007; Larsson & Sues 2007; Martinelli et al. 2012; Barrios et al. 2016) and personal observations (see Appendix for documentation of changes).

We incorporated notosuchians from parallel daughter matrices, utilising scores presented in those datasets, and a review of the literature. These consist of *Razanandrongobe sakalavae* from the Bathonian (Middle Jurassic) of Madagascar (Maganuco et al. 2006; Dal Sasso et al. 2017), the probable peirosaurids *Bayomesasuchus hernandezi* (Barrios et al. 2016) and *Barrosasuchus neuquenianus* (Coria et al. 2019) from the early Late Cretaceous (Turonian and Santonian, respectively) of Argentina, the sphagesaurid *Caipirasuchus mineirus* from the late Campanian–early Maastrichtian (latest Cretaceous) of Brazil (Martinelli et al. 2018), and the sebecid *Ogresuchus furatus* from the early Maastrichtian of Spain (Sellés et al. 2020). We also expanded the sampling of putative peirosaurids that had not previously been incorporated into iterations of the Pol et al. (2014) data matrix via the inclusion of *Rukwasuchus yajabalijekundu* from the Late Cretaceous of Tanzania (Sertich & O'Connor 2014) and *Miadanasuchus oblita* from the Maastrichtian of Madagascar (Rasmusson Simons & Buckley 2009). The OTU for *Hamadasuchus rebouli* followed previous iterations of this data matrix, although we made a small number of character state changes (see Appendix). The resultant data matrix consists of 121 OTUs scored for 443 characters, including 63 putative notosuchian taxa. *Antaeusuchus taouzensis* could be scored for 51 of these characters.

The data matrix was analysed under maximum parsimony using the ‘Stabilize Consensus’ option in the ‘New Technology Search’ in TNT v. 1.5 (Goloboff et al. 2008). The search was executed using sectorial searches, drift, and tree fusing, and the consensus was stabilized five times with a factor 75, prior to using the resultant trees as the starting trees for a ‘Traditional Search’ using Tree Bisection-Reconstruction. Subsequently, a strict consensus tree was calculated. We applied two different weighting schemes, using equal weighting (EQW) and extended implied weighting (EIW). Shown to perform well on morphological datasets (Goloboff et al. 2018), EIW downweights homoplastic characters in relation to their average homoplasy, whilst reducing the possible impact of missing data (Goloboff 2014). The concavity constant, represented by the *k*-value, denotes the strength of downweighting, with lower values having been shown to downweight homoplastic characters more severely than higher values (Goloboff et al. 2018). Following analytical protocols in recent analyses of neosuchians (Groh et al. 2020; Nicholl et al. 2020; Rio et al. 2020; Rio & Mannion 2021), we applied EIW to notosuchians for the first time, using *k*-values of 8 and 12. Characters with missing entries were downweighted faster assuming 50% the homoplasy of observed entries, and weighting strength did not exceed 5 times that of characters with no missing entries. Forty-three characters representing nested sets of homologies were ordered (1, 3, 6, 10, 23, 37, 43, 44, 45,49, 65, 67, 69, 71, 73, 77, 79, 86, 90, 91, 96, 97, 105, 116, 126, 140, 142, 143, 149, 167,182, 187, 193, 197, 226, 228, 279, 339, 356, 357, 364, 368, 401). Character 5 was made inactive due to “dependence with the modified definition of character 6” (Pol et al. 2014: supplementary information p. 3). Following the identification of problematic, unstable taxa by Pol et al. (2014), confirmed by our preliminary searches, three species known from fragmentary remains were excluded from our analyses *a priori* (i.e. *Coringasuchus anisodontis*, *Pabwehshi pakistanensis*, and *Pehuenchesuchus enderi*). The character list and data matrix are provided as nexus and tnt files (electronic supplementary material), with stored settings for assigning characters as ordered and inactive.

4.2. Results

Under EQW, our analysis produced 11520 trees with a tree length of 1778 steps. The overall tree topology is broadly consistent with the analyses of Pol et al. (2014)

and subsequent iterations. Notosuchia comprises a main bifurcation into Ziphosuchia (plus *Candidodon itapecuruense* and *Libycosuchus brevirostris*), and a clade in which Uruguaysuchidae is recovered as the sister taxon of Mahajangasuchidae + Peirosauridae (following the recent phylogenetic definition of Geroto & Bertini 2018 [see below]) (Fig. 7). Although *Peirosaurus torminni* is not included in our data matrix, *Uberabasuchus terrificus* has been consistently recovered as a close relative, with some authors regarding the latter as a junior synonym of the former (e.g. Larsson & Sues 2007; Martinelli et al. 2012). As such, we regard the *Uberabasuchus* OTU as a proxy for *Peirosaurus* in terms of identifying Peirosauridae. Bremer values are generally low across the tree, ranging from 1–3.

Antaeusuchus is recovered within Peirosauridae, as the sister taxon to *Hamadasuchus* (Fig. 7). The two Kem Kem OTUs form a clade with *Bayomesasuchus* that is the sister group to nearly all other peirosaurids. Within this latter group, *Barrosasuchus* and *Miadanasuchus* form a clade that is the sister taxon to a polytomy comprising *Rukwasuchus*, *Gasparinisuchus peirosauroides*, *Lomasuchus palpebrosus*, *Uberabasuchus*, and *Montealtosuchus arrudacamposi.* This polytomy can be resolved through the *a posteriori* pruning of *Gasparinisuchus* in the agreement subtree, which results in *Lomasuchus* and *Montealtosuchus* recovered as sister taxa, forming a clade with *Uberabasuchus*, with *Rukwasuchus* placed at the 'base' of this grouping. *Stolokrosuchus lapparenti* is recovered as the earliest diverging member of Peirosauridae.

Under EIW, with both *k*-values, the overall topology is largely similar to that recovered using EQW. With a *k*-value of 8, the analysis produced 45 trees with a tree length of 89.3, and with a *k*-value of 12, 15 MPTs were found of length 68.3. The main difference with results obtained from EQW is that the taxonomic content of Peirosauridae is now expanded, as a result of *Stolokrosuchus* being recovered in a clade with *Lorosuchus nodosus* and Mahajangasuchidae (Fig. 8). The phylogenetic definition proposed by Geroto and Bertini (2018) means that Mahajangasuchidae is a clade within Peirosauridae according to our EIW topology.

5. Comparisons

Given the results of our phylogenetic analyses, which provide robust and consistent support for a peirosaurid placement for *Antaeusuchus*, we largely restrict our anatomical comparisons to members of this clade.

5.1. Comparisons with other peirosaurids

Characteristic of all members of Peirosauridae (Martinelli et al. 2012), *Antaeusuchus* possesses an undulatory dorsal margin of the dentary comprising two distinct waves, the apices of which coincide with the position of the two largest dentary teeth (Ortega et al. 1996; Pol et al. 2014). In all peirosaurids in which the relevant region is preserved, with the exception of *Stolokrosuchus* (Larsson & Gado 2000), the 4th dentary tooth is the largest of those in the first wave, and it coincides with the apex of the anterior dentary region. The position of the largest tooth (the apex of the posterior wave) also varies amongst peirosaurids (Pol et al. 2014). The apex of this posterior wave corresponds to the 13th tooth position in *Antaeusuchus*, *Barrosasuchus, Gasparinisuchus, and Kinesuchus overoi* (Martinelli et al., 2012; Filippi et al. 2018; Coria et al. 2019), whereas it occurs at the level of the 12th tooth in *Hamadasuchus* and *Montealtosuchus* (Carvalho et al. 2007; Larsson & Sues 2007). In *Stolokrosuchus*, the jaw gradually increases in dorsoventral height posteriorly, corresponding with a progressively larger tooth size towards the posterior region of the dentary (Larsson & Gado 2000). In lateral view, the dorsoventrally expanded posterior region of the mandible of *Antaeusuchus* more closely resembles that of *Hamadasuchus*, *Montealtosuchus*, and *Uberabasuchus* (Carvalho et al. 2004, 2007; Larsson & Sues 2007) than it does in taxa such as *Barrosasuchus* and *Kinesuchus* (and potentially *Pepesuchus deiseae*) (Campos et al., 2011; Filippi et al. 2018; Coria et al. 2019), in which the region is more dorsoventrally compressed.

All peirosaurid taxa, except for the longirostrine-snouted *Stolokrosuchus* (Larsson & Gado 2000), are characterised by a mediolaterally broad mandibular symphysis (Fig. 9). This is most prominent in *Colhuehuapisuchus lunai*, *Barrosasuchus*, and *Gasparinisuchus* (Martinelli et al. 2012; Coria et al. 2019; Lamanna et al. 2019), in which the anteroposterior length to mediolateral width ratio of the symphyseal dorsal surface is less than 1.0 (values range from 0.8–0.9). Although still broad in comparison with many other notosuchian taxa, such as sphagesaurians (Ruiz et al.

2021), which often have length to width ratios exceeding 2.0 (Pol et al. 2014), *Antaeusuchus*, as well as *Hamadasuchus*, possess some of the anteroposteriorly longest mandibular symphyses amongst Peirosauridae, with a ratio of 1.4 and 1.5 for *Antaeusuchus* and *Hamadasuchus*, respectively (Larsson & Sues 2007). The ratios are 1.2 in *Montealtosuchus* and 1.1 in both *Uberabasuchus* and *Bayomesasuchus* (Carvalho et al. 2004; Carvalho et al. 2007; Barrios et al. 2016). *Kinesuchus* preserves the anteroposteriorly longest mandibular symphyses of any peirosaurid, with a ratio of 2.0 (Filippi et al. 2018).

As is the case in all notosuchians (Pol et al. 2014), the splenials of *Antaeusuchus* participate in the mandibular symphysis, although the extent to which this is the case varies between peirosaurids (Fig. 9). The splenial of *Antaeusuchus* occupies 39% of the anteroposterior length of the symphysis in dorsal view. A relatively long dorsal symphyseal contribution is also present in *Hamadasuchus* (49%), *Bayomesasuchus* (40%), *Kinesuchus* (44%), *Patagosuchus anielensis* (~44%), and potentially *Uberabasuchus*, although the latter cannot be observed in dorsal view (Carvalho et al. 2004; Barrios et al. 2016; Lio et al. 2016; Filippi et al. 2018). A much shorter splenial contribution to the symphysis characterizes *Gasparinisuchus* (16%), *Barrosasuchus* (21%), and *Colhuehuapisuchus* (~26%) (Martinelli et al., 2012; Coria et al. 2019; Lamanna et al. 2019).

Where the splenial meets the dentary on the symphyseal dorsal surface of *Antaeusuchus*, the suture forms an approximate ‘V’ shape. A similar morphology is present in *Hamadasuchus* (Larsson & Sues 2007), *Bayomesasuchus* (Barrios et al. 2016), *Kinesuchus* (Filippi et al. 2018), and *Stolokrosuchus* (Larsson & Gado 2000), as well as *Patagosuchus* (Lio et al. 2016) and *Montealtosuchus* (Carvalho et al. 2007), although the ‘V’ is slightly broader in the latter two species, forming a less acute angle. This morphology contrasts with that of *Barrosasuchus*, *Gasparinisuchus*, *Colhuehuapisuchus*, and *Miadanasuchus* (Rasmusson Simons & Buckley 2009; Martinelli et al. 2012; Coria et al. 2019; Lamanna et al. 2019), in which the dentary-splenial suture forms a broad ‘U’ shape. As with all other peirosaurids (Pol et al. 2014), the dorsal surface of the mandibular symphysis on which this suture occurs is very slightly transversely concave in *Antaeusuchus*.

In *Antaeusuchus*, as well as *Hamadasuchus* (Larsson & Sues 2007), the dentary-splenial suture exposed on the dorsal surface of the mandibular symphysis diverges gradually from the midline until the level of the 12th dentary tooth, at which point it becomes parallel to the toothrow. A similar morphology characterizes *Kinesuchus*, except that the change in orientation of the suture is less acute in that species (Filippi et al. 2018). In *Montealtosuchus* and *Patagosuchus*, the suture becomes parallel with the toothrow at the level of the 10th dentary tooth (Carvalho et al. 2007; Lio et al. 2015). By contrast, the dentary-splenial suture in *Stolokrosuchus* parallels the toothrow only at the level of the 25th tooth (Larsson & Gado 2000). Although the morphology of the suture is 'U'-shaped, as opposed to the 'V'-shape that characterizes *Antaeusuchus*, it becomes approximately parallel with the toothrow at the level of the 11th and 12th tooth in *Gasparinisuchus* and *Barrosasuchus*, respectively (Martinelli et al. 2012; Coria et al. 2019).

Posterior to the symphysis, the mandibular rami of *Antaeusuchus* diverge at an angle of approximately 44° to each other. A value of between ~40–45° is fairly consistent amongst peirosaurids; this contrasts with some other notosuchians, including sphagesaurians (Pol et al. 2014; Martinelli et al. 2018), whereby the skull is mediolaterally broader, and the rami diverge from one another at a less acute angle. Immediately posterior to the symphysis, the splenial of *Antaeusuchus* is largely exposed in ventral view, and forms approximately 40% of the mediolateral width of the mandibular rami. A comparably broad splenial also characterizes *Uberabasuchus*, *Montealtosuchus*, and *Kinesuchus* (Carvalho et al. 2004; Carvalho et al. 2007; Filippi et al. 2018), whereas the splenial comprises only 25–30% of the rami transverse cross section in *Gasparinisuchus*, *Stolokrosuchus, Colhuehuapisuchus*, and *Barrosasuchus* (Larsson & Gado 2000; Martinelli et al. 2012; Coria et al. 2019; Lamanna et al. 2019).

In numerous peirosaurids, including *Antaeusuchus*, *Hamadasuchus*, *Uberabasuchus, Montealtosuchus*, *Pepesuchus*, *Stolokrosuchus*, and *Lomasuchus*, an anteroposteriorly elongate groove runs parallel to the dentary toothrow, just ventral to the dorsal margin of the lateral surface of the mandible (Gasparini et al. 1991; Larsson & Gado 2000; Carvalho et al. 2004; Carvalho et al. 2007; Larsson & Sues 2007; Campos et al. 2011). The lateral surface of the dentary is also typically sculpted with pits and/or grooves in peirosaurids; however, there is interspecific variation in the degree to which this sculpting continues over the entire surface. In *Antaeusuchus*, the lateral surface of the dentary is similar in its texture and sculpting both above and below the groove. In this regard, the morphology is similar to that of *Uberabasuchus*, *Barrosasuchus*, and *Kinesuchus* (Carvalho et al. 2004; Filippi et al. 2018; Coria et al. 2019). In *Hamadasuchus*, *Montealtosuchus*, *Pepesuchus*, and *Patagosuchus*, the region above the groove is smooth, differing markedly from the remainder of the highly sculpted lateral dentary surface (Carvalho et al. 2007; Larsson & Sues 2007; Campos et al. 2011; Lio et al. 2016). Although *Stolokrosuchus* shows no difference in bone surface texture above and below the anteroposterior groove (Larsson & Gado 2002), it differs from *Antaeusuchus* in that the majority of the lateral dentary surface is smooth and unornamented.

The degree of sculpting on the lateral surface of the dentary varies across notosuchian taxa, including within Peirosauridae. Whereas the surface is covered in deep pits in *Hamadasuchus*, *Uberabasuchus*, *Montealtosuchus*, *Patagosuchus*, *Bayomesasuchus*, and *Miadanasuchus* (Carvalho et al. 2004; 2007; Larsson & Sues 2007; Rasmusson Simons & Buckley 2009; Barrios et al. 2016; Lio et al. 2016), the surface of *Antaeusuchus* is considerably smoother and is textured with narrow, shallow grooves.

Unlike *Montealtosuchus*, *Gasparinisuchus*, *Bayomesasuchus*, Stolokrosuchus, *Patagosuchus*, *Pepesuchus*, and *Colhuehuapisuchus* (Buckley & Brochu 1999; Larsson & Gado 2000; Carvalho et al. 2007; Campos et al. 2011; Martinelli et al. 2012; Lamanna et al. 2019), the lateral surface of the dentary adjacent to the 5th–8th teeth forms a distinct anteroposteriorly elongate concavity in *Antaeusuchus*. This is otherwise known only in *Hamadasuchus* (Larsson & Sues 2007), although a shallower concavity also characterizes *Barrosasuchus* (Coria et al. 2019). This depression would likely have functioned to receive an enlarged premaxillary tooth during occlusion.

Although incompletely preserved, the mandibular fenestra in *Antaeusuchus* is almost certainly large and anteroposteriorly elongate, as is the case in *Hamadasuchus*, *Montealtosuchus*, and *Uberabasuchus* (Carvalho et al. 2004; Carvalho et al. 2007;

Ibrahim et al. 2020), but differing from *Barrosasuchus* in which the fenestra is greatly reduced (Coria et al. 2019). However, *Montealtosuchus* and *Uberabasuchus* differ from the dentaries of *Antaeusuchus* and *Hamadasuchus* (Ibrahim et al. 2020) in that the latter two have a small posterior process that extends ventral to the mandibular fenestra. This process is absent in *Montealtosuchus* and *Uberabasuchus*, in which the dentary-angular contact is entirely anterior to the mandibular fenestra instead (Carvalho et al. 2004; Carvalho et al. 2007). The dentary-surangular contact is similar in *Antaeusuchus*, *Hamadasuchus*, *Montealtosuchus*, and *Uberabasuchus*, with the surangular contacted by two posterior processes: the dorsal process intrudes entirely into the surangular, whereas the second process forms the ventral margin of the surangular and the anterodorsal margin of the mandibular fenestra (Carvalho et al. 2004; Carvalho et al. 2007; Larsson & Sues 2007). This feature cannot be assessed in other peirosaurid taxa, in which the relevant region of the mandible is not preserved.

When complete, each dentary of *Antaeusuchus* has 18 tooth positions. This count is common amongst peirosaurids, e.g. *Montealtosuchus*, *Gasparinisuchus*, *Kinesuchus, Pepesuchus,* and possibly *Barrosasuchus* (Carvalho et al. 2007; Campos et al. 2011; Martinelli et al. 2012; Filippi et al. 2018; Coria et al. 2019), but differs from *Stolokrosuchus*, in which there are at least 30 dentary alveoli (Larsson & Gado 2000). As in all peirosaurids (Pol et al. 2014), the first two dentary teeth of *Antaeusuchus* are strongly procumbent.

The dentary teeth posterior to the 5th alveolus are closely spaced and are mostly situated in a continuous groove in *Antaeusuchus*, *Hamadasuchus* (Larsson & Sues 2007), *Gasparinisuchus* (Martinelli et al. 2012), and *Barrosasuchus* (Coria et al. 2019). This differs from the condition in *Kinesuchus* (Filippi et al. 2018) and *Patagosuchus* (Lio et al. 2016), in which the teeth are separated by distinct septa that extend fully to the dorsal margin of the dentary.

5.2. Detailed comparisons with *Hamadasuchus rebouli*

Although several crocodyliform taxa, including notosuchians, have been identified from the Kem Kem Group (Ibrahim et al. 2020), only one peirosaurid species is

currently recognised from these beds: *Hamadasuchus rebouli* (Buffetaut 1994; Larsson & Sues 2007). Since the original description of the holotype dentary by Buffetaut (1994), several specimens have been referred to *Hamadasuchus* (Larsson & Sidor 1999; Rauhut & López-Arbarello 2006; Larsson & Sues 2007; Ibrahim et al. 2020). In our CTM (and previous iterations), the OTU of *Hamadasuchus* comprises the holotype mandibular fragment, MDEC001, plus the cranial material, ROM 52620, referred by Larsson & Sues (2007). Almost all characters that could be assessed for *Antaeusuchus* received the same score as *Hamadasuchus*, resulting in their consistent recovery as sister taxa in our phylogenetic analyses. The only differences in scores are present in characters 77 (scored as 2 and 1&2 for *Antaeusuchus* and *Hamadasuchus*, respectively), 155 (scored as 1 and 0&1 for *Antaeusuchus* and *Hamadasuchus*, respectively), and 393 (scored as 0 and 0&1 for *Antaeusuchus* and *Hamadasuchus*, respectively). The score of 1&2 for character 77 reflects the fragmentary nature of the *Hamadasuchus* type specimen and uncertainty of the precise length of the splenial contribution to the mandibular symphysis, rather than representing a polymorphism, whereas the score of 0&1 for characters 155 and 393 represents the definite presence of both states in this OTU. Given the similarity of the scores of both Kem Kem specimens, and that those provided for the mandible of *Hamadasuchus* are based only on the holotype specimen and not any referred material, we provide more detailed comparisons in the following section.
Antaeusuchus is compared to several anatomically overlapping specimens currently assigned to *Hamadasuchus*, namely the holotype dentary (MDEC001), several partial mandibles (ROM 49282, 52045, and 52047) described by Larsson & Sues (2007), a complete skull and lower jaws (BSPG 2005 I 83) figured by Rauhut & López-Arbarello (2006), and two mandibular symphyses (MNHN-MRS 3110 & NMC 41784) illustrated in Ibrahim et al. (2020). Despite being largely similar in overall morphology, *Antaeusuchus* differs in several respects from all specimens assigned to *Hamadasuchus* (Fig. 10).

Although only one dentary is preserved in the holotype (MDEC001), the angle of divergence of the mandibular rami can be inferred by measuring the angle of deviation of one dentary from the exposed symphyseal suture. Estimated mandibular rami divergence angles of ~20° for ROM 52047, ~25° for MDEC001 and ~30° for

ROM 49282, 52045, are much narrower than that of *Antaeusuchus* (43–44°). This suggests that *Hamadasuchus* had a slenderer rostrum than that of *Antaeusuchus*.

The surface texture of the *Antaeusuchus* dentary differs from all three specimens referred to *Hamadasuchus* in that it is not covered in deep pits and grooves. Instead, it is ornamented with relatively narrow and shallow grooves. *Antaeusuchus* also differs from these specimens in the dorsal region of the dentary lateral surface. In MDEC001, the area just ventral to the toothrow is smooth and lacks pits, differing from the remainder of the lateral surface (Buffetaut 1994). Instead, this dorsal region has a corrugated morphology, with broad, shallow dorsoventral grooves that do not correspond to the position of the dentary teeth (Fig. 10). A similar morphology characterizes ROM 49282, BSPG 2005 I 83, and NMC 41784, although it is not as prominent in those specimens. In *Antaeusuchus*, the degree of ornamentation is much the same across the lateral surface of the dentary and a fluted dorsal region is absent.

The apex of the second mandibular wave is marked by the position of the 13th tooth in *Antaeusuchus*, as well as ROM 49282, BSPG 2005 I 83, and probably MNHN-MRS 3110. By contrast, the tip of the second dentary wave is most likely marked by the 12th tooth in the holotype MDEC001, which is significantly larger than the 13th tooth (Buffetaut 1994).

Posterior to the 7th dentary tooth, the teeth of MDEC001 are strongly labiolingually compressed, and possess serrated carinae on their anterior and posterior cutting edges. A similar morphology is also present in *Antaeusuchus*, as well as MNHN-MRS 3110, but not in ROM 49282, in which the teeth are compressed only from the 10th tooth. The 5th to 9th teeth are damaged in BSPG 2005 I 83 and so it is unclear at which tooth position the compression commences. The posterior teeth in MDEC001 have a lanceolate shape (Buffetaut 1994) that is not present in *Antaeusuchus*, but which is most reminiscent of the morphology in MNHN-MRS 3110. In NHMUK PV R36829, teeth 11, 12, 14, and 15 are the only ones which are fully preserved; the anterior two of these have rounded crowns that do not form an angular tip. Although the 14th and 15th teeth of NHMUK PV R36829 are slightly pointed at their apices, they are not comparable to the almost triangular shape of those in the holotype MDEC001 (Buffetaut 1994). In NHMUK PV R36874, the 10th–14th teeth are slightly more angular in appearance, but their anterior and posterior margins are parallel for most of their length, converging to a point only at the crown apex (Fig. 10).

The only fully preserved tooth in the ROM 49282 dentary is the 13th one (Larsson & Sues 2007). Comparing the broad morphology, it is most similar to the teeth at a similar dentary position in *Antaeusuchus*, in that its apical margin is rounded. However, the tooth enamel of ROM 49282 is essentially smooth. By contrast, the enamel in *Antaeusuchus* is wrinkled into anastomosing apicobasal ridges (approximately 2–3 ridges per mm) (Fig. 10). Both morphologies differ from that of the teeth of MDEC001, in which the enamel is textured, but has an irregular, globular pattern towards its base, and anastomosing ridges towards the apex of the crown (Buffetaut 1994). ROM 49282 also displays a unique condition in which the tooth enamel is fluted with broad apicobasal ridges around its circumference.

The teeth of all specimens assigned to *Hamadasuchus*, as well as those of *Antaeusuchus*, have very finely serrated carinae on their anterior and posterior cutting edges, with individual serrations spaced at approximately 3–5 per mm. Although most prominent in MDEC001, vertical fluting on the anterior and posterior regions of the crowns is visible in the posterior dentary teeth of all the specimens discussed in this section.

Finally, *Antaeusuchus* is significantly larger than all *Hamadasuchus* specimens, such that it is almost double the size of MDEC001, ROM 49282, and BSPG 2005 I 83. Although the size of the specimen alone should not be a reason to erect a new species (e.g. Griffin et al. 2021), we believe it to be a valid morphological difference as part of a large, unique combination of features. Furthermore, *Hamadasuchus* is already known from an ontogenetic series, including specimens considered 'adult' (Larsson & Sues 2007); as such, it is difficult to reconcile the numerous anatomical differences merely as a result of *Antaeusuchus* being an even older individual of Hamadasuchus).

6. Discussion

6.1. Taxonomic affinities of NHMUK PV R36829 and R36874

In all of our analyses, the NHMUK PV R36829 + R36874 OTU (i.e. *Antaeusuchus*) is recovered as the sister taxon of *Hamadasuchus*. This relationship is supported by a single unambiguous synapomorphy (a distinct concavity adjacent to the 5th to 10th dentary teeth for the reception of the enlarged maxillary tooth), and one ambiguous synapomorphy (a short distance between the fourth and fifth mandibular teeth). In total, 34 characters in our CTM can be scored for both the *Hamadasuchus* OTU and *Antaeusuchus*, with only three of these receiving different scores (characters 77, 155, 393). The first of these describes the contribution of the splenial to the mandibular symphysis in dorsal view and only partially differs: whereas *Hamadasuchus* is polymorphic (1/2), *Antaeusuchus* is characterised solely by state 2. Nonetheless, both taxa exhibit splenials that are anteroposteriorly more elongate than other peirosaurid taxa, with the exception of *Bayomesasuchus*. The second character in which scores differ describes the sculpting of the dentary region below the toothrow. Again, the difference is only partial, with *Hamadasuchus* polymorphic (0/1) and *Antaeusuchus* possessing the derived condition (i.e. state 1). The elevated sections of this region in the *Hamadasuchus* holotype are characterized by a pitted surface, whereas the depressed areas are smooth. Finally, the third differing character describes the rugose texture of the tooth enamel, for which *Hamadasuchus* is scored as 0 & 1, whereas *Antaeusuchus* is characterized by the plesiomorphic condition (i.e. state 0). The tooth enamel in the *Hamadasuchus* holotype is more globular towards the middle and basal regions of the tooth crown, becoming more linear and ridgelike towards its apex. In *Antaeusuchus*, elongate, anastomosing ridges run from the apex to the base of the enamel.

Although there are only three differences captured in our CTM, our detailed comparisons demonstrate numerous additional features that indicate that NHMUK PV R36829 and R3687 are not referrable to *Hamadasuchus rebouli*. NHMUK PV R36829 and R36874 differ from *Hamadasuchus rebouli* in their large size as well as the possession of a unique combination of features: (1) a high angle of divergence between mandibular rami; (2) a rugose dentary tooth enamel shaped into anastomosing apicobasal ridges; (3) the largest dentary tooth in the second wave is located in alveolus 13; (4) sub-triangular tooth crowns (in lateral view) with a gently curved apex; (5) minor labiolingual compression of the posterior dentary teeth; (6) a lack of fluting on the dorsal region of the lateral dentary surface; (7) a relatively unornamented surface texture of the dentary adorned with narrow, shallow ridges rather than deep pits or grooves; and (8) dentary teeth more widely spaced at their base.

As such, it seems clear that NHMUK PV R36829 + R3687 represents a second peirosaurid in the Kem Kem Group, and thus supports our erection of *Antaeusuchus taouzensis* n. gen. n. sp. In addition, material currently referred to *Hamadasuchus* also differs from the type specimen (MDEC001), as well as *Antaeusuchus*. In particular, the partial mandible, ROM 49282, described by Larsson & Sues (2007), differs from both taxa in several features, including: (1) distinctive apicobasal fluting on the 13th tooth; (2) a highly elongate contribution of the splenial to the mandibular fenestra; (3) a mandibular rami divergence of approximately 30°; and (4) possession of relatively smooth tooth enamel. The unique combination of characters in each of MDEC001, ROM 49282, and NHMUK PV R36829 + R36874, therefore suggests the presence of at least three separate, albeit closely related, peirosaurid species from the Kem Kem Group. Although we erect a new name for NHMUK PV R36829 + R3687, we refrain from naming a new taxon for ROM 49282 pending the description and assessment of additional materials currently assigned to *Hamadasuchus rebouli* (namely BSPG 2005 I 83 and additional ROM specimens).

6.2. Implications for peirosaurid relationships

Peirosauridae was erected by Gasparini (1982) to accommodate *Peirosaurus torminni* (Price 1955) from the late Maastrichtian Marília Formation of Brazil. This family was subsequently expanded by Gasparini et al. (1991) to include *Lomasuchus* from the late Turonian–early Coniacian of Argentina. Geroto & Bertini (2019 p. 328) provided a phylogenetic definition for Peirosauridae as “the least inclusive clade containing *P. tormini* [sic] Price, 1955, *Itasuchus jesuinoi* Price, 1955, and *Stolokrosuchus lapparenti* Larsson & Gado, 2000, but not including *Notosuchus terrestris* Woodward, 1896, *Baurusuchus pachecoi* Price, 1945, *Sphagesaurus huenei* Price, 1950, *Araripesuchus gomesii* Price, 1959, *Sebecus icaeorhinus* Simpson, 1937, *Mariliasuchus amarali* Carvalho & Bertini, 1999, and *Crocodylus niloticus* Laurent, 1768”. Although a phylogenetic definition based on two well-nested and stable species-level specifiers would be preferable (e.g. Sereno 1998, 2005; Lee 2005), we follow the definition of Geroto & Bertini (2019) here, pending a detailed re-evaluation of the interrelationships of this part of the notosuchian tree.

Following Geroto & Bertini’s (2019) definition, Peirosauridae comprises a taxonomically rich array of crocodyliforms from across the Cretaceous of South America, Africa, and Madagascar (e.g. Price 1955; Carvalho et al. 2004; Carvalho et al. 2007; Larsson & Sues 2007; Leardi & Pol 2009; Sertich O’Connor 2014; Campos et al. 2011; Martinelli et al. 2012; Lio et al. 2016; Barrios et al. 2016; Filippi et al. 2018; Coria et al. 2019). However, there is little consensus regarding the position of Peirosauridae. A number of analyses have recovered Peirosauridae within Notosuchia, as the sister taxon to Mahajangasuchidae (i.e. *Kaprosuchus* + *Mahajangasuchus*), with these lineages forming a clade with Uruguaysuchidae that is the sister taxon to all other notosuchians (e.g. Pol et al. 2014; Sertich & O’Connor 2014; Coria et al. 2019). Others have recovered Peirosauridae as part of Sebecia, forming a clade with Sebecidae (e.g. Larsson & Sues 2007; Sereno & Larsson 2009), and sometimes also including Mahajangasuchidae (e.g. Geroto & Bertini 2019; Ruiz et al. 2021). Whereas some of these analyses place Sebecia as the sister taxon to all other notosuchians (e.g. Geroto & Bertini 2019; Ruiz et al. 2021), others recover Sebecia within Neosuchia (e.g. Larsson & Sues 2007; Sereno & Larsson 2009). Peirosauridae has also been recovered as an early diverging neosuchian clade in some studies (e.g. Pol & Apesteguía 2005; Gasparini 2006; Turner & Buckley 2008; Leardi & Pol 2009).

In several recent phylogenetic analyses (e.g. Pol et al. 2014; Geroto & Bertini 2019; Coria et al. 2019), *Hamadasuchus* has been recovered as the sister taxon to a group of exclusively South American Cretaceous peirosaurids (comprising various combinations of *Montealtosuchus*, *Uberabasuchus*, *Lomasuchus*, *Gasparinisuchus*, and *Barcinosuchus*). Similarly, Barrios et al. (2016) recovered *Hamadasuchus* in a polytomy with most of these taxa, along with *Bayomesasuchus* from the Turonian (Late Cretaceous) of Argentina. Sertich & O’Connor (2014) recovered

Hamadasuchus in an unresolved trichotomy with *Rukwasuchus* and *Stolokrosuchus*, forming a clade of African peirosaurids.

Here, under both equal and extended implied weighting schemes, the position of Peirosauridae is consistent with the results of Pol et al. (2014) and subsequent studies based on this dataset (e.g. Leardi et at 2015; Fiorelli et al. 2016; Iori et al. 2018; Leardi et al. 2018; Martinelli et al. 2018; Coria et al. 2019). Under its broadened taxonomic content, following the phylogenetic definition of Geroto & Bertini (2019), Peirosauridae includes Mahajangasuchidae in our EIW analyses (Fig. 8). This occurs because *Stolokrosuchus* is recovered as more closely related to Mahajangasuchidae than to other peirosaurids in the EIW topology. Our equal weights analysis recovers *Stolokrosuchus* as the most 'basal' member of Peirosauridae instead, with Mahajangasuchidae outside of this clade (Fig. 7). In both cases, our peirosaurid + mahajangasuchid grouping is the sister taxon of Uruguaysuchidae, with this clade the sister taxon to all other notosuchians.

In our strict consensus trees, the clade comprising *Antaeusuchus* and *Hamadasuchus* is most closely related to *Bayomesasuchus*. This grouping is the sister taxon to other peirosaurids (excluding *Stolokrosuchus* and Mahajangasuchidae) (Fig. 7). The remaining South American taxa are grouped in a polytomy with the African taxon *Rukwasuchus*, with this recovered as the sister taxon of a clade comprising the Malagasy taxon *Miadanasuchus* and the Argentinean species *Barrosasuchus*. The aforementioned polytomy can be resolved via *a posteriori* pruning of *Gasparinisuchus*, resulting in *Rukwasuchus* as the sister taxon of (*Uberabasuchus* + (*Lomasuchus* + *Montealtosuchus*)).

The fact that our analyses produce topologies more consistent with those derived from the data matrix of Pol et al. (2014) than alternative matrices is not surprising given that this is the underlying dataset for our study. As such, the interrelationships of Peirosauridae within Metasuchia will require further testing, ideally merging characters and taxa from across studies with competing hypotheses. However, the recovery of Peirosauridae as an early diverging metasuchian clade outside of the ziphosuchian notosuchian radiation is consistent across analyses, regardless of the underlying dataset.

One of the notable results of our analyses is the placement of *Miadanasuchus* within Peirosauridae, which was independently recovered in this clade by Geroto and Bertini (2019). This species from the Maastrichtian of Madagascar was originally described as *Trematochampsa oblita* (Buffetaut & Taquet 1979), before being assigned to a new genus by Rasmusson Simons & Buckley (2009). The type species of *Trematochampsa*, *T. taqueti*, is based on fragmentary remains from the Coniacian–Santonian In Beceten Formation of Niger (Buffetaut 1974; 1976a, b), for which the family Trematochampsidae was also erected (Buffetaut 1974). Several additional crocodyliform taxa have been assigned to Trematochampsidae (e.g. *Amargasuchus minor* [Chiappe 1988], *Barreirosuchus franciscoi* [Iori et al. 2012], *Hamadasuchus*, *Itasuchus*, *Mahajangasuchus*), spanning the Cretaceous of Africa, Europe, Madagascar, and South America, with most of these known from fragmentary remains (see review in Meunier & Larsson 2018). Buffetaut (1988, 1989) also included *Peirosaurus torminni* as a member of Trematochampsidae, which would therefore have priority over Peirosauridae. However, multiple authors have questioned or rejected the monophyly of Trematochampsidae, which appears to have become a wastebasket taxon (e.g. Gasparini et al. 1991; Ortega et al. 1996; Buckley & Brochu 1999; Turner & Calvo 2005; Larsson & Sues 2007; Rasmusson Simons et al. 2009; Meunier & Larsson 2018). Furthermore, Meunier & Larsson (2018) demonstrated that *Trematochampsa taqueti* is a nomen dubium, based on non-diagnostic, chimeric remains, with some of these displaying peirosaurid affinities. Our analyses provide further evidence that most, if not all, Cretaceous taxa previously assigned to Trematochampsidae belong to Peirosauridae, and confirm the presence of this latter clade in the Maastrichtian of Madagascar. Given the lack of diagnostic features in the type remains of '*Trematochampsa taqueti*' and the absence of a formal definition for 'Trematochampsidae', coupled with its approximate synonymy with the formally defined and widely used Peirosauridae, we support the proposal of Meunier & Larsson (2018) to abandon the name *Trematochampsa* and its coordinated rank taxa.

6.3. Gondwanan notosuchian diversity outside of South America

During the Mesozoic, notosuchians (*sensu* Pol et al. 2014) were the most diverse clade of Gondwanan crocodyliforms (Turner & Sertich 2010), although this high species richness varied through both time and space (Pol & Leardi 2015; De Celis et al. 2020). At least 70% of known notosuchian diversity is found on Gondwanan continents (Pol & Leardi 2015), with a small number of species recognised from Europe (Kuhn 1968; Antunes 1975; Rossman et al. 2000; Company et al. 2005; Dalla Vecchia & Cau 2011; Rabi & Sebök 2015; Martin 2016; Sellés et al. 2020) and Asia (Wu et al. 1995; Wu & Sues 1996). Though most numerous in South America, Gondwanan notosuchian occurrences are also known from mainland Africa, Madagascar, India, and Pakistan, as well as possibly the Arabian Peninsula. Currently no notosuchians are known from Australasia or Antarctica, although it remains unclear whether this represents a genuine absence, perhaps pertaining to a high-latitude environmental dispersal barrier, or it reflects a sampling bias (e.g. see Poropat et al. 2021). Here, we provide a critical reappraisal of the Gondwanan record of notosuchians outside of South America.

6.3.1. Jurassic

The stratigraphically oldest known notosuchian is *Razanandrongobe sakalavae* (Maganuco et al. 2006) from the Bathonian (Middle Jurassic) Isalo IIIb Formation in northwestern Madagascar. Originally named as an archosaur of uncertain affinities on the basis of teeth and a fragmentary maxilla (Maganuco et al. 2006), several more skull fragments, including a right premaxilla and an incomplete left dentary, have since been assigned to the taxon, enabling its identification as a large-bodied notosuchian (Dal Sasso et al. 2017). Considering that the next stratigraphically oldest notosuchians are from the Aptian (late Early Cretaceous), resulting in a ~40 million-year ghost lineage, *Razanandrongobe* is a stratigraphic outlier and its affinities might seem doubtful. However, based on the sister taxon relationship of Notosuchia and Neosuchia, with the latter clade known from the Early Jurassic (Tykoski et al., 2002), *Razanandrongobe* instead partly fills the inferred ghost lineage of notosuchians, which otherwise would extend back approximately 65–75 million years (Dal Sasso et al. 2017; Mannion et al. 2019). In the small number of phylogenetic analyses to have incorporated it (Dal Sasso et al. 2017; Sellés et al. 2020), including ours, *Razanandrongobe* is recovered in a position close to the ‘base’ of Sebecosuchia. This nested position within Notosuchia for such a stratigraphically early species necessitates the extension of multiple unsampled lineages back into the Jurassic (Fig. 11). As such, the phylogenetic affinities of *Razanandrongobe* require further evaluation to test whether this poor stratigraphic fit is genuine.

6.3.2. Early Cretaceous

In southeastern Africa, the Aptian Dinosaur Beds of northern Malawi (Fig. 12) have yielded numerous remains of *Malawisuchus mwakasyungutiensis*, preserving most of the skeleton (Gomani 1997). Recognised in part for its unusual mammal-like multicuspid teeth, some analyses have placed *Malawisuchus* in a nested position within Sphagesauria (e.g. Gomani 1997; Sereno & Larsson 2009; O'Connor et al. 2010). However, most recent analyses typically recover *Malawisuchus* as an early diverging ziphosuchian, with spaghesaurians currently restricted to South America (e.g. Pol et al. 2014; Ruiz et al. 2021; this study). Unlike the topology of Martin and Lapparent de Broin (2016), *Malawisuchus* is not recovered within Candidodontidae in our analyses (Fig. 7).

The Aptian–Albian Elrhaz Formation exposed at Gadoufaoua, central Niger (Fig. 12), has yielded the remains of three morphologically diverse notosuchian species (*Anatosuchus minor*, *Araripesuchus wegeneri*, and *Stolokrosuchus lapparenti*). The bizarre, 'duck-billed' *Anatosuchus* is known from several individuals, including a skull and associated partial postcranial skeleton, as well as a skull of a juvenile animal (Sereno et al. 2003; Sereno & Larsson 2009). *Anatosuchus* has often been recovered as a member of Uruguaysuchidae (e.g. Sereno & Larsson 2009; Pol et al. 2014); some analyses have placed it outside of this clade, although these tend to recover it as a 'basal' member of Notosuchia. The small and gracile species *Araripesuchus wegeneri* was erected from the anterior region of an articulated upper and lower snout (Buffetaut & Taquet 1979). Multiple remains have since been assigned to the taxon, including a block preserving at least five separate individuals, three of which are essentially complete, partially articulated skeletons (Sereno & Larsson 2009). In our analyses, *Araripesuchus wegeneri* and *Anatosuchus* are recovered as sister taxa within Uruguaysuchidae, further questioning the monophyly of *Araripesuchus* (see Sereno & Larsson 2009: p. 31). The longirostrine-snouted

Stolokrosuchus is known from an almost complete skull (Larsson & Gado 2000). Originally referred to Peirosauridae (Larsson & Gado 2000; see also Larsson & Sues 2007; Sereno & Larsson 2009; Geroto & Bertini 2019), subsequent analyses have shown the position of *Stolokrosuchus* to be highly labile, such that it has also been placed as an early diverging member of both Notosuchia (e.g. Dal Sasso et al. 2017) and Neosuchia (e.g. Turner & Sertich 2010; Andrade et al. 2011). Following the definition of Peirosauridae provided by Geroto & Bertini (2019), our analyses recover *Stolokrosuchus* as the earliest diverging member of this clade, which is consistent with previous analyses that have continued to place it close to the 'base' of Metasuchia.

Several isolated teeth from the Aptian–Albian Koum Formation of northeastern Cameroon (Fig. 12) were reported by Flynn et al. (1988) and Congleton (1990), who recognised their possible affinities with *Araripesuchus,* especially *A*. *wegeneri*. Kellner (1994 p. 618) questioned this referral, suggesting that these strongly serrated, laterally compressed, leaf-shaped teeth differed from those in the posterior toothrow of *Araripesuchus gomesii*, which he described as "weakly serrated" and "less leaf-shaped". It is unclear why Kellner (1994) limited comparisons to *Araripesuchus gomesii*; nonetheless, the description of additional specimens of *Araripesuchus wegeneri* from Niger (Sereno & Larsson 2009), along with other species of this genus (e.g. Pol & Apesteguia 2005; Ortega et al. 2000; Turner 2006; Sereno & Larsson 2009; Dumont et al. 2020; Ibrahim et al. 2020), allows for more thorough comparisons with the teeth from Cameroon. Given that none of the South American *Araripesuchus* species, nor *Araripesuchus tsangatsangana*, have denticles, the labiolingually compressed, lanceolate shape of these teeth, with serrated carinae along their posteriormost and anteriormost margins, is supportive of a referral to either *Araripesuchus wegeneri* or *Araripesuchus rattoides* (the latter comparison is based on referred material, BSPG 2008 I 41, rather than the holotype specimen [Ibrahim et al. 2020]). However, because of variation in crown morphology along the toothrow in all species of *Araripesuchus*, and given that teeth in the middle-to-posterior toothrow are either absent or poorly preserved in *Araripesuchus rattoides*, it is not currently possible to provide a species-level referral.

The Albian Aïn el Guettar Formation in southern Tunisia (Fig. 12) has yielded numerous crocodyliform remains, including teeth assigned to *Araripesuchus wegeneri*, *Araripesuchus* sp., and aff. *Hamadasuchus* sp. (Le Loeuff et al. 2000; Cuny et al. 2010; Fanti et al. 2012). The specimens assigned to *Araripesuchus* (Cuny et al. 2010, fig. 4.7; Fanti et al. 2012, fig. 12U–X) are labiolingually compressed and triangular, with serrated carinae and relatively smooth enamel. Based on the slightly dorsoventrally constricted lanceolate shape of the teeth in lateral view, it is likely that they come from the middle region of the toothrow. All of these features support their referral to *Araripesuchus*, widening the spatial distribution of the genus to north-central Africa. Although serrated tooth margins are known to be present in *Araripesuchus wegeneri* and a referred specimen of *Araripesuchus rattoides* (Ibrahim et al. 2020), we refrain from assigning these specimens beyond generic level as was “cautiously” proposed by Cuny et al. (2010: p. 625) for the same reasons outlined in the preceding paragraph. A single tooth referred to aff. *Hamadasuchus* sp. is labiolingually compressed and approximately triangular in lateral view, with “remnants of clear serration” (Cuny et al. 2010: fig. 4.8, p. 625). Although the more extreme labiolingual compression towards the anterior and posterior margins of the tooth is reminiscent of *Hamadasuchus*, the apparent lack of rugose enamel is unusual given its presence in all teeth associated with the holotype specimen of *Hamadasuchus*. The only other named crocodyliforms from the Early Cretaceous of Africa to possess serrated carinae are *Araripesuchus wegeneri* and referred material of *Araripesuchus rattoides*, both of which possess dentition more similar in size to the tooth reported in Cuny et al. (2010). However, given that the Tunisian specimen is clearly well-worn and is not dissimilar in broad morphology from either *Hamadasuchus* or *Araripesuchus*, we regard this specimen as an indeterminate notosuchian. Re-evaluation and full description of specimens referred to *Hamadasuchus* that have teeth with smooth enamel (e.g. BSPG 2005 I 83) might enable referral to a particular genus.

6.3.3. Late Cretaceous

In northwestern Africa, the Cenomanian Kem Kem Group of Morocco has yielded three previously named notosuchian species (*Araripesuchus rattoides*, *Hamadasuchus rebouli*, *Lavocatchampsa sigogneaurussellae*), in addition to the new species, *Antaeusuchus taouzensis*, described herein (Fig. 12). *Araripesuchus rattoides* is known from the holotypic partial dentary, as well as several referred dentary fragments (Sereno & Larsson 2009; Ibrahim et al 2020). It differs from *A. wegeneri* in several features, including its possession of a narrower and deeper snout, highly procumbent teeth, and potentially a greater number of teeth. Though not included in our phylogenetic analyses because of its fragmentary nature, *Araripesuchus rattoides* was recovered by Sereno & Larsson (2009) in a polytomy with three *Araripesuchus* species (*A*. *gomesii* and *A*. *patagonicus* from South America, and *A*. *tsangatsangana* from Madagascar), with this the sister group to a clade comprising the remaining uruguaysuchids (including *A*. *wegeneri*). *Lavocatchampsa sigogneaurussellae* was erected based on a small anterior snout region, which displays unusually heterodont teeth that are convergent with those of mammals (Martin & Lapparent de Broin 2016). Using the data matrix of Pol et al. (2014), Martin & Lapparent de Broin (2016) recovered *Lavocatchampsa* as a 'basal' ziphosuchian within Candidodontidae, a small clade otherwise known only from the Cretaceous of South America (Carvalho et al. 2004, Montefeltro et al. 2009).

As discussed in detail above, the peirosaurid *Hamadasuchus rebouli* was erected based on a single dentary fragment from the Kem Kem Group (Buffetaut 1994), but numerous cranial and mandibular remains have since been referred to this species from this stratigraphic unit (Larsson & Sues 2007; Ibrahim et al., 2020), including a skull table previously assigned to *Libycosuchus* sp. (Buffetaut 1976a, b). Although we do not disagree with referral of these remains to Peirosauridae, it is currently unclear if all of them are attributable to *Hamadasuchus rebouli*. Isolated teeth described by Larsson & Sidor (1999) were also referred to this species. One tooth, inferred to be from the middle of the toothrow (Larsson & Sidor 1999: fig. 1B), is very reminiscent of those preserved in the holotype of *Hamadasuchus rebouli*, based on its triangular shape in lateral view, its labiolingual compression, and the density of serrations. A second tooth shares the globular texture of the enamel towards the base of the crown, which transitions into more linear ridges towards the apex (Larsson & Sidor 1999: fig. 1C), which is again consistent with a referral to *Hamadasuchus rebouli*. However, a conical, retro-curved caniniform tooth shows distinctive fluting (Larsson & Sidor 1999: fig. 1A), which is absent from the holotypic specimen, but present in some of the specimens previously referred to the species

(ROM 49282 and 52620, BSPG 2005 I 83, and possibly NMC 41892 [Ibrahim et al. 2020]).

Larsson & Sidor (1999) described several additional crocodyliform teeth from the Kem Kem Group that have been suggested to represent additional notosuchian taxa (Ibrahim et al., 2020). Material referred to “Indet. crocodyliform 1” (Larsson & Sidor 1999 p. 398) is represented by two small, subtriangular crowns (SGM-Rep 4, SGM-Rep 5) in labiolingual view, each with three approximately parallel rows of relatively large cuspids that terminate in angular apices towards the anteroposterior midpoint of the tooth (Larsson & Sidor 1999, fig. 2 A–D]). On one of these teeth, a large planar wear facet bisects the rows of cusps on the buccal surface. A third tooth (SGM-Rep 6) referred to by Larsson & Sidor (1999 p. 399) as “Indet. crocodyliform 2” is more elliptical in dorsal view, and has a central, anteroposterior row of cuspids surrounded labially and lingually by two less dorsally raised rows of smaller cusps (Larsson & Sidor 1999, fig. 3). The outer two rows merge at the anteriormost and posteriormost margins of the tooth, forming a cingulum. Unlike the other multicuspid teeth, the rows of cusps in this third tooth are much closer to horizontal in their orientation, forming a less acute apex. Furthermore, the cusps of the central row are relatively larger in comparison to the tooth size and are fewer in number, forming an apex either mesially or distally (depending on tooth orientation in the jaw) rather than centrally. *Lavocatchampsa sigogneaurussellae* is the only crocodyliform from the Kem Kem Group that exhibits a multicuspid tooth morphology (Martin & Lapparent de Broin 2016); however, we agree with the observations of Ibrahim et al. (2020) that both morphologies are distinct from this taxon. We do note that the less acute tooth described as ‘Indet. crocodyliform 2’ is most similar in its morphology to the taxon described by Martin & de Lapparent de Broin (2016) based on its elliptical shape in occlusal view, and the presence of a cingulum bearing multiple cuspids that surround a central carina formed of a relatively small number (four) of cusps.

In summary, the Kem Kem Group seems to record the presence of at least seven potential notosuchians, represented by three peirosaurids (*Hamadasuchus rebouli*, *Antaeusuchus taouzensis*, and at least one unnamed species), *Araripesuchus rattoides*, and three species with multicuspid teeth (*Lavocatchampsa sigogneaurussellae* and two unnamed species). However, given poor stratigraphic constraints for many of these species, it remains possible that these were not all contemporaneous.

The Cenomanian Bahariya Formation of north-central Egypt has yielded just a single notosuchian species (Fig. 12), with *Libycosuchus brevirostris* represented by a complete skull and lower jaws, as well as several isolated vertebrae (Stromer 1914; Buffetaut 1976). *Libycosuchus* has an anteroposteriorly short skull and is fairly consistently recovered as an early diverging ziphosuchian (e.g. Sertich & O'Connor 2014; Pol et al. 2014; Martin & Lapparent de Broin 2016; Geroto & Bertini 2019), as is also the case in our analyses.

The large-bodied species *Kaprosuchus saharicus* is the only published notosuchian currently known from the Cenomanian Echkar Formation of northwestern Niger (Sereno & Larsson 2009) (Fig. 12). This species is based on an essentially complete skull and mandible and has been informally referred to as the "boar croc" due to its enlarged caniniform teeth. *Kaprosuchus* has been consistently recovered as the sister taxon to *Mahajangasuchus insignis* from the Maastrichtian of Madagascar (see below), and is thus a member of Mahajangasuchidae (e.g. Sereno & Larsson, 2009; Pol et al. 2014, Geroto & Bertini 2019; this analysis) (Fig. 6). Sereno & Pol (2019) reported an undescribed partial skeleton from the Echkar Formation that appears to be most closely related to the Maastrichtian Malagasy species, *Araripesuchus tsangatsangana*.

In the southeastern region of Africa, two notosuchian taxa are known from the Namba Member of the Galula Formation of western Tanzania (Fig. 12). Originally thought to be Aptian–Cenomanian (O'Connor et al. 2010; Roberts et al. 2010), new dates indicate either a Cenomanian–Santonian or more likely a Campanian age for this stratigraphic unit (Widlansky et al. 2018). Represented by the posterior region of the skull, the medium-to large-bodied *Rukwasuchus yajabalijekundu* was recovered by Sertich & O'Connor (2014) as a peirosaurid. It had not been included in a subsequent phylogenetic analysis prior to ours, which provides further support for a peirosaurid placement (Figs 6 & 7). Known from an essentially complete skeleton, *Pakasuchus kapilimai* is one of several small notosuchians with multicuspid teeth from the Cretaceous of Gondwana that appears to fill an ecological niche that would later be occupied by mammals (O’Connor et al. 2010; Sertich & O’Connor 2014). As is the case in several previous studies (e.g. O’Connor et al. 2010; Pol et al. 2014; Sertich & O’Connor 2014; Martin and Lapparent de Broin 2016), our analyses recover *Pakasuchus* as an early diverging member of Ziphosuchia, closely related to *Malawisuchus* (Fig. 7).

The Coniacian–Santonian In Beceten Formation of Niger (Fig. 12) has yielded the type material (an incomplete lacrimal) of *Trematochampsa taqueti* (Buffetaut 1974). As discussed in Section 6.2, Meunier & Larsson (2018) demonstrated that *Trematochampsa taqueti* is a nomen dubium, and suggested that isolated bones and teeth informally referred to the taxon represent at least three different small-medium sized crocodyliform species. They noted that many of these specimens show potential affinities to peirosaurids (especially *Hamadasuchus*), uruguaysuchids (especially *Araripesuchus wegeneri* and *Anatosuchus minor*), ziphosuchians, and/or neosuchians, which we follow here.

The Wadi Milk Formation of northern Sudan (Fig. 12) has traditionally been regarded as Cenomanian (e.g. Buffetaut et al. 1990; Rage & Werner 1999), but more recent work indicates that it should be assigned to the Campanian–Maastrichtian (Owusu Agyemang et al. 2019). An undescribed peirosaurid has been briefly reported, consisting of partial mandibles and part of the skull roof, and which is notable for its large size (Evans et al. 2014).

Putative notosuchian remains from the Maastrichtian Dukamaje Formation in western Niger have been mentioned in the literature, but not described. Moody and Sutcliffe (1991: table 2) listed the presence of *Trematochampsa taqueti* and *Libycosuchus* sp. in this formation, but they provided no further details. We suspect that that this was a mistake, with the In Beceten faunal list accidentally incorporated, but this cannot currently be confirmed.

A mandibular fragment preserving the middle portion of a right dentary could potentially represent the only occurrence of a notosuchian from the Arabian Peninsula (Buscalioni et al. 2004). Buscalioni et al. (2004) tentatively assigned the specimen from the Maastrichtian Al-Khod Conglomerate Formation of northern

Oman as cf. *Trematochampsa* indet. and noted similarities with *Miadanosuchus* (‘*Trematochampsa*’) *oblita* from the Maastrichtian of Madagascar. These similarities included the presence of an enlarged tooth in the 10th alveolus, and a morphology indicative of a long and wide mandibular symphysis (despite this region not being preserved). Our analyses recover *Miadanosuchus* within Peirosauridae, a clade characterised by two distinct waves on the dorsal margin of the dentary. The very straight, only slightly inclined dorsal edge of the dentary in the Oman specimen is therefore not indicative of a specimen belonging to this clade, especially as the presence of an enlarged tooth would be expected to be accompanied by the dorsoventral expansion of the dentary. Furthermore, the dentary of *Miadanosuchus* maintains its mediolateral width posterior to the enlarged tenth tooth for at least the distance of two alveoli. The Oman specimen shows gradual, but distinct narrowing posterior to the enlarged tooth. Given the highly fragmentary nature of the specimen, and the few preserved anatomical features of phylogenetic relevance, we suggest that the material can only be assigned to an indeterminate crocodyliform.

The Maastrichtian Maevarano Formation that outcrops in northwestern Madagascar has thus far yielded four notosuchian taxa (Fig. 12). The bizarre “pug-nosed” *Simosuchus clarki* is represented by multiple individuals preserving most of the skeleton (Buckley et al. 2000; Georgi & Krause 2010; Hill 2010; Kley et al. 2010; Sertich & Groenke 2010). Most analyses recover *Simosuchus* as an early diverging ziphosuchian (e.g. Turner & Sertich 2010; Pol & Powell 2011; Pol et al. 2014; Geroto & Bertini 2019; this study). The large-bodied *Mahajangasuchus insignis* is known from an almost complete skull and much of the postcranial skeleton (Buckley & Brochu 1999; Turner & Buckley 2008). Initially thought to have affinities with ‘Trematochampsidae’, the taxon has since been recovered as a peirosaurid (e.g. Turner & Calvo 2005), or just outside of this clade (e.g. Pol et al. 2014). It is now the clade specifier for Mahajangasuchidae (Sereno & Larsson 2009), with our analyses providing evidence for a position both within (EIW) and just outside (equal weighting) of Peirosauridae. *Araripesuchus tsangatsangana* is represented by a nearly complete skull, as well as a second individual preserving a nearly complete skeleton (Turner 2006). *Miadanasuchus* (‘*Trematochampsa*’) *oblita* is known from partial dentaries, part of the skull roof, and a vertebra (Buffetaut & Taquet 1979;

Rasmusson Simons & Buckley 2009), and it appears to represent a peirosaurid (Geroto & Bertini (2019; this study).

Pabwehshi pakistanensis, recovered from the Maastrichtian Pab Formation of southwestern Pakistan (Fig. 12), is known from fragmentary specimens, which preserve the anterior region of the snout and the associated section of the mandible of two individuals (Wilson et al. 2001). The limited remains of *Pabwehshi* mean that its phylogenetic position is labile (Pol et al. 2014), although most authors have supported a close relationship with Baurusuchidae (e.g. Wilson et al. 2001; Turner & Calvo 2005; Nascimento & Hussam 2010; Turner & Sertich 2010; Pol & Powell 2011; Carvalho et al. 2011; Dal Sasso et al. 2017; Geroto & Bertini 2019; Coria et al. 2019), which is otherwise known only from South America (e.g. Montefeltro et al. 2020; Darlim et al. 2021). By contrast, Larsson & Sues (2007) recovered *Pabwehshi* as the most 'basal' member of Sebecia, i.e. as the sister taxon to a clade comprising Peirosauridae and Sebecidae. *Pabwehshi pakistanensis* was excluded from our analyses because of its labile position, but more complete material will ultimately be needed to robustly resolve its phylogenetic position.

An isolated tooth from the Maastrichtian Kallamedu Formation of southern India (Fig. 12) was described by Prasad et at. (2013), who identified it as cf. *Simosuchus* sp. Based on comparisons with *Simosuchus clarki*, Prasad et al. (2013) suggested that the tooth is probably from the posterior region of the dentary. We fully agree with the evaluation and assignment of this specimen.

6.3.4. Paleogene

Buffetaut (1989) erected *Eremosuchus elkoholicus* from the El Kohol Formation of southwest Algeria (Fig. 12), which is dated to the Ypresian, early Eocene (Coster et al. 2012). This species is known from a partial mandible, teeth, vertebrae, and a fibula. When initially described, *Eremosuchus* was placed in the family Trematochampsidae (Buffetaut 1989), but more recently it has been included in Sebecosuchia by several authors (e.g. Gasparini et al. 1991; Ortega et al. 1996; Turner & Calvo 2005). However, it has not been included in most phylogenetic analyses, presumably because of its incomplete nature, and has largely been neglected in treatments of crocodyliform evolutionary history. A detailed redescription and analysis of the phylogenetic relationships of *Eremosuchus* is needed to establish its systematic and biogeographic affinities.

Finally, the late Eocene Birket Qarun Formation (Seiffert 2006) in northeastern Egypt (Fig. 12) has yielded a fragmentary right dentary with ziphodont dentition (Stefanic et al. 2020). Though not assigned to a genus, the specimen clearly has sebecosuchian affinities and extends the temporal range of Notosuchia in Africa (Stefanic et al. 2020).

6.3.5. Summary

Our review of the Gondwanan record of notosuchians outside of South America demonstrates their spatiotemporal distribution in the Middle Jurassic, from the Aptian–Maastrichtian, and in the Eocene, with their remains known from Africa and Indo-Madagascar. A possible occurrence from the latest Cretaceous of Oman (Buscalioni et al. 2004) cannot be confidently referred to Notosuchia. The African and Indo-Madagascan Cretaceous record indicates the presence of several lineages, all with close ties to South American clades, with many faunas demonstrating multiple sympatric species. Given that notosuchians only first appeared in the Aptian in South America (and Asia), coupled with palaeogeographic reconstructions documenting the increasing fragmentation of Gondwana at this time (e.g. Seton et al. 2012), this diverse record supports previous suggestions regarding an undocumented pre-Aptian radiation of Notosuchia (e.g. Martin and Lapparent de Broin 2016; Mannion et al. 2019). By contrast, their Gondwanan Paleogene record outside of South America is currently limited to just two occurrences, both from the Eocene of north Africa and both belonging to Sebecosuchia. No stratigraphically younger remains have been assigned to Notosuchia from this region, with their last Laurasian occurrences from the middle Eocene of western Europe (e.g. Martin 2016), indicating their extirpation outside of South America by the end of the Eocene.

7. Conclusions

Two new crocodyliform specimens from the Cenomanian Kem Kem Group of Morocco are described and incorporated into a phylogenetic analysis. Both specimens are referrable to *Antaeusuchus taouzensis* n. gen. n. sp., which is recovered within the notosuchian clade Peirosauridae, as the sister taxon to the contemporaneous *Hamadasuchus rebouli*. Comparisons of materials previously assigned to *Hamadasuchus* indicate the presence of at least three distinct peirosaurid species from the same spatiotemporal interval. Coupled with a critical reappraisal of the non-South American Gondwanan record of Notosuchia, we recognise a much greater taxonomic and ecomorphological diversity within this clade during the Cretaceous.

Acknowledgements

We are grateful to Paul Barrett and Susannah Maidment for their help in providing access to NHMUK PV R36829 and R36874, as well as to Kevin Webb for providing photographs of the specimens (all at the Natural History Museum, London). Paul Barrett also provided help with species name formulation. Access to specimens of *Hamadasuchus rebouli* and other peirosaurid material from Morocco was provided by David Evans and Brian Iwama (both Royal Ontario Museum, Toronto), as well as Oliver Rauhut (Bayerische Staatssammlung für Paläontologie und Geologie, Munich), to whom we are also grateful. Photographs of other specimens referred to *Hamadasuchus rebouli* were kindly provided by Diego Pol (Museo Paleontológico Egidio Feruglio, Trelew) including that used in Fig. 10 C. We also acknowledge the Willi Hennig Society, which has sponsored the development and free distribution of TNT. Finally, we are grateful for comments provided by Mario Bronzati and one anonymous reviewer that helped to improve the quality of this manuscript.

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. C.S.C.N and P.D.M. conceived of the study and interpreted the results. All authors contributed to the design of the study and to the drafting of the manuscript. Analyses were conducted by C.S.C.N. Figures were produced by C.S.C.N. and E.S.E.H. All authors approved the final version of the manuscript.

Competing interests. We declare we have no competing interests.

Funding. C.S.C.N. is funded by a Royal Society research grant (RGF\R1\180020) awarded to P.D.M. E.S.E.H. received funding from a Palaeontological Association Undergraduate Research Bursary (PA-UB201804) and her work is supported by a Natural Environment Research Council studentship (NE/S007415/1). P.D.M.'s contribution was supported by grants from the Royal Society (UF160216, RGF\R1\180020, and RGF\EA\201037).

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Tables

Table 1

Mandibular measurements of the holotypic specimen (NHMUK PV R36829) of *Antaeusuchus taouzensis* n. gen. n. sp.

	Dimension (mm)
Maximum mandibular anteroposterior length	415
Maximum mandibular symphysis anteroposterior length	123
Maximum mandibular symphysis mediolateral width	83
Maximum dentary anteroposterior length	371
Maximum dorsoventral height of mandibular ramus	92

Table 2

Tooth and alveolus measurements of the holotypic specimen (NHMUK PV R36829) of *Antaeusuchus taouzensis* n. gen. n. sp.

Tooth position	**Apicobasal length (mm)**	**Alveolar dimension (mm)**			
		Left mandible, anteroposterior length	Right mandible, anteroposterior length	Left mandible, Mediolateral width	Right mandible, Mediolateral width
1	-	11.0	11.5	14.1	14.1
2	-	7.4	7.0	8.7	8.4
3	-	5.0	5.0	5.0	5.4
4	12.1	17.5	12.5	16.0	12.0
5	-	10.0	10.0	10.0	9.5
6	-	5.6	5.5	6.5	7.0
7	-	4.6	5.2	6.8	6.1
8	-		5.1		6.0
9	-	6.6	5.4	6.5	6.2
10	11.0	11.2	11.1	10.5	10.0
11	18.0	14.2	-	13.0	-

12	19.0	15.6	-	12.2	-
13	16.0	23.1	-	16.2	-
14	10.0	14.4	-	11.5	-
15	13.0	13.0	-	8.5	-
16	8.0	10.0	-	7.0	-
17	-	7.0	-	6.0	-
18	-	8.0	-	7.0	-

Table 3

Spatiotemporal distribution and phylogenetic affinities of non-South American, Gondwanan named notosuchian species.

Taxon	**Stratigraphic and geographic provenance**	**Age**	**Phylogenetic position**	**Reference**
Razanandrongobe sakalavae	Isalo IIIB Fm., Madagascar	Bathonian, Middle Jurassic	Sebecosuchia?	Maganuco et al., 2006
Malawisuchus mwakasyungutiensis	Dinosaur Beds Fm., Malawi	Aptian, Early Cretaceous	Basal Ziphosuchia	Gomani, 1997
Stolokrosuchus lapparenti	Elrhaz Fm., Niger	Aptian–Albian, Early Cretaceous	Peirosauridae	Larsson and Gado, 2000
Araripesuchus wegeneri	Elrhaz Fm., Niger	Aptian–Albian, Early Cretaceous	Uruguaysuchidae	Buffetaut, 1981
Anatosuchus minor	Elrhaz Fm., Niger	Aptian–Albian, Early Cretaceous	Uruguaysuchidae	Sereno et al., 2003
Hamadasuchus rebouli	Kem Kem Group, Morocco	Cenomanian, Late Cretaceous	Peirosauridae	Buffetaut, 1994
Lavocatchampsa sigogneaurusselae	Kem Kem Group, Morocco	Cenomanian, Late Cretaceous	Basal Ziphosuchia	Martin and Lapparent de Broin, 2016
Araripesuchus rattoides	Kem Kem Group, Morocco	Cenomanian, Late Cretaceous	Uruguaysuchidae	Sereno and Larsson, 2009
Libycosuchus brevirostris	Bahariya Fm., Egypt	Cenomanian, Late Cretaceous	Basal Ziphosuchia	Stromer, 1914
Kaprosuchus saharicus	Echkar Fm., Niger	Cenomanian, Late Cretaceous	Mahajangasuchidae	Sereno and Larsson, 2009

Rukwasuchus yajabalijekundu	Galula Fm., Tanzania	Cenomanian–Campanian, Late Cretaceous	Peirosauridae	Sertich and O'Connor, 2014
Pakasuchus kapilimai	Galula Fm., Tanzania	Cenomanian–Campanian, Late Cretaceous	Basal Ziphosuchia	O'Connor et al., 2010
Araripesuchus tsangatsangana	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Uruguaysuchidae	Turner, 2006
Simosuchus clarki	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Basal Ziphosuchia	Buckley et al., 2000
Mahajangasuchus insignis	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Mahajangasuchidae	Buckley and Brochu, 1999
Miadanosuchus oblita	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Peirosauridae	Rasmusson Simons and Buckley, 2009
Pabwehshi pakistanensis	Pab Fm., Pakistan	Maastrichtian, Late Cretaceous	Sebecosuchia?	Wilson et al., 2001
Eremosucus elkoholicus	El Kohol Fm., Algeria	Ypresian, early Eocene	Sebecosuchia?	Buffetaut, 1989

Figure captions

Figure 1

Map showing locality of the new fossil remains. White star indicates the approximate geographic position of *Antaeusuchus taouzensis* n. gen. n. sp. (NHMUK PV R36829 and R36874) within the Kem Kem Group of Morocco.

Figure 2

Line drawings and photographs of *Antaeusuchus taouzensis* n. gen. n. sp. (NHMUK PV R36829 [A&C] and NHMUK PV R36874 [B&D]) in right lateral view. Scale bar represents 100 mm.

Figure 3

Line drawings and photographs of *Antaeusuchus taouzensis* n. gen. n. sp. (NHMUK PV R36829 [A&C] and NHMUK PV R36874 [B&D]) in left lateral view. Scale bar represents 100 mm.

Figure 4

Line drawings and photographs of *Antaeusuchus taouzensis* n. gen. n. sp. (NHMUK PV R36829 [A&C] and NHMUK PV R36874 [B&D]) in dorsal view. Scale bar represents 100 mm.

Figure 5

Line drawings and photographs of *Antaeusuchus taouzensis* n. gen. n. sp. (NHMUK PV R36829 [A&C] and NHMUK PV R36874 [B&D]) in ventral view. Scale bar represents 100 mm.

Figure 6

Teeth of *Antaeusuchus taouzensis* n. gen. n. sp. A, teeth 12–14 of NHMUK PV R36874. B, tooth 14 of NHMUK PV R36829. Abbreviations: cbc, constricted base of crown; dc, denticulated carina; rre, ridged rugose enamel. Scale bar represents 10 mm.

Figure 7

Strict consensus tree showing the relationships of notosuchians using equal weighting of characters. Numbers at the nodes indicate Bremer support values.

Figure 8

Strict consensus tree showing the relationships of notosuchians using extended implied weighting at *k*-values of 8 and 12. Some clades (Uruguaysuchidae and Ziphosuchia) have been condensed.

Figure 9

Comparison of the dorsal mandibular surfaces of several notosuchians: A, *Antaeusuchus taouzensis* n. gen. n. sp. (NHMUK PV 36829*); B, *Antaeusuchus taouzensis* (NHMUK PV R36874); C, *Montealtosuchus arrudacamposi* (MPMA 16-0007-04*); D, *Gasparinisuchus peirosauroides* (MOZ 1750 PV*); E, *Hamadasuchus rebouli* (ROM 49282); F, *Hamadasuchus rebouli* (MDE C001*); G, *Barrosasuchus neuquenianus* (MCF-PVPH-413*); H, *Araripesuchus rattoides* (CMN 41893*); I, *Bayomesasuchus hernandezi* (MCF PVPH-822). Asterisk indicates a holotype specimen.

Figure 10

Comparison of peirosaurid mandibles from the Kem Kem Group in lateral view: A, NHMUK PV 36829 (*Antaeusuchus taouzensis* n. gen. n. sp. holotype); B, NHMUK PV R36874 (*Antaeusuchus taouzensis* paratype); C, MDEC001 (*Hamadasuchus rebouli* holotype); D, ROM 49282; E, BSPG 2005 I 83. A1–E1 show close-up images of the teeth of each respective taxon. Image B is reversed. Scale bars represent 50 mm.

Figure 11

Time-calibrated phylogenetic topology showing the agreement subtree of notosuchians using equal weighting of characters. Some clades are condensed and the polytomy including *Razanandrongobe sakalavae* is shown despite being pruned from the agreement subtree.

Figure 12

Spatiotemporal distribution of notosuchian occurrences from Africa and Indo-Madagascar. A, Present-day map and stratigraphic column. Stars indicate the location of all named notosuchian taxa. The size of each star is proportional to the number of named taxa at each locality. Circles indicate other remains referred to Notosuchia. B–F, Palaeogeographic reconstructions showing the distribution of notosuchian occurrences for the Middle Jurassic (B), Early Cretaceous (C), early Late Cretaceous (D), late Late Cretaceous (E), and Eocene (F). Plots modified from the Paleobiology Database Navigator (https://paleobiodb.org/navigator/).

Appendix

Character scores modified from the respective matrices of Martínez et al. (2018) and are listed below:

Hamadasuchus rebouli:

103 ? -> 0**;** **363** ? -> 0**;** **365** ? -> 0**;** **383** ? -> 0; **384** ? -> 0; **388** ? -> 0; **389** ? -> 0; **392** ? -> 1; **393** ? -> 0&1; **394** ? -> 0; **443** 0 -> 1

Gasparinisuchus peirosauroides:

443 0 -> 0&1

Montealtosuchus arrudacamposi:

443 0 -> 1

Libycosuchus brevirostris:

441 ? -> 0

Malawisuchus mwakasyungutiensis:
441 ? -> 0

Caipirasuchus stenognathus:

441 ? -> 0

Caipirasuchus montealtensis:

441 ? -> 0

Baurusuchus salgadoensis:

441 ? -> 0

Stolokrosuchus lapparenti:

441 ? -> 0

A second peirosaurid crocodyliform from the mid-Cretaceous Kem Kem Group of Morocco and the diversity of Gondwanan notosuchians outside South America

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RRH: SECOND MOROCCAN PEIROSAURID
LRH: NICHOLL, HUNT, OUARHACHE & MANNION

Abstract

Notosuchians are an extinct clade of terrestrial crocodyliforms with a particularly rich record in the late Early to Late Cretaceous (~130–66 Ma) of Gondwana. Although much of this diversity comes from South America, Africa and Indo-Madagascar have also yielded numerous notosuchian remains. Three notosuchian species are currently recognised from the early Late Cretaceous (~100 Ma) Kem Kem Group of Morocco, including the peirosaurid *Hamadasuchus rebouli*. Here, we describe two new specimens that demonstrate the presence of at least a fourth notosuchian species in this fauna. *Antaeusuchus taouzensis* n. gen. n. sp. is incorporated into one of the largest notosuchian-focused character-taxon matrices yet to be compiled, comprising 443 characters scored for 63 notosuchian species, with increased sampling of African and peirosaurid species. Parsimony analyses run under equal and extended implied weighting consistently recover *Antaeusuchus* as a peirosaurid notosuchian, supported by the presence of two distinct waves on the dorsal dentary surface, a surangular which laterally overlaps the dentary above the mandibular fenestra, and a relatively broad mandibular symphysis. Within Peirosauridae, *Antaeusuchus* is recovered as the sister taxon of *Hamadasuchus*. However, it differs from *Hamadasuchus* with respect to several features, including the ornamentation of the lateral surface of the mandible, the angle of divergence of the mandibular rami, the texture of tooth enamel, and the shape of the teeth, supporting their generic distinction. We present a critical reappraisal of the non-South American Gondwanan notosuchian record, which spans the Middle Jurassic–late Eocene. This review, as well as our phylogenetic analyses, indicate the existence of at least three approximately contemporaneous peirosaurid lineages within the Kem Kem Group, alongside other notosuchians, and support the peirosaurid affinities of the 'trematochampsid' *Miadanasuchus oblita* from the Maastrichtian of Madagascar. Furthermore, the Cretaceous record demonstrates the presence of multiple lineages of approximately contemporaneous notosuchians in several African and Madagascan faunas, and supports previous suggestions regarding an undocumented pre-Aptian radiation of Notosuchia. By contrast, the post-Cretaceous record is depauperate, comprising rare occurrences of sebecosuchians in north Africa prior to their extirpation.

Keywords: Notosuchia, Crocodylomorpha, Gondwana, Kem Kem, Mesozoic, Africa

1. Introduction

Today's crocodylians are the remnants of a once much more diverse and widespread clade, Crocodyliformes (Brochu 2003; Carvalho et al. 2010; Mannion et al. 2015; Wilberg et al. 2019; Stubbs et al. 2021). One extinct group, Notosuchia, comprises a morphologically diverse, speciose clade of terrestrial crocodyliforms (Carvalho et al. 2010; Pol et al. 2014; Pol & Leardi, 2015). Often noted to exhibit bizarre bauplans relative to other crocodyliforms, notosuchians include species characterised by features such as 'pug-nosed' and 'duck'-like snouts (e.g. Buckley et al. 2000; Sereno et al. 2003; Kley et al. 2010), elongate limbs indicative of a parasagittal posture (e.g. Gasparini 1971; Pol 2005; Riff and Kellner 2011; Godoy et al. 2016), mammal-like heterodont dentition (e.g. Carvalho 1994; Wu et al. 1995; Buckley et al. 2000; Ősi 2014), and even herbivory (e.g. O'Connor et al. 2010; Melstrom & Irmis 2019). Notosuchians have predominantly been recovered from Gondwanan landmasses, especially South America (e.g. Carvalho et al. 2010; Pol et al. 2014; Ruiz et al. 2021), from which more than 70% of species have been discovered (Pol & Leardi 2015). Although the group had its highest apparent (i.e. 'raw number of') species diversity in the middle–Late Cretaceous (~120–66 Ma) (Riff et al., 2012; Pol & Leardi, 2015), notosuchians survived until the middle Miocene (~12 Ma) (Langston 1965; Langston & Gasparini 1997; Paolillo & Linares 2007), with putative remains extending their record back to the Middle Jurassic (~168 Ma) (Dal Sasso et al. 2017).

Despite severe and pervasive under-sampling of fossiliferous localities relative to most other continents (Mannion et al. 2019), diverse assemblages of extinct crocodyliforms have been discovered from several spatiotemporal intervals in Africa (e.g. Jouve 2007; Sereno & Larsson 2009; Brochu & Storrs 2012; Stefanic et al. 2020), including those yielding notosuchians. One such interval is represented by the 'middle' Cretaceous Kem Kem Group, a series of highly fossiliferous continental strata exposed in the east of Morocco along its border with Algeria, forming the northwestern edge of the Sahara Desert (Lavocat 1948; Russell 1996; Sereno et al. 1996; Bardet et al. 2010; Cavin et al. 2010; Ibrahim et al. 2020) (Fig. 1). The Kem

Kem Group is generally considered to be either late Albian or Cenomanian (~105–94 Ma) (e.g. Martin and Lapparent de Broin 2016), with the most recent stratigraphic reappraisal favouring this younger age (Ibrahim et al. 2020). A diverse vertebrate fauna has been recovered from the Kem Kem Group, including sharks, bony fishes, lissamphibians, turtles, squamates, pterosaurs, non-avian dinosaurs, and crocodyliforms (Sereno et al. 1996; Rage & Dutheil 2008; Sereno & Larsson 2009; Bardet et al. 2010; Cavin et al., 2010; Ibrahim et al. 2020).

The Kem Kem crocodyliforms comprise the neosuchians *Aegisuchus witmeri* (Holliday & Gardner 2012), *Elosuchus cherifiensis* (Lavocat 1955; Lapparent de Broin 2002), and *Laganosuchus maghrebensis* (Sereno & Larsson 2009), as well as three notosuchians (Ibrahim et al. 2020). The first of these notosuchians to be named, the peirosaurid *Hamadasuchus rebouli* (Buffetaut 1994), was erected based on a fragmentary dentary. Several specimens have since been referred to this taxon, including a nearly complete cranium and lower jaws (Larsson & Sidor 1999; Rauhut & López-Arbarello 2006; Larsson & Sues 2007; Ibrahim et al. 2020). Sereno & Larsson (2009) described a second Kem Kem notosuchian species, the small-bodied uruguaysuchid *Araripesuchus rattoides*, which is currently known from several dentaries (Ibrahim et al. 2020). The third notosuchian species to be described, the candidodontid *Lavocatchampsa sigogneaurussellae* (Martin & Lapparent de Broin 2016), is known from a small partial skull with unusual mammal-like multicuspid teeth. Ibrahim et al. (2020) suggested that multicuspid crocodyliform teeth described by Larsson & Sidor (1999) might represent additional notosuchian taxa. Finally, Ibrahim et al. (2020) also noted anatomical differences between the type and referred material of *Hamadasuchus* that could indicate yet higher crocodyliform diversity in the Kem Kem Group.

Here, we describe new notosuchian remains from the Kem Kem Group of Morocco that support Ibrahim et al.'s (2020) suggestion of higher crocodyliform diversity in this fauna. We test the phylogenetic position of these new specimens in an expanded version of an existing data set. Finally, we provide a critical reappraisal of the Gondwanan record of non-South American notosuchians, in which we reassess the group's diversity through time and space.

1.1. Institutional abbreviations — **BSPG**, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **CMN (formerly NMC)**, Canadian Museum of Nature, Ottawa, Canada; **MDE**, Musée des Dinosaures, Espéraza, France; **MNHM**, Muséum national d'Histoire naturelle, Paris, France; **NHMUK**, Natural History Museum, London, UK; **ROM**, Royal Ontario Museum, Toronto, Canada.

2. Systematic Palaeontology

Crocodylomorpha Walker, 1970

Crocodyliformes Hay, 1930 (sensu Clark in Benton and Clark, 1988)

Mesoeucrocodylia Whetstone and Whybrow, 1983

Notosuchia Gasparini, 1971

Peirosauridae Gasparini, 1982

Antaeusuchus taouzensis gen. et sp. nov.

urn:lsid:zoobank.org:act:62C4F680-CCFD-41CF-A328-8552E7B086C0
urn:lsid:zoobank.org:act:13959FDD-B1B1-472D-B2C6-DBD935721892

Commented [NC1]: I have included the LSID link from ZooBank; however, I am unsure if this is the appropriate place to provide this information.

Etymology—Genus name after the giant *Antaeus* from Berber and Greek mythology, who is said to be buried at Msoura in northern Morocco, and *suchus*, from the Greek *souchos*, meaning crocodile. Species name after the township *Taouz* from where the holotype and paratype specimens were recovered.

Holotype—NHMUK PV R36829: paired mandibles, comprising an essentially complete left dentary and splenial, along with a partial angular and surangular, in articulation with the anterior portion of the right dentary and splenial.

Paratype—NHMUK PV R36874: a partial right mandible, comprising an incomplete dentary, surangular, and angular.

Locality and horizon—Near to Jebel Beg'aa, Taouz township, Errachidia Province, eastern Morocco. The specimens were commercially collected and recovered from unspecified beds within the Cenomanian (lower Upper Cretaceous) Kem Kem Group.

Diagnosis—A crocodyliform characterized by the following unique combination of features: (1) wide divergence angle (40–45°) of the mandibular rami; (2) dorsal margin of dentary sinusoidal with two distinct waves; (3) relatively unornamented surface texture of dentary adorned with narrow, shallow ridges; (4) ventrolateral dentary surface anterior to mandibular fenestra transversely compressed and vertical; (5) dentary extends posteriorly beneath the mandibular fenestra; (6) anterior alveoli of dentary strongly procumbent; (7) concavity for the reception of the enlarged maxillary tooth lateral to the 7th alveolus of the dentary; (8) splenial forming approximately 40% of the total mandibular anteroposterior length; (9) surangular overlaps dentary above the mandibular fenestra; (10) rugose tooth enamel formed by anastomosing grooves and ridges; (11) enlarged 4th and 13th dentary teeth; (12) tooth margins in posterior region of the dentary toothrow with denticulate carinae formed by homogeneous and symmetrical denticles with a sharp cutting edge; and (13) sub-triangular dentary tooth crowns (in lateral view) with a gently curved apex.

3. Description

After detailed description and comparison of the two specimens, we consider both NHMUK PV R36874 and R36829 to belong to the new species, *Antaeusuchus taouzensis*, and as such they are described together. In instances where the feature being described is preserved in only one specimen, the relevant museum accession number is provided.

3.1. Preservation

The preserved parts of both specimens are undistorted and in good condition, such that small-scale morphological details are still visible. Damage is restricted mainly to the teeth, several of which are missing.

3.2. General Shape

The anterior region of the mandible is characterised by a broad, ’U’-shaped symphysis that forms at least one quarter of the total anteroposterior mandibular length. Each mandibular ramus diverges at an angle of approximately 22° from the sagittal midline. The ramus remains approximately straight along the majority of its preserved length, curving very slightly medially close to its posterior margin (visible on the left side of NHMUK PV R36829). The anterior half of the mandibular dorsal margin is characterized by two distinct ‘waves’, whereas the strongly sloping posterior half is largely straight, with the dentary increasing in dorsoventral height towards the surangular.

3.3. Dentary

The dentary is anteroposteriorly elongate, and its lateral, ventral, and dorsal surfaces are sculpted by neurovascular foramina and vermiform grooves. On the lateral surface, the foramina are largest and most numerous in the anterodorsal region of the snout. In the middle region of the snout, a series of short grooves run anteroposteriorly along the lateral surface, ~10 mm ventral to the toothrow. These grooves meet an anteroposteriorly elongate groove that extends to the dorsal suture of the dentary and surangular process (Figs 2 & 3). Another prominent, anteroposteriorly elongate vascular groove runs from the anterior-most point of the mandibular fenestra to the level of the posterior tip of the toothrow.

In lateral view, the dentary has a sinusoidal dorsal margin composed of two distinct waves. The most anterior wave spans teeth 1–6, whereas the most posterior wave is dorsally raised between teeth 9–15. The dorsoventrally tallest region of each wave corresponds with the position of dentary teeth 4 and 13, the posteriormost of which is more dorsally elevated than the anterior (Figs 2 & 3). The dentary forms the anterior region of a relatively wide mandibular symphysis (Fig. 4), the dorsal surface of which is very mildly concave. In dorsal view, the midline dentary suture extends posteriorly to the level of the 8th tooth (Fig. 4). The bone in this region is relatively unornamented, with the exception of a series of foramina immediately adjacent to the toothrow. On the ventral surface of the mandibular symphysis, the medial dentary suture extends posteriorly to a level between the 7th–8th teeth. A concavity is situated lateral to the 5th–10th teeth, most likely for the reception of an enlarged maxillary tooth. The posterior region of the lateral dentary surface dorsal to the mandibular fenestra is divided into two major acute posterior processes, separated by an anterior process of the surangular (Fig. 2). The ventral-most dentary extension forms the anterodorsal margin of the external mandibular fenestra and is dorsoventrally wide, forming approximately three quarters of the dorsoventral height of the mandible at the same level. The dorsal-most process is much narrower; its dorsal and ventral margins converge posteriorly to form an acute angle. An anteroposteriorly short dentary process is situated ventral to the external mandibular fenestra, although this does not contact the fenestral border. In NHMUK PV R36874, the splenial is not preserved, exposing the dentary's medial surface (Fig. 3).

The dentary has 18 tooth positions. On the left side of NHMUK PV R36829, whole or partial teeth are preserved in alveoli 1–16, whereas 17–18 are empty. On the right side of the specimen, 10 alveoli are preserved, with whole or partial teeth preserved in all but one (alveolus 9). Although the anterior region of NHMUK PV R36874 has broken away, the first preserved alveolus is large, and is assumed to be the fourth in the series. Whole or partial teeth are present in alveoli 5–6, 8, and 10–16 in NHMUK PV R36874. The largest tooth is the 13th, followed closely by the 4th, 11th, and 12th, which are approximately equidimensional in their circumference. In dorsal view, the tooth row is slightly sinusoidal, with lateral waves corresponding to the position of the 4th and 13th teeth (Fig. 4). Although not fully preserved in either specimen, the anteriormost two teeth appear to be procumbent. Dentary teeth 3–10 project slightly anterolaterally. All of the dentary teeth are closely arranged, without the presence of diastemas.

3.4. Splenial

The splenials are only preserved in NHMUK PV R36829. They participate in a relatively wide mandibular symphysis (Table 1) and occupy approximately 38% of the anteroposterior symphyseal length on the dorsal surface of the mandible, extending anteromedially to the position of the 8th alveolus (Fig. 4). On the dorsal surface of the symphysis, the splenial-dentary suture diverges gradually from the sagittal midline. This suture is slightly concave until the 11th tooth, from which point it is parallel to the tooth row. A line of small foramina run parallel to the toothrow along the lateral margin of the dorsal surface of the splenial. On the ventral surface of the mandible, the splenial occupies approximately 31% of the anteroposterior length of the symphysis, and it extends anteriorly to the position of the 9th tooth. The ventromedial splenial surface of the mandibular symphysis is dorsally displaced relative to the lateral margin. A posterior peg is located on the ventromedial surface of the symphysis (Fig. 4). The splenial is transversely thin and dorsoventrally tall, covering the inner surface of the mandibular ramus from the ventral margin of the dentary to the lingual alveolar groove. Positioned just posterior to the mandibular symphysis, on the medial surface of the splenial, is an opening, likely homologous to the intermandibularis oralis of living crocodylians (Iordansky 1973). This is elliptical, such that its anteroposterior length is approximately twice that of its dorsoventral height.

3.5. Surangular

The surangular is more completely preserved in NHMUK PV R36829, extending from the posterior margin of the toothrow to its broken posterior margin at the dorsal-most region of the mandibular fenestra. Its lateral surface is covered with interconnected shallow grooves. Of the surangular’s two acute anterior processes, the most anteroposteriorly elongate is located on the dorsal and medial surfaces of the mandible and extends to the posterior margin of the toothrow (Fig. 4). A second anterior process is present on the dorsal region of the lateral mandibular surface (Figs 2 & 3). Approximately halfway between the anterior margin of the mandibular fenestra and the posterior margin of the toothrow, the dorsal and ventral margins of this second anterior process meet anteriorly to form a subtriangular tip. An anteroposteriorly elongate dorsal coronoid tuberosity protrudes from the dorsomedial surangular surface, running anteroposteriorly for a distance of approximately 30 mm; its anterior margin is at the same level as the posterior-most point of the posterodorsal dentary process. The surangular forms the dorsal-most margin of the mandibular fenestra.

3.6. Angular

Albeit highly incomplete, the angular is best preserved in NHMUK PV R36874. The angular has an elongate anterior process that extends along the ventromedial surface of the mandible to the level of the 14th dentary tooth (Fig. 5). A second, smaller anterior process is present on the lateral surface of the skull (Fig. 3). This extends to the anterior margin of the mandibular fenestra, such that the angular forms the latter’s entire ventral margin. The posteriormost preserved region of the angular projects laterally, forming a prominent ventrolateral ridge beneath the mandibular fenestra.

3.7. Mandibular Fenestra

Although not fully preserved in either specimen, the mandibular fenestra can be inferred to be large and anteroventrally–posterodorsally elongate, as indicated by its extensive, straight anterodorsal margin in NHMUK PV R36874 (Figs 2 & 3). Its anteriormost margin is positioned at approximately the same level as the posteriormost extension of the dorsal-most dentary process; however, the posterior fenestral margin is not preserved in either specimen.

3.8. Dentition

In the anterior region of the snout, the approximately circular alveoli suggest that the teeth are essentially conical; however, those towards the posterior of the toothrow (from the tenth tooth posteriorly) become more labiolingually compressed (Table 2). More extreme labiolingual flattening is present on the anterior and posterior margins of all preserved teeth (Fig. 6). These labiolingually flattened margins are adorned with denticulated carinae forming the anteriormost and posteriormost cutting edges of the teeth. The denticles are small and subtle, showing no significant size variation along the carinae (Fig. 6). There are approximately 35–40 denticles per 10 mm. All preserved teeth are covered by a layer of red-brown enamel upon which apicobasal striations are evident around the whole circumference of the tooth. There are approximately 3–4 bifurcating striations per 1 mm, giving the enamel a wrinkled appearance.

4. Phylogenetic analysis and results

4.1. Dataset and analytical approach

Specimens NHMUK PV R36829 and R36874 were combined as one operational taxonomic unit (OTU), *Antaeusuchus taouzensis*, into a character-taxon matrix (CTM) sampling a large number of crocodyliforms, with particular emphasis on notosuchians. This matrix was originally published by Pol et al. (2014) and has since formed the underlying dataset for phylogenetic analysis in a number of studies, with each one making minor additions and/or revisions to taxa and/or characters. Unfortunately, many of these iterations have occurred in parallel, rather than representing a continuous series of revisions to one dataset, meaning that there is no single dataset incorporating all of these changes to the original Pol et al. (2014) data matrix. Here, we united many of these ‘daughter’ matrices, using that of Martínez et al. (2018) as a starting point. The latter is a successive iteration of the data matrices of Leardi et al. (2015) and Fiorelli et al. (2016), which emanated from that of Pol at al. (2014). We included two additional characters, following Leardi et al. (2018), and revised 20 existing character scores based on observations from recent studies (Stromer 1914; Gomani 1997; Larsson & Gado 2000; Carvalho et al. 2005; Carvalho et al. 2007; Larsson & Sues 2007; Martinelli et al. 2012; Barrios et al. 2016) and personal observations (see Appendix for documentation of changes).

We incorporated notosuchians from parallel daughter matrices, utilising scores presented in those datasets, and a review of the literature. These consist of *Razanandrongobe sakalavae* from the Bathonian (Middle Jurassic) of Madagascar (Maganuco et al. 2006; Dal Sasso et al. 2017), the probable peirosaurids *Bayomesasuchus hernandezi* (Barrios et al. 2016) and *Barrosasuchus neuquenianus* (Coria et al. 2019) from the early Late Cretaceous (Turonian and Santonian, respectively) of Argentina, the sphagesaurid *Caipirasuchus mineirus* from the late Campanian–early Maastrichtian (latest Cretaceous) of Brazil (Martinelli et al. 2018), and the sebecid *Ogresuchus furatus* from the early Maastrichtian of Spain (Sellés et al. 2020). We also expanded the sampling of putative peirosaurids that had not previously been incorporated into iterations of the Pol et al. (2014) data matrix via the inclusion of *Rukwasuchus yajabalijekundu* from the Late Cretaceous of Tanzania (Sertich & O'Connor 2014) and *Miadanasuchus oblita* from the Maastrichtian of Madagascar (Rasmusson Simons & Buckley 2009). The OTU for *Hamadasuchus rebouli* followed previous iterations of this data matrix, although we made a small number of character state changes (see Appendix). The resultant data matrix consists of 121 OTUs scored for 443 characters, including 63 putative notosuchian taxa. *Antaeusuchus taouzensis* could be scored for 51 of these characters.

The data matrix was analysed under maximum parsimony using the ‘Stabilize Consensus’ option in the ‘New Technology Search’ in TNT v. 1.5 (Goloboff et al. 2008). The search was executed using sectorial searches, drift, and tree fusing, and the consensus was stabilized five times with a factor 75, prior to using the resultant trees as the starting trees for a ‘Traditional Search’ using Tree Bisection-Reconstruction. Subsequently, a strict consensus tree was calculated. We applied two different weighting schemes, using equal weighting (EQW) and extended implied weighting (EIW). Shown to perform well on morphological datasets (Goloboff et al. 2018), EIW downweights homoplastic characters in relation to their average homoplasy, whilst reducing the possible impact of missing data (Goloboff 2014). The concavity constant, represented by the *k*-value, denotes the strength of downweighting, with lower values having been shown to downweight homoplastic characters more severely than higher values (Goloboff et al. 2018). Following analytical protocols in recent analyses of neosuchians (Groh et al. 2020; Nicholl et al. 2020; Rio et al. 2020; Rio & Mannion 2021), we applied EIW to notosuchians for the first time, using *k*-values of 8 and 12. Characters with missing entries were downweighted faster assuming 50% the homoplasy of observed entries, and weighting strength did not exceed 5 times that of characters with no missing entries. Forty-three characters representing nested sets of homologies were ordered (1, 3, 6, 10, 23, 37, 43, 44, 45,49, 65, 67, 69, 71, 73, 77, 79, 86, 90, 91, 96, 97, 105, 116, 126, 140, 142, 143, 149, 167,182, 187, 193, 197, 226, 228, 279, 339, 356, 357, 364, 368, 401). Character 5 was made inactive due to “dependence with the modified definition of character 6” (Pol et al. 2014: supplementary information p. 3). Following the identification of problematic, unstable taxa by Pol et al. (2014), confirmed by our preliminary searches, three species known from fragmentary remains were excluded from our analyses *a priori* (i.e. *Coringasuchus anisodontis*, *Pabwehshi pakistanensis*, and *Pehuenchesuchus enderi*). The character list and data matrix are provided as nexus and tnt files (electronic supplementary material), with stored settings for assigning characters as ordered and inactive.

4.2. Results

Under EQW, our analysis produced 11520 trees with a tree length of 1778 steps. The overall tree topology is broadly consistent with the analyses of Pol et al. (2014)

and subsequent iterations. Notosuchia comprises a main bifurcation into Ziphosuchia (plus *Candidodon itapecuruense* and *Libycosuchus brevirostris*), and a clade in which Uruguaysuchidae is recovered as the sister taxon of Mahajangasuchidae + Peirosauridae (following the recent phylogenetic definition of Geroto & Bertini 2018 [see below]) (Fig. 7). Although *Peirosaurus torminni* is not included in our data matrix, *Uberabasuchus terrificus* has been consistently recovered as a close relative, with some authors regarding the latter as a junior synonym of the former (e.g. Larsson & Sues 2007; Martinelli et al. 2012). As such, we regard the *Uberabasuchus* OTU as a proxy for *Peirosaurus* in terms of identifying Peirosauridae. Bremer values are generally low across the tree, ranging from 1–3.

Antaeusuchus is recovered within Peirosauridae, as the sister taxon to *Hamadasuchus* (Fig. 7). The two Kem Kem OTUs form a clade with *Bayomesasuchus* that is the sister group to nearly all other peirosaurids. Within this latter group, *Barrosasuchus* and *Miadanasuchus* form a clade that is the sister taxon to a polytomy comprising *Rukwasuchus*, *Gasparinisuchus peirosauroides*, *Lomasuchus palpebrosus*, *Uberabasuchus*, and *Montealtosuchus arrudacamposi.* This polytomy can be resolved through the *a posteriori* pruning of *Gasparinisuchus* in the agreement subtree, which results in *Lomasuchus* and *Montealtosuchus* recovered as sister taxa, forming a clade with *Uberabasuchus*, with *Rukwasuchus* placed at the ‘base’ of this grouping. *Stolokrosuchus lapparenti* is recovered as the earliest diverging member of Peirosauridae.

Under EIW, with both *k*-values, the overall topology is largely similar to that recovered using EQW. With a *k*-value of 8, the analysis produced 45 trees with a tree length of 89.3, and with a *k*-value of 12, 15 MPTs were found of length 68.3. The main difference with results obtained from EQW is that the taxonomic content of Peirosauridae is now expanded, as a result of *Stolokrosuchus* being recovered in a clade with *Lorosuchus nodosus* and Mahajangasuchidae (Fig. 8). The phylogenetic definition proposed by Geroto and Bertini (2018) means that Mahajangasuchidae is a clade within Peirosauridae according to our EIW topology.

5. Comparisons

Given the results of our phylogenetic analyses, which provide robust and consistent support for a peirosaurid placement for *Antaeusuchus*, we largely restrict our anatomical comparisons to members of this clade.

5.1. Comparisons with other peirosaurids

Characteristic of all members of Peirosauridae (Martinelli et al. 2012), *Antaeusuchus* possesses an undulatory dorsal margin of the dentary comprising two distinct waves, the apices of which coincide with the position of the two largest dentary teeth (Ortega et al. 1996; Pol et al. 2014). In all peirosaurids in which the relevant region is preserved, with the exception of *Stolokrosuchus* (Larsson & Gado 2000), the 4th dentary tooth is the largest of those in the first wave, and it coincides with the apex of the anterior dentary region. The position of the largest tooth (the apex of the posterior wave) also varies amongst peirosaurids (Pol et al. 2014). The apex of this posterior wave corresponds to the 13th tooth position in *Antaeusuchus*, *Barrosasuchus, Gasparinisuchus, and Kinesuchus overoi* (Martinelli et al., 2012; Filippi et al. 2018; Coria et al. 2019), whereas it occurs at the level of the 12th tooth in *Hamadasuchus* and *Montealtosuchus* (Carvalho et al. 2007; Larsson & Sues 2007). In *Stolokrosuchus*, the jaw gradually increases in dorsoventral height posteriorly, corresponding with a progressively larger tooth size towards the posterior region of the dentary (Larsson & Gado 2000). In lateral view, the dorsoventrally expanded posterior region of the mandible of *Antaeusuchus* more closely resembles that of *Hamadasuchus*, *Montealtosuchus*, and *Uberabasuchus* (Carvalho et al. 2004, 2007; Larsson & Sues 2007) than it does in taxa such as *Barrosasuchus* and *Kinesuchus* (and potentially *Pepesuchus deiseae*) (Campos et al., 2011; Filippi et al. 2018; Coria et al. 2019), in which the region is more dorsoventrally compressed.

All peirosaurid taxa, except for the longirostrine-snouted *Stolokrosuchus* (Larsson & Gado 2000), are characterised by a mediolaterally broad mandibular symphysis (Fig. 9). This is most prominent in *Colhuehuapisuchus lunai*, *Barrosasuchus*, and *Gasparinisuchus* (Martinelli et al. 2012; Coria et al. 2019; Lamanna et al. 2019), in which the anteroposterior length to mediolateral width ratio of the symphyseal dorsal surface is less than 1.0 (values range from 0.8–0.9). Although still broad in comparison with many other notosuchian taxa, such as sphagesaurians (Ruiz et al.

2021), which often have length to width ratios exceeding 2.0 (Pol et al. 2014), *Antaeusuchus*, as well as *Hamadasuchus*, possess some of the anteroposteriorly longest mandibular symphyses amongst Peirosauridae, with a ratio of 1.4 and 1.5 for *Antaeusuchus* and *Hamadasuchus*, respectively (Larsson & Sues 2007). The ratios are 1.2 in *Montealtosuchus* and 1.1 in both *Uberabasuchus* and *Bayomesasuchus* (Carvalho et al. 2004; Carvalho et al. 2007; Barrios et al. 2016). *Kinesuchus* preserves the anteroposteriorly longest mandibular symphyses of any peirosaurid, with a ratio of 2.0 (Filippi et al. 2018).

As is the case in all notosuchians (Pol et al. 2014), the splenials of *Antaeusuchus* participate in the mandibular symphysis, although the extent to which this is the case varies between peirosaurids (Fig. 9). The splenial of *Antaeusuchus* occupies 39% of the anteroposterior length of the symphysis in dorsal view. A relatively long dorsal symphyseal contribution is also present in *Hamadasuchus* (49%), *Bayomesasuchus* (40%), *Kinesuchus* (44%), *Patagosuchus anielensis* (~44%), and potentially *Uberabasuchus*, although the latter cannot be observed in dorsal view (Carvalho et al. 2004; Barrios et al. 2016; Lio et al. 2016; Filippi et al. 2018). A much shorter splenial contribution to the symphysis characterizes *Gasparinisuchus* (16%), *Barrosasuchus* (21%), and *Colhuehuapisuchus* (~26%) (Martinelli et al., 2012; Coria et al. 2019; Lamanna et al. 2019).

Where the splenial meets the dentary on the symphyseal dorsal surface of *Antaeusuchus*, the suture forms an approximate 'V' shape. A similar morphology is present in *Hamadasuchus* (Larsson & Sues 2007), *Bayomesasuchus* (Barrios et al. 2016), *Kinesuchus* (Filippi et al. 2018), and *Stolokrosuchus* (Larsson & Gado 2000), as well as *Patagosuchus* (Lio et al. 2016) and *Montealtosuchus* (Carvalho et al. 2007), although the 'V' is slightly broader in the latter two species, forming a less acute angle. This morphology contrasts with that of *Barrosasuchus*, *Gasparinisuchus*, *Colhuehuapisuchus*, and *Miadanasuchus* (Rasmusson Simons & Buckley 2009; Martinelli et al. 2012; Coria et al. 2019; Lamanna et al. 2019), in which the dentary-splenial suture forms a broad 'U' shape. As with all other peirosaurids (Pol et al. 2014), the dorsal surface of the mandibular symphysis on which this suture occurs is very slightly transversely concave in *Antaeusuchus*.

In *Antaeusuchus*, as well as *Hamadasuchus* (Larsson & Sues 2007), the dentary-splenial suture exposed on the dorsal surface of the mandibular symphysis diverges gradually from the midline until the level of the 12th dentary tooth, at which point it becomes parallel to the toothrow. A similar morphology characterizes *Kinesuchus*, except that the change in orientation of the suture is less acute in that species (Filippi et al. 2018). In *Montealtosuchus* and *Patagosuchus*, the suture becomes parallel with the toothrow at the level of the 10th dentary tooth (Carvalho et al. 2007; Lio et al. 2015). By contrast, the dentary-splenial suture in *Stolokrosuchus* parallels the toothrow only at the level of the 25th tooth (Larsson & Gado 2000). Although the morphology of the suture is 'U'-shaped, as opposed to the 'V'-shape that characterizes *Antaeusuchus*, it becomes approximately parallel with the toothrow at the level of the 11th and 12th tooth in *Gasparinisuchus* and *Barrosasuchus*, respectively (Martinelli et al. 2012; Coria et al. 2019).

Posterior to the symphysis, the mandibular rami of *Antaeusuchus* diverge at an angle of approximately 44° to each other. A value of between ~40–45° is fairly consistent amongst peirosaurids; this contrasts with some other notosuchians, including sphagesaurians (Pol et al. 2014; Martinelli et al. 2018), whereby the skull is mediolaterally broader, and the rami diverge from one another at a less acute angle. Immediately posterior to the symphysis, the splenial of *Antaeusuchus* is largely exposed in ventral view, and forms approximately 40% of the mediolateral width of the mandibular rami. A comparably broad splenial also characterizes *Uberabasuchus*, *Montealtosuchus*, and *Kinesuchus* (Carvalho et al. 2004; Carvalho et al. 2007; Filippi et al. 2018), whereas the splenial comprises only 25–30% of the rami transverse cross section in *Gasparinisuchus*, *Stolokrosuchus, Colhuehuapisuchus*, and *Barrosasuchus* (Larsson & Gado 2000; Martinelli et al. 2012; Coria et al. 2019; Lamanna et al. 2019).

In numerous peirosaurids, including *Antaeusuchus*, *Hamadasuchus*, *Uberabasuchus, Montealtosuchus*, *Pepesuchus*, *Stolokrosuchus*, and *Lomasuchus*, an anteroposteriorly elongate groove runs parallel to the dentary toothrow, just ventral to the dorsal margin of the lateral surface of the mandible (Gasparini et al. 1991; Larsson & Gado 2000; Carvalho et al. 2004; Carvalho et al. 2007; Larsson & Sues 2007; Campos et al. 2011). The lateral surface of the dentary is also typically sculpted with pits and/or grooves in peirosaurids; however, there is interspecific variation in the degree to which this sculpting continues over the entire surface. In *Antaeusuchus*, the lateral surface of the dentary is similar in its texture and sculpting both above and below the groove. In this regard, the morphology is similar to that of *Uberabasuchus*, *Barrosasuchus*, and *Kinesuchus* (Carvalho et al. 2004; Filippi et al. 2018; Coria et al. 2019). In *Hamadasuchus*, *Montealtosuchus*, *Pepesuchus*, and *Patagosuchus*, the region above the groove is smooth, differing markedly from the remainder of the highly sculpted lateral dentary surface (Carvalho et al. 2007; Larsson & Sues 2007; Campos et al. 2011; Lio et al. 2016). Although *Stolokrosuchus* shows no difference in bone surface texture above and below the anteroposterior groove (Larsson & Gado 2002), it differs from *Antaeusuchus* in that the majority of the lateral dentary surface is smooth and unornamented.

The degree of sculpting on the lateral surface of the dentary varies across notosuchian taxa, including within Peirosauridae. Whereas the surface is covered in deep pits in *Hamadasuchus*, *Uberabasuchus*, *Montealtosuchus*, *Patagosuchus*, *Bayomesasuchus*, and *Miadanasuchus* (Carvalho et al. 2004; 2007; Larsson & Sues 2007; Rasmusson Simons & Buckley 2009; Barrios et al. 2016; Lio et al. 2016), the surface of *Antaeusuchus* is considerably smoother and is textured with narrow, shallow grooves.

Unlike *Montealtosuchus*, *Gasparinisuchus*, *Bayomesasuchus*, Stolokrosuchus, *Patagosuchus*, *Pepesuchus*, and *Colhuehuapisuchus* (Buckley & Brochu 1999; Larsson & Gado 2000; Carvalho et al. 2007; Campos et al. 2011; Martinelli et al. 2012; Lamanna et al. 2019), the lateral surface of the dentary adjacent to the 5th–8th teeth forms a distinct anteroposteriorly elongate concavity in *Antaeusuchus*. This is otherwise known only in *Hamadasuchus* (Larsson & Sues 2007), although a shallower concavity also characterizes *Barrosasuchus* (Coria et al. 2019). This depression would likely have functioned to receive an enlarged premaxillary tooth during occlusion.

Although incompletely preserved, the mandibular fenestra in *Antaeusuchus* is almost certainly large and anteroposteriorly elongate, as is the case in *Hamadasuchus*, *Montealtosuchus*, and *Uberabasuchus* (Carvalho et al. 2004; Carvalho et al. 2007;

Ibrahim et al. 2020), but differing from *Barrosasuchus* in which the fenestra is greatly reduced (Coria et al. 2019). However, *Montealtosuchus* and *Uberabasuchus* differ from the dentaries of *Antaeusuchus* and *Hamadasuchus* (Ibrahim et al. 2020) in that the latter two have a small posterior process that extends ventral to the mandibular fenestra. This process is absent in *Montealtosuchus* and *Uberabasuchus*, in which the dentary-angular contact is entirely anterior to the mandibular fenestra instead (Carvalho et al. 2004; Carvalho et al. 2007). The dentary-surangular contact is similar in *Antaeusuchus*, *Hamadasuchus*, *Montealtosuchus*, and *Uberabasuchus*, with the surangular contacted by two posterior processes: the dorsal process intrudes entirely into the surangular, whereas the second process forms the ventral margin of the surangular and the anterodorsal margin of the mandibular fenestra (Carvalho et al. 2004; Carvalho et al. 2007; Larsson & Sues 2007). This feature cannot be assessed in other peirosaurid taxa, in which the relevant region of the mandible is not preserved.

When complete, each dentary of *Antaeusuchus* has 18 tooth positions. This count is common amongst peirosaurids, e.g. *Montealtosuchus*, *Gasparinisuchus*, *Kinesuchus, Pepesuchus,* and possibly *Barrosasuchus* (Carvalho et al. 2007; Campos et al. 2011; Martinelli et al. 2012; Filippi et al. 2018; Coria et al. 2019), but differs from *Stolokrosuchus*, in which there are at least 30 dentary alveoli (Larsson & Gado 2000). As in all peirosaurids (Pol et al. 2014), the first two dentary teeth of *Antaeusuchus* are strongly procumbent.

The dentary teeth posterior to the 5th alveolus are closely spaced and are mostly situated in a continuous groove in *Antaeusuchus*, *Hamadasuchus* (Larsson & Sues 2007), *Gasparinisuchus* (Martinelli et al. 2012), and *Barrosasuchus* (Coria et al. 2019). This differs from the condition in *Kinesuchus* (Filippi et al. 2018) and *Patagosuchus* (Lio et al. 2016), in which the teeth are separated by distinct septa that extend fully to the dorsal margin of the dentary.

5.2. Detailed comparisons with *Hamadasuchus rebouli*

Although several crocodyliform taxa, including notosuchians, have been identified from the Kem Kem Group (Ibrahim et al. 2020), only one peirosaurid species is currently recognised from these beds: *Hamadasuchus rebouli* (Buffetaut 1994; Larsson & Sues 2007). Since the original description of the holotype dentary by Buffetaut (1994), several specimens have been referred to *Hamadasuchus* (Larsson & Sidor 1999; Rauhut & López-Arbarello 2006; Larsson & Sues 2007; Ibrahim et al. 2020). In our CTM (and previous iterations), the OTU of *Hamadasuchus* comprises the holotype mandibular fragment, MDEC001, plus the cranial material, ROM 52620, referred by Larsson & Sues (2007). Almost all characters that could be assessed for *Antaeusuchus* received the same score as *Hamadasuchus*, resulting in their consistent recovery as sister taxa in our phylogenetic analyses. The only differences in scores are present in characters 77 (scored as 2 and 1&2 for *Antaeusuchus* and *Hamadasuchus*, respectively), 155 (scored as 1 and 0&1 for *Antaeusuchus* and *Hamadasuchus*, respectively), and 393 (scored as 0 and 0&1 for *Antaeusuchus* and *Hamadasuchus*, respectively). The score of 1&2 for character 77 reflects the fragmentary nature of the *Hamadasuchus* type specimen and uncertainty of the precise length of the splenial contribution to the mandibular symphysis, rather than representing a polymorphism, whereas the score of 0&1 for characters 155 and 393 represents the definite presence of both states in this OTU. Given the similarity of the scores of both Kem Kem specimens, and that those provided for the mandible of *Hamadasuchus* are based only on the holotype specimen and not any referred material, we provide more detailed comparisons in the following section. *Antaeusuchus* is compared to several anatomically overlapping specimens currently assigned to *Hamadasuchus*, namely the holotype dentary (MDEC001), several partial mandibles (ROM 49282, 52045, and 52047) described by Larsson & Sues (2007), a complete skull and lower jaws (BSPG 2005 I 83) figured by Rauhut & López-Arbarello (2006), and two mandibular symphyses (MNHN-MRS 3110 & NMC 41784) illustrated in Ibrahim et al. (2020). Despite being largely similar in overall morphology, *Antaeusuchus* differs in several respects from all specimens assigned to *Hamadasuchus* (Fig. 10).

Although only one dentary is preserved in the holotype (MDEC001), the angle of divergence of the mandibular rami can be inferred by measuring the angle of deviation of one dentary from the exposed symphyseal suture. Estimated mandibular rami divergence angles of ~20° for ROM 52047, ~25° for MDEC001 and ~30° for

ROM 49282, 52045, are much narrower than that of *Antaeusuchus* (43–44°). This suggests that *Hamadasuchus* had a slenderer rostrum than that of *Antaeusuchus*.

The surface texture of the *Antaeusuchus* dentary differs from all three specimens referred to *Hamadasuchus* in that it is not covered in deep pits and grooves. Instead, it is ornamented with relatively narrow and shallow grooves. *Antaeusuchus* also differs from these specimens in the dorsal region of the dentary lateral surface. In MDEC001, the area just ventral to the toothrow is smooth and lacks pits, differing from the remainder of the lateral surface (Buffetaut 1994). Instead, this dorsal region has a corrugated morphology, with broad, shallow dorsoventral grooves that do not correspond to the position of the dentary teeth (Fig. 10). A similar morphology characterizes ROM 49282, BSPG 2005 I 83, and NMC 41784, although it is not as prominent in those specimens. In *Antaeusuchus*, the degree of ornamentation is much the same across the lateral surface of the dentary and a fluted dorsal region is absent.

The apex of the second mandibular wave is marked by the position of the 13th tooth in *Antaeusuchus*, as well as ROM 49282, BSPG 2005 I 83, and probably MNHN-MRS 3110. By contrast, the tip of the second dentary wave is most likely marked by the 12th tooth in the holotype MDEC001, which is significantly larger than the 13th tooth (Buffetaut 1994).

Posterior to the 7th dentary tooth, the teeth of MDEC001 are strongly labiolingually compressed, and possess serrated carinae on their anterior and posterior cutting edges. A similar morphology is also present in *Antaeusuchus*, as well as MNHN-MRS 3110, but not in ROM 49282, in which the teeth are compressed only from the 10th tooth. The 5th to 9th teeth are damaged in BSPG 2005 I 83 and so it is unclear at which tooth position the compression commences. The posterior teeth in MDEC001 have a lanceolate shape (Buffetaut 1994) that is not present in *Antaeusuchus*, but which is most reminiscent of the morphology in MNHN-MRS 3110. In NHMUK PV R36829, teeth 11, 12, 14, and 15 are the only ones which are fully preserved; the anterior two of these have rounded crowns that do not form an angular tip. Although the 14th and 15th teeth of NHMUK PV R36829 are slightly pointed at their apices, they are not comparable to the almost triangular shape of those in the holotype MDEC001 (Buffetaut 1994). In NHMUK PV R36874, the 10^{th}–14^{th} teeth are slightly more angular in appearance, but their anterior and posterior margins are parallel for most of their length, converging to a point only at the crown apex (Fig. 10).

The only fully preserved tooth in the ROM 49282 dentary is the 13^{th} one (Larsson & Sues 2007). Comparing the broad morphology, it is most similar to the teeth at a similar dentary position in *Antaeusuchus*, in that its apical margin is rounded. However, the tooth enamel of ROM 49282 is essentially smooth. By contrast, the enamel in *Antaeusuchus* is wrinkled into anastomosing apicobasal ridges (approximately 2–3 ridges per mm) (Fig. 10). Both morphologies differ from that of the teeth of MDEC001, in which the enamel is textured, but has an irregular, globular pattern towards its base, and anastomosing ridges towards the apex of the crown (Buffetaut 1994). ROM 49282 also displays a unique condition in which the tooth enamel is fluted with broad apicobasal ridges around its circumference.

The teeth of all specimens assigned to *Hamadasuchus*, as well as those of *Antaeusuchus*, have very finely serrated carinae on their anterior and posterior cutting edges, with individual serrations spaced at approximately 3–5 per mm. Although most prominent in MDEC001, vertical fluting on the anterior and posterior regions of the crowns is visible in the posterior dentary teeth of all the specimens discussed in this section.

Finally, *Antaeusuchus* is significantly larger than all *Hamadasuchus* specimens, such that it is almost double the size of MDEC001, ROM 49282, and BSPG 2005 I 83. Although the size of the specimen alone should not be a reason to erect a new species (e.g. Griffin et al. 2021), we believe it to be a valid morphological difference as part of a large, unique combination of features. Furthermore, *Hamadasuchus* is already known from an ontogenetic series, including specimens considered ‘adult’ (Larsson & Sues 2007); as such, it is difficult to reconcile the numerous anatomical differences merely as a result of *Antaeusuchus* being an even older individual of Hamadasuchus).

6. Discussion

6.1. Taxonomic affinities of NHMUK PV R36829 and R36874

In all of our analyses, the NHMUK PV R36829 + R36874 OTU (i.e. *Antaeusuchus*) is recovered as the sister taxon of *Hamadasuchus*. This relationship is supported by a single unambiguous synapomorphy (a distinct concavity adjacent to the 5th to 10th dentary teeth for the reception of the enlarged maxillary tooth), and one ambiguous synapomorphy (a short distance between the fourth and fifth mandibular teeth). In total, 34 characters in our CTM can be scored for both the *Hamadasuchus* OTU and *Antaeusuchus*, with only three of these receiving different scores (characters 77, 155, 393). The first of these describes the contribution of the splenial to the mandibular symphysis in dorsal view and only partially differs: whereas *Hamadasuchus* is polymorphic (1/2), *Antaeusuchus* is characterised solely by state 2. Nonetheless, both taxa exhibit splenials that are anteroposteriorly more elongate than other peirosaurid taxa, with the exception of *Bayomesasuchus*. The second character in which scores differ describes the sculpting of the dentary region below the toothrow. Again, the difference is only partial, with *Hamadasuchus* polymorphic (0/1) and *Antaeusuchus* possessing the derived condition (i.e. state 1). The elevated sections of this region in the *Hamadasuchus* holotype are characterized by a pitted surface, whereas the depressed areas are smooth. Finally, the third differing character describes the rugose texture of the tooth enamel, for which *Hamadasuchus* is scored as 0 & 1, whereas *Antaeusuchus* is characterized by the plesiomorphic condition (i.e. state 0). The tooth enamel in the *Hamadasuchus* holotype is more globular towards the middle and basal regions of the tooth crown, becoming more linear and ridgelike towards its apex. In *Antaeusuchus*, elongate, anastomosing ridges run from the apex to the base of the enamel.

Although there are only three differences captured in our CTM, our detailed comparisons demonstrate numerous additional features that indicate that NHMUK PV R36829 and R3687 are not referrable to *Hamadasuchus rebouli*. NHMUK PV R36829 and R36874 differ from *Hamadasuchus rebouli* in their large size as well as the possession of a unique combination of features: (1) a high angle of divergence between mandibular rami; (2) a rugose dentary tooth enamel shaped into anastomosing apicobasal ridges; (3) the largest dentary tooth in the second wave is located in alveolus 13; (4) sub-triangular tooth crowns (in lateral view) with a gently curved apex; (5) minor labiolingual compression of the posterior dentary teeth; (6) a lack of fluting on the dorsal region of the lateral dentary surface; (7) a relatively unornamented surface texture of the dentary adorned with narrow, shallow ridges rather than deep pits or grooves; and (8) dentary teeth more widely spaced at their base.

As such, it seems clear that NHMUK PV R36829 + R3687 represents a second peirosaurid in the Kem Kem Group, and thus supports our erection of *Antaeusuchus taouzensis* n. gen. n. sp. In addition, material currently referred to *Hamadasuchus* also differs from the type specimen (MDEC001), as well as *Antaeusuchus*. In particular, the partial mandible, ROM 49282, described by Larsson & Sues (2007), differs from both taxa in several features, including: (1) distinctive apicobasal fluting on the 13th tooth; (2) a highly elongate contribution of the splenial to the mandibular fenestra; (3) a mandibular rami divergence of approximately 30°; and (4) possession of relatively smooth tooth enamel. The unique combination of characters in each of MDEC001, ROM 49282, and NHMUK PV R36829 + R36874, therefore suggests the presence of at least three separate, albeit closely related, peirosaurid species from the Kem Kem Group. Although we erect a new name for NHMUK PV R36829 + R3687, we refrain from naming a new taxon for ROM 49282 pending the description and assessment of additional materials currently assigned to *Hamadasuchus rebouli* (namely BSPG 2005 I 83 and additional ROM specimens).

6.2. Implications for peirosaurid relationships

Peirosauridae was erected by Gasparini (1982) to accommodate *Peirosaurus torminni* (Price 1955) from the late Maastrichtian Marília Formation of Brazil. This family was subsequently expanded by Gasparini et al. (1991) to include *Lomasuchus* from the late Turonian–early Coniacian of Argentina. Geroto & Bertini (2019 p. 328) provided a phylogenetic definition for Peirosauridae as “the least inclusive clade containing *P. tormini* [sic] Price, 1955, *Itasuchus jesuinoi* Price, 1955, and *Stolokrosuchus lapparenti* Larsson & Gado, 2000, but not including *Notosuchus terrestris* Woodward, 1896, *Baurusuchus pachecoi* Price, 1945, *Sphagesaurus huenei* Price, 1950, *Araripesuchus gomesii* Price, 1959, *Sebecus icaeorhinus* Simpson, 1937, *Mariliasuchus amarali* Carvalho & Bertini, 1999, and *Crocodylus niloticus* Laurent, 1768”. Although a phylogenetic definition based on two well-nested and stable species-level specifiers would be preferable (e.g. Sereno 1998, 2005; Lee 2005), we follow the definition of Geroto & Bertini (2019) here, pending a detailed re-evaluation of the interrelationships of this part of the notosuchian tree.

Following Geroto & Bertini’s (2019) definition, Peirosauridae comprises a taxonomically rich array of crocodyliforms from across the Cretaceous of South America, Africa, and Madagascar (e.g. Price 1955; Carvalho et al. 2004; Carvalho et al. 2007; Larsson & Sues 2007; Leardi & Pol 2009; Sertich O’Connor 2014; Campos et al. 2011; Martinelli et al. 2012; Lio et al. 2016; Barrios et al. 2016; Filippi et al. 2018; Coria et al. 2019). However, there is little consensus regarding the position of Peirosauridae. A number of analyses have recovered Peirosauridae within Notosuchia, as the sister taxon to Mahajangasuchidae (i.e. *Kaprosuchus* + *Mahajangasuchus*), with these lineages forming a clade with Uruguaysuchidae that is the sister taxon to all other notosuchians (e.g. Pol et al. 2014; Sertich & O’Connor 2014; Coria et al. 2019). Others have recovered Peirosauridae as part of Sebecia, forming a clade with Sebecidae (e.g. Larsson & Sues 2007; Sereno & Larsson 2009), and sometimes also including Mahajangasuchidae (e.g. Geroto & Bertini 2019; Ruiz et al. 2021). Whereas some of these analyses place Sebecia as the sister taxon to all other notosuchians (e.g. Geroto & Bertini 2019; Ruiz et al. 2021), others recover Sebecia within Neosuchia (e.g. Larsson & Sues 2007; Sereno & Larsson 2009). Peirosauridae has also been recovered as an early diverging neosuchian clade in some studies (e.g. Pol & Apesteguía 2005; Gasparini 2006; Turner & Buckley 2008; Leardi & Pol 2009).

In several recent phylogenetic analyses (e.g. Pol et al. 2014; Geroto & Bertini 2019; Coria et al. 2019), *Hamadasuchus* has been recovered as the sister taxon to a group of exclusively South American Cretaceous peirosaurids (comprising various combinations of *Montealtosuchus*, *Uberabasuchus*, *Lomasuchus*, *Gasparinisuchus*, and *Barcinosuchus*). Similarly, Barrios et al. (2016) recovered *Hamadasuchus* in a polytomy with most of these taxa, along with *Bayomesasuchus* from the Turonian (Late Cretaceous) of Argentina. Sertich & O’Connor (2014) recovered

Hamadasuchus in an unresolved trichotomy with *Rukwasuchus* and *Stolokrosuchus*, forming a clade of African peirosaurids.

Here, under both equal and extended implied weighting schemes, the position of Peirosauridae is consistent with the results of Pol et al. (2014) and subsequent studies based on this dataset (e.g. Leardi et at 2015; Fiorelli et al. 2016; Iori et al. 2018; Leardi et al. 2018; Martinelli et al. 2018; Coria et al. 2019). Under its broadened taxonomic content, following the phylogenetic definition of Geroto & Bertini (2019), Peirosauridae includes Mahajangasuchidae in our EIW analyses (Fig. 8). This occurs because *Stolokrosuchus* is recovered as more closely related to Mahajangasuchidae than to other peirosaurids in the EIW topology. Our equal weights analysis recovers *Stolokrosuchus* as the most ‘basal’ member of Peirosauridae instead, with Mahajangasuchidae outside of this clade (Fig. 7). In both cases, our peirosaurid + mahajangasuchid grouping is the sister taxon of Uruguaysuchidae, with this clade the sister taxon to all other notosuchians.

In our strict consensus trees, the clade comprising *Antaeusuchus* and *Hamadasuchus* is most closely related to *Bayomesasuchus*. This grouping is the sister taxon to other peirosaurids (excluding *Stolokrosuchus* and Mahajangasuchidae) (Fig. 7). The remaining South American taxa are grouped in a polytomy with the African taxon *Rukwasuchus*, with this recovered as the sister taxon of a clade comprising the Malagasy taxon *Miadanasuchus* and the Argentinean species *Barrosasuchus*. The aforementioned polytomy can be resolved via *a posteriori* pruning of *Gasparinisuchus*, resulting in *Rukwasuchus* as the sister taxon of (*Uberabasuchus* + (*Lomasuchus* + *Montealtosuchus*)).

The fact that our analyses produce topologies more consistent with those derived from the data matrix of Pol et al. (2014) than alternative matrices is not surprising given that this is the underlying dataset for our study. As such, the interrelationships of Peirosauridae within Metasuchia will require further testing, ideally merging characters and taxa from across studies with competing hypotheses. However, the recovery of Peirosauridae as an early diverging metasuchian clade outside of the ziphosuchian notosuchian radiation is consistent across analyses, regardless of the underlying dataset.

One of the notable results of our analyses is the placement of *Miadanasuchus* within Peirosauridae, which was independently recovered in this clade by Geroto and Bertini (2019). This species from the Maastrichtian of Madagascar was originally described as *Trematochampsa oblita* (Buffetaut & Taquet 1979), before being assigned to a new genus by Rasmusson Simons & Buckley (2009). The type species of *Trematochampsa*, *T. taqueti*, is based on fragmentary remains from the Coniacian–Santonian In Beceten Formation of Niger (Buffetaut 1974; 1976a, b), for which the family Trematochampsidae was also erected (Buffetaut 1974). Several additional crocodyliform taxa have been assigned to Trematochampsidae (e.g. *Amargasuchus minor* [Chiappe 1988], *Barreirosuchus franciscoi* [Iori et al. 2012], *Hamadasuchus*, *Itasuchus*, *Mahajangasuchus*), spanning the Cretaceous of Africa, Europe, Madagascar, and South America, with most of these known from fragmentary remains (see review in Meunier & Larsson 2018). Buffetaut (1988, 1989) also included *Peirosaurus torminni* as a member of Trematochampsidae, which would therefore have priority over Peirosauridae. However, multiple authors have questioned or rejected the monophyly of Trematochampsidae, which appears to have become a wastebasket taxon (e.g. Gasparini et al. 1991; Ortega et al. 1996; Buckley & Brochu 1999; Turner & Calvo 2005; Larsson & Sues 2007; Rasmusson Simons et al. 2009; Meunier & Larsson 2018). Furthermore, Meunier & Larsson (2018) demonstrated that *Trematochampsa taqueti* is a nomen dubium, based on non-diagnostic, chimeric remains, with some of these displaying peirosaurid affinities. Our analyses provide further evidence that most, if not all, Cretaceous taxa previously assigned to Trematochampsidae belong to Peirosauridae, and confirm the presence of this latter clade in the Maastrichtian of Madagascar. Given the lack of diagnostic features in the type remains of '*Trematochampsa taqueti*' and the absence of a formal definition for 'Trematochampsidae', coupled with its approximate synonymy with the formally defined and widely used Peirosauridae, we support the proposal of Meunier & Larsson (2018) to abandon the name *Trematochampsa* and its coordinated rank taxa.

6.3. Gondwanan notosuchian diversity outside of South America

During the Mesozoic, notosuchians (*sensu* Pol et al. 2014) were the most diverse clade of Gondwanan crocodyliforms (Turner & Sertich 2010), although this high species richness varied through both time and space (Pol & Leardi 2015; De Celis et al. 2020). At least 70% of known notosuchian diversity is found on Gondwanan continents (Pol & Leardi 2015), with a small number of species recognised from Europe (Kuhn 1968; Antunes 1975; Rossman et al. 2000; Company et al. 2005; Dalla Vecchia & Cau 2011; Rabi & Sebök 2015; Martin 2016; Sellés et al. 2020) and Asia (Wu et al. 1995; Wu & Sues 1996). Though most numerous in South America, Gondwanan notosuchian occurrences are also known from mainland Africa, Madagascar, India, and Pakistan, as well as possibly the Arabian Peninsula. Currently no notosuchians are known from Australasia or Antarctica, although it remains unclear whether this represents a genuine absence, perhaps pertaining to a high-latitude environmental dispersal barrier, or it reflects a sampling bias (e.g. see Poropat et al. 2021). Here, we provide a critical reappraisal of the Gondwanan record of notosuchians outside of South America.

6.3.1. Jurassic

The stratigraphically oldest known notosuchian is *Razanandrongobe sakalavae* (Maganuco et al. 2006) from the Bathonian (Middle Jurassic) Isalo IIIb Formation in northwestern Madagascar. Originally named as an archosaur of uncertain affinities on the basis of teeth and a fragmentary maxilla (Maganuco et al. 2006), several more skull fragments, including a right premaxilla and an incomplete left dentary, have since been assigned to the taxon, enabling its identification as a large-bodied notosuchian (Dal Sasso et al. 2017). Considering that the next stratigraphically oldest notosuchians are from the Aptian (late Early Cretaceous), resulting in a ~40 million-year ghost lineage, *Razanandrongobe* is a stratigraphic outlier and its affinities might seem doubtful. However, based on the sister taxon relationship of Notosuchia and Neosuchia, with the latter clade known from the Early Jurassic (Tykoski et al., 2002), *Razanandrongobe* instead partly fills the inferred ghost lineage of notosuchians, which otherwise would extend back approximately 65–75 million years (Dal Sasso et al. 2017; Mannion et al. 2019). In the small number of phylogenetic analyses to have incorporated it (Dal Sasso et al. 2017; Sellés et al. 2020), including ours, *Razanandrongobe* is recovered in a position close to the ‘base’ of Sebecosuchia. This nested position within Notosuchia for such a stratigraphically early species necessitates the extension of multiple unsampled lineages back into the Jurassic (Fig. 11). As such, the phylogenetic affinities of *Razanandrongobe* require further evaluation to test whether this poor stratigraphic fit is genuine.

6.3.2. Early Cretaceous

In southeastern Africa, the Aptian Dinosaur Beds of northern Malawi (Fig. 12) have yielded numerous remains of *Malawisuchus mwakasyungutiensis*, preserving most of the skeleton (Gomani 1997). Recognised in part for its unusual mammal-like multicuspid teeth, some analyses have placed *Malawisuchus* in a nested position within Sphagesauria (e.g. Gomani 1997; Sereno & Larsson 2009; O'Connor et al. 2010). However, most recent analyses typically recover *Malawisuchus* as an early diverging ziphosuchian, with spaghesaurians currently restricted to South America (e.g. Pol et al. 2014; Ruiz et al. 2021; this study). Unlike the topology of Martin and Lapparent de Broin (2016), *Malawisuchus* is not recovered within Candidodontidae in our analyses (Fig. 7).

The Aptian–Albian Elrhaz Formation exposed at Gadoufaoua, central Niger (Fig. 12), has yielded the remains of three morphologically diverse notosuchian species (*Anatosuchus minor*, *Araripesuchus wegeneri*, and *Stolokrosuchus lapparenti*). The bizarre, 'duck-billed' *Anatosuchus* is known from several individuals, including a skull and associated partial postcranial skeleton, as well as a skull of a juvenile animal (Sereno et al. 2003; Sereno & Larsson 2009). *Anatosuchus* has often been recovered as a member of Uruguaysuchidae (e.g. Sereno & Larsson 2009; Pol et al. 2014); some analyses have placed it outside of this clade, although these tend to recover it as a 'basal' member of Notosuchia. The small and gracile species *Araripesuchus wegeneri* was erected from the anterior region of an articulated upper and lower snout (Buffetaut & Taquet 1979). Multiple remains have since been assigned to the taxon, including a block preserving at least five separate individuals, three of which are essentially complete, partially articulated skeletons (Sereno & Larsson 2009). In our analyses, *Araripesuchus wegeneri* and *Anatosuchus* are recovered as sister taxa within Uruguaysuchidae, further questioning the monophyly of *Araripesuchus* (see Sereno & Larsson 2009: p. 31). The longirostrine-snouted

Stolokrosuchus is known from an almost complete skull (Larsson & Gado 2000). Originally referred to Peirosauridae (Larsson & Gado 2000; see also Larsson & Sues 2007; Sereno & Larsson 2009; Geroto & Bertini 2019), subsequent analyses have shown the position of *Stolokrosuchus* to be highly labile, such that it has also been placed as an early diverging member of both Notosuchia (e.g. Dal Sasso et al. 2017) and Neosuchia (e.g. Turner & Sertich 2010; Andrade et al. 2011). Following the definition of Peirosauridae provided by Geroto & Bertini (2019), our analyses recover *Stolokrosuchus* as the earliest diverging member of this clade, which is consistent with previous analyses that have continued to place it close to the 'base' of Metasuchia.

Several isolated teeth from the Aptian–Albian Koum Formation of northeastern Cameroon (Fig. 12) were reported by Flynn et al. (1988) and Congleton (1990), who recognised their possible affinities with *Araripesuchus,* especially *A. wegeneri*. Kellner (1994 p. 618) questioned this referral, suggesting that these strongly serrated, laterally compressed, leaf-shaped teeth differed from those in the posterior toothrow of *Araripesuchus gomesii*, which he described as "weakly serrated" and "less leaf-shaped". It is unclear why Kellner (1994) limited comparisons to *Araripesuchus gomesii*; nonetheless, the description of additional specimens of *Araripesuchus wegeneri* from Niger (Sereno & Larsson 2009), along with other species of this genus (e.g. Pol & Apesteguia 2005; Ortega et al. 2000; Turner 2006; Sereno & Larsson 2009; Dumont et al. 2020; Ibrahim et al. 2020), allows for more thorough comparisons with the teeth from Cameroon. Given that none of the South American *Araripesuchus* species, nor *Araripesuchus tsangatsangana*, have denticles, the labiolingually compressed, lanceolate shape of these teeth, with serrated carinae along their posteriormost and anteriormost margins, is supportive of a referral to either *Araripesuchus wegeneri* or *Araripesuchus rattoides* (the latter comparison is based on referred material, BSPG 2008 I 41, rather than the holotype specimen [Ibrahim et al. 2020]). However, because of variation in crown morphology along the toothrow in all species of *Araripesuchus*, and given that teeth in the middle-to-posterior toothrow are either absent or poorly preserved in *Araripesuchus rattoides*, it is not currently possible to provide a species-level referral.

The Albian Aïn el Guettar Formation in southern Tunisia (Fig. 12) has yielded numerous crocodyliform remains, including teeth assigned to *Araripesuchus wegeneri*, *Araripesuchus* sp., and aff. *Hamadasuchus* sp. (Le Loeuff et al. 2000; Cuny et al. 2010; Fanti et al. 2012). The specimens assigned to *Araripesuchus* (Cuny et al. 2010, fig. 4.7; Fanti et al. 2012, fig. 12U–X) are labiolingually compressed and triangular, with serrated carinae and relatively smooth enamel. Based on the slightly dorsoventrally constricted lanceolate shape of the teeth in lateral view, it is likely that they come from the middle region of the toothrow. All of these features support their referral to *Araripesuchus*, widening the spatial distribution of the genus to north-central Africa. Although serrated tooth margins are known to be present in *Araripesuchus wegeneri* and a referred specimen of *Araripesuchus rattoides* (Ibrahim et al. 2020), we refrain from assigning these specimens beyond generic level as was “cautiously” proposed by Cuny et al. (2010: p. 625) for the same reasons outlined in the preceding paragraph. A single tooth referred to aff. *Hamadasuchus* sp. is labiolingually compressed and approximately triangular in lateral view, with “remnants of clear serration” (Cuny et al. 2010: fig. 4.8, p. 625). Although the more extreme labiolingual compression towards the anterior and posterior margins of the tooth is reminiscent of *Hamadasuchus*, the apparent lack of rugose enamel is unusual given its presence in all teeth associated with the holotype specimen of *Hamadasuchus*. The only other named crocodyliforms from the Early Cretaceous of Africa to possess serrated carinae are *Araripesuchus wegeneri* and referred material of *Araripesuchus rattoides*, both of which possess dentition more similar in size to the tooth reported in Cuny et al. (2010). However, given that the Tunisian specimen is clearly well-worn and is not dissimilar in broad morphology from either *Hamadasuchus* or *Araripesuchus*, we regard this specimen as an indeterminate notosuchian. Re-evaluation and full description of specimens referred to *Hamadasuchus* that have teeth with smooth enamel (e.g. BSPG 2005 I 83) might enable referral to a particular genus.

6.3.3. Late Cretaceous

In northwestern Africa, the Cenomanian Kem Kem Group of Morocco has yielded three previously named notosuchian species (*Araripesuchus rattoides*, *Hamadasuchus rebouli*, *Lavocatchampsa sigogneaurussellae*), in addition to the new species, *Antaeusuchus taouzensis*, described herein (Fig. 12). *Araripesuchus rattoides* is known from the holotypic partial dentary, as well as several referred dentary fragments (Sereno & Larsson 2009; Ibrahim et al 2020). It differs from *A. wegeneri* in several features, including its possession of a narrower and deeper snout, highly procumbent teeth, and potentially a greater number of teeth. Though not included in our phylogenetic analyses because of its fragmentary nature, *Araripesuchus rattoides* was recovered by Sereno & Larsson (2009) in a polytomy with three *Araripesuchus* species (*A. gomesii* and *A. patagonicus* from South America, and *A. tsangatsangana* from Madagascar), with this the sister group to a clade comprising the remaining uruguaysuchids (including *A. wegeneri*). *Lavocatchampsa sigogneaurussellae* was erected based on a small anterior snout region, which displays unusually heterodont teeth that are convergent with those of mammals (Martin & Lapparent de Broin 2016). Using the data matrix of Pol et al. (2014), Martin & Lapparent de Broin (2016) recovered *Lavocatchampsa* as a 'basal' ziphosuchian within Candidodontidae, a small clade otherwise known only from the Cretaceous of South America (Carvalho et al. 2004, Montefeltro et al. 2009).

As discussed in detail above, the peirosaurid *Hamadasuchus rebouli* was erected based on a single dentary fragment from the Kem Kem Group (Buffetaut 1994), but numerous cranial and mandibular remains have since been referred to this species from this stratigraphic unit (Larsson & Sues 2007; Ibrahim et al., 2020), including a skull table previously assigned to *Libycosuchus* sp. (Buffetaut 1976a, b). Although we do not disagree with referral of these remains to Peirosauridae, it is currently unclear if all of them are attributable to *Hamadasuchus rebouli*. Isolated teeth described by Larsson & Sidor (1999) were also referred to this species. One tooth, inferred to be from the middle of the toothrow (Larsson & Sidor 1999: fig. 1B), is very reminiscent of those preserved in the holotype of *Hamadasuchus rebouli*, based on its triangular shape in lateral view, its labiolingual compression, and the density of serrations. A second tooth shares the globular texture of the enamel towards the base of the crown, which transitions into more linear ridges towards the apex (Larsson & Sidor 1999: fig. 1C), which is again consistent with a referral to *Hamadasuchus rebouli*. However, a conical, retro-curved caniniform tooth shows distinctive fluting (Larsson & Sidor 1999: fig. 1A), which is absent from the holotypic specimen, but present in some of the specimens previously referred to the species

(ROM 49282 and 52620, BSPG 2005 I 83, and possibly NMC 41892 [Ibrahim et al. 2020]).

Larsson & Sidor (1999) described several additional crocodyliform teeth from the Kem Kem Group that have been suggested to represent additional notosuchian taxa (Ibrahim et al., 2020). Material referred to “Indet. crocodyliform 1” (Larsson & Sidor 1999 p. 398) is represented by two small, subtriangular crowns (SGM-Rep 4, SGM-Rep 5) in labiolingual view, each with three approximately parallel rows of relatively large cuspids that terminate in angular apices towards the anteroposterior midpoint of the tooth (Larsson & Sidor 1999, fig. 2 A–D]). On one of these teeth, a large planar wear facet bisects the rows of cusps on the buccal surface. A third tooth (SGM-Rep 6) referred to by Larsson & Sidor (1999 p. 399) as “Indet. crocodyliform 2” is more elliptical in dorsal view, and has a central, anteroposterior row of cuspids surrounded labially and lingually by two less dorsally raised rows of smaller cusps (Larsson & Sidor 1999, fig. 3). The outer two rows merge at the anteriormost and posteriormost margins of the tooth, forming a cingulum. Unlike the other multicuspid teeth, the rows of cusps in this third tooth are much closer to horizontal in their orientation, forming a less acute apex. Furthermore, the cusps of the central row are relatively larger in comparison to the tooth size and are fewer in number, forming an apex either mesially or distally (depending on tooth orientation in the jaw) rather than centrally. *Lavocatchampsa sigogneaurussellae* is the only crocodyliform from the Kem Kem Group that exhibits a multicuspid tooth morphology (Martin & Lapparent de Broin 2016); however, we agree with the observations of Ibrahim et al. (2020) that both morphologies are distinct from this taxon. We do note that the less acute tooth described as ‘Indet. crocodyliform 2’ is most similar in its morphology to the taxon described by Martin & de Lapparent de Broin (2016) based on its elliptical shape in occlusal view, and the presence of a cingulum bearing multiple cuspids that surround a central carina formed of a relatively small number (four) of cusps.

In summary, the Kem Kem Group seems to record the presence of at least seven potential notosuchians, represented by three peirosaurids (*Hamadasuchus rebouli*, *Antaeusuchus taouzensis*, and at least one unnamed species), *Araripesuchus rattoides*, and three species with multicuspid teeth (*Lavocatchampsa sigogneaurussellae* and two unnamed species). However, given poor stratigraphic constraints for many of these species, it remains possible that these were not all contemporaneous.

The Cenomanian Bahariya Formation of north-central Egypt has yielded just a single notosuchian species (Fig. 12), with *Libycosuchus brevirostris* represented by a complete skull and lower jaws, as well as several isolated vertebrae (Stromer 1914; Buffetaut 1976). *Libycosuchus* has an anteroposteriorly short skull and is fairly consistently recovered as an early diverging ziphosuchian (e.g. Sertich & O'Connor 2014; Pol et al. 2014; Martin & Lapparent de Broin 2016; Geroto & Bertini 2019), as is also the case in our analyses.

The large-bodied species *Kaprosuchus saharicus* is the only published notosuchian currently known from the Cenomanian Echkar Formation of northwestern Niger (Sereno & Larsson 2009) (Fig. 12). This species is based on an essentially complete skull and mandible and has been informally referred to as the "boar croc" due to its enlarged caniniform teeth. *Kaprosuchus* has been consistently recovered as the sister taxon to *Mahajangasuchus insignis* from the Maastrichtian of Madagascar (see below), and is thus a member of Mahajangasuchidae (e.g. Sereno & Larsson, 2009; Pol et al. 2014, Geroto & Bertini 2019; this analysis) (Fig. 6). Sereno & Pol (2019) reported an undescribed partial skeleton from the Echkar Formation that appears to be most closely related to the Maastrichtian Malagasy species, *Araripesuchus tsangatsangana*.

In the southeastern region of Africa, two notosuchian taxa are known from the Namba Member of the Galula Formation of western Tanzania (Fig. 12). Originally thought to be Aptian–Cenomanian (O'Connor et al. 2010; Roberts et al. 2010), new dates indicate either a Cenomanian–Santonian or more likely a Campanian age for this stratigraphic unit (Widlansky et al. 2018). Represented by the posterior region of the skull, the medium-to large-bodied *Rukwasuchus yajabalijekundu* was recovered by Sertich & O'Connor (2014) as a peirosaurid. It had not been included in a subsequent phylogenetic analysis prior to ours, which provides further support for a peirosaurid placement (Figs 6 & 7). Known from an essentially complete skeleton, *Pakasuchus kapilimai* is one of several small notosuchians with multicuspid teeth from the Cretaceous of Gondwana that appears to fill an ecological niche that would later be occupied by mammals (O'Connor et al. 2010; Sertich & O'Connor 2014). As is the case in several previous studies (e.g. O'Connor et al. 2010; Pol et al. 2014; Sertich & O'Connor 2014; Martin and Lapparent de Broin 2016), our analyses recover *Pakasuchus* as an early diverging member of Ziphosuchia, closely related to *Malawisuchus* (Fig. 7).

The Coniacian–Santonian In Beceten Formation of Niger (Fig. 12) has yielded the type material (an incomplete lacrimal) of *Trematochampsa taqueti* (Buffetaut 1974). As discussed in Section 6.2, Meunier & Larsson (2018) demonstrated that *Trematochampsa taqueti* is a nomen dubium, and suggested that isolated bones and teeth informally referred to the taxon represent at least three different small-medium sized crocodyliform species. They noted that many of these specimens show potential affinities to peirosaurids (especially *Hamadasuchus*), uruguaysuchids (especially *Araripesuchus wegeneri* and *Anatosuchus minor*), ziphosuchians, and/or neosuchians, which we follow here.

The Wadi Milk Formation of northern Sudan (Fig. 12) has traditionally been regarded as Cenomanian (e.g. Buffetaut et al. 1990; Rage & Werner 1999), but more recent work indicates that it should be assigned to the Campanian–Maastrichtian (Owusu Agyemang et al. 2019). An undescribed peirosaurid has been briefly reported, consisting of partial mandibles and part of the skull roof, and which is notable for its large size (Evans et al. 2014).

Putative notosuchian remains from the Maastrichtian Dukamaje Formation in western Niger have been mentioned in the literature, but not described. Moody and Sutcliffe (1991: table 2) listed the presence of *Trematochampsa taqueti* and *Libycosuchus* sp. in this formation, but they provided no further details. We suspect that that this was a mistake, with the In Beceten faunal list accidentally incorporated, but this cannot currently be confirmed.

A mandibular fragment preserving the middle portion of a right dentary could potentially represent the only occurrence of a notosuchian from the Arabian Peninsula (Buscalioni et al. 2004). Buscalioni et al. (2004) tentatively assigned the specimen from the Maastrichtian Al-Khod Conglomerate Formation of northern

Oman as cf. *Trematochampsa* indet. and noted similarities with *Miadanosuchus* (‘*Trematochampsa*’) *oblita* from the Maastrichtian of Madagascar. These similarities included the presence of an enlarged tooth in the 10th alveolus, and a morphology indicative of a long and wide mandibular symphysis (despite this region not being preserved). Our analyses recover *Miadanosuchus* within Peirosauridae, a clade characterised by two distinct waves on the dorsal margin of the dentary. The very straight, only slightly inclined dorsal edge of the dentary in the Oman specimen is therefore not indicative of a specimen belonging to this clade, especially as the presence of an enlarged tooth would be expected to be accompanied by the dorsoventral expansion of the dentary. Furthermore, the dentary of *Miadanosuchus* maintains its mediolateral width posterior to the enlarged tenth tooth for at least the distance of two alveoli. The Oman specimen shows gradual, but distinct narrowing posterior to the enlarged tooth. Given the highly fragmentary nature of the specimen, and the few preserved anatomical features of phylogenetic relevance, we suggest that the material can only be assigned to an indeterminate crocodyliform.

The Maastrichtian Maevarano Formation that outcrops in northwestern Madagascar has thus far yielded four notosuchian taxa (Fig. 12). The bizarre “pug-nosed” *Simosuchus clarki* is represented by multiple individuals preserving most of the skeleton (Buckley et al. 2000; Georgi & Krause 2010; Hill 2010; Kley et al. 2010; Sertich & Groenke 2010). Most analyses recover *Simosuchus* as an early diverging ziphosuchian (e.g. Turner & Sertich 2010; Pol & Powell 2011; Pol et al. 2014; Geroto & Bertini 2019; this study). The large-bodied *Mahajangasuchus insignis* is known from an almost complete skull and much of the postcranial skeleton (Buckley & Brochu 1999; Turner & Buckley 2008). Initially thought to have affinities with ‘Trematochampsidae’, the taxon has since been recovered as a peirosaurid (e.g. Turner & Calvo 2005), or just outside of this clade (e.g. Pol et al. 2014). It is now the clade specifier for Mahajangasuchidae (Sereno & Larsson 2009), with our analyses providing evidence for a position both within (EIW) and just outside (equal weighting) of Peirosauridae. *Araripesuchus tsangatsangana* is represented by a nearly complete skull, as well as a second individual preserving a nearly complete skeleton (Turner 2006). *Miadanasuchus* (‘*Trematochampsa*’) *oblita* is known from partial dentaries, part of the skull roof, and a vertebra (Buffetaut & Taquet 1979;

Rasmusson Simons & Buckley 2009), and it appears to represent a peirosaurid (Geroto & Bertini (2019; this study).

Pabwehshi pakistanensis, recovered from the Maastrichtian Pab Formation of southwestern Pakistan (Fig. 12), is known from fragmentary specimens, which preserve the anterior region of the snout and the associated section of the mandible of two individuals (Wilson et al. 2001). The limited remains of *Pabwehshi* mean that its phylogenetic position is labile (Pol et al. 2014), although most authors have supported a close relationship with Baurusuchidae (e.g. Wilson et al. 2001; Turner & Calvo 2005; Nascimento & Hussam 2010; Turner & Sertich 2010; Pol & Powell 2011; Carvalho et al. 2011; Dal Sasso et al. 2017; Geroto & Bertini 2019; Coria et al. 2019), which is otherwise known only from South America (e.g. Montefeltro et al. 2020; Darlim et al. 2021). By contrast, Larsson & Sues (2007) recovered *Pabwehshi* as the most ‘basal’ member of Sebecia, i.e. as the sister taxon to a clade comprising Peirosauridae and Sebecidae. *Pabwehshi pakistanensis* was excluded from our analyses because of its labile position, but more complete material will ultimately be needed to robustly resolve its phylogenetic position.

An isolated tooth from the Maastrichtian Kallamedu Formation of southern India (Fig. 12) was described by Prasad et at. (2013), who identified it as cf. *Simosuchus* sp. Based on comparisons with *Simosuchus clarki*, Prasad et al. (2013) suggested that the tooth is probably from the posterior region of the dentary. We fully agree with the evaluation and assignment of this specimen.

6.3.4. Paleogene

Buffetaut (1989) erected *Eremosuchus elkoholicus* from the El Kohol Formation of southwest Algeria (Fig. 12), which is dated to the Ypresian, early Eocene (Coster et al. 2012). This species is known from a partial mandible, teeth, vertebrae, and a fibula. When initially described, *Eremosuchus* was placed in the family Trematochampsidae (Buffetaut 1989), but more recently it has been included in Sebecosuchia by several authors (e.g. Gasparini et al. 1991; Ortega et al. 1996; Turner & Calvo 2005). However, it has not been included in most phylogenetic analyses, presumably because of its incomplete nature, and has largely been neglected in treatments of crocodyliform evolutionary history. A detailed redescription and analysis of the phylogenetic relationships of *Eremosuchus* is needed to establish its systematic and biogeographic affinities.

Finally, the late Eocene Birket Qarun Formation (Seiffert 2006) in northeastern Egypt (Fig. 12) has yielded a fragmentary right dentary with ziphodont dentition (Stefanic et al. 2020). Though not assigned to a genus, the specimen clearly has sebecosuchian affinities and extends the temporal range of Notosuchia in Africa (Stefanic et al. 2020).

6.3.5. Summary

Our review of the Gondwanan record of notosuchians outside of South America demonstrates their spatiotemporal distribution in the Middle Jurassic, from the Aptian–Maastrichtian, and in the Eocene, with their remains known from Africa and Indo-Madagascar. A possible occurrence from the latest Cretaceous of Oman (Buscalioni et al. 2004) cannot be confidently referred to Notosuchia. The African and Indo-Madagascan Cretaceous record indicates the presence of several lineages, all with close ties to South American clades, with many faunas demonstrating multiple sympatric species. Given that notosuchians only first appeared in the Aptian in South America (and Asia), coupled with palaeogeographic reconstructions documenting the increasing fragmentation of Gondwana at this time (e.g. Seton et al. 2012), this diverse record supports previous suggestions regarding an undocumented pre-Aptian radiation of Notosuchia (e.g. Martin and Lapparent de Broin 2016; Mannion et al. 2019). By contrast, their Gondwanan Paleogene record outside of South America is currently limited to just two occurrences, both from the Eocene of north Africa and both belonging to Sebecosuchia. No stratigraphically younger remains have been assigned to Notosuchia from this region, with their last Laurasian occurrences from the middle Eocene of western Europe (e.g. Martin 2016), indicating their extirpation outside of South America by the end of the Eocene.

7. Conclusions

Two new crocodyliform specimens from the Cenomanian Kem Kem Group of Morocco are described and incorporated into a phylogenetic analysis. Both specimens are referrable to *Antaeusuchus taouzensis* n. gen. n. sp., which is recovered within the notosuchian clade Peirosauridae, as the sister taxon to the contemporaneous *Hamadasuchus rebouli*. Comparisons of materials previously assigned to *Hamadasuchus* indicate the presence of at least three distinct peirosaurid species from the same spatiotemporal interval. Coupled with a critical reappraisal of the non-South American Gondwanan record of Notosuchia, we recognise a much greater taxonomic and ecomorphological diversity within this clade during the Cretaceous.

Acknowledgements

We are grateful to Paul Barrett and Susannah Maidment for their help in providing access to NHMUK PV R36829 and R36874, as well as to Kevin Webb for providing photographs of the specimens (all at the Natural History Museum, London). Paul Barrett also provided help with species name formulation. Access to specimens of *Hamadasuchus rebouli* and other peirosaurid material from Morocco was provided by David Evans and Brian Iwama (both Royal Ontario Museum, Toronto), as well as Oliver Rauhut (Bayerische Staatssammlung für Paläontologie und Geologie, Munich), to whom we are also grateful. Photographs of other specimens referred to *Hamadasuchus rebouli* were kindly provided by Diego Pol (Museo Paleontológico Egidio Feruglio, Trelew) including that used in Fig. 10 C. We also acknowledge the Willi Hennig Society, which has sponsored the development and free distribution of TNT. Finally, we are grateful for comments provided by Mario Bronzati and one anonymous reviewer that helped to improve the quality of this manuscript.

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. C.S.C.N and P.D.M. conceived of the study and interpreted the results. All authors contributed to the design of the study and to the drafting of the manuscript. Analyses were conducted by C.S.C.N. Figures were produced by C.S.C.N. and E.S.E.H. All authors approved the final version of the manuscript.

Competing interests. We declare we have no competing interests.

Funding. C.S.C.N. is funded by a Royal Society research grant (RGF\R1\180020) awarded to P.D.M. E.S.E.H. received funding from a Palaeontological Association Undergraduate Research Bursary (PA-UB201804) and her work is supported by a Natural Environment Research Council studentship (NE/S007415/1). P.D.M.'s contribution was supported by grants from the Royal Society (UF160216, RGF\R1\180020, and RGF\EA\201037).

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Tables

Table 1

Mandibular measurements of the holotypic specimen (NHMUK PV R36829) of *Antaeusuchus taouzensis* n. gen. n. sp.

	Dimension (mm)
Maximum mandibular anteroposterior length	415
Maximum mandibular symphysis anteroposterior length	123
Maximum mandibular symphysis mediolateral width	83
Maximum dentary anteroposterior length	371
Maximum dorsoventral height of mandibular ramus	92

Table 2

Tooth and alveolus measurements of the holotypic specimen (NHMUK PV R36829) of *Antaeusuchus taouzensis* n. gen. n. sp.

Tooth position	**Apicobasal length (mm)**	**Alveolar dimension (mm)**			
		Left mandible, anteroposterior length	Right mandible, anteroposterior length	Left mandible, Mediolateral width	Right mandible, Mediolateral width
1	-	11.0	11.5	14.1	14.1
2	-	7.4	7.0	8.7	8.4
3	-	5.0	5.0	5.0	5.4
4	12.1	17.5	12.5	16.0	12.0
5	-	10.0	10.0	10.0	9.5
6	-	5.6	5.5	6.5	7.0
7	-	4.6	5.2	6.8	6.1
8	-		5.1		6.0
9	-	6.6	5.4	6.5	6.2
10	11.0	11.2	11.1	10.5	10.0
11	18.0	14.2	-	13.0	-

12	19.0	15.6	-	12.2	-
13	16.0	23.1	-	16.2	-
14	10.0	14.4	-	11.5	-
15	13.0	13.0	-	8.5	-
16	8.0	10.0	-	7.0	-
17	-	7.0	-	6.0	-
18	-	8.0	-	7.0	-

Table 3

Spatiotemporal distribution and phylogenetic affinities of non-South American, Gondwanan named notosuchian species.

Taxon	**Stratigraphic and geographic provenance**	**Age**	**Phylogenetic position**	**Reference**
Razanandrongobe sakalavae	Isalo IIIB Fm., Madagascar	Bathonian, Middle Jurassic	Sebecosuchia?	Maganuco et al., 2006
Malawisuchus mwakasyungutiensis	Dinosaur Beds Fm., Malawi	Aptian, Early Cretaceous	Basal Ziphosuchia	Gomani, 1997
Stolokrosuchus lapparenti	Elrhaz Fm., Niger	Aptian–Albian, Early Cretaceous	Peirosauridae	Larsson and Gado, 2000
Araripesuchus wegeneri	Elrhaz Fm., Niger	Aptian–Albian, Early Cretaceous	Uruguaysuchidae	Buffetaut, 1981
Anatosuchus minor	Elrhaz Fm., Niger	Aptian–Albian, Early Cretaceous	Uruguaysuchidae	Sereno et al., 2003
Hamadasuchus rebouli	Kem Kem Group, Morocco	Cenomanian, Late Cretaceous	Peirosauridae	Buffetaut, 1994
Lavocatchampsa sigogneaurusselae	Kem Kem Group, Morocco	Cenomanian, Late Cretaceous	Basal Ziphosuchia	Martin and Lapparent de Broin, 2016
Araripesuchus rattoides	Kem Kem Group, Morocco	Cenomanian, Late Cretaceous	Uruguaysuchidae	Sereno and Larsson, 2009
Libycosuchus brevirostris	Bahariya Fm., Egypt	Cenomanian, Late Cretaceous	Basal Ziphosuchia	Stromer, 1914
Kaprosuchus saharicus	Echkar Fm., Niger	Cenomanian, Late Cretaceous	Mahajangasuchidae	Sereno and Larsson, 2009

Rukwasuchus yajabalijekundu	Galula Fm., Tanzania	Cenomanian–Campanian, Late Cretaceous	Peirosauridae	Sertich and O'Connor, 2014
Pakasuchus kapilimai	Galula Fm., Tanzania	Cenomanian–Campanian, Late Cretaceous	Basal Ziphosuchia	O'Connor et al., 2010
Araripesuchus tsangatsangana	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Uruguaysuchidae	Turner, 2006
Simosuchus clarki	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Basal Ziphosuchia	Buckley et al., 2000
Mahajangasuchus insignis	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Mahajangasuchidae	Buckley and Brochu, 1999
Miadanosuchus oblita	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Peirosauridae	Rasmusson Simons and Buckley, 2009
Pabwehshi pakistanensis	Pab Fm., Pakistan	Maastrichtian, Late Cretaceous	Sebecosuchia?	Wilson et al., 2001
Eremosucus elkoholicus	El Kohol Fm., Algeria	Ypresian, early Eocene	Sebecosuchia?	Buffetaut, 1989

Figure captions

Figure 1

Map showing locality of the new fossil remains. White star indicates the approximate geographic position of *Antaeusuchus taouzensis* n. gen. n. sp. (NHMUK PV R36829 and R36874) within the Kem Kem Group of Morocco.

Figure 2

Line drawings and photographs of *Antaeusuchus taouzensis* n. gen. n. sp. (NHMUK PV R36829 [A&C] and NHMUK PV R36874 [B&D]) in right lateral view. Scale bar represents 100 mm.

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Figure 6

Teeth of *Antaeusuchus taouzensis* n. gen. n. sp. A, teeth 12–14 of NHMUK PV R36874. B, tooth 14 of NHMUK PV R36829. Abbreviations: cbc, constricted base of crown; dc, denticulated carina; rre, ridged rugose enamel. Scale bar represents 10 mm.

Figure 7

Strict consensus tree showing the relationships of notosuchians using equal weighting of characters. Numbers at the nodes indicate Bremer support values.

Figure 8

Strict consensus tree showing the relationships of notosuchians using extended implied weighting at *k*-values of 8 and 12. Some clades (Uruguaysuchidae and Ziphosuchia) have been condensed.

Figure 9

Comparison of the dorsal mandibular surfaces of several notosuchians: A, *Antaeusuchus taouzensis* n. gen. n. sp. (NHMUK PV 36829*); B, *Antaeusuchus taouzensis* (NHMUK PV R36874); C, *Montealtosuchus arrudacamposi* (MPMA 16-0007-04*); D, *Gasparinisuchus peirosauroides* (MOZ 1750 PV*); E, *Hamadasuchus rebouli* (ROM 49282); F, *Hamadasuchus rebouli* (MDE C001*); G, *Barrosasuchus neuquenianus* (MCF-PVPH-413*); H, *Araripesuchus rattoides* (CMN 41893*); I, *Bayomesasuchus hernandezi* (MCF PVPH-822). Asterisk indicates a holotype specimen.

Figure 10

Comparison of peirosaurid mandibles from the Kem Kem Group in lateral view: A, NHMUK PV 36829 (*Antaeusuchus taouzensis* n. gen. n. sp. holotype); B, NHMUK PV R36874 (*Antaeusuchus taouzensis* paratype); C, MDEC001 (*Hamadasuchus rebouli* holotype); D, ROM 49282; E, BSPG 2005 I 83. A1–E1 show close-up images of the teeth of each respective taxon. Image B is reversed. Scale bars represent 50 mm.

Figure 11

Time-calibrated phylogenetic topology showing the agreement subtree of notosuchians using equal weighting of characters. Some clades are condensed and the polytomy including *Razanandrongobe sakalavae* is shown despite being pruned from the agreement subtree.

Figure 12

Spatiotemporal distribution of notosuchian occurrences from Africa and Indo-Madagascar. A, Present-day map and stratigraphic column. Stars indicate the location of all named notosuchian taxa. The size of each star is proportional to the number of named taxa at each locality. Circles indicate other remains referred to Notosuchia. B–F, Palaeogeographic reconstructions showing the distribution of notosuchian occurrences for the Middle Jurassic (B), Early Cretaceous (C), early Late Cretaceous (D), late Late Cretaceous (E), and Eocene (F). Plots modified from the Paleobiology Database Navigator (https://paleobiodb.org/navigator/).

Appendix

Character scores modified from the respective matrices of Martínez et al. (2018) and are listed below:

Hamadasuchus rebouli:

103 ? -> 0**;** **363** ? -> 0**;** **365** ? -> 0**;** **383** ? -> 0; **384** ? -> 0; **388** ? -> 0; **389** ? -> 0; **392** ? -> 1; **393** ? -> 0&1; **394** ? -> 0; **443** 0 -> 1

Gasparinisuchus peirosauroides:

443 0 -> 0&1

Montealtosuchus arrudacamposi:

443 0 -> 1

Libycosuchus brevirostris:

441 ? -> 0

Malawisuchus mwakasyungutiensis:
441 ? -> 0

Caipirasuchus stenognathus:

441 ? -> 0

Caipirasuchus montealtensis:

441 ? -> 0

Baurusuchus salgadoensis:

441 ? -> 0

Stolokrosuchus lapparenti:

441 ? -> 0

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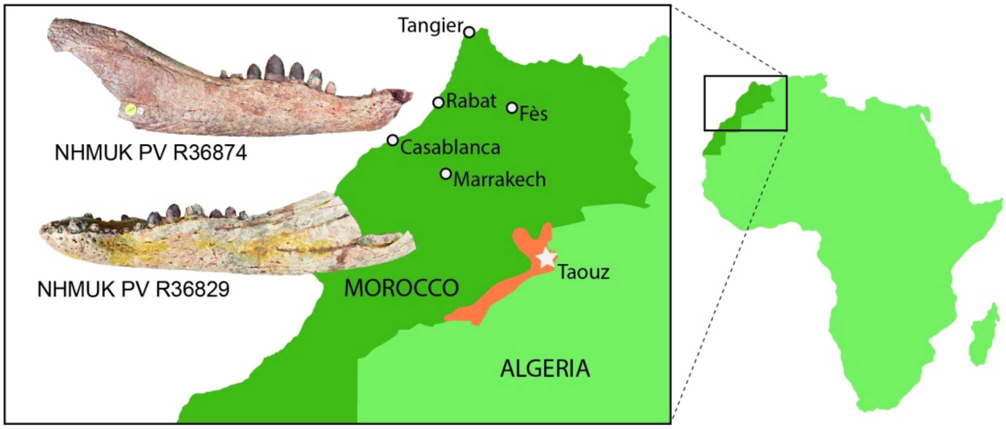

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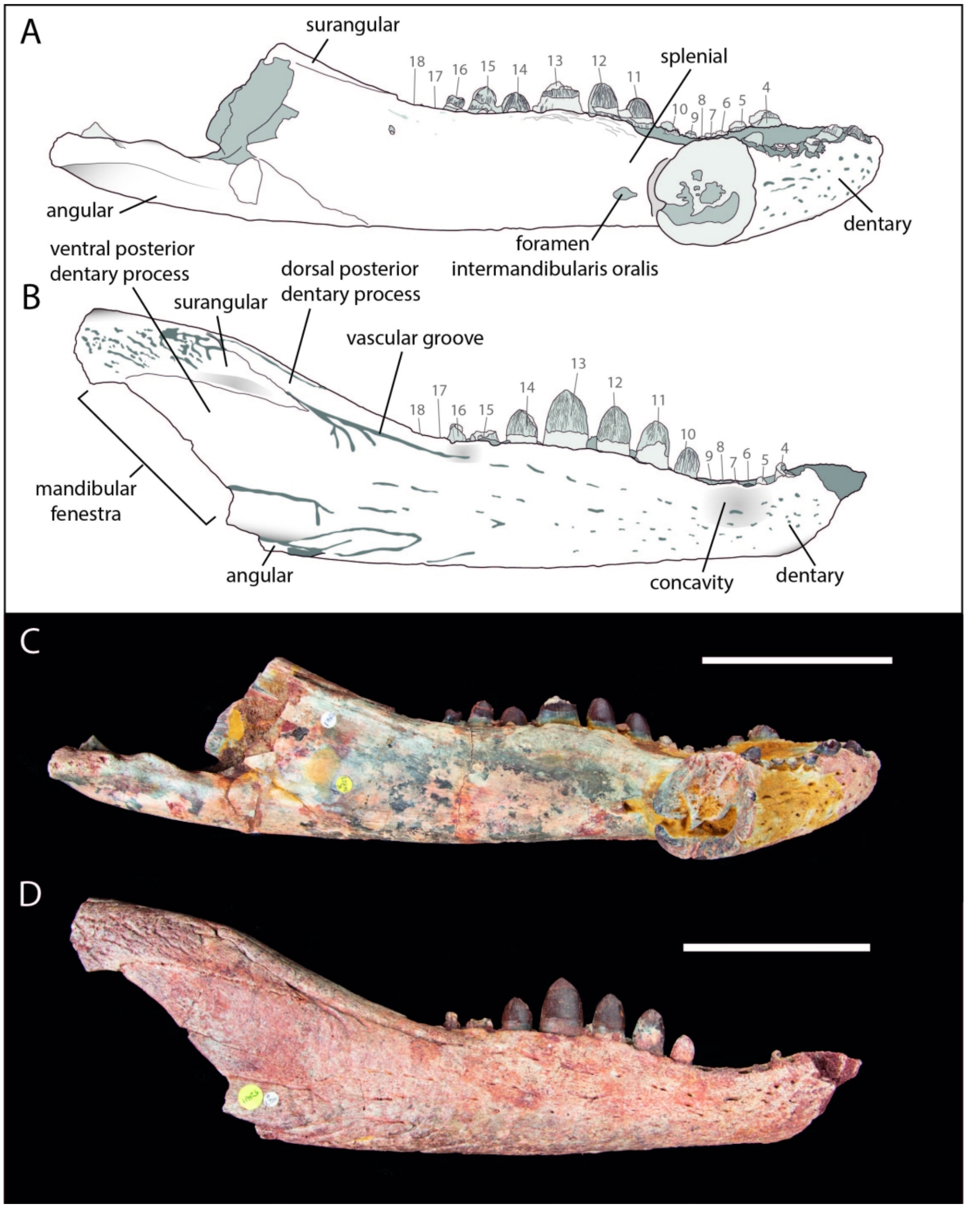
189x83mm (300 x 300 DPI)



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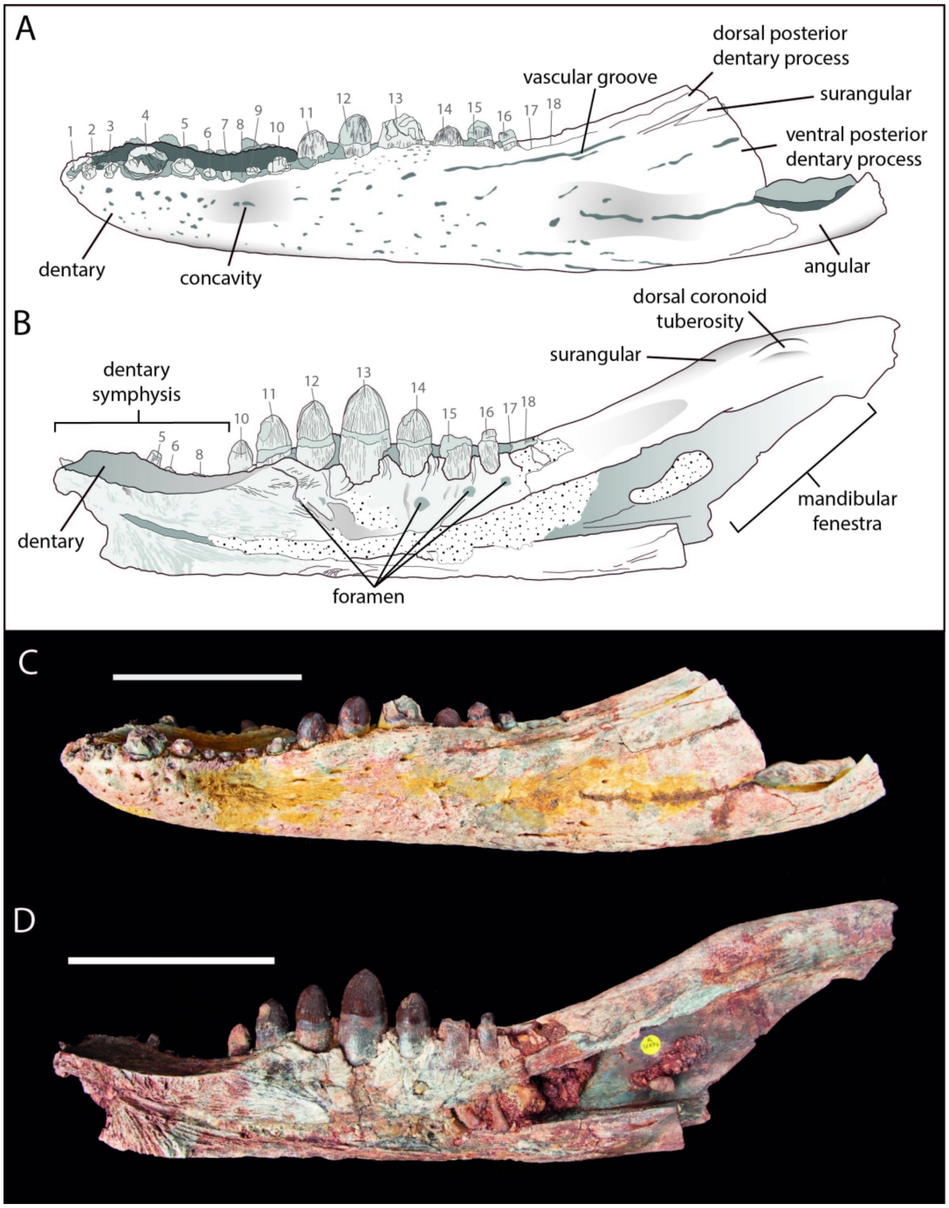

Figure 3
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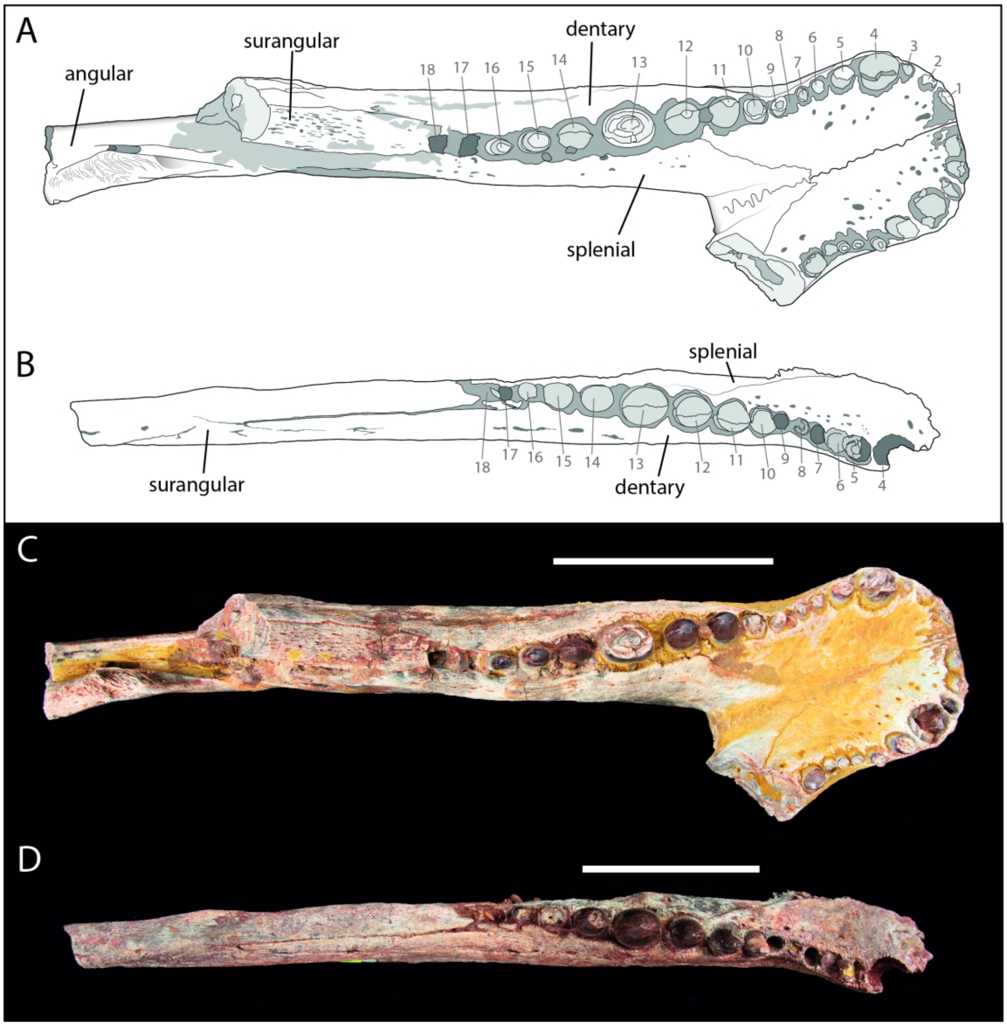

Figure 4
Line drawings and photographs of *Antaeusuchus taouzensis* n. gen. n. sp. (NHMUK PV R36829 [A&C] and NHMUK PV R36874 [B&D]) in dorsal view. Scale bar represents 100 mm.

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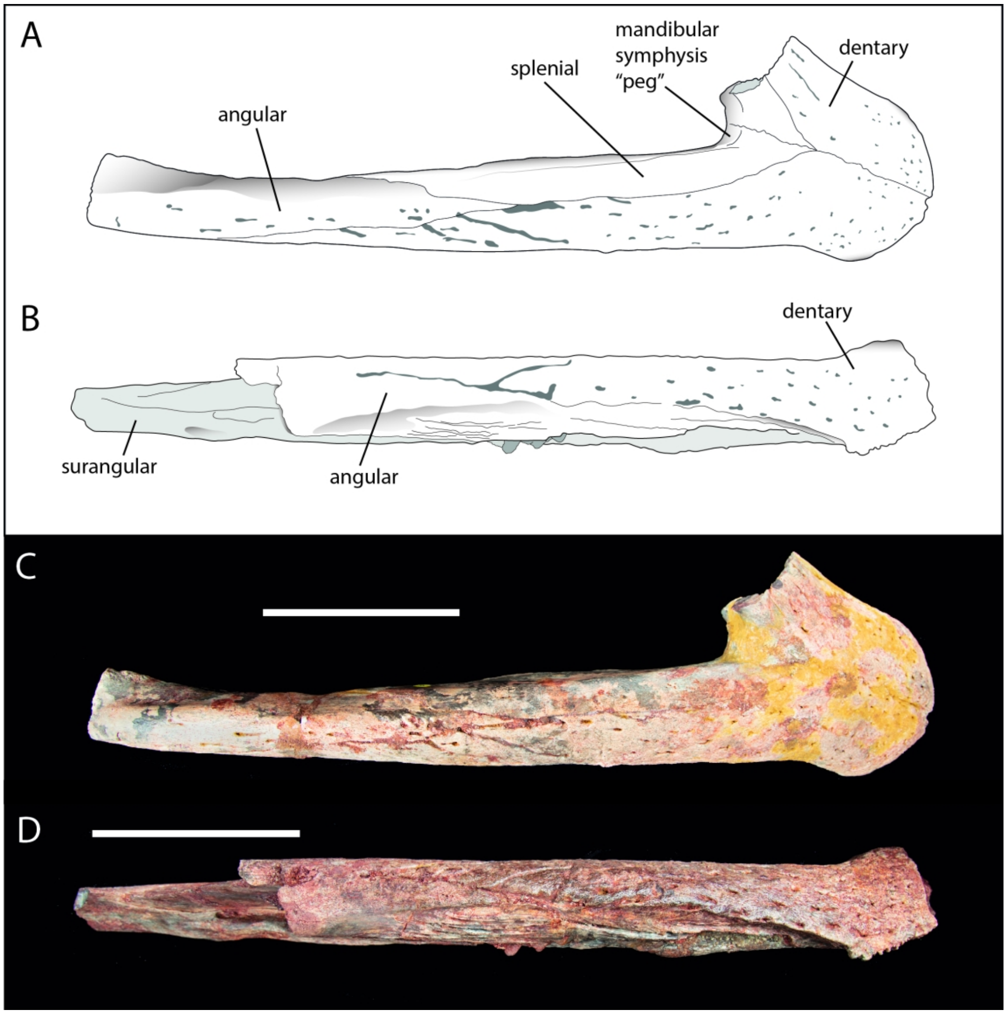

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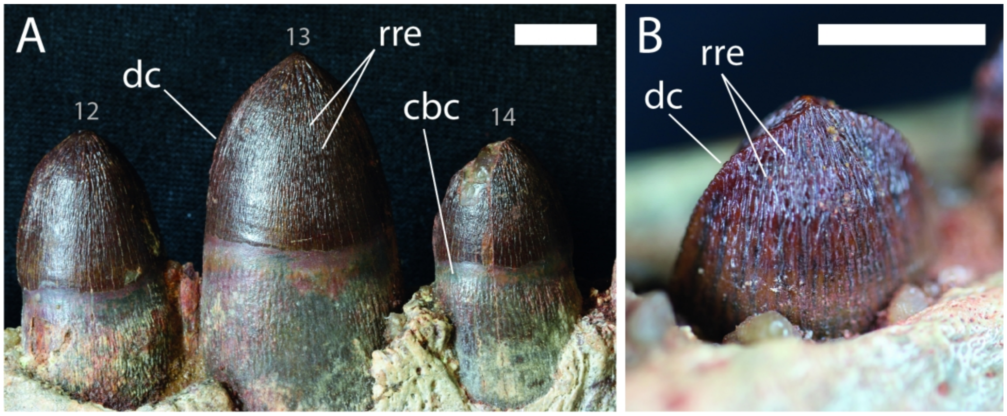

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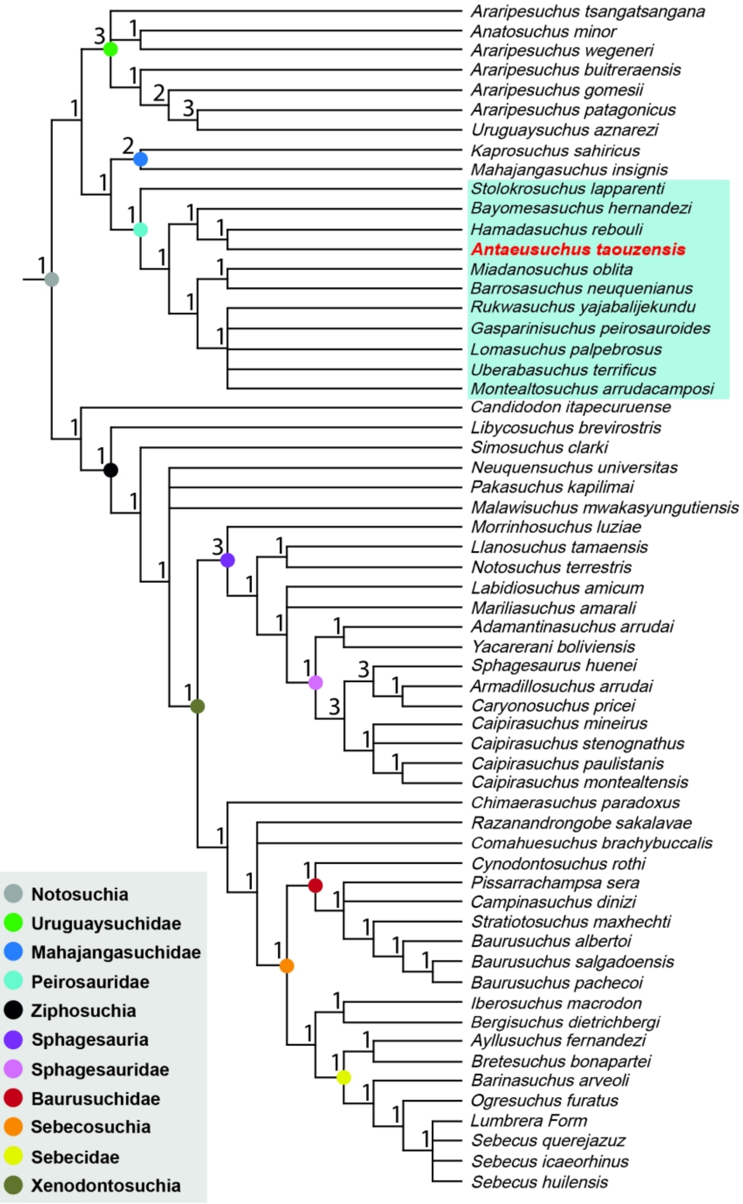
188x77mm (300 x 300 DPI)



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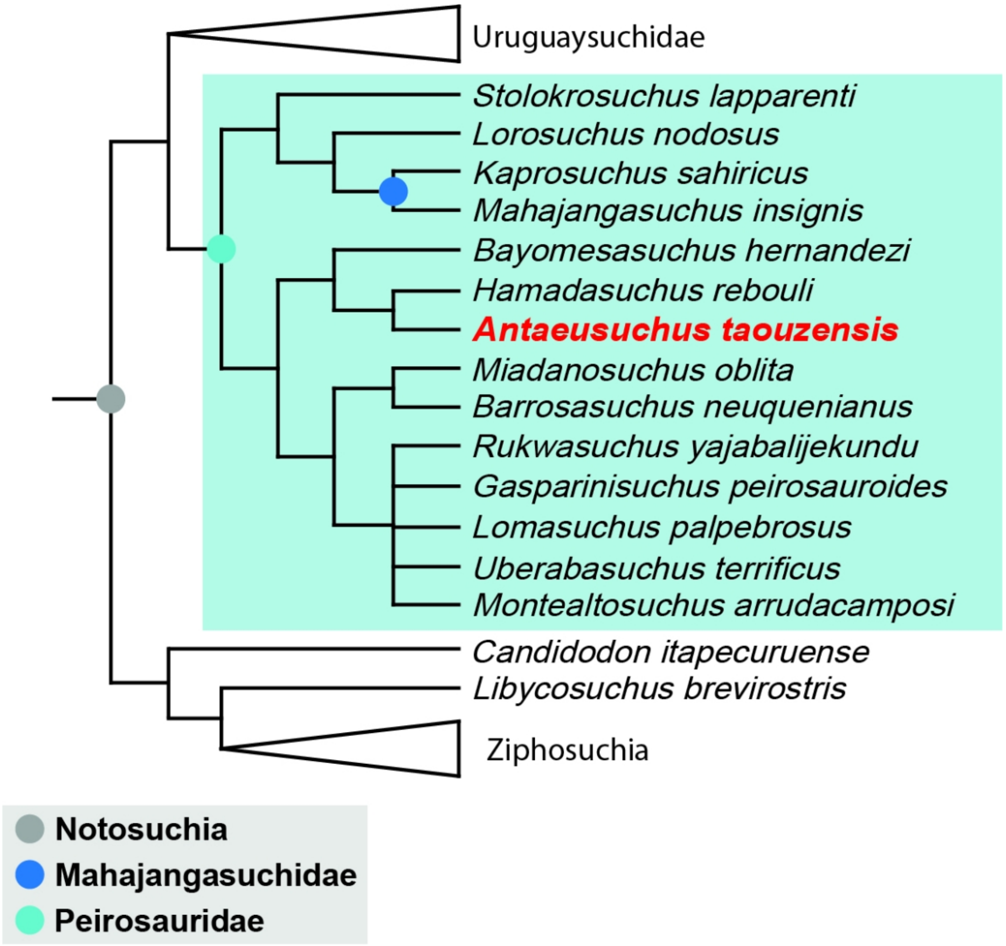

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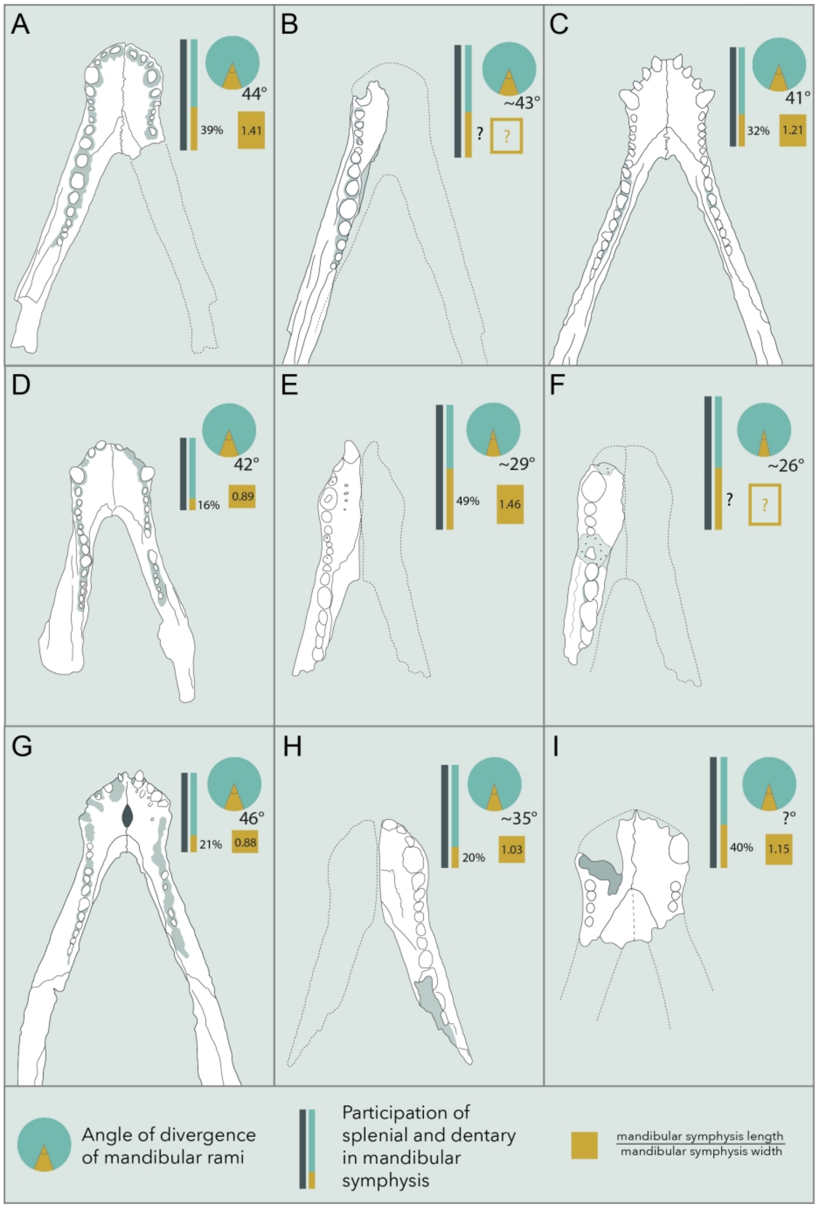
99x93mm (300 x 300 DPI)



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Comparison of the dorsal mandibular surfaces of several notosuchians: A, *Antaeusuchus taouzensis* n. gen. n. sp. (NHMUK PV 36829*); B, *Antaeusuchus taouzensis* (NHMUK PV R36874); C, *Montealtosuchus arrudacamposi* (MPMA 16-0007-04*); D, *Gasparinisuchus peirosauroides* (MOZ 1750 PV*); E, *Hamadasuchus rebouli* (ROM 49282); F, *Hamadasuchus rebouli* (MDE C001*); G, *Barrosasuchus neuquenianus* (MCF-PVPH-413*); H, *Araripesuchus rattoides* (CMN 41893*); I, *Bayomesasuchus hernandezi* (MCF PVPH-822). Asterisk indicates a holotype specimen.

185x270mm (300 x 300 DPI)

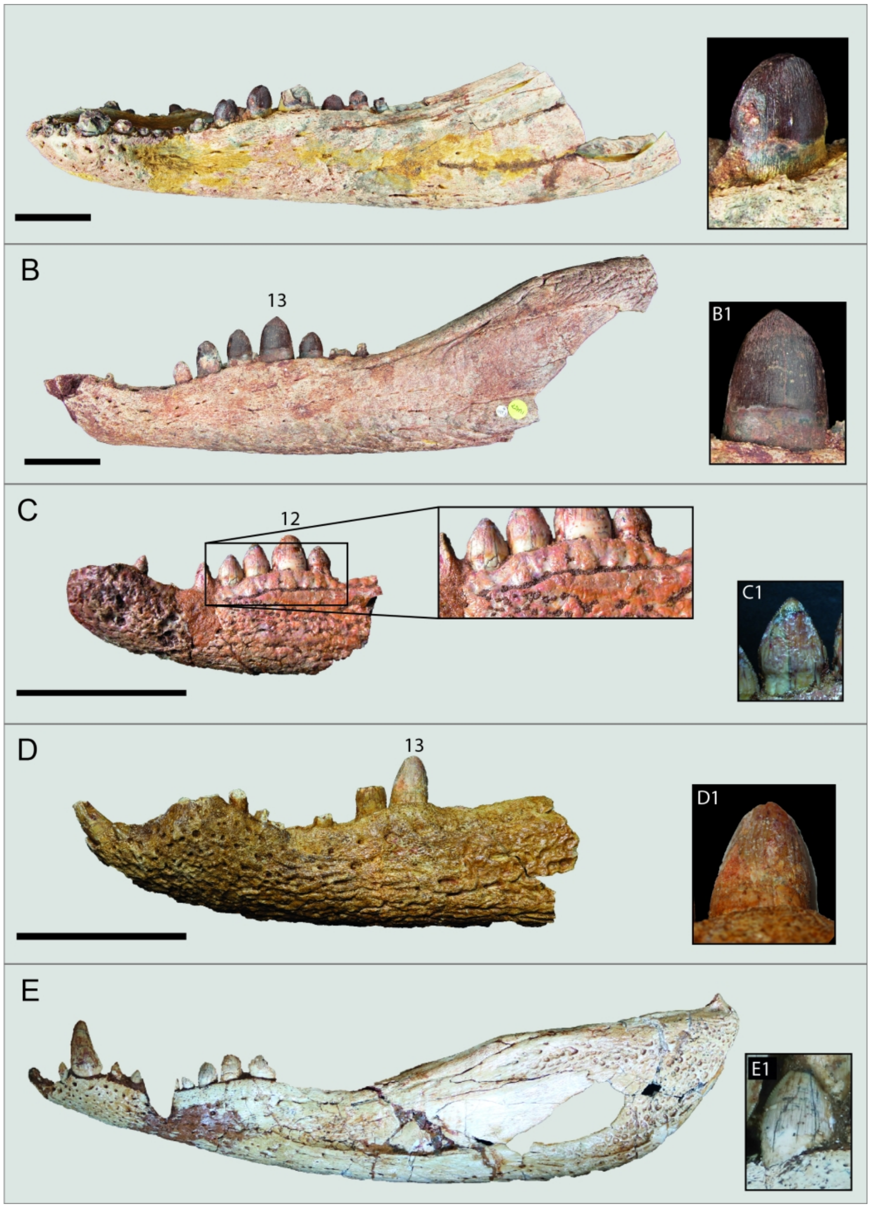

Figure 10
Comparison of peirosaurid mandibles from the Kem Kem Group in lateral view: A, NHMUK PV 36829 (*Antaeusuchus taouzensis* n. gen. n. sp. holotype); B, NHMUK PV R36874 (*Antaeusuchus taouzensis* paratype); C, MDEC001 (*Hamadasuchus rebouli* holotype); D, ROM 49282; E, BSPG 2005 I 83. A1–E1 show close-up images of the teeth of each respective taxon. Image B is reversed. Scale bars represent 50 mm.

182x253mm (300 x 300 DPI)

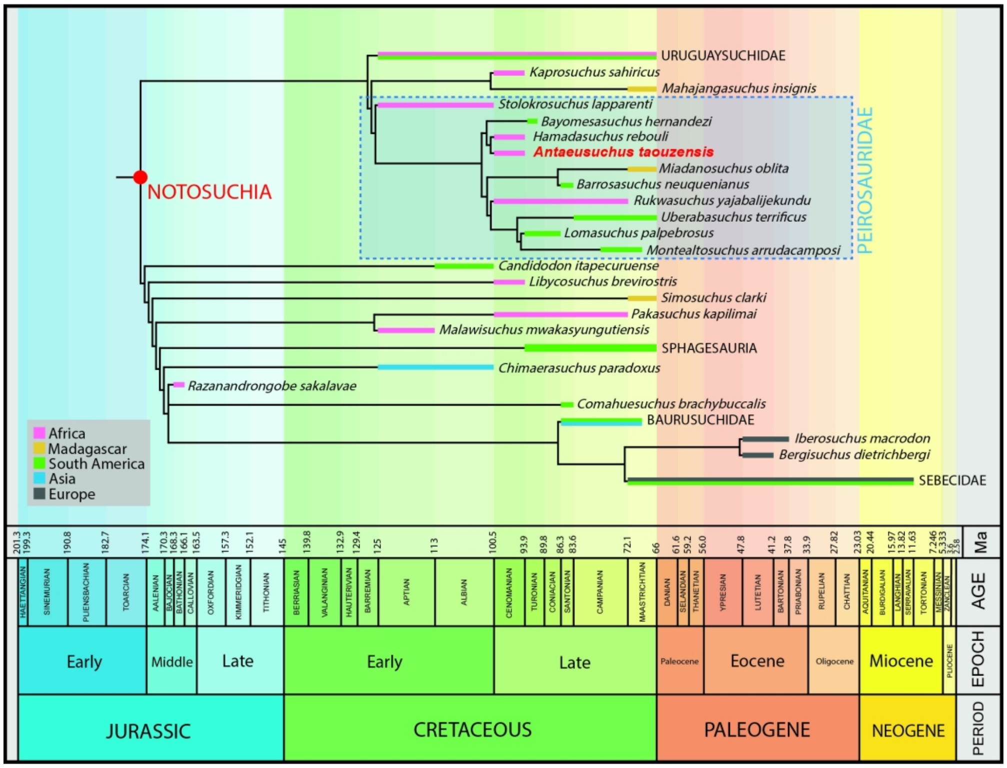

Figure 11
Time-calibrated phylogenetic topology showing the agreement subtree of notosuchians using equal weighting of characters. Some clades are condensed and the polytomy including Razanandrongobe sakalavae is shown despite being pruned from the agreement subtree.

198x150mm (300 x 300 DPI)

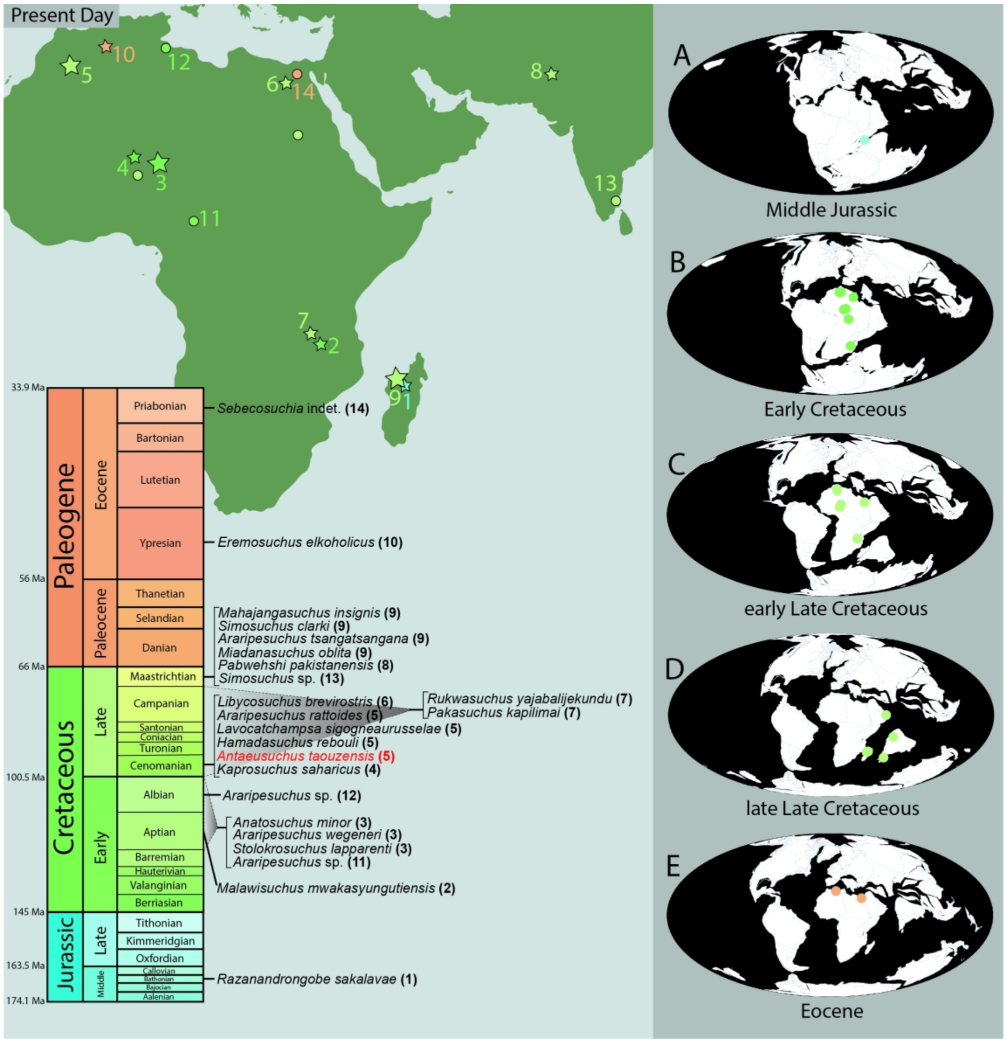

Figure 12

Spatiotemporal distribution of notosuchian occurrences from Africa and Indo-Madagascar. A, Present-day map and stratigraphic column. Stars indicate the location of all named notosuchian taxa. The size of each star is proportional to the number of named taxa at each locality. Circles indicate other remains referred to Notosuchia. B–F, Palaeogeographic reconstructions showing the distribution of notosuchian occurrences for the Middle Jurassic (B), Early Cretaceous (C), early Late Cretaceous (D), late Late Cretaceous (E), and Eocene (F). Plots modified from the Paleobiology Database Navigator (https://paleobiodb.org/navigator/).

204x210mm (300 x 300 DPI)