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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**

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Manuscripts

**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  $\alpha$ -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

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3 specimen, we provide the definition we have used for Peirosauridae, within which  
4 *Antaeosuchus* is recovered. We believe that the specific clades used throughout the  
5 manuscript are standard, widely used terminology used by authors working on this topic,  
6 and are not especially pertinent to the key focus of the paper. It is our understanding that  
7 explicit clade definitions are not usually required for work such as this. Furthermore, there is  
8 only currently a single proposed phylogenetic definition for Notosuchia, Ziphosuchia, and  
9 Metasuchia, and these have been in usage for most of the last two decades.  
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14 **3) Although it is not particularly relevant, the revised phylogeny presented by the MS is**  
15 **not the largest notosuchian-focused character-taxon matrices yet to be compiled.**  
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17  
18 The text states that the matrix is “one of the largest” rather than “the largest” which we  
19 believe to be true given the high degree of character and taxon sampling, and our particular  
20 focus on including more peirosaurid taxa. As such, we have made no changes in response to  
21 this comment.  
22  
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25 **4) We have proposed a phylogenetic definition for Notosuchia in our paper (Ruiz, et al.**  
26 **2021), perhaps include it on the Systematic Palaeontology section.**  
27  
28

29 As mentioned above, the aim of this paper is to present a new crocodylomorph specimen,  
30 not to review broader notosuchian taxonomy. We do not believe the inclusion of  
31 phylogenetic definitions of all clades relating to notosuchians to be standard procedure in  
32 work such as this. Furthermore, the definition of Notosuchia in that paper is identical to the  
33 original phylogenetic definition provided by Sereno et al. (2001).  
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38 **5) In relation to the anatomy of *Antaeosuchus*, I suggest the authors to take a look on**  
39 **Pinheiro’s et al. (2020, Plos One) description of the enamel of *Roxochampsa*.**  
40

41 The paper suggested by the reviewer describes a Late Cretaceous Brazilian notosuchian,  
42 which was recovered outside of Peirosauridae. In our manuscript, detailed comparisons  
43 with other crocodylomorphs are restricted to Peirosauridae given the position recovered by  
44 *Antaeosuchus* in our phylogenetic analyses. As such, we feel it is unnecessary to include text  
45 regarding *Roxochampsa* within the manuscript based on its recovery in a different clade and  
46 lack of spatiotemporal overlap. If the reviewer is suggesting potential similarities between  
47 the two taxa, we note that the enamel in *Roxochampsa* differs from that of *Antaeosuchus* in  
48 several aspects, most notably in that the apicobasal enamel ridges are themselves  
49 crenulated along their length. As such, we have not added in comparisons to this taxon.  
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54 **6) Which are the parameters used during sectorial searches, drift and tree fusing?**  
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57 We have modified the text to confirm the exact parameters used during our analyses. These  
58 sections have been highlighted in the marked-up draft.  
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4 **7) I did not understand what the authors mean when they say that *Uberabasuchus* can be**  
5 **used as a proxy for *Peirosaurus*?**  
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8 We described in the preceding sentence how *Uberabasuchus terrificus* has been  
9 consistently recovered as a close relative of *Peirosaurus torminni*, with some authors  
10 regarding the latter as a junior synonym of the former (e.g. Larsson & Sues 2007; Martinelli  
11 et al. 2012). As such, we think the existing text is clear and explicit in terms of what we  
12 mean, i.e. “Although *Peirosaurus torminni* is not included in our data matrix, *Uberabasuchus*  
13 *terrificus* has been consistently recovered as a close relative, with some authors regarding  
14 the latter as a junior synonym of the former (e.g. Larsson & Sues 2007; Martinelli et al.  
15 2012). As such, we regard the *Uberabasuchus* OTU as a proxy for *Peirosaurus* in terms of  
16 identifying Peirosauridae.”  
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21 **8) In the discussion about the multicuspid teeth described by Larsson & Sidor (1999), I**  
22 **suggest the authors to also take a look on the papers by Montefeltro et al. (2009) and**  
23 **Pinheiro et al. (2021, *Coronelsuchus*).**  
24  
25

26 The paper by Montefeltro et al. (2009) describes six multicuspid teeth from the Upper  
27 Cretaceous of Brazil. Though similar in broad morphology to those described from Morocco,  
28 the authors note that they are “not related to two unnamed forms” from the Kem Kem  
29 beds. Pinheiro et al. (2021) also describe a notosuchian with heterodont, multicuspid  
30 dentition from the Bauru Basin of Brazil. Although both papers describe multicuspid teeth,  
31 this is not a particularly unusual morphology amongst notosuchians. The condition is more  
32 widespread than the papers mentioned by the reviewer and so it is unclear why these two  
33 precisely have been chosen. We refrain from including these specific examples in this work  
34 as our review focuses on the Gondwanan record outside of South America.  
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40 **9) The reference Evans et al. 2014 cited in the text is not listed. There is a reference cited**  
41 **as Montefeltro et al. (2019). I guess it is Montefeltro (2019, JVP) or Montefeltro et al.**  
42 **(2020, J. Anato).**  
43  
44

45 We have added the appropriate citations to the manuscript. The latter has been corrected  
46 to Montefeltro et al. (2020) in the References.  
47  
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49

50 **Reviewer 2:**  
51

52 **1) The authors used two different protocols for their phylogenetic analyses, one**  
53 **employing equally weighting of characters, and the other employed the extend implied**  
54 **weighting protocol. I do think it is interesting to see the results using two alternative**  
55 **weighting methods. However, if two alternative methods are used in the paper, I think that the**  
56 **authors should then explain if they prefer any of the methods employed. If they do prefer**  
57 **one of the two methods, justify. If no, just mention that you are using different methods**  
58 **because there is no study so far that says that we should ‘definitely’ opt for one instead of**  
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3 **the other. In this context, sentence like “we applied extend implied weighting to**  
4 **notosuchians for the first time’ are not very relevant, especially when the authors use the**  
5 **phylogeny obtained from their analysis using equal weighting in their Figure 11. In this**  
6 **case, I think there should be a justification for the reason why you selected the equal**  
7 **weighting analysis for this figure.**  
8  
9

10 We are pleased to hear that the reviewer is interested to see the results of the alternative  
11 methods in this paper. Goloboff (2014; 2017) described the potential benefits of using  
12 extended implied weighting on morphological datasets, and several recent neosuchian-  
13 focused studies (e.g. Groh et al. 2020; Rio et al. 2020; Rio and Mannion 2021) also show that  
14 analyses run using extended implied weighting (EIW) score higher in measures of  
15 phylogenetic accuracy. We do not “prefer” any particular method, nor do we analyse the  
16 benefits and pitfalls of each as it is beyond the remit of this paper. We do, however, think  
17 that it is important to mention that the method has not yet been used on notosuchians  
18 given the discrepancies seen in tree topologies between both methods. Given that we do  
19 not have a preferred analysis, the method used to illustrate the tree in Figure 11 is not  
20 important: given that our analyses had broadly congruent results we merely chose to  
21 represent one tree as a time calibrated figure given that both are already figured as  
22 cladograms.  
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29 **2. The authors did a good job in providing comparisons between the new species with**  
30 **other peirosaurids. Also, by the end of this section, they list the differences the**  
31 **differences between Antaeusuchus and the other peirosaurids from the Kem Kem,**  
32 **Hamadasuchus. The authors mention that one of the differences is that specimens**  
33 **assigned to Antaeusuchus are much larger than species assigned to Hamadasuchus. Thus, I**  
34 **think that an interesting addition to their study would be to try ruling out the possibilities**  
35 **that the differences between Antaeusuchus and Hamadasuchus are not related to**  
36 **ontogeny – i.e. that individuals of Antaeusuchus do not correspond to larger individuals of**  
37 **Hamadasuchus. I’m not sure it is possible to check this for all the different characteristics**  
38 **they mentioned based on the differences observed in extant crocodylians – but anyway,**  
39 **this might strength their argument to separate the two species.**  
40  
41  
42

43 We agree with the reviewer that this would be an interesting aspect to include in the study.  
44 Griffin et al. (2020) suggested that the best measure of ontogeny in crocodylomorphs can  
45 be ascertained from long bone histology and neurocentral fusion in vertebrae, neither of  
46 which are applicable in this paper given the preserved material. The sister taxon to  
47 *Antaeusuchus*, and therefore potentially the best proxy for evaluating ontogenetic changes  
48 in the new specimens, *Hamadasuchus rebouli* is known from several specimens that are  
49 described by Larsson & Sues (2007) as representing an ontogenetic series. Within the paper  
50 they refer to several morphological differences that are evident between the various growth  
51 stages. These almost entirely relate to the cranium (e.g. the reduction of a sagittal crest on  
52 the frontoparietal suture, the reduction of medial rims of the supratemporal fenestra, and  
53 the reduction of a crest on the posterodorsal surface of the quadrate), and thus are not  
54 helpful in assessing the growth stage of the *Antaeusuchus* mandible. The final morphological  
55 feature mentioned by Larsson & Sues (2007) relates to shape changes in the posterior  
56 dentary teeth, and describes a change from more gracile, labiolingually compressed  
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3 morphology to more robust, wider teeth in relatively mature individuals. The teeth in  
4 *Antaeusuchus* are actually closer in diameter to the less mature specimens of  
5 *Hamadasuchus*, going some way to ruling out that the former is a more mature than the  
6 latter. Though we understand the reviewer's concerns about using size as a justification for  
7 the erection of a new species, *Antaeusuchus* is significantly larger than even the largest of  
8 all known specimens referred to *Hamadasuchus*, which is already known from an  
9 ontogenetic series Larsson & Sues (2007). We agree that as a sole comparison, size would  
10 be an insufficient reason to justify a new species, but as part of a large, unique combination  
11 of morphological features, we believe it to be a valid difference. A paragraph explaining this  
12 has been added to the text.  
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18 **3. I have mixed feelings about the last section of the discussion, which brings a revision of**  
19 **the notosuchians outside South America. Whereas I think it is interesting to see this kind**  
20 **of information compiled in a single study, I do not think that the authors used the**  
21 **information already available in the literature in order to provide any new insight on the**  
22 **evolution of African notosuchians. For example, the section dealing with the presence of**  
23 ***Razanandrongo* in the Middle Jurassic of Madagascar brings no novel information that**  
24 **is worth being included in the discussion section of this manuscript. In sum, there is not**  
25 **much of new insights or new perspectives in all the sections of this part of the discussion**  
26 **that would justify the inclusion of this part of the manuscript together with the**  
27 **description of the new taxon and discussions on the phylogenetic analysis of peirosaurids.**  
28 **For example, section 6.3.5 would better fit as part of an introduction of a manuscript on**  
29 **the fossil record of notosuchians.**  
30  
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33

34 We believe that a revision of Gondwanan notosuchians outside of South America is an  
35 integral part of this manuscript. We provide the first ever comprehensive overview of all  
36 notosuchians from this region, several of which we reidentify. Our reappraisal deals with  
37 multiple putative remains, the assignment of which will significantly affect the outcome of  
38 macroevolutionary studies for notosuchians outside of South America. In terms of  
39 biogeography, the notosuchian record from the Arabian Peninsula is removed. Furthermore,  
40 the review provides updated stratigraphic information which is often missed by many  
41 authors. As such, we strongly disagree with the reviewer and have retained this section.  
42  
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## 47 **Comments from Reviewer 2 provided in the attached PDF:**

48  
49  
50 **1. Please add dates in millions of years - this will facilitate readers to locate themselves in**  
51 **geologic time.**  
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54 We have included all relevant dates within the abstract as well as at their first mention in  
55 the main body of text.  
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3 **2. In the way that it is written, it seems that an analysis of the fossil record is what**  
4 **indicates that *Miadanosuchus* might be a peirosaurid. Is that really what is intended to be**  
5 **said here? My view is that only a phylogenetic analysis can indicate the phylogenetic**  
6 **affinities of a taxon.**  
7  
8

9 The wording has been altered to reflect the role of phylogenetic analyses in the designation  
10 of *Miadanosuchus* as a peirosaurid as opposed to solely the reappraisal of the non-South  
11 American notosuchian record.  
12  
13

14  
15 **3. Usually, I like to see a final sentence wrapping up the main point of the manuscript, and**  
16 **also bringing some directions for future studies. The authors might want to consider to**  
17 **include something like this to the abstract.**  
18  
19

20 We feel that the abstract as a whole does a sufficient job of summarising the main points of  
21 the manuscript and so we refrain from adding a further sentence, especially given that we  
22 were already at the word limit in our original submission. Furthermore, our entire abstract  
23 summarises our study – having a final sentence that summarises the abstract seems  
24 somewhat redundant. A future studies section is not needed and we have already noted  
25 several things that need doing in the existing text (e.g. revision of *Hamadasuchus*).  
26  
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29

30 **4. You can also cite Ruiz et al. 2020 here.**  
31

32 Requested citation has been added to the text.  
33  
34  
35

36 **5. What do you mean by apparent diversity here? Number of known species? Please**  
37 **specify.**  
38  
39

40 Text has been clarified to indicate that we are referring to the raw number of species.  
41  
42  
43

44 **6. Could you indicate where each wave starts and ends?**  
45

46 Information regarding the positioning of the waves has been added.  
47  
48  
49

50 **7. Is it possible that the suture extends further posteriorly? Are the splenials overlapping**  
51 **the dentaries in this region?**  
52

53 We have not amended this section as it simply describes the dentary suture visible in dorsal  
54 view. The suture is seen to extend to the 8<sup>th</sup> tooth in specimen PV R36829, and its shape can  
55 also be inferred in PV R36874. On the ventral surface the dentary extends to the 7<sup>th</sup>/8<sup>th</sup>  
56 teeth. The exposure of the suture in medial view in PV R36874 indicates that the suture did  
57 not extend further posteriorly due to intrusion of the splenials between the dentaries.  
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4 **8. These two processes, the one forming the dorsal margin of the mandibular fenestra and**  
5 **the one dorsal to it, are they really processes or is it just the case that the surangular is**  
6 **overlapping the dentary in this region?**  
7  
8

9 Although the surangular does marginally overlap the dentary as scored in character 366, an  
10 oblique suture can be seen in both lateral and medial view indicating that these are distinct,  
11 separate processes rather than superficial ones formed just by a surangular process  
12 overlapping the dentary.  
13  
14

15  
16 **9. It would be great to have these processes labelled in the figure.**  
17  
18

19 As requested, the posterior processes have been labelled in figures 2 and 3.  
20  
21

22  
23 **10. However, shouldn't it be three processes, as you consider as the process ventral to the**  
24 **mandibular fenestra as a posterior process as well?**  
25

26 The addition of this text clarifies the specific processes we are referring to. The “third”  
27 process is described later in the text and is not referred to here as it cannot be considered  
28 “major”, forming only a short protrusion.  
29  
30

31  
32 **11. I suggest changing to: and occupy approximately 38% of the anteroposterior**  
33 **symphyseal length on the dorsal surface of the mandible.**  
34  
35

36 The text has been changed as requested.  
37  
38

39  
40 **12. On the ventral surface.**  
41

42 The text has been changed as requested.  
43  
44

45  
46 **13. It is better to cite the work of Lordansky, cited in Larsson & Sues, than to cite the**  
47 **latter. Should then change the sentence slightly - likely homologous the foramen**  
48 **intermandibularis oralis of living crocodylians.**  
49

50 We have cited Lordansky (1973), and have changed the text as requested.  
51  
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53  
54 **14. I couldn't see it on the figures.**  
55

56 A label has been added to figures 2 and 3.  
57  
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3 **15. For the angular and some of the other bones previously described, I missed a more**  
4 **general description of each bone, detailing the general shape of the bone and indicating**  
5 **the bones that it contacts.**  
6  
7

8 We have added in several additional descriptions of general morphology; however, we feel  
9 that we have already been fairly consistent with describing the contact between bones.  
10  
11

12  
13 **16. I think that if you are using a whole new section for the description of the mandibular**  
14 **fenestra, you could provide some more details, even if it is incomplete. For example, is it**  
15 **possible to add some relative measurements to the description of this structure?**  
16  
17

18 We have added in an additional comment although refrain from too many descriptions  
19 given the fragmentary nature of the fenestra.  
20  
21

22  
23 **17. Which are the parameters used during sectorial searches, drift and tree fusing?**  
24

25 Precise parameters have been included.  
26  
27

28  
29 **18. Not necessary to include this. Just cite Goloboff.**  
30

31 We have kept this text as we feel that it provides an overview of the benefits of using  
32 extended implied weighting on a dataset, especially as the method has not previously been  
33 applied to notosuchian crocodylomorphs. We do not believe that the inclusion of the text  
34 detracts from the manuscript in any way.  
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38  
39 **19. A better approach would be to try different values of 'k' instead of adopting the values**  
40 **from previous studies.**  
41

42 We selected these specific values as previous studies (e.g. Goloboff et al. 2017) have  
43 indicated that lower values of  $k$  can be excessive in downweighting putative homoplastic  
44 characters. Despite extended implied weighting never having been used before in a  
45 notosuchian-focused matrix, such effects can be seen in datasets for neosuchian  
46 crocodylomorphs (e.g. Rio & Mannion 2021) in which low  $k$ -values consistently produce  
47 trees that score poorly in measures of phylogenetic accuracy. Whilst attempting to avoid  
48 lower values of  $k$ , we still undertake multiple analyses to determine the possible impact of  
49 different  $k$ -values.  
50  
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52

53 **20. If a taxon is included in the matrix, I think that it also should be included in the**  
54 **analyses. So, you should either show the topology of the strict consensus with these**  
55 **unstable taxa, or simply generate a reduced consensus tree using the prunnelsen**  
56 **command (Goloboff & Szumik, 2015 or 2016). I think that the last option is more**  
57 **appropriate because it shows where these problematic taxa are floating on your tree.**  
58  
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3 We refrain from changing the analysis on the basis that if these taxa were not included  
4 within the matrix at all then the issue would not have been raised. We are unaware of a  
5 similar paper which includes all described species of notosuchian. We therefore follow the  
6 recommendations of Pol et al. (2014) to exclude this taxa.  
7  
8

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

10  
11 Precise parameters have been included.  
12  
13

14  
15 **22. This should be tree length - not branch length.**

16  
17 Changed as requested.  
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21 **23. I think it will be easier to follow the results if you already mention the phylogenetic**  
22 **definition here.**

23  
24  
25 The definition is written out later on in a separate section of text relating to peirosaurids,  
26 and therefore we refrain from including it here. We feel that writing the full definition of  
27 clades in this section of the manuscript would potentially make the text harder to follow,  
28 especially given that these are generally widely used clade terms in notosuchian-focused  
29 literature.  
30  
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33 **24. How did you recover this? You used the prunnelsen command or you removed**  
34 ***Gasparinisuchus* and ran a new analysis? Please indicate that.**

35  
36  
37 *Gasparinisuchus* was removed from the analysis in the agreement subtree.  
38  
39

40  
41 **25. I'm not very convinced that you can use this characteristic for comparisons between**  
42 ***Antaeusuchus* and other taxa, because it is not entirely preserved in the former.**

43  
44  
45 We still include this morphology in our comparisons, as despite the fenestra being  
46 incomplete in either single specimen, the majority of its border is preserved across both  
47 NHMUK PV R36829 and R36874. In both specimens the preserved margins indicate that the  
48 opening is clearly larger than in *Barrosasuchus* with which it is compared.  
49  
50

51  
52 **26. I think that in this case, you should score your taxon with '?' rather than 1 and 2.**

53  
54  
55 We have chosen not to alter the score to '?' as the splenial is clearly elongate and would be  
56 scored for either state 1 or 2 if complete. We feel in this instance it is better to score for  
57 either scenario rather than to exclude morphological information. Furthermore, the  
58 character construction needs to be addressed given the large gap between states 1 and 2,  
59 however, this is beyond the scope of this paper.  
60

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6 **27. Don't you think that this polymorphism could also exist in specimens assigned to**  
7 ***Hamadasuchus*?**  
8

9  
10 There is definitely variation amongst taxa referred to *Hamadasuchus*, as discussed in our  
11 comparisons section. Given the character state boundaries for character 77, we felt it best  
12 to provide a detailed account of the measurements in each specimen. A comprehensive  
13 review of notosuchian characters would help to produce definite scores for many taxa with  
14 polymorphic scoring; However, this is not the aim of the paper.  
15  
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18 **28. That is not necessarily true - you should remove this sentence.**  
19

20 We have removed the sentence as requested.  
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3 **A second peirosaurid crocodyliform from the mid-Cretaceous Kem Kem Group**  
4 **of Morocco and the diversity of Gondwanan notosuchians outside South**  
5 **America**  
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40 RRH: SECOND MOROCCAN PEIROSAURID

41 LRH: NICHOLL, HUNT, OUARHACHE & MANNION  
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## 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; Ósi 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

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

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12 The Kem Kem crocodyliforms comprise the neosuchians *Aegisuchus witmeri*  
13 (Holliday & Gardner 2012), *Elosuchus cherifiensis* (Lavocat 1955; Lapparent de  
14 Broin 2002), and *Laganosuchus maghrebensis* (Sereno & Larsson 2009), as well as  
15 three notosuchians (Ibrahim et al. 2020). The first of these notosuchians to be  
16 named, the peirosaurid *Hamadasuchus rebouli* (Buffetaut 1994), was erected based  
17 on a fragmentary dentary. Several specimens have since been referred to this taxon,  
18 including a nearly complete cranium and lower jaws (Larsson & Sidor 1999; Rauhut  
19 & López-Arbarello 2006; Larsson & Sues 2007; Ibrahim et al. 2020). Sereno &  
20 Larsson (2009) described a second Kem Kem notosuchian species, the small-bodied  
21 uruguaysuchid *Araripesuchus rattoides*, which is currently known from several  
22 dentaries (Ibrahim et al. 2020). The third notosuchian species to be described, the  
23 candidodontid *Lavocatchampsa sigogneaurussellae* (Martin & Lapparent de Broin  
24 2016), is known from a small partial skull with unusual mammal-like multicuspid  
25 teeth. Ibrahim et al. (2020) suggested that multicuspid crocodyliform teeth described  
26 by Larsson & Sidor (1999) might represent additional notosuchian taxa. Finally,  
27 Ibrahim et al. (2020) also noted anatomical differences between the type and  
28 referred material of *Hamadasuchus* that could indicate yet higher crocodyliform  
29 diversity in the Kem Kem Group.

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



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3 **1.1. Institutional abbreviations** — **BSPG**, Bayerische Staatssammlung für  
4 Paläontologie und Geologie, Munich, Germany; **CMN (formerly NMC)**, Canadian  
5 Museum of Nature, Ottawa, Canada; **MDE**, Musée des Dinosauriens, Espéraza,  
6 France; **MNHM**, Muséum national d'Histoire naturelle, Paris, France; **NHMUK**,  
7 Natural History Museum, London, UK; **ROM**, Royal Ontario Museum, Toronto,  
8 Canada.  
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## 14 **2. Systematic Palaeontology**

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18 Crocodylomorpha Walker, 1970  
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22 Crocodyliformes Hay, 1930 (sensu Clark in Benton and Clark, 1988)  
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25 Mesoeucrocodylia Whetstone and Whybrow, 1983  
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28 Notosuchia Gasparini, 1971  
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31 Peirosauridae Gasparini, 1982  
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35 *Antaeusuchus taouzensis* gen. et sp. nov.  
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37 urn:lsid:zoobank.org:act:62C4F680-CCFD-41CF-A328-8552E7B086C0

38 urn:lsid:zoobank.org:act:13959FDD-B1B1-472D-B2C6-DBD935721892  
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42 **Etymology**—Genus name after the giant *Antaeus* from Berber and Greek  
43 mythology, who is said to be buried at Msoura in northern Morocco, and *suchus*,  
44 from the Greek *souchos*, meaning crocodile. Species name after the township *Taouz*  
45 from where the holotype and paratype specimens were recovered.  
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51 **Holotype**—NHMUK PV R36829: paired mandibles, comprising an essentially  
52 complete left dentary and splenial, along with a partial angular and surangular, in  
53 articulation with the anterior portion of the right dentary and splenial.  
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57 **Paratype**—NHMUK PV R36874: a partial right mandible, comprising an incomplete  
58 dentary, surangular, and angular.  
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5 **Locality and horizon**—Near to Jebel Beg'aa, Taouz township, Errachidia Province,  
6 eastern Morocco. The specimens were commercially collected and recovered from  
7 unspecified beds within the Cenomanian (lower Upper Cretaceous) Kem Kem  
8 Group.  
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13 **Diagnosis**—A crocodyliform characterized by the following unique combination of  
14 features: (1) wide divergence angle (40–45°) of the mandibular rami; (2) dorsal  
15 margin of dentary sinusoidal with two distinct waves; (3) relatively unornamented  
16 surface texture of dentary adorned with narrow, shallow ridges; (4) ventrolateral  
17 dentary surface anterior to mandibular fenestra transversely compressed and  
18 vertical; (5) dentary extends posteriorly beneath the mandibular fenestra; (6) anterior  
19 alveoli of dentary strongly procumbent; (7) concavity for the reception of the enlarged  
20 maxillary tooth lateral to the 7<sup>th</sup> alveolus of the dentary; (8) splenial forming  
21 approximately 40% of the total mandibular anteroposterior length; (9) surangular  
22 overlaps dentary above the mandibular fenestra; (10) rugose tooth enamel formed  
23 by anastomosing grooves and ridges; (11) enlarged 4<sup>th</sup> and 13<sup>th</sup> dentary teeth; (12)  
24 tooth margins in posterior region of the dentary toothrow with denticulate carinae  
25 formed by homogeneous and symmetrical denticles with a sharp cutting edge; and  
26 (13) sub-triangular dentary tooth crowns (in lateral view) with a gently curved apex.  
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### 39 **3. Description**

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41 After detailed description and comparison of the two specimens, we consider both  
42 NHMUK PV R36874 and R36829 to belong to the new species, *Antaeusuchus*  
43 *taouzensis*, and as such they are described together. In instances where the feature  
44 being described is preserved in only one specimen, the relevant museum accession  
45 number is provided.  
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#### 51 **3.1. Preservation**

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

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3 The anterior region of the mandible is characterised by a broad, 'U'-shaped symphysis  
4 that forms at least one quarter of the total anteroposterior mandibular length. Each  
5 mandibular ramus diverges at an angle of approximately 22° from the sagittal midline.  
6 The ramus remains approximately straight along the majority of its preserved length,  
7 curving very slightly medially close to its posterior margin (visible on the left side of  
8 NHMUK PV R36829). The anterior half of the mandibular dorsal margin is  
9 characterized by two distinct 'waves', whereas the strongly sloping posterior half is  
10 largely straight, with the dentary increasing in dorsoventral height towards the  
11 surangular.  
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### 20 **3.3. Dentary**

21 The dentary is anteroposteriorly elongate, and its lateral, ventral, and dorsal surfaces  
22 are sculpted by neurovascular foramina and vermiform grooves. On the lateral  
23 surface, the foramina are largest and most numerous in the anterodorsal region of the  
24 snout. In the middle region of the snout, a series of short grooves run anteroposteriorly  
25 along the lateral surface, ~10 mm ventral to the toothrow. These grooves meet an  
26 anteroposteriorly elongate groove that extends to the dorsal suture of the dentary and  
27 surangular process (Figs 2 & 3). Another prominent, anteroposteriorly elongate  
28 vascular groove runs from the anterior-most point of the mandibular fenestra to the  
29 level of the posterior tip of the toothrow.  
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39 In lateral view, the dentary has a sinusoidal dorsal margin composed of two distinct  
40 waves. The most anterior wave spans teeth 1–6, whereas the most posterior wave is  
41 dorsally raised between teeth 9–15. The dorsoventrally tallest region of each wave  
42 corresponds with the position of dentary teeth 4 and 13, the posteriormost of which is  
43 more dorsally elevated than the anterior (Figs 2 & 3). The dentary forms the anterior  
44 region of a relatively wide mandibular symphysis (Fig. 4), the dorsal surface of which  
45 is very mildly concave. In dorsal view, the midline dentary suture extends posteriorly  
46 to the level of the 8<sup>th</sup> tooth (Fig. 4). The bone in this region is relatively unornamented,  
47 with the exception of a series of foramina immediately adjacent to the toothrow. On  
48 the ventral surface of the mandibular symphysis, the medial dentary suture extends  
49 posteriorly to a level between the 7<sup>th</sup>–8<sup>th</sup> teeth. A concavity is situated lateral to the  
50 5<sup>th</sup>–10<sup>th</sup> teeth, most likely for the reception of an enlarged maxillary tooth. The posterior  
51 region of the lateral dentary surface dorsal to the mandibular fenestra is divided into  
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3 two major acute posterior processes, separated by an anterior process of the  
4 surangular (Fig. 2). The ventral-most dentary extension forms the anterodorsal margin  
5 of the external mandibular fenestra and is dorsoventrally wide, forming approximately  
6 three quarters of the dorsoventral height of the mandible at the same level. The dorsal-  
7 most process is much narrower; its dorsal and ventral margins converge posteriorly to  
8 form an acute angle. An anteroposteriorly short dentary process is situated ventral to  
9 the external mandibular fenestra, although this does not contact the fenestral border.  
10 In NHMUK PV R36874, the splenial is not preserved, exposing the dentary's medial  
11 surface (Fig. 3).  
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20 The dentary has 18 tooth positions. On the left side of NHMUK PV R36829, whole or  
21 partial teeth are preserved in alveoli 1–16, whereas 17–18 are empty. On the right  
22 side of the specimen, 10 alveoli are preserved, with whole or partial teeth preserved  
23 in all but one (alveolus 9). Although the anterior region of NHMUK PV R36874 has  
24 broken away, the first preserved alveolus is large, and is assumed to be the fourth in  
25 the series. Whole or partial teeth are present in alveoli 5–6, 8, and 10–16 in NHMUK  
26 PV R36874. The largest tooth is the 13<sup>th</sup>, followed closely by the 4<sup>th</sup>, 11<sup>th</sup>, and 12<sup>th</sup>,  
27 which are approximately equidimensional in their circumference. In dorsal view, the  
28 tooth row is slightly sinusoidal, with lateral waves corresponding to the position of the  
29 4<sup>th</sup> and 13<sup>th</sup> teeth (Fig. 4). Although not fully preserved in either specimen, the  
30 anteriormost two teeth appear to be procumbent. Dentary teeth 3–10 project slightly  
31 anterolaterally. All of the dentary teeth are closely arranged, without the presence of  
32 diastemas.  
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### 44 **3.4. Splenial**

45 The splenials are only preserved in NHMUK PV R36829. They participate in a  
46 relatively wide mandibular symphysis (Table 1) and occupy approximately 38% of the  
47 anteroposterior symphyseal length on the dorsal surface of the mandible, extending  
48 anteromedially to the position of the 8<sup>th</sup> alveolus (Fig. 4). On the dorsal surface of the  
49 symphysis, the splenial-dentary suture diverges gradually from the sagittal midline.  
50 This suture is slightly concave until the 11<sup>th</sup> tooth, from which point it is parallel to the  
51 tooth row. A line of small foramina run parallel to the toothrow along the lateral margin  
52 of the dorsal surface of the splenial. On the ventral surface of the mandible, the  
53 splenial occupies approximately 31% of the anteroposterior length of the symphysis,  
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3 and it extends anteriorly to the position of the 9<sup>th</sup> tooth. The ventromedial splenial  
4 surface of the mandibular symphysis is dorsally displaced relative to the lateral margin.  
5 A posterior peg is located on the ventromedial surface of the symphysis (Fig. 4). The  
6 splenial is transversely thin and dorsoventrally tall, covering the inner surface of the  
7 mandibular ramus from the ventral margin of the dentary to the lingual alveolar groove.  
8 Positioned just posterior to the mandibular symphysis, on the medial surface of the  
9 splenial, is an opening, likely homologous to the intermandibularis oralis of living  
10 crocodylians (Iordansky 1973). This is elliptical, such that its anteroposterior length is  
11 approximately twice that of its dorsoventral height.  
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### 20 **3.5. Surangular**

21 The surangular is more completely preserved in NHMUK PV R36829, extending from  
22 the posterior margin of the toothrow to its broken posterior margin at the dorsal-most  
23 region of the mandibular fenestra. Its lateral surface is covered with interconnected  
24 shallow grooves. Of the surangular's two acute anterior processes, the most  
25 anteroposteriorly elongate is located on the dorsal and medial surfaces of the  
26 mandible and extends to the posterior margin of the toothrow (Fig. 4). A second  
27 anterior process is present on the dorsal region of the lateral mandibular surface (Figs  
28 2 & 3). Approximately halfway between the anterior margin of the mandibular fenestra  
29 and the posterior margin of the toothrow, the dorsal and ventral margins of this second  
30 anterior process meet anteriorly to form a subtriangular tip. An anteroposteriorly  
31 elongate dorsal coronoid tuberosity protrudes from the dorsomedial surangular  
32 surface, running anteroposteriorly for a distance of approximately 30 mm; its anterior  
33 margin is at the same level as the posterior-most point of the posterodorsal dentary  
34 process. The surangular forms the dorsal-most margin of the mandibular fenestra.  
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### 50 **3.6. Angular**

51 Albeit highly incomplete, the angular is best preserved in NHMUK PV R36874. The  
52 angular has an elongate anterior process that extends along the ventromedial surface  
53 of the mandible to the level of the 14<sup>th</sup> dentary tooth (Fig. 5). A second, smaller anterior  
54 process is present on the lateral surface of the skull (Fig. 3). This extends to the  
55 anterior margin of the mandibular fenestra, such that the angular forms the latter's  
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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

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3 each one making minor additions and/or revisions to taxa and/or characters.  
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5 Unfortunately, many of these iterations have occurred in parallel, rather than  
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7 representing a continuous series of revisions to one dataset, meaning that there is  
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9 no single dataset incorporating all of these changes to the original Pol et al. (2014)  
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11 data matrix. Here, we united many of these 'daughter' matrices, using that of  
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13 Martínez et al. (2018) as a starting point. The latter is a successive iteration of the  
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15 data matrices of Leardi et al. (2015) and Fiorelli et al. (2016), which emanated from  
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17 that of Pol et al. (2014). We included two additional characters, following Leardi et al.  
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19 (2018), and revised 20 existing character scores based on observations from recent  
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21 studies (Stromer 1914; Gomani 1997; Larsson & Gado 2000; Carvalho et al. 2005;  
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23 Carvalho et al. 2007; Larsson & Sues 2007; Martinelli et al. 2012; Barrios et al. 2016)  
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25 and personal observations (see Appendix for documentation of changes).

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27 We incorporated notosuchians from parallel daughter matrices, utilising scores  
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29 presented in those datasets, and a review of the literature. These consist of  
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31 *Razanandrongobe sakalavae* from the Bathonian (Middle Jurassic) of Madagascar  
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33 (Maganuco et al. 2006; Dal Sasso et al. 2017), the probable peirosaurids  
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35 *Bayomesasuchus hernandesi* (Barrios et al. 2016) and *Barrosasuchus*  
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37 *neuquenianus* (Coria et al. 2019) from the early Late Cretaceous (Turonian and  
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39 Santonian, respectively) of Argentina, the sphagesaurid *Caipirasuchus mineirus* from  
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41 the late Campanian–early Maastrichtian (latest Cretaceous) of Brazil (Martinelli et al.  
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43 2018), and the sebecid *Ogresuchus furatus* from the early Maastrichtian of Spain  
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45 (Sellés et al. 2020). We also expanded the sampling of putative peirosaurids that  
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47 had not previously been incorporated into iterations of the Pol et al. (2014) data  
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49 matrix via the inclusion of *Rukwasuchus yajabaliyekundu* from the Late Cretaceous of  
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51 Tanzania (Sertich & O'Connor 2014) and *Miadasuchus oblita* from the  
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53 Maastrichtian of Madagascar (Rasmusson Simons & Buckley 2009). The OTU for  
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55 *Hamadasuchus rebouli* followed previous iterations of this data matrix, although we  
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57 made a small number of character state changes (see Appendix). The resultant data  
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59 matrix consists of 121 OTUs scored for 443 characters, including 63 putative  
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notosuchian taxa. *Antaeusuchus taouzensis* could be scored for 51 of these  
characters.

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3 The data matrix was analysed under maximum parsimony using the ‘Stabilize  
4 Consensus’ option in the ‘New Technology Search’ in TNT v. 1.5 (Goloboff et  
5 al. 2008). The search was executed using sectorial searches, drift, and tree fusing,  
6 and the consensus was stabilized five times with a factor 75, prior to using the  
7 resultant trees as the starting trees for a ‘Traditional Search’ using Tree Bisection-  
8 Reconstruction. Subsequently, a strict consensus tree was calculated. We applied  
9 two different weighting schemes, using equal weighting (EQW) and extended implied  
10 weighting (EIW). Shown to perform well on morphological datasets (Goloboff et al.  
11 2018), EIW downweights homoplastic characters in relation to their average  
12 homoplasy, whilst reducing the possible impact of missing data (Goloboff 2014). The  
13 concavity constant, represented by the  $k$ -value, denotes the strength of  
14 downweighting, with lower values having been shown to downweight homoplastic  
15 characters more severely than higher values (Goloboff et al. 2018). Following  
16 analytical protocols in recent analyses of neosuchians (Groh et al. 2020; Nicholl et  
17 al. 2020; Rio et al. 2020; Rio & Mannion 2021), we applied EIW to notosuchians for  
18 the first time, using  $k$ -values of 8 and 12. Characters with missing entries were  
19 downweighted faster assuming 50% the homoplasy of observed entries, and  
20 weighting strength did not exceed 5 times that of characters with no missing entries.  
21 Forty-three characters representing nested sets of homologies were ordered (1, 3, 6,  
22 10, 23, 37, 43, 44, 45, 49, 65, 67, 69, 71, 73, 77, 79, 86, 90, 91, 96, 97, 105, 116,  
23 126, 140, 142, 143, 149, 167, 182, 187, 193, 197, 226, 228, 279, 339, 356, 357, 364,  
24 368, 401). Character 5 was made inactive due to “dependence with the modified  
25 definition of character 6” (Pol et al. 2014: supplementary information p. 3). Following  
26 the identification of problematic, unstable taxa by Pol et al. (2014), confirmed by our  
27 preliminary searches, three species known from fragmentary remains were excluded  
28 from our analyses *a priori* (i.e. *Coringasuchus anisodontis*, *Pabwehshi pakistanensis*,  
29 and *Pehuenchesuchus enderi*). The character list and data matrix are provided as  
30 nexus and tnt files (electronic supplementary material), with stored settings for  
31 assigning characters as ordered and inactive.  
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## 54 55 **4.2. Results**

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58 Under EQW, our analysis produced 11520 trees with a tree length of 1778 steps.  
59 The overall tree topology is broadly consistent with the analyses of Pol et al. (2014)  
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3 and subsequent iterations. Notosuchia comprises a main bifurcation into Ziphosuchia  
4 (plus *Candidodon itapecuruense* and *Libycosuchus brevirostris*), and a clade in  
5 which Uruguaysuchidae is recovered as the sister taxon of Mahajangasuchidae +  
6 Peirosauridae (following the recent phylogenetic definition of Geroto & Bertini 2018  
7 [see below]) (Fig. 7). Although *Peirosaurus torminni* is not included in our data  
8 matrix, *Uberabasuchus terrificus* has been consistently recovered as a close relative,  
9 with some authors regarding the latter as a junior synonym of the former (e.g.  
10 Larsson & Sues 2007; Martinelli et al. 2012). As such, we regard the *Uberabasuchus*  
11 OTU as a proxy for *Peirosaurus* in terms of identifying Peirosauridae. Bremer values  
12 are generally low across the tree, ranging from 1–3.  
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22 *Antaeusuchus* is recovered within Peirosauridae, as the sister taxon to  
23 *Hamadasuchus* (Fig. 7). The two Kem Kem OTUs form a clade with  
24 *Bayomesasuchus* that is the sister group to nearly all other peirosaurids. Within this  
25 latter group, *Barrosasuchus* and *Miadanasuchus* form a clade that is the sister taxon  
26 to a polytomy comprising *Rukwasuchus*, *Gasparinisuchus peirosauroides*,  
27 *Lomasuchus palpebrosus*, *Uberabasuchus*, and *Montealtosuchus arrudacamposi*.  
28 This polytomy can be resolved through the *a posteriori* pruning of *Gasparinisuchus* in  
29 the agreement subtree, which results in *Lomasuchus* and *Montealtosuchus*  
30 recovered as sister taxa, forming a clade with *Uberabasuchus*, with *Rukwasuchus*  
31 placed at the 'base' of this grouping. *Stolokrosuchus lapparenti* is recovered as the  
32 earliest diverging member of Peirosauridae.  
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43 Under EIW, with both *k*-values, the overall topology is largely similar to that  
44 recovered using EQW. With a *k*-value of 8, the analysis produced 45 trees with a  
45 tree length of 89.3, and with a *k*-value of 12, 15 MPTs were found of length 68.3. The  
46 main difference with results obtained from EQW is that the taxonomic content of  
47 Peirosauridae is now expanded, as a result of *Stolokrosuchus* being recovered in a  
48 clade with *Lorosuchus nodosus* and Mahajangasuchidae (Fig. 8). The phylogenetic  
49 definition proposed by Geroto and Bertini (2018) means that Mahajangasuchidae is  
50 a clade within Peirosauridae according to our EIW topology.  
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## 58 **5. Comparisons**

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3 Given the results of our phylogenetic analyses, which provide robust and consistent  
4 support for a peirosaurid placement for *Antaeusuchus*, we largely restrict our  
5 anatomical comparisons to members of this clade.  
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### 10 **5.1. Comparisons with other peirosaurids**

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13 Characteristic of all members of Peirosauridae (Martinelli et al. 2012), *Antaeusuchus*  
14 possesses an undulatory dorsal margin of the dentary comprising two distinct waves,  
15 the apices of which coincide with the position of the two largest dentary teeth (Ortega  
16 et al. 1996; Pol et al. 2014). In all peirosaurids in which the relevant region is  
17 preserved, with the exception of *Stolokrosuchus* (Larsson & Gado 2000), the 4<sup>th</sup>  
18 dentary tooth is the largest of those in the first wave, and it coincides with the apex of  
19 the anterior dentary region. The position of the largest tooth (the apex of the  
20 posterior wave) also varies amongst peirosaurids (Pol et al. 2014). The apex of this  
21 posterior wave corresponds to the 13<sup>th</sup> tooth position in *Antaeusuchus*,  
22 *Barrosasuchus*, *Gasparinisuchus*, and *Kinesuchus overoi* (Martinelli et al., 2012;  
23 Filippi et al. 2018; Coria et al. 2019), whereas it occurs at the level of the 12<sup>th</sup> tooth in  
24 *Hamadasuchus* and *Montealtosuchus* (Carvalho et al. 2007; Larsson & Sues 2007).  
25 In *Stolokrosuchus*, the jaw gradually increases in dorsoventral height posteriorly,  
26 corresponding with a progressively larger tooth size towards the posterior region of  
27 the dentary (Larsson & Gado 2000). In lateral view, the dorsoventrally expanded  
28 posterior region of the mandible of *Antaeusuchus* more closely resembles that of  
29 *Hamadasuchus*, *Montealtosuchus*, and *Uberabasuchus* (Carvalho et al. 2004, 2007;  
30 Larsson & Sues 2007) than it does in taxa such as *Barrosasuchus* and *Kinesuchus*  
31 (and potentially *Pepesuchus deiseae*) (Campos et al., 2011; Filippi et al. 2018; Coria  
32 et al. 2019), in which the region is more dorsoventrally compressed.  
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50 All peirosaurid taxa, except for the longirostrine-snouted *Stolokrosuchus* (Larsson &  
51 Gado 2000), are characterised by a mediolaterally broad mandibular symphysis (Fig.  
52 9). This is most prominent in *Colhuehuapisuchus lunai*, *Barrosasuchus*, and  
53 *Gasparinisuchus* (Martinelli et al. 2012; Coria et al. 2019; Lamanna et al. 2019), in  
54 which the anteroposterior length to mediolateral width ratio of the symphyseal dorsal  
55 surface is less than 1.0 (values range from 0.8–0.9). Although still broad in  
56 comparison with many other notosuchian taxa, such as sphagesaurians (Ruiz et al.  
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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*.

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3 In *Antaeusuchus*, as well as *Hamadasuchus* (Larsson & Sues 2007), the dentary-  
4 splenial suture exposed on the dorsal surface of the mandibular symphysis diverges  
5 gradually from the midline until the level of the 12<sup>th</sup> dentary tooth, at which point it  
6 becomes parallel to the toothrow. A similar morphology characterizes *Kinesuchus*,  
7 except that the change in orientation of the suture is less acute in that species  
8 (Filippi et al. 2018). In *Montealtosuchus* and *Patagosuchus*, the suture becomes  
9 parallel with the toothrow at the level of the 10<sup>th</sup> dentary tooth (Carvalho et al. 2007;  
10 Lio et al. 2015). By contrast, the dentary-splenial suture in *Stolokrosuchus* parallels  
11 the toothrow only at the level of the 25<sup>th</sup> tooth (Larsson & Gado 2000). Although the  
12 morphology of the suture is 'U'-shaped, as opposed to the 'V'-shape that  
13 characterizes *Antaeusuchus*, it becomes approximately parallel with the toothrow at  
14 the level of the 11<sup>th</sup> and 12<sup>th</sup> tooth in *Gasparinisuchus* and *Barrosasuchus*,  
15 respectively (Martinelli et al. 2012; Coria et al. 2019).  
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27 Posterior to the symphysis, the mandibular rami of *Antaeusuchus* diverge at an  
28 angle of approximately 44° to each other. A value of between ~40–45° is fairly  
29 consistent amongst peirosaurids; this contrasts with some other notosuchians,  
30 including sphagesaurians (Pol et al. 2014; Martinelli et al. 2018), whereby the skull is  
31 mediolaterally broader, and the rami diverge from one another at a less acute angle.  
32 Immediately posterior to the symphysis, the splenial of *Antaeusuchus* is largely  
33 exposed in ventral view, and forms approximately 40% of the mediolateral width of  
34 the mandibular rami. A comparably broad splenial also characterizes  
35 *Uberabasuchus*, *Montealtosuchus*, and *Kinesuchus* (Carvalho et al. 2004; Carvalho  
36 et al. 2007; Filippi et al. 2018), whereas the splenial comprises only 25–30% of the  
37 rami transverse cross section in *Gasparinisuchus*, *Stolokrosuchus*,  
38 *Colhuehuapisuchus*, and *Barrosasuchus* (Larsson & Gado 2000; Martinelli et al.  
39 2012; Coria et al. 2019; Lamanna et al. 2019).  
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51 In numerous peirosaurids, including *Antaeusuchus*, *Hamadasuchus*,  
52 *Uberabasuchus*, *Montealtosuchus*, *Pepesuchus*, *Stolokrosuchus*, and *Lomasuchus*,  
53 an anteroposteriorly elongate groove runs parallel to the dentary toothrow, just  
54 ventral to the dorsal margin of the lateral surface of the mandible (Gasparini et al.  
55 1991; Larsson & Gado 2000; Carvalho et al. 2004; Carvalho et al. 2007; Larsson &  
56 Sues 2007; Campos et al. 2011). The lateral surface of the dentary is also typically  
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3 sculpted with pits and/or grooves in peirosaurids; however, there is interspecific  
4 variation in the degree to which this sculpting continues over the entire surface. In  
5 *Antaeosuchus*, the lateral surface of the dentary is similar in its texture and sculpting  
6 both above and below the groove. In this regard, the morphology is similar to that of  
7 *Uberabasuchus*, *Barrosasuchus*, and *Kinesuchus* (Carvalho et al. 2004; Filippi et al.  
8 2018; Coria et al. 2019). In *Hamadasuchus*, *Montealtosuchus*, *Pepesuchus*, and  
9 *Patagosuchus*, the region above the groove is smooth, differing markedly from the  
10 remainder of the highly sculpted lateral dentary surface (Carvalho et al. 2007;  
11 Larsson & Sues 2007; Campos et al. 2011; Lio et al. 2016). Although *Stolokrosuchus*  
12 shows no difference in bone surface texture above and below the anteroposterior  
13 groove (Larsson & Gado 2002), it differs from *Antaeosuchus* in that the majority of  
14 the lateral dentary surface is smooth and unornamented.

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26 The degree of sculpting on the lateral surface of the dentary varies across  
27 notosuchian taxa, including within Peirosauridae. Whereas the surface is covered in  
28 deep pits in *Hamadasuchus*, *Uberabasuchus*, *Montealtosuchus*, *Patagosuchus*,  
29 *Bayomesasuchus*, and *Miadasuchus* (Carvalho et al. 2004; 2007; Larsson & Sues  
30 2007; Rasmusson Simons & Buckley 2009; Barrios et al. 2016; Lio et al. 2016), the  
31 surface of *Antaeosuchus* is considerably smoother and is textured with narrow,  
32 shallow grooves.

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39 Unlike *Montealtosuchus*, *Gasparinisuchus*, *Bayomesasuchus*, *Stolokrosuchus*,  
40 *Patagosuchus*, *Pepesuchus*, and *Colhuehuapisuchus* (Buckley & Brochu 1999;  
41 Larsson & Gado 2000; Carvalho et al. 2007; Campos et al. 2011; Martinelli et al.  
42 2012; Lamanna et al. 2019), the lateral surface of the dentary adjacent to the 5<sup>th</sup>–8<sup>th</sup>  
43 teeth forms a distinct anteroposteriorly elongate concavity in *Antaeosuchus*. This is  
44 otherwise known only in *Hamadasuchus* (Larsson & Sues 2007), although a  
45 shallower concavity also characterizes *Barrosasuchus* (Coria et al. 2019). This  
46 depression would likely have functioned to receive an enlarged premaxillary tooth  
47 during occlusion.

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

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3 Ibrahim et al. 2020), but differing from *Barrosasuchus* in which the fenestra is greatly  
4 reduced (Coria et al. 2019). However, *Montealtosuchus* and *Uberabasuchus* differ  
5 from the dentaries of *Antaeusuchus* and *Hamadasuchus* (Ibrahim et al. 2020) in that  
6 the latter two have a small posterior process that extends ventral to the mandibular  
7 fenestra. This process is absent in *Montealtosuchus* and *Uberabasuchus*, in which  
8 the dentary-angular contact is entirely anterior to the mandibular fenestra instead  
9 (Carvalho et al. 2004; Carvalho et al. 2007). The dentary-surangular contact is  
10 similar in *Antaeusuchus*, *Hamadasuchus*, *Montealtosuchus*, and *Uberabasuchus*,  
11 with the surangular contacted by two posterior processes: the dorsal process  
12 intrudes entirely into the surangular, whereas the second process forms the ventral  
13 margin of the surangular and the anterodorsal margin of the mandibular fenestra  
14 (Carvalho et al. 2004; Carvalho et al. 2007; Larsson & Sues 2007). This feature  
15 cannot be assessed in other peirosaurid taxa, in which the relevant region of the  
16 mandible is not preserved.  
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29 When complete, each dentary of *Antaeusuchus* has 18 tooth positions. This count is  
30 common amongst peirosaurids, e.g. *Montealtosuchus*, *Gasparinisuchus*,  
31 *Kinesuchus*, *Pepesuchus*, and possibly *Barrosasuchus* (Carvalho et al. 2007;  
32 Campos et al. 2011; Martinelli et al. 2012; Filippi et al. 2018; Coria et al. 2019), but  
33 differs from *Stolokrosuchus*, in which there are at least 30 dentary alveoli (Larsson &  
34 Gado 2000). As in all peirosaurids (Pol et al. 2014), the first two dentary teeth of  
35 *Antaeusuchus* are strongly procumbent.  
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43 The dentary teeth posterior to the 5<sup>th</sup> alveolus are closely spaced and are mostly  
44 situated in a continuous groove in *Antaeusuchus*, *Hamadasuchus* (Larsson & Sues  
45 2007), *Gasparinisuchus* (Martinelli et al. 2012), and *Barrosasuchus* (Coria et al.  
46 2019). This differs from the condition in *Kinesuchus* (Filippi et al. 2018) and  
47 *Patagosuchus* (Lio et al. 2016), in which the teeth are separated by distinct septa  
48 that extend fully to the dorsal margin of the dentary.  
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## 55 **5.2. Detailed comparisons with *Hamadasuchus rebouli***

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58 Although several crocodyliform taxa, including notosuchians, have been identified  
59 from the Kem Kem Group (Ibrahim et al. 2020), only one peirosaurid species is  
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3 currently recognised from these beds: *Hamadasuchus rebouli* (Buffetaut 1994;  
4 Larsson & Sues 2007). Since the original description of the holotype dentary by  
5 Buffetaut (1994), several specimens have been referred to *Hamadasuchus* (Larsson  
6 & Sidor 1999; Rauhut & López-Arbarello 2006; Larsson & Sues 2007; Ibrahim et al.  
7 2020). In our CTM (and previous iterations), the OTU of *Hamadasuchus* comprises  
8 the holotype mandibular fragment, MDEC001, plus the cranial material, ROM 52620,  
9 referred by Larsson & Sues (2007). Almost all characters that could be assessed for  
10 *Antaeusuchus* received the same score as *Hamadasuchus*, resulting in their  
11 consistent recovery as sister taxa in our phylogenetic analyses. The only differences  
12 in scores are present in characters 77 (scored as 2 and 1&2 for *Antaeusuchus* and  
13 *Hamadasuchus*, respectively), 155 (scored as 1 and 0&1 for *Antaeusuchus* and  
14 *Hamadasuchus*, respectively), and 393 (scored as 0 and 0&1 for *Antaeusuchus* and  
15 *Hamadasuchus*, respectively). The score of 1&2 for character 77 reflects the  
16 fragmentary nature of the *Hamadasuchus* type specimen and uncertainty of the  
17 precise length of the splenial contribution to the mandibular symphysis, rather than  
18 representing a polymorphism, whereas the score of 0&1 for characters 155 and 393  
19 represents the definite presence of both states in this OTU. Given the similarity of  
20 the scores of both Kem Kem specimens, and that those provided for the mandible of  
21 *Hamadasuchus* are based only on the holotype specimen and not any referred  
22 material, we provide more detailed comparisons in the following section.

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24 *Antaeusuchus* is compared to several anatomically overlapping specimens currently  
25 assigned to *Hamadasuchus*, namely the holotype dentary (MDEC001), several  
26 partial mandibles (ROM 49282, 52045, and 52047) described by Larsson & Sues  
27 (2007), a complete skull and lower jaws (BSPG 2005 I 83) figured by Rauhut &  
28 López-Arbarello (2006), and two mandibular symphyses (MNHN-MRS 3110 & NMC  
29 41784) illustrated in Ibrahim et al. (2020). Despite being largely similar in overall  
30 morphology, *Antaeusuchus* differs in several respects from all specimens assigned  
31 to *Hamadasuchus* (Fig. 10).

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34 Although only one dentary is preserved in the holotype (MDEC001), the angle of  
35 divergence of the mandibular rami can be inferred by measuring the angle of  
36 deviation of one dentary from the exposed symphyseal suture. Estimated mandibular  
37 rami divergence angles of ~20° for ROM 52047, ~25° for MDEC001 and ~30° for  
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3 ROM 49282, 52045, are much narrower than that of *Antaeosuchus* (43–44°). This  
4 suggests that *Hamadasuchus* had a slenderer rostrum than that of *Antaeosuchus*.  
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8 The surface texture of the *Antaeosuchus* dentary differs from all three specimens  
9 referred to *Hamadasuchus* in that it is not covered in deep pits and grooves. Instead,  
10 it is ornamented with relatively narrow and shallow grooves. *Antaeosuchus* also  
11 differs from these specimens in the dorsal region of the dentary lateral surface. In  
12 MDEC001, the area just ventral to the toothrow is smooth and lacks pits, differing  
13 from the remainder of the lateral surface (Buffetaut 1994). Instead, this dorsal region  
14 has a corrugated morphology, with broad, shallow dorsoventral grooves that do not  
15 correspond to the position of the dentary teeth (Fig. 10). A similar morphology  
16 characterizes ROM 49282, BSPG 2005 I 83, and NMC 41784, although it is not as  
17 prominent in those specimens. In *Antaeosuchus*, the degree of ornamentation is  
18 much the same across the lateral surface of the dentary and a fluted dorsal region is  
19 absent.  
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31 The apex of the second mandibular wave is marked by the position of the 13<sup>th</sup> tooth  
32 in *Antaeosuchus*, as well as ROM 49282, BSPG 2005 I 83, and probably MNHN-  
33 MRS 3110. By contrast, the tip of the second dentary wave is most likely marked by  
34 the 12<sup>th</sup> tooth in the holotype MDEC001, which is significantly larger than the 13<sup>th</sup>  
35 tooth (Buffetaut 1994).  
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41 Posterior to the 7<sup>th</sup> dentary tooth, the teeth of MDEC001 are strongly labiolingually  
42 compressed, and possess serrated carinae on their anterior and posterior cutting  
43 edges. A similar morphology is also present in *Antaeosuchus*, as well as MNHN-  
44 MRS 3110, but not in ROM 49282, in which the teeth are compressed only from the  
45 10<sup>th</sup> tooth. The 5<sup>th</sup> to 9<sup>th</sup> teeth are damaged in BSPG 2005 I 83 and so it is unclear at  
46 which tooth position the compression commences. The posterior teeth in MDEC001  
47 have a lanceolate shape (Buffetaut 1994) that is not present in *Antaeosuchus*, but  
48 which is most reminiscent of the morphology in MNHN-MRS 3110. In NHMUK PV  
49 R36829, teeth 11, 12, 14, and 15 are the only ones which are fully preserved; the  
50 anterior two of these have rounded crowns that do not form an angular tip. Although  
51 the 14<sup>th</sup> and 15<sup>th</sup> teeth of NHMUK PV R36829 are slightly pointed at their apices,  
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3 they are not comparable to the almost triangular shape of those in the holotype  
4 MDEC001 (Buffetaut 1994). In NHMUK PV R36874, the 10<sup>th</sup>–14<sup>th</sup> teeth are slightly  
5 more angular in appearance, but their anterior and posterior margins are parallel for  
6 most of their length, converging to a point only at the crown apex (Fig. 10).  
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11 The only fully preserved tooth in the ROM 49282 dentary is the 13<sup>th</sup> one (Larsson &  
12 Sues 2007). Comparing the broad morphology, it is most similar to the teeth at a  
13 similar dentary position in *Antaeosuchus*, in that its apical margin is rounded.  
14 However, the tooth enamel of ROM 49282 is essentially smooth. By contrast, the  
15 enamel in *Antaeosuchus* is wrinkled into anastomosing apicobasal ridges  
16 (approximately 2–3 ridges per mm) (Fig. 10). Both morphologies differ from that of  
17 the teeth of MDEC001, in which the enamel is textured, but has an irregular, globular  
18 pattern towards its base, and anastomosing ridges towards the apex of the crown  
19 (Buffetaut 1994). ROM 49282 also displays a unique condition in which the tooth  
20 enamel is fluted with broad apicobasal ridges around its circumference.  
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31 The teeth of all specimens assigned to *Hamadasuchus*, as well as those of  
32 *Antaeosuchus*, have very finely serrated carinae on their anterior and posterior  
33 cutting edges, with individual serrations spaced at approximately 3–5 per mm.  
34 Although most prominent in MDEC001, vertical fluting on the anterior and posterior  
35 regions of the crowns is visible in the posterior dentary teeth of all the specimens  
36 discussed in this section.  
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43 Finally, *Antaeosuchus* is significantly larger than all *Hamadasuchus* specimens, such  
44 that it is almost double the size of MDEC001, ROM 49282, and BSPG 2005 I 83.  
45 Although the size of the specimen alone should not be a reason to erect a new species  
46 (e.g. Griffin et al. 2021), we believe it to be a valid morphological difference as part of  
47 a large, unique combination of features. Furthermore, *Hamadasuchus* is already  
48 known from an ontogenetic series, including specimens considered ‘adult’ (Larsson &  
49 Sues 2007); as such, it is difficult to reconcile the numerous anatomical differences  
50 merely as a result of *Antaeosuchus* being an even older individual of *Hamadasuchus*.  
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## 58 **6. Discussion**

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## 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 5<sup>th</sup> to 10<sup>th</sup> 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 referable 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

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3 curved apex; (5) minor labiolingual compression of the posterior dentary teeth; (6) a  
4 lack of fluting on the dorsal region of the lateral dentary surface; (7) a relatively  
5 unornamented surface texture of the dentary adorned with narrow, shallow ridges  
6 rather than deep pits or grooves; and (8) dentary teeth more widely spaced at their  
7 base.  
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13 As such, it seems clear that NHMUK PV R36829 + R3687 represents a second  
14 peirosaurid in the Kem Kem Group, and thus supports our erection of *Antaeusuchus*  
15 *taouzensis* n. gen. n. sp. In addition, material currently referred to *Hamadasuchus*  
16 also differs from the type specimen (MDEC001), as well as *Antaeusuchus*. In  
17 particular, the partial mandible, ROM 49282, described by Larsson & Sues (2007),  
18 differs from both taxa in several features, including: (1) distinctive apicobasal fluting  
19 on the 13<sup>th</sup> tooth; (2) a highly elongate contribution of the splenial to the mandibular  
20 fenestra; (3) a mandibular rami divergence of approximately 30°; and (4) possession  
21 of relatively smooth tooth enamel. The unique combination of characters in each of  
22 MDEC001, ROM 49282, and NHMUK PV R36829 + R36874, therefore suggests the  
23 presence of at least three separate, albeit closely related, peirosaurid species from  
24 the Kem Kem Group. Although we erect a new name for NHMUK PV R36829 +  
25 R3687, we refrain from naming a new taxon for ROM 49282 pending the description  
26 and assessment of additional materials currently assigned to *Hamadasuchus rebouli*  
27 (namely BSPG 2005 I 83 and additional ROM specimens).  
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## 41 **6.2. Implications for peirosaurid relationships**

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43 Peirosauridae was erected by Gasparini (1982) to accommodate *Peirosaurus*  
44 *torminni* (Price 1955) from the late Maastrichtian Marília Formation of Brazil. This  
45 family was subsequently expanded by Gasparini et al. (1991) to include *Lomasuchus*  
46 from the late Turonian–early Coniacian of Argentina. Geroto & Bertini (2019 p. 328)  
47 provided a phylogenetic definition for Peirosauridae as “the least inclusive clade  
48 containing *P. tormini* [sic] Price, 1955, *Itasuchus jesuinoi* Price, 1955,  
49 and *Stolokrosuchus lapparenti* Larsson & Gado, 2000, but not including *Notosuchus*  
50 *terrestris* Woodward, 1896, *Baurusuchus pachecoi* Price, 1945, *Sphagesaurus*  
51 *huenei* Price, 1950, *Araripesuchus gomesii* Price, 1959, *Sebecus*  
52 *icaeorhinus* Simpson, 1937, *Marillasuchus amarali* Carvalho & Bertini, 1999,  
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3 and *Crocodylus niloticus* Laurent, 1768". Although a phylogenetic definition based on  
4 two well-nested and stable species-level specifiers would be preferable (e.g. Sereno  
5 1998, 2005; Lee 2005), we follow the definition of Geroto & Bertini (2019) here,  
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7 pending a detailed re-evaluation of the interrelationships of this part of the  
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9 notosuchian tree.  
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13 Following Geroto & Bertini's (2019) definition, Peirosauridae comprises a  
14 taxonomically rich array of crocodyliforms from across the Cretaceous of South  
15 America, Africa, and Madagascar (e.g. Price 1955; Carvalho et al. 2004; Carvalho et  
16 al. 2007; Larsson & Sues 2007; Leardi & Pol 2009; Sertich O'Connor 2014; Campos  
17 et al. 2011; Martinelli et al. 2012; Lio et al. 2016; Barrios et al. 2016; Filippi et al.  
18 2018; Coria et al. 2019). However, there is little consensus regarding the position of  
19 Peirosauridae. A number of analyses have recovered Peirosauridae within  
20 Notosuchia, as the sister taxon to Mahajangasuchidae (i.e. *Kaprosuchus* +  
21 *Mahajangasuchus*), with these lineages forming a clade with Uruguaysuchidae that  
22 is the sister taxon to all other notosuchians (e.g. Pol et al. 2014; Sertich & O'Connor  
23 2014; Coria et al. 2019). Others have recovered Peirosauridae as part of Sebecia,  
24 forming a clade with Sebecidae (e.g. Larsson & Sues 2007; Sereno & Larsson  
25 2009), and sometimes also including Mahajangasuchidae (e.g. Geroto & Bertini  
26 2019; Ruiz et al. 2021). Whereas some of these analyses place Sebecia as the  
27 sister taxon to all other notosuchians (e.g. Geroto & Bertini 2019; Ruiz et al. 2021),  
28 others recover Sebecia within Neosuchia (e.g. Larsson & Sues 2007; Sereno &  
29 Larsson 2009). Peirosauridae has also been recovered as an early diverging  
30 neosuchian clade in some studies (e.g. Pol & Apesteguía 2005; Gasparini 2006;  
31 Turner & Buckley 2008; Leardi & Pol 2009).  
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50 In several recent phylogenetic analyses (e.g. Pol et al. 2014; Geroto & Bertini 2019;  
51 Coria et al. 2019), *Hamadasuchus* has been recovered as the sister taxon to a group  
52 of exclusively South American Cretaceous peirosaurids (comprising various  
53 combinations of *Montealtosuchus*, *Uberabasuchus*, *Lomasuchus*, *Gasparinisuchus*,  
54 and *Barcinosuchus*). Similarly, Barrios et al. (2016) recovered *Hamadasuchus* in a  
55 polytomy with most of these taxa, along with *Bayomesasuchus* from the Turonian  
56 (Late Cretaceous) of Argentina. Sertich & O'Connor (2014) recovered  
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3 *Hamadasuchus* in an unresolved trichotomy with *Rukwasuchus* and *Stolokrosuchus*,  
4 forming a clade of African peirosaurids.  
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8 Here, under both equal and extended implied weighting schemes, the position of  
9 Peirosauridae is consistent with the results of Pol et al. (2014) and subsequent  
10 studies based on this dataset (e.g. Leardi et al. 2015; Fiorelli et al. 2016; Iori et al.  
11 2018; Leardi et al. 2018; Martinelli et al. 2018; Coria et al. 2019). Under its  
12 broadened taxonomic content, following the phylogenetic definition of Geroto &  
13 Bertini (2019), Peirosauridae includes Mahajangasuchidae in our EIW analyses (Fig.  
14 8). This occurs because *Stolokrosuchus* is recovered as more closely related to  
15 Mahajangasuchidae than to other peirosaurids in the EIW topology. Our equal  
16 weights analysis recovers *Stolokrosuchus* as the most 'basal' member of  
17 Peirosauridae instead, with Mahajangasuchidae outside of this clade (Fig. 7). In both  
18 cases, our peirosaurid + mahajangasuchid grouping is the sister taxon of  
19 Uruguaysuchidae, with this clade the sister taxon to all other notosuchians.  
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30 In our strict consensus trees, the clade comprising *Antaeusuchus* and  
31 *Hamadasuchus* is most closely related to *Bayomesasuchus*. This grouping is the  
32 sister taxon to other peirosaurids (excluding *Stolokrosuchus* and  
33 Mahajangasuchidae) (Fig. 7). The remaining South American taxa are grouped in a  
34 polytomy with the African taxon *Rukwasuchus*, with this recovered as the sister  
35 taxon of a clade comprising the Malagasy taxon *Miadanasuchus* and the  
36 Argentinean species *Barrosasuchus*. The aforementioned polytomy can be resolved  
37 via *a posteriori* pruning of *Gasparinisuchus*, resulting in *Rukwasuchus* as the sister  
38 taxon of a clade comprising the Malagasy taxon *Miadanasuchus* and the  
39 Argentinean species *Barrosasuchus*. The aforementioned polytomy can be resolved  
40 via *a posteriori* pruning of *Gasparinisuchus*, resulting in *Rukwasuchus* as the sister  
41 taxon of (*Uberabasuchus* + (*Lomasuchus* + *Montealtosuchus*)).  
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48 The fact that our analyses produce topologies more consistent with those derived  
49 from the data matrix of Pol et al. (2014) than alternative matrices is not surprising  
50 given that this is the underlying dataset for our study. As such, the interrelationships  
51 of Peirosauridae within Metasuchia will require further testing, ideally merging  
52 characters and taxa from across studies with competing hypotheses. However, the  
53 recovery of Peirosauridae as an early diverging metasuchian clade outside of the  
54 ziphosuchian notosuchian radiation is consistent across analyses, regardless of the  
55 underlying dataset.  
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5 One of the notable results of our analyses is the placement of *Miadanasuchus* within  
6 Peirosauridae, which was independently recovered in this clade by Geroto and  
7 Bertini (2019). This species from the Maastrichtian of Madagascar was originally  
8 described as *Trematochampsia oblita* (Buffetaut & Taquet 1979), before being  
9 assigned to a new genus by Rasmusson Simons & Buckley (2009). The type species  
10 of *Trematochampsia*, *T. taqueti*, is based on fragmentary remains from the  
11 Coniacian–Santonian In Beceten Formation of Niger (Buffetaut 1974; 1976a, b), for  
12 which the family Trematochampsidae was also erected (Buffetaut 1974). Several  
13 additional crocodyliform taxa have been assigned to Trematochampsidae (e.g.  
14 *Amargasuchus minor* [Chiappe 1988], *Barreirosuchus franciscoi* [Iori et al. 2012],  
15 *Hamadasuchus*, *Itasuchus*, *Mahajangasuchus*), spanning the Cretaceous of Africa,  
16 Europe, Madagascar, and South America, with most of these known from  
17 fragmentary remains (see review in Meunier & Larsson 2018). Buffetaut  
18 (1988, 1989) also included *Peirosaurus torminni* as a member of  
19 Trematochampsidae, which would therefore have priority over Peirosauridae.  
20 However, multiple authors have questioned or rejected the monophyly of  
21 Trematochampsidae, which appears to have become a wastebasket taxon (e.g.  
22 Gasparini et al. 1991; Ortega et al. 1996; Buckley & Brochu 1999; Turner & Calvo  
23 2005; Larsson & Sues 2007; Rasmusson Simons et al. 2009; Meunier & Larsson  
24 2018). Furthermore, Meunier & Larsson (2018) demonstrated that *Trematochampsia*  
25 *taqueti* is a nomen dubium, based on non-diagnostic, chimeric remains, with some of  
26 these displaying peirosaurid affinities. Our analyses provide further evidence that  
27 most, if not all, Cretaceous taxa previously assigned to Trematochampsidae belong  
28 to Peirosauridae, and confirm the presence of this latter clade in the Maastrichtian of  
29 Madagascar. Given the lack of diagnostic features in the type remains of  
30 ‘*Trematochampsia taqueti*’ and the absence of a formal definition for  
31 ‘Trematochampsidae’, coupled with its approximate synonymy with the formally  
32 defined and widely used Peirosauridae, we support the proposal of Meunier &  
33 Larsson (2018) to abandon the name *Trematochampsia* and its coordinated rank  
34 taxa.

### 6.3. Gondwanan notosuchian diversity outside of South America

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3 During the Mesozoic, notosuchians (*sensu* Pol et al. 2014) were the most diverse  
4 clade of Gondwanan crocodyliforms (Turner & Sertich 2010), although this high  
5 species richness varied through both time and space (Pol & Leardi 2015; De Celis et  
6 al. 2020). At least 70% of known notosuchian diversity is found on Gondwanan  
7 continents (Pol & Leardi 2015), with a small number of species recognised from  
8 Europe (Kuhn 1968; Antunes 1975; Rossman et al. 2000; Company et al. 2005;  
9 Dalla Vecchia & Cau 2011; Rabi & Sebök 2015; Martin 2016; Sellés et al. 2020) and  
10 Asia (Wu et al. 1995; Wu & Sues 1996). Though most numerous in South America,  
11 Gondwanan notosuchian occurrences are also known from mainland Africa,  
12 Madagascar, India, and Pakistan, as well as possibly the Arabian Peninsula.  
13 Currently no notosuchians are known from Australasia or Antarctica, although it  
14 remains unclear whether this represents a genuine absence, perhaps pertaining to a  
15 high-latitude environmental dispersal barrier, or it reflects a sampling bias (e.g. see  
16 Poropat et al. 2021). Here, we provide a critical reappraisal of the Gondwanan  
17 record of notosuchians outside of South America.  
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### 30 **6.3.1. Jurassic**

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32 The stratigraphically oldest known notosuchian is *Razanandrongobe sakalavae*  
33 (Maganuco et al. 2006) from the Bathonian (Middle Jurassic) Isalo IIIb Formation in  
34 northwestern Madagascar. Originally named as an archosaur of uncertain affinities  
35 on the basis of teeth and a fragmentary maxilla (Maganuco et al. 2006), several  
36 more skull fragments, including a right premaxilla and an incomplete left dentary,  
37 have since been assigned to the taxon, enabling its identification as a large-bodied  
38 notosuchian (Dal Sasso et al. 2017). Considering that the next stratigraphically  
39 oldest notosuchians are from the Aptian (late Early Cretaceous), resulting in a ~40  
40 million-year ghost lineage, *Razanandrongobe* is a stratigraphic outlier and its  
41 affinities might seem doubtful. However, based on the sister taxon relationship of  
42 Notosuchia and Neosuchia, with the latter clade known from the Early Jurassic  
43 (Tykoski et al., 2002), *Razanandrongobe* instead partly fills the inferred ghost lineage  
44 of notosuchians, which otherwise would extend back approximately 65–75 million  
45 years (Dal Sasso et al. 2017; Mannion et al. 2019). In the small number of  
46 phylogenetic analyses to have incorporated it (Dal Sasso et al. 2017; Sellés et al.  
47 2020), including ours, *Razanandrongobe* is recovered in a position close to the  
48 'base' of Sebecosuchia. This nested position within Notosuchia for such a  
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3 stratigraphically early species necessitates the extension of multiple unsampled  
4 lineages back into the Jurassic (Fig. 11). As such, the phylogenetic affinities of  
5 *Razanandrongobe* require further evaluation to test whether this poor stratigraphic fit  
6 is genuine.  
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### 10 11 12 **6.3.2. Early Cretaceous** 13

14 In southeastern Africa, the Aptian Dinosaur Beds of northern Malawi (Fig. 12) have  
15 yielded numerous remains of *Malawisuchus mwakasyungutiensis*, preserving most  
16 of the skeleton (Gomani 1997). Recognised in part for its unusual mammal-like  
17 multicuspid teeth, some analyses have placed *Malawisuchus* in a nested position  
18 within Sphagesauria (e.g. Gomani 1997; Sereno & Larsson 2009; O'Connor et al.  
19 2010). However, most recent analyses typically recover *Malawisuchus* as an early  
20 diverging ziphosuchian, with sphagesaurians currently restricted to South America  
21 (e.g. Pol et al. 2014; Ruiz et al. 2021; this study). Unlike the topology of Martin and  
22 Lapparent de Broin (2016), *Malawisuchus* is not recovered within Candidodontidae  
23 in our analyses (Fig. 7).  
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33 The Aptian–Albian Elrhaz Formation exposed at Gadoufaoua, central Niger (Fig. 12),  
34 has yielded the remains of three morphologically diverse notosuchian species  
35 (*Anatosuchus minor*, *Araripesuchus wegneri*, and *Stolokrosuchus lapparenti*). The  
36 bizarre, 'duck-billed' *Anatosuchus* is known from several individuals, including a skull  
37 and associated partial postcranial skeleton, as well as a skull of a juvenile animal  
38 (Sereno et al. 2003; Sereno & Larsson 2009). *Anatosuchus* has often been  
39 recovered as a member of Uruguaysuchidae (e.g. Sereno & Larsson 2009; Pol et al.  
40 2014); some analyses have placed it outside of this clade, although these tend to  
41 recover it as a 'basal' member of Notosuchia. The small and gracile species  
42 *Araripesuchus wegneri* was erected from the anterior region of an articulated upper  
43 and lower snout (Buffetaut & Taquet 1979). Multiple remains have since been  
44 assigned to the taxon, including a block preserving at least five separate individuals,  
45 three of which are essentially complete, partially articulated skeletons (Sereno &  
46 Larsson 2009). In our analyses, *Araripesuchus wegneri* and *Anatosuchus* are  
47 recovered as sister taxa within Uruguaysuchidae, further questioning the monophyly  
48 of *Araripesuchus* (see Sereno & Larsson 2009: p. 31). The longirostrine-snouted  
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3 *Stolokrosuchus* is known from an almost complete skull (Larsson & Gado 2000).  
4 Originally referred to Peirosauridae (Larsson & Gado 2000; see also Larsson & Sues  
5 2007; Sereno & Larsson 2009; Geroto & Bertini 2019), subsequent analyses have  
6 shown the position of *Stolokrosuchus* to be highly labile, such that it has also been  
7 placed as an early diverging member of both Notosuchia (e.g. Dal Sasso et al. 2017)  
8 and Neosuchia (e.g. Turner & Sertich 2010; Andrade et al. 2011). Following the  
9 definition of Peirosauridae provided by Geroto & Bertini (2019), our analyses recover  
10 *Stolokrosuchus* as the earliest diverging member of this clade, which is consistent  
11 with previous analyses that have continued to place it close to the ‘base’ of  
12 Metasuchia.  
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22 Several isolated teeth from the Aptian–Albian Koum Formation of northeastern  
23 Cameroon (Fig. 12) were reported by Flynn et al. (1988) and Congleton (1990), who  
24 recognised their possible affinities with *Araripesuchus*, especially *A. wegneri*.  
25 Kellner (1994 p. 618) questioned this referral, suggesting that these strongly  
26 serrated, laterally compressed, leaf-shaped teeth differed from those in the posterior  
27 toothrow of *Araripesuchus gomesii*, which he described as “weakly serrated” and  
28 “less leaf-shaped”. It is unclear why Kellner (1994) limited comparisons to  
29 *Araripesuchus gomesii*; nonetheless, the description of additional specimens of  
30 *Araripesuchus wegneri* from Niger (Sereno & Larsson 2009), along with other  
31 species of this genus (e.g. Pol & Apesteguia 2005; Ortega et al. 2000; Turner 2006;  
32 Sereno & Larsson 2009; Dumont et al. 2020; Ibrahim et al. 2020), allows for more  
33 thorough comparisons with the teeth from Cameroon. Given that none of the South  
34 American *Araripesuchus* species, nor *Araripesuchus tsangatsangana*, have  
35 denticles, the labiolingually compressed, lanceolate shape of these teeth, with  
36 serrated carinae along their posteriormost and anteriormost margins, is supportive of  
37 a referral to either *Araripesuchus wegneri* or *Araripesuchus rattoides* (the latter  
38 comparison is based on referred material, BSPG 2008 I 41, rather than the holotype  
39 specimen [Ibrahim et al. 2020]). However, because of variation in crown morphology  
40 along the toothrow in all species of *Araripesuchus*, and given that teeth in the  
41 middle-to-posterior toothrow are either absent or poorly preserved in *Araripesuchus*  
42 *rattoides*, it is not currently possible to provide a species-level referral.  
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3 The Albian Aïn el Guettar Formation in southern Tunisia (Fig. 12) has yielded  
4 numerous crocodyliform remains, including teeth assigned to *Araripesuchus*  
5 *wegeneri*, *Araripesuchus* sp., and aff. *Hamadasuchus* sp. (Le Loeuff et al. 2000;  
6 Cuny et al. 2010; Fanti et al. 2012). The specimens assigned to *Araripesuchus*  
7 (Cuny et al. 2010, fig. 4.7; Fanti et al. 2012, fig. 12U–X) are labiolingually  
8 compressed and triangular, with serrated carinae and relatively smooth enamel.  
9 Based on the slightly dorsoventrally constricted lanceolate shape of the teeth in  
10 lateral view, it is likely that they come from the middle region of the toothrow. All of  
11 these features support their referral to *Araripesuchus*, widening the spatial  
12 distribution of the genus to north-central Africa. Although serrated tooth margins are  
13 known to be present in *Araripesuchus wegeneri* and a referred specimen of  
14 *Araripesuchus rattoides* (Ibrahim et al. 2020), we refrain from assigning these  
15 specimens beyond generic level as was “cautiously” proposed by Cuny et al. (2010:  
16 p. 625) for the same reasons outlined in the preceding paragraph. A single tooth  
17 referred to aff. *Hamadasuchus* sp. is labiolingually compressed and approximately  
18 triangular in lateral view, with “remnants of clear serration” (Cuny et al. 2010: fig. 4.8,  
19 p. 625). Although the more extreme labiolingual compression towards the anterior  
20 and posterior margins of the tooth is reminiscent of *Hamadasuchus*, the apparent  
21 lack of rugose enamel is unusual given its presence in all teeth associated with the  
22 holotype specimen of *Hamadasuchus*. The only other named crocodyliforms from  
23 the Early Cretaceous of Africa to possess serrated carinae are *Araripesuchus*  
24 *wegeneri* and referred material of *Araripesuchus rattoides*, both of which possess  
25 dentition more similar in size to the tooth reported in Cuny et al. (2010). However,  
26 given that the Tunisian specimen is clearly well-worn and is not dissimilar in broad  
27 morphology from either *Hamadasuchus* or *Araripesuchus*, we regard this specimen  
28 as an indeterminate notosuchian. Re-evaluation and full description of specimens  
29 referred to *Hamadasuchus* that have teeth with smooth enamel (e.g. BSPG 2005 I  
30 83) might enable referral to a particular genus.  
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### 52 53 **6.3.3. Late Cretaceous**

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56 In northwestern Africa, the Cenomanian Kem Kem Group of Morocco has yielded  
57 three previously named notosuchian species (*Araripesuchus rattoides*,  
58 *Hamadasuchus rebouli*, *Lavocatchampsa sigogneaurussellae*), in addition to the new  
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3 species, *Antaeusuchus taouzensis*, described herein (Fig. 12). *Araripesuchus*  
4 *rattoides* is known from the holotypic partial dentary, as well as several referred  
5 dentary fragments (Sereno & Larsson 2009; Ibrahim et al 2020). It differs from *A.*  
6 *wegeneri* in several features, including its possession of a narrower and deeper  
7 snout, highly procumbent teeth, and potentially a greater number of teeth. Though  
8 not included in our phylogenetic analyses because of its fragmentary nature,  
9 *Araripesuchus rattoides* was recovered by Sereno & Larsson (2009) in a polytomy  
10 with three *Araripesuchus* species (*A. gomesii* and *A. patagonicus* from South  
11 America, and *A. tsangatsangana* from Madagascar), with this the sister group to a  
12 clade comprising the remaining uruguaysuchids (including *A. wegeneri*).  
13 *Lavocatchampsa sigogneaurussellae* was erected based on a small anterior snout  
14 region, which displays unusually heterodont teeth that are convergent with those of  
15 mammals (Martin & Lapparent de Broin 2016). Using the data matrix of Pol et al.  
16 (2014), Martin & Lapparent de Broin (2016) recovered *Lavocatchampsa* as a 'basal'  
17 ziphosuchian within Candidodontidae, a small clade otherwise known only from the  
18 Cretaceous of South America (Carvalho et al. 2004, Montefeltro et al. 2009).

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

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3 constraints for many of these species, it remains possible that these were not all  
4 contemporaneous.  
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8 The Cenomanian Bahariya Formation of north-central Egypt has yielded just a single  
9 notosuchian species (Fig. 12), with *Libycosuchus brevirostris* represented by a  
10 complete skull and lower jaws, as well as several isolated vertebrae (Stromer 1914;  
11 Buffetaut 1976). *Libycosuchus* has an anteroposteriorly short skull and is fairly  
12 consistently recovered as an early diverging ziphosuchian (e.g. Sertich & O'Connor  
13 2014; Pol et al. 2014; Martin & Lapparent de Broin 2016; Geroto & Bertini 2019), as  
14 is also the case in our analyses.  
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22 The large-bodied species *Kaprosuchus saharicus* is the only published notosuchian  
23 currently known from the Cenomanian Echkar Formation of northwestern Niger  
24 (Sereno & Larsson 2009) (Fig. 12). This species is based on an essentially complete  
25 skull and mandible and has been informally referred to as the “boar croc” due to its  
26 enlarged caniniform teeth. *Kaprosuchus* has been consistently recovered as the sister  
27 taxon to *Mahajangasuchus insignis* from the Maastrichtian of Madagascar (see  
28 below), and is thus a member of Mahajangasuchidae (e.g. Sereno & Larsson, 2009;  
29 Pol et al. 2014, Geroto & Bertini 2019; this analysis) (Fig. 6). Sereno & Pol (2019)  
30 reported an undescribed partial skeleton from the Echkar Formation that appears to  
31 be most closely related to the Maastrichtian Malagasy species, *Araripesuchus*  
32 *tsangatsangana*.  
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43 In the southeastern region of Africa, two notosuchian taxa are known from the Namba  
44 Member of the Galula Formation of western Tanzania (Fig. 12). Originally thought to  
45 be Aptian–Cenomanian (O'Connor et al. 2010; Roberts et al. 2010), new dates  
46 indicate either a Cenomanian–Santonian or more likely a Campanian age for this  
47 stratigraphic unit (Widlansky et al. 2018). Represented by the posterior region of the  
48 skull, the medium-to large-bodied *Rukwasuchus yajabaliyekundu* was recovered by  
49 Sertich & O'Connor (2014) as a peirosaurid. It had not been included in a subsequent  
50 phylogenetic analysis prior to ours, which provides further support for a peirosaurid  
51 placement (Figs 6 & 7). Known from an essentially complete skeleton, *Pakasuchus*  
52 *kapilimai* is one of several small notosuchians with multicuspid teeth from the  
53 Cretaceous of Gondwana that appears to fill an ecological niche that would later be  
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3 occupied by mammals (O'Connor et al. 2010; Sertich & O'Connor 2014). As is the  
4 case in several previous studies (e.g. O'Connor et al. 2010; Pol et al. 2014; Sertich &  
5 O'Connor 2014; Martin and Lapparent de Broin 2016), our analyses recover  
6 *Pakasuchus* as an early diverging member of Ziphosuchia, closely related to  
7 *Malawisuchus* (Fig. 7).  
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13 The Coniacian–Santonian In Beceten Formation of Niger (Fig. 12) has yielded the  
14 type material (an incomplete lacrimal) of *Trematochampsia taqueti* (Buffetaut 1974).  
15 As discussed in Section 6.2, Meunier & Larsson (2018) demonstrated that  
16 *Trematochampsia taqueti* is a nomen dubium, and suggested that isolated bones and  
17 teeth informally referred to the taxon represent at least three different small-medium  
18 sized crocodyliform species. They noted that many of these specimens show  
19 potential affinities to peirosaurids (especially *Hamadasuchus*), uruguaysuchids  
20 (especially *Araripesuchus wegneri* and *Anatosuchus minor*), ziphosuchians, and/or  
21 neosuchians, which we follow here.  
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30 The Wadi Milk Formation of northern Sudan (Fig. 12) has traditionally been regarded  
31 as Cenomanian (e.g. Buffetaut et al. 1990; Rage & Werner 1999), but more recent  
32 work indicates that it should be assigned to the Campanian–Maastrichtian (Owusu  
33 Agyemang et al. 2019). An undescribed peirosaurid has been briefly reported,  
34 consisting of partial mandibles and part of the skull roof, and which is notable for its  
35 large size (Evans et al. 2014).  
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43 Putative notosuchian remains from the Maastrichtian Dukamaje Formation in  
44 western Niger have been mentioned in the literature, but not described. Moody and  
45 Sutcliffe (1991: table 2) listed the presence of *Trematochampsia taqueti* and  
46 *Libycosuchus* sp. in this formation, but they provided no further details. We suspect  
47 that that this was a mistake, with the In Beceten faunal list accidentally incorporated,  
48 but this cannot currently be confirmed.  
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54 A mandibular fragment preserving the middle portion of a right dentary could  
55 potentially represent the only occurrence of a notosuchian from the Arabian  
56 Peninsula (Buscalioni et al. 2004). Buscalioni et al. (2004) tentatively assigned the  
57 specimen from the Maastrichtian Al-Khod Conglomerate Formation of northern  
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3 Oman as cf. *Trematochampsia* indet. and noted similarities with *Miadanosuchus*  
4 ('*Trematochampsia*') *oblita* from the Maastrichtian of Madagascar. These similarities  
5 included the presence of an enlarged tooth in the 10<sup>th</sup> alveolus, and a morphology  
6 indicative of a long and wide mandibular symphysis (despite this region not being  
7 preserved). Our analyses recover *Miadanosuchus* within Peirosauridae, a clade  
8 characterised by two distinct waves on the dorsal margin of the dentary. The very  
9 straight, only slightly inclined dorsal edge of the dentary in the Oman specimen is  
10 therefore not indicative of a specimen belonging to this clade, especially as the  
11 presence of an enlarged tooth would be expected to be accompanied by the  
12 dorsoventral expansion of the dentary. Furthermore, the dentary of *Miadanosuchus*  
13 maintains its mediolateral width posterior to the enlarged tenth tooth for at least the  
14 distance of two alveoli. The Oman specimen shows gradual, but distinct narrowing  
15 posterior to the enlarged tooth. Given the highly fragmentary nature of the specimen,  
16 and the few preserved anatomical features of phylogenetic relevance, we suggest  
17 that the material can only be assigned to an indeterminate crocodyliform.  
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31 The Maastrichtian Maevarano Formation that outcrops in northwestern Madagascar  
32 has thus far yielded four notosuchian taxa (Fig. 12). The bizarre “pug-nosed”  
33 *Simosuchus clarki* is represented by multiple individuals preserving most of the  
34 skeleton (Buckley et al. 2000; Georgi & Krause 2010; Hill 2010; Kley et al. 2010;  
35 Sertich & Groenke 2010). Most analyses recover *Simosuchus* as an early diverging  
36 ziphosuchian (e.g. Turner & Sertich 2010; Pol & Powell 2011; Pol et al. 2014; Geroto  
37 & Bertini 2019; this study). The large-bodied *Mahajangasuchus insignis* is known  
38 from an almost complete skull and much of the postcranial skeleton (Buckley &  
39 Brochu 1999; Turner & Buckley 2008). Initially thought to have affinities with  
40 ‘Trematochampsidae’, the taxon has since been recovered as a peirosaurid (e.g.  
41 Turner & Calvo 2005), or just outside of this clade (e.g. Pol et al. 2014). It is now the  
42 clade specifier for Mahajangasuchidae (Sereno & Larsson 2009), with our analyses  
43 providing evidence for a position both within (EIW) and just outside (equal weighting)  
44 of Peirosauridae. *Araripesuchus tsangatsangana* is represented by a nearly  
45 complete skull, as well as a second individual preserving a nearly complete skeleton  
46 (Turner 2006). *Miadanosuchus* ('*Trematochampsia*') *oblita* is known from partial  
47 dentaries, part of the skull roof, and a vertebra (Buffetaut & Taquet 1979;  
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3 Rasmusson Simons & Buckley 2009), and it appears to represent a peirosaurid  
4 (Geroto & Bertini (2019; this study).  
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8 *Pabwehshi pakistanensis*, recovered from the Maastrichtian Pab Formation of  
9 southwestern Pakistan (Fig. 12), is known from fragmentary specimens, which  
10 preserve the anterior region of the snout and the associated section of the mandible  
11 of two individuals (Wilson et al. 2001). The limited remains of *Pabwehshi* mean that  
12 its phylogenetic position is labile (Pol et al. 2014), although most authors have  
13 supported a close relationship with Baurusuchidae (e.g. Wilson et al. 2001; Turner &  
14 Calvo 2005; Nascimento & Hussam 2010; Turner & Sertich 2010; Pol & Powell 2011;  
15 Carvalho et al. 2011; Dal Sasso et al. 2017; Geroto & Bertini 2019; Coria et al.  
16 2019), which is otherwise known only from South America (e.g. Montefeltro et al.  
17 2020; Darlim et al. 2021). By contrast, Larsson & Sues (2007) recovered *Pabwehshi*  
18 as the most 'basal' member of Sebecia, i.e. as the sister taxon to a clade comprising  
19 Peirosauridae and Sebecidae. *Pabwehshi pakistanensis* was excluded from our  
20 analyses because of its labile position, but more complete material will ultimately be  
21 needed to robustly resolve its phylogenetic position.  
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34 An isolated tooth from the Maastrichtian Kallamedu Formation of southern India (Fig.  
35 12) was described by Prasad et al. (2013), who identified it as cf. *Simosuchus* sp.  
36 Based on comparisons with *Simosuchus clarki*, Prasad et al. (2013) suggested that  
37 the tooth is probably from the posterior region of the dentary. We fully agree with the  
38 evaluation and assignment of this specimen.  
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#### 44 **6.3.4. Paleogene**

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48 Buffetaut (1989) erected *Eremosuchus elkoholicus* from the El Kohol Formation of  
49 southwest Algeria (Fig. 12), which is dated to the Ypresian, early Eocene (Coster et  
50 al. 2012). This species is known from a partial mandible, teeth, vertebrae, and a  
51 fibula. When initially described, *Eremosuchus* was placed in the family  
52 Trematochampsidae (Buffetaut 1989), but more recently it has been included in  
53 Sebecosuchia by several authors (e.g. Gasparini et al. 1991; Ortega et al. 1996;  
54 Turner & Calvo 2005). However, it has not been included in most phylogenetic  
55 analyses, presumably because of its incomplete nature, and has largely been  
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3 neglected in treatments of crocodyliform evolutionary history. A detailed  
4 redescription and analysis of the phylogenetic relationships of *Eremosuchus* is  
5 needed to establish its systematic and biogeographic affinities.  
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10 Finally, the late Eocene Birket Qarun Formation (Seiffert 2006) in northeastern Egypt  
11 (Fig. 12) has yielded a fragmentary right dentary with ziphodont dentition (Stefanic et  
12 al. 2020). Though not assigned to a genus, the specimen clearly has sebecosuchian  
13 affinities and extends the temporal range of Notosuchia in Africa (Stefanic et al.  
14 2020).  
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### 20 **6.3.5. Summary**

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23 Our review of the Gondwanan record of notosuchians outside of South America  
24 demonstrates their spatiotemporal distribution in the Middle Jurassic, from the  
25 Aptian–Maastrichtian, and in the Eocene, with their remains known from Africa and  
26 Indo-Madagascar. A possible occurrence from the latest Cretaceous of Oman  
27 (Buscalioni et al. 2004) cannot be confidently referred to Notosuchia. The African  
28 and Indo-Madagascan Cretaceous record indicates the presence of several  
29 lineages, all with close ties to South American clades, with many faunas  
30 demonstrating multiple sympatric species. Given that notosuchians only first  
31 appeared in the Aptian in South America (and Asia), coupled with palaeogeographic  
32 reconstructions documenting the increasing fragmentation of Gondwana at this time  
33 (e.g. Seton et al. 2012), this diverse record supports previous suggestions regarding  
34 an undocumented pre-Aptian radiation of Notosuchia (e.g. Martin and Lapparent de  
35 Broin 2016; Mannion et al. 2019). By contrast, their Gondwanan Paleogene record  
36 outside of South America is currently limited to just two occurrences, both from the  
37 Eocene of north Africa and both belonging to Sebecosuchia. No stratigraphically  
38 younger remains have been assigned to Notosuchia from this region, with their last  
39 Laurasian occurrences from the middle Eocene of western Europe (e.g. Martin  
40 2016), indicating their extirpation outside of South America by the end of the Eocene.  
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## 56 **7. Conclusions**

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3 Two new crocodyliform specimens from the Cenomanian Kem Kem Group of  
4 Morocco are described and incorporated into a phylogenetic analysis. Both  
5 specimens are referable to *Antaeosuchus taouzensis* n. gen. n. sp., which is  
6 recovered within the notosuchian clade Peirosauridae, as the sister taxon to the  
7 contemporaneous *Hamadasuchus rebouli*. Comparisons of materials previously  
8 assigned to *Hamadasuchus* indicate the presence of at least three distinct  
9 peirosaurid species from the same spatiotemporal interval. Coupled with a critical  
10 reappraisal of the non-South American Gondwanan record of Notosuchia, we  
11 recognise a much greater taxonomic and ecomorphological diversity within this clade  
12 during the Cretaceous.  
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50 Data accessibility. The datasets supporting this article have been uploaded as part of  
51 the electronic supplementary material.  
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54 Authors' contributions. C.S.C.N and P.D.M. conceived of the study and interpreted  
55 the results. All authors contributed to the design of the study and to the drafting of  
56 the manuscript. Analyses were conducted by C.S.C.N. Figures were produced by  
57 C.S.C.N. and E.S.E.H. All authors approved the final version of the manuscript.  
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5 Competing interests. We declare we have no competing interests.  
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## Tables

### Table 1

Mandibular measurements of the holotypic specimen (NHMUK PV R36829) of *Antaeosuchus 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 *Antaeosuchus 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	-

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

**Table 3**

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

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

<i>Rukwasuchus yajabalijekundu</i>	Galula Fm., Tanzania	Cenomanian–Campanian, Late Cretaceous	Peirosauridae	Sertich and O'Connor, 2014
<i>Pakasuchus kapilimai</i>	Galula Fm., Tanzania	Cenomanian–Campanian, Late Cretaceous	Basal Ziphosuchia	O'Connor et al., 2010
<i>Araripesuchus tsangatsangana</i>	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Uruguaysuchidae	Turner, 2006
<i>Simosuchus clarki</i>	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Basal Ziphosuchia	Buckley et al., 2000
<i>Mahajangasuchus insignis</i>	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Mahajangasuchidae	Buckley and Brochu, 1999
<i>Miadanosuchus oblita</i>	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Peirosauridae	Rasmusson Simons and Buckley, 2009
<i>Pabwehshi pakistanensis</i>	Pab Fm., Pakistan	Maastrichtian, Late Cretaceous	Sebecosuchia?	Wilson et al., 2001
<i>Eremosucus elkoholicus</i>	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 *Antaeosuchus taouzensis* n. gen. n. sp. (NHMUK PV R36829 and R36874) within the Kem Kem Group of Morocco.

### Figure 2

Line drawings and photographs of *Antaeosuchus 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 *Antaeosuchus 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 *Antaeosuchus 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 *Antaeosuchus 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 *Antaeosuchus 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, *Antaeosuchus taouzensis* n. gen. n. sp. (NHMUK PV 36829\*); B, *Antaeosuchus 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,

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3 *Bayomesasuchus hernandezii* (MCF PVPH-822). Asterisk indicates a holotype  
4 specimen.  
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### 8 **Figure 10**

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10 Comparison of peirosaurid mandibles from the Kem Kem Group in lateral view: A,  
11 NHMUK PV 36829 (*Antaeosuchus taouzensis* n. gen. n. sp. holotype); B, NHMUK  
12 PV R36874 (*Antaeosuchus taouzensis* paratype); C, MDEC001 (*Hamadasuchus*  
13 *rebouli* holotype); D, ROM 49282; E, BSPG 2005 I 83. A1–E1 show close-up images  
14 of the teeth of each respective taxon. Image B is reversed. Scale bars represent 50  
15 mm.  
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### 22 **Figure 11**

23  
24 Time-calibrated phylogenetic topology showing the agreement subtree of  
25 notosuchians using equal weighting of characters. Some clades are condensed and  
26 the polytomy including *Razanandrongobe sakalavae* is shown despite being pruned  
27 from the agreement subtree.  
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### 32 **Figure 12**

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

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5 **441 ? -> 0**  
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8 *Stolokrosuchus lapparenti*:  
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11 **441 ? -> 0**  
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10 **A second peirosaurid crocodyliform from the mid-Cretaceous Kem Kem Group**  
11 **of Morocco and the diversity of Gondwanan notosuchians outside South**  
12 **America**  
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38 RRH: SECOND MOROCCAN PEIROSAURID

39 LRH: NICHOLL, HUNT, OUARHACHE & MANNION  
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## 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 Madagascar 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; Ōsi 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

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

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20 The Kem Kem crocodyliforms comprise the neosuchians *Aegisuchus witmeri*  
21 (Holliday & Gardner 2012), *Elosuchus cheriffensis* (Lavocat 1955; Lapparent de  
22 Broin 2002), and *Laganosuchus maghrebensis* (Sereno & Larsson 2009), as well as  
23 three notosuchians (Ibrahim et al. 2020). The first of these notosuchians to be  
24 named, the peirosaurid *Hamadasuchus rebouli* (Buffetaut 1994), was erected based  
25 on a fragmentary dentary. Several specimens have since been referred to this taxon,  
26 including a nearly complete cranium and lower jaws (Larsson & Sidor 1999; Rauhut  
27 & López-Arbarelo 2006; Larsson & Sues 2007; Ibrahim et al. 2020). Sereno &  
28 Larsson (2009) described a second Kem Kem notosuchian species, the small-bodied  
29 uruguaysuchid *Araripesuchus rattoides*, which is currently known from several  
30 dentaries (Ibrahim et al. 2020). The third notosuchian species to be described, the  
31 candidodontid *Lavocatchampsia sigogneaurussellae* (Martin & Lapparent de Broin  
32 2016), is known from a small partial skull with unusual mammal-like multicuspid  
33 teeth. Ibrahim et al. (2020) suggested that multicuspid crocodyliform teeth described  
34 by Larsson & Sidor (1999) might represent additional notosuchian taxa. Finally,  
35 Ibrahim et al. (2020) also noted anatomical differences between the type and  
36 referred material of *Hamadasuchus* that could indicate yet higher crocodyliform  
37 diversity in the Kem Kem Group.

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45 Here, we describe new notosuchian remains from the Kem Kem Group of Morocco  
46 that support Ibrahim et al.'s (2020) suggestion of higher crocodyliform diversity in this  
47 fauna. We test the phylogenetic position of these new specimens in an expanded  
48 version of an existing data set. Finally, we provide a critical reappraisal of the  
49 Gondwanan record of non-South American notosuchians, in which we reassess the  
50 group's diversity through time and space.  
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10 **1.1. Institutional abbreviations** — **BSPG**, Bayerische Staatssammlung für  
11 Paläontologie und Geologie, Munich, Germany; **CMN (formerly NMC)**, Canadian  
12 Museum of Nature, Ottawa, Canada; **MDE**, Musée des Dinosaurés, Espéraza,  
13 France; **MNHM**, Muséum national d'Histoire naturelle, Paris, France; **NHMUK**,  
14 Natural History Museum, London, UK; **ROM**, Royal Ontario Museum, Toronto,  
15 Canada.  
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## 18 **2. Systematic Palaeontology**

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21 Crocodylomorpha Walker, 1970  
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24 Crocodyliformes Hay, 1930 (sensu Clark in Benton and Clark, 1988)  
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27 Mesoeucrocodylia Whetstone and Whybrow, 1983  
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30 Notosuchia Gasparini, 1971  
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33 Peirosauridae Gasparini, 1982  
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36 *Antaeusuchus taouzensis* gen. et sp. nov.

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40 **Etymology**—Genus name after the giant *Antaeus* from Berber and Greek  
41 mythology, who is said to be buried at Msoura in northern Morocco, and *suchus*,  
42 from the Greek *souchos*, meaning crocodile. Species name after the township *Taouz*  
43 from where the holotype and paratype specimens were recovered.  
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46 **Holotype**—NHMUK PV R36829: paired mandibles, comprising an essentially  
47 complete left dentary and splenial, along with a partial angular and surangular, in  
48 articulation with the anterior portion of the right dentary and splenial.  
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51 **Paratype**—NHMUK PV R36874: a partial right mandible, comprising an incomplete  
52 dentary, surangular, and angular.  
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11 **Locality and horizon**—Near to Jebel Beg'aa, Taouz township, Errachidia Province,  
12 eastern Morocco. The specimens were commercially collected and recovered from  
13 unspecified beds within the Cenomanian (lower Upper Cretaceous) Kem Kem  
14 Group.  
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18 **Diagnosis**—A crocodyliform characterized by the following unique combination of  
19 features: (1) wide divergence angle (40–45°) of the mandibular rami; (2) dorsal  
20 margin of dentary sinusoidal with two distinct waves; (3) relatively unornamented  
21 surface texture of dentary adorned with narrow, shallow ridges; (4) ventrolateral  
22 dentary surface anterior to mandibular fenestra transversely compressed and  
23 vertical; (5) dentary extends posteriorly beneath the mandibular fenestra; (6) anterior  
24 alveoli of dentary strongly procumbent; (7) concavity for the reception of the enlarged  
25 maxillary tooth lateral to the 7<sup>th</sup> alveolus of the dentary; (8) splenial forming  
26 approximately 40% of the total mandibular anteroposterior length; (9) surangular  
27 overlaps dentary above the mandibular fenestra; (10) rugose tooth enamel formed  
28 by anastomosing grooves and ridges; (11) enlarged 4<sup>th</sup> and 13<sup>th</sup> dentary teeth; (12)  
29 tooth margins in posterior region of the dentary toothrow with denticulate carinae  
30 formed by homogeneous and symmetrical denticles with a sharp cutting edge; and  
31 (13) sub-triangular dentary tooth crowns (in lateral view) with a gently curved apex.  
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### 38 **3. Description**

39 After detailed description and comparison of the two specimens, we consider both  
40 NHMUK PV R36874 and R36829 to belong to the new species, *Antaeusuchus*  
41 *taouzensis*, and as such they are described together. In instances where the feature  
42 being described is preserved in only one specimen, the relevant museum accession  
43 number is provided.  
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#### 47 **3.1. Preservation**

48 The preserved parts of both specimens are undistorted and in good condition, such  
49 that small-scale morphological details are still visible. Damage is restricted mainly to  
50 the teeth, several of which are missing.  
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#### 53 **3.2. General Shape**

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10 The anterior region of the mandible is characterised by a broad, 'U'-shaped symphysis  
11 that forms at least one quarter of the total anteroposterior mandibular length. Each  
12 mandibular ramus diverges at an angle of approximately 22° from the sagittal midline.  
13 The ramus remains approximately straight along the majority of its preserved length,  
14 curving very slightly medially close to its posterior margin (visible on the left side of  
15 NHMUK PV R36829). The anterior half of the mandibular dorsal margin is  
16 characterized by two distinct 'waves', whereas the strongly sloping posterior half is  
17 largely straight, with the dentary increasing in dorsoventral height towards the  
18 surangular.  
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### 23 3.3. Dentary

24 **The dentary is anteroposteriorly elongate**, and its lateral, ventral, and dorsal surfaces  
25 are sculpted by neurovascular foramina and vermiform grooves. On the lateral  
26 surface, the foramina are largest and most numerous in the anterodorsal region of the  
27 snout. In the middle region of the snout, a series of short grooves run anteroposteriorly  
28 along the lateral surface, ~10 mm ventral to the toothrow. These grooves meet an  
29 anteroposteriorly elongate groove that extends to the dorsal suture of the dentary and  
30 surangular process (Figs 2 & 3). Another prominent, anteroposteriorly elongate  
31 vascular groove runs from the anterior-most point of the mandibular fenestra to the  
32 level of the posterior tip of the toothrow.  
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37 In lateral view, the dentary has a sinusoidal dorsal margin composed of two distinct  
38 waves. **The most anterior wave spans teeth 1–6, whereas the most posterior wave is**  
39 **dorsally raised between teeth 9–15**. The dorsoventrally tallest region of each wave  
40 corresponds with the position of dentary teeth 4 and 13, the posteriormost of which is  
41 more dorsally elevated than the anterior (Figs 2 & 3). The dentary forms the anterior  
42 region of a relatively wide mandibular symphysis (Fig. 4), the dorsal surface of which  
43 is very mildly concave. In dorsal view, the midline dentary suture extends posteriorly  
44 to the level of the 8<sup>th</sup> tooth (Fig. 4). The bone in this region is relatively unornamented,  
45 with the exception of a series of foramina immediately adjacent to the toothrow. On  
46 the ventral surface of the mandibular symphysis, the medial dentary suture extends  
47 posteriorly to a level between the 7<sup>th</sup>–8<sup>th</sup> teeth. A concavity is situated lateral to the  
48 5<sup>th</sup>–10<sup>th</sup> teeth, most likely for the reception of an enlarged maxillary tooth. The posterior  
49 region of the lateral dentary surface **dorsal to the mandibular fenestra** is divided into  
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10 two major acute posterior processes, separated by an anterior process of the  
11 surangular (Fig. 2). The ventral-most dentary extension forms the anterodorsal margin  
12 of the external mandibular fenestra and is dorsoventrally wide, forming approximately  
13 three quarters of the dorsoventral height of the mandible at the same level. The dorsal-  
14 most process is much narrower; its dorsal and ventral margins converge posteriorly to  
15 form an acute angle. An anteroposteriorly short dentary process is situated ventral to  
16 the external mandibular fenestra, although this does not contact the fenestral border.  
17 In NHMUK PV R36874, the splenial is not preserved, exposing the dentary's medial  
18 surface (Fig. 3).  
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23 The dentary has 18 tooth positions. On the left side of NHMUK PV R36829, whole or  
24 partial teeth are preserved in alveoli 1–16, whereas 17–18 are empty. On the right  
25 side of the specimen, 10 alveoli are preserved, with whole or partial teeth preserved  
26 in all but one (alveolus 9). Although the anterior region of NHMUK PV R36874 has  
27 broken away, the first preserved alveolus is large, and is assumed to be the fourth in  
28 the series. Whole or partial teeth are present in alveoli 5–6, 8, and 10–16 in NHMUK  
29 PV R36874. The largest tooth is the 13<sup>th</sup>, followed closely by the 4<sup>th</sup>, 11<sup>th</sup>, and 12<sup>th</sup>,  
30 which are approximately equidimensional in their circumference. In dorsal view, the  
31 tooth row is slightly sinusoidal, with lateral waves corresponding to the position of the  
32 4<sup>th</sup> and 13<sup>th</sup> teeth (Fig. 4). Although not fully preserved in either specimen, the  
33 anteriormost two teeth appear to be procumbent. Dentary teeth 3–10 project slightly  
34 anterolaterally. All of the dentary teeth are closely arranged, without the presence of  
35 diastemas.  
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#### 41 3.4. Splenial

42 The splenials are only preserved in NHMUK PV R36829. They participate in a  
43 relatively wide mandibular symphysis (Table 1) and occupy approximately 38% of the  
44 anteroposterior symphyseal length on the dorsal surface of the mandible, extending  
45 anteromedially to the position of the 8<sup>th</sup> alveolus (Fig. 4). On the dorsal surface of the  
46 symphysis, the splenial-dentary suture diverges gradually from the sagittal midline.  
47 This suture is slightly concave until the 11<sup>th</sup> tooth, from which point it is parallel to the  
48 tooth row. A line of small foramina run parallel to the toothrow along the lateral margin  
49 of the dorsal surface of the splenial. On the ventral surface of the mandible, the  
50 splenial occupies approximately 31% of the anteroposterior length of the symphysis,  
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10 and it extends anteriorly to the position of the 9<sup>th</sup> tooth. The ventromedial splenial  
11 surface of the mandibular symphysis is dorsally displaced relative to the lateral margin.  
12 A posterior peg is located on the ventromedial surface of the symphysis (Fig. 4). The  
13 splenial is transversely thin and dorsoventrally tall, covering the inner surface of the  
14 mandibular ramus from the ventral margin of the dentary to the lingual alveolar groove.  
15 Positioned just posterior to the mandibular symphysis, on the medial surface of the  
16 splenial, is an opening, likely homologous to the intermandibularis oralis of living  
17 crocodylians (Iordansky 1973). This is elliptical, such that its anteroposterior length is  
18 approximately twice that of its dorsoventral height.  
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### 23 3.5. Surangular

24 The surangular is more completely preserved in NHMUK PV R36829, extending from  
25 the posterior margin of the toothrow to its broken posterior margin at the dorsal-most  
26 region of the mandibular fenestra. Its lateral surface is covered with interconnected  
27 shallow grooves. Of the surangular's two acute anterior processes, the most  
28 anteroposteriorly elongate is located on the dorsal and medial surfaces of the  
29 mandible and extends to the posterior margin of the toothrow (Fig. 4). A second  
30 anterior process is present on the dorsal region of the lateral mandibular surface (Figs  
31 2 & 3). Approximately halfway between the anterior margin of the mandibular fenestra  
32 and the posterior margin of the toothrow, the dorsal and ventral margins of this second  
33 anterior process meet anteriorly to form a subtriangular tip. An anteroposteriorly  
34 elongate dorsal coronoid tuberosity protrudes from the dorsomedial surangular  
35 surface, running anteroposteriorly for a distance of approximately 30 mm; its anterior  
36 margin is at the same level as the posterior-most point of the posterodorsal dentary  
37 process. The surangular forms the dorsal-most margin of the mandibular fenestra.  
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### 45 3.6. Angular

46 Albeit highly incomplete, the angular is best preserved in NHMUK PV R36874. The  
47 angular has an elongate anterior process that extends along the ventromedial surface  
48 of the mandible to the level of the 14<sup>th</sup> dentary tooth (Fig. 5). A second, smaller anterior  
49 process is present on the lateral surface of the skull (Fig. 3). This extends to the  
50 anterior margin of the mandibular fenestra, such that the angular forms the latter's  
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10 entire ventral margin. The posteriormost preserved region of the angular projects  
11 laterally, forming a prominent ventrolateral ridge beneath the mandibular fenestra.  
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### 13 14 **3.7. Mandibular Fenestra**

15 Although not fully preserved in either specimen, the mandibular fenestra can be  
16 inferred to be large and anteroventrally–posterodorsally elongate, as indicated by its  
17 extensive, straight anterodorsal margin in NHMUK PV R36874 (Figs 2 & 3). Its  
18 anteriormost margin is positioned at approximately the same level as the  
19 posteriormost extension of the dorsal-most dentary process; however, the posterior  
20 fenestral margin is not preserved in either specimen.  
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### 24 **3.8. Dentition**

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

### 44 **4.1. Dataset and analytical approach**

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47 Specimens NHMUK PV R36829 and R36874 were combined as one operational  
48 taxonomic unit (OTU), *Antaeosuchus taouzensis*, into a character-taxon matrix  
49 (CTM) sampling a large number of crocodyliforms, with particular emphasis on  
50 notosuchians. This matrix was originally published by Pol et al. (2014) and has since  
51 formed the underlying dataset for phylogenetic analysis in a number of studies, with  
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10 each one making minor additions and/or revisions to taxa and/or characters.  
11 Unfortunately, many of these iterations have occurred in parallel, rather than  
12 representing a continuous series of revisions to one dataset, meaning that there is  
13 no single dataset incorporating all of these changes to the original Pol et al. (2014)  
14 data matrix. Here, we united many of these 'daughter' matrices, using that of  
15 Martínez et al. (2018) as a starting point. The latter is a successive iteration of the  
16 data matrices of Leardi et al. (2015) and Fiorelli et al. (2016), which emanated from  
17 that of Pol et al. (2014). We included two additional characters, following Leardi et al.  
18 (2018), and revised 20 existing character scores based on observations from recent  
19 studies (Stromer 1914; Gomani 1997; Larsson & Gado 2000; Carvalho et al. 2005;  
20 Carvalho et al. 2007; Larsson & Sues 2007; Martinelli et al. 2012; Barrios et al. 2016)  
21 and personal observations (see Appendix for documentation of changes).  
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27 We incorporated notosuchians from parallel daughter matrices, utilising scores  
28 presented in those datasets, and a review of the literature. These consist of  
29 *Razanandrongoibe sakalavae* from the Bathonian (Middle Jurassic) of Madagascar  
30 (Maganuco et al. 2006; Dal Sasso et al. 2017), the probable peirosaurids  
31 *Bayomesasuchus hernandezii* (Barrios et al. 2016) and *Barrosasuchus*  
32 *neuquenianus* (Coria et al. 2019) from the early Late Cretaceous (Turonian and  
33 Santonian, respectively) of Argentina, the sphagesaurid *Caipirasuchus mineirus* from  
34 the late Campanian–early Maastrichtian (latest Cretaceous) of Brazil (Martinelli et al.  
35 2018), and the sebecid *Ogresuchus furatus* from the early Maastrichtian of Spain  
36 (Sellés et al. 2020). We also expanded the sampling of putative peirosaurids that  
37 had not previously been incorporated into iterations of the Pol et al. (2014) data  
38 matrix via the inclusion of *Rukwasuchus yjabalijekundu* from the Late Cretaceous of  
39 Tanzania (Sertich & O'Connor 2014) and *Miadasuchus oblita* from the  
40 Maastrichtian of Madagascar (Rasmusson Simons & Buckley 2009). The OTU for  
41 *Hamadasuchus rebouli* followed previous iterations of this data matrix, although we  
42 made a small number of character state changes (see Appendix). The resultant data  
43 matrix consists of 121 OTUs scored for 443 characters, including 63 putative  
44 notosuchian taxa. *Antaeusuchus taouzensis* could be scored for 51 of these  
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10 The data matrix was analysed under maximum parsimony using the 'Stabilize  
11 Consensus' option in the 'New Technology Search' in TNT v. 1.5 (Goloboff et  
12 al. 2008). The search was executed using sectorial searches, drift, and tree fusing,  
13 and the consensus was stabilized five times with a factor 75, prior to using the  
14 resultant trees as the starting trees for a 'Traditional Search' using Tree Bisection-  
15 Reconstruction. Subsequently, a strict consensus tree was calculated. We applied  
16 two different weighting schemes, using equal weighting (EQW) and extended implied  
17 weighting (EIW). Shown to perform well on morphological datasets (Goloboff et al.  
18 2018), EIW downweights homoplastic characters in relation to their average  
19 homoplasy, whilst reducing the possible impact of missing data (Goloboff 2014). The  
20 concavity constant, represented by the  $k$ -value, denotes the strength of  
21 downweighting, with lower values having been shown to downweight homoplastic  
22 characters more severely than higher values (Goloboff et al. 2018). Following  
23 analytical protocols in recent analyses of neosuchians (Groh et al. 2020; Nicholl et  
24 al. 2020; Rio et al. 2020; Rio & Mannion 2021), we applied EIW to notosuchians for  
25 the first time, using  $k$ -values of 8 and 12. Characters with missing entries were  
26 downweighted faster assuming 50% the homoplasy of observed entries, and  
27 weighting strength did not exceed 5 times that of characters with no missing entries.  
28 Forty-three characters representing nested sets of homologies were ordered (1, 3, 6,  
29 10, 23, 37, 43, 44, 45, 49, 65, 67, 69, 71, 73, 77, 79, 86, 90, 91, 96, 97, 105, 116,  
30 126, 140, 142, 143, 149, 167, 182, 187, 193, 197, 226, 228, 279, 339, 356, 357, 364,  
31 368, 401). Character 5 was made inactive due to "dependence with the modified  
32 definition of character 6" (Pol et al. 2014: supplementary information p. 3). Following  
33 the identification of problematic, unstable taxa by Pol et al. (2014), confirmed by our  
34 preliminary searches, three species known from fragmentary remains were excluded  
35 from our analyses *a priori* (i.e. *Coringasuchus anisodontis*, *Pabwehshi pakistanensis*,  
36 and *Pehuenchesuchus enderi*). The character list and data matrix are provided as  
37 nexus and tnt files (electronic supplementary material), with stored settings for  
38 assigning characters as ordered and inactive.

## 4.2. Results

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51 Under EQW, our analysis produced 11520 trees with a tree length of 1778 steps.  
52 The overall tree topology is broadly consistent with the analyses of Pol et al. (2014)  
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10 and subsequent iterations. Notosuchia comprises a main bifurcation into Ziphosuchia  
11 (plus *Candidodon itapecuruense* and *Libycosuchus brevirostris*), and a clade in  
12 which Uruguaysuchidae is recovered as the sister taxon of Mahajangasuchidae +  
13 Peirosauridae (following the recent phylogenetic definition of Geroto & Bertini 2018  
14 [see below]) (Fig. 7). Although *Peirosaurus torminni* is not included in our data  
15 matrix, *Uberabasuchus terrificus* has been consistently recovered as a close relative,  
16 with some authors regarding the latter as a junior synonym of the former (e.g.  
17 Larsson & Sues 2007; Martinelli et al. 2012). As such, we regard the *Uberabasuchus*  
18 OTU as a proxy for *Peirosaurus* in terms of identifying Peirosauridae. Bremer values  
19 are generally low across the tree, ranging from 1–3.  
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24 *Antaeusuchus* is recovered within Peirosauridae, as the sister taxon to  
25 *Hamadasuchus* (Fig. 7). The two Kem Kem OTUs form a clade with  
26 *Bayomesasuchus* that is the sister group to nearly all other peirosaurids. Within this  
27 latter group, *Barrosasuchus* and *Miadanasuchus* form a clade that is the sister taxon  
28 to a polytomy comprising *Rukwasuchus*, *Gasparinisuchus peirosauroides*,  
29 *Lomasuchus palpebrosus*, *Uberabasuchus*, and *Montealtosuchus arrudacamposi*.  
30 This polytomy can be resolved through the *a posteriori* pruning of *Gasparinisuchus* in  
31 the agreement subtree, which results in *Lomasuchus* and *Montealtosuchus*  
32 recovered as sister taxa, forming a clade with *Uberabasuchus*, with *Rukwasuchus*  
33 placed at the 'base' of this grouping. *Stolokrosuchus lapparenti* is recovered as the  
34 earliest diverging member of Peirosauridae.  
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40 Under EIW, with both *k*-values, the overall topology is largely similar to that  
41 recovered using EQW. With a *k*-value of 8, the analysis produced 45 trees with a  
42 tree length of 89.3, and with a *k*-value of 12, 15 MPTs were found of length 68.3. The  
43 main difference with results obtained from EQW is that the taxonomic content of  
44 Peirosauridae is now expanded, as a result of *Stolokrosuchus* being recovered in a  
45 clade with *Lorosuchus nodosus* and Mahajangasuchidae (Fig. 8). The phylogenetic  
46 definition proposed by Geroto and Bertini (2018) means that Mahajangasuchidae is  
47 a clade within Peirosauridae according to our EIW topology.  
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## 51 **5. Comparisons**

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10 Given the results of our phylogenetic analyses, which provide robust and consistent  
11 support for a peirosaurid placement for *Antaeusuchus*, we largely restrict our  
12 anatomical comparisons to members of this clade.  
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### 15 **5.1. Comparisons with other peirosaurids**

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18 Characteristic of all members of Peirosauridae (Martinelli et al. 2012), *Antaeusuchus*  
19 possesses an undulatory dorsal margin of the dentary comprising two distinct waves,  
20 the apices of which coincide with the position of the two largest dentary teeth (Ortega  
21 et al. 1996; Pol et al. 2014). In all peirosaurids in which the relevant region is  
22 preserved, with the exception of *Stolokrosuchus* (Larsson & Gado 2000), the 4<sup>th</sup>  
23 dentary tooth is the largest of those in the first wave, and it coincides with the apex of  
24 the anterior dentary region. The position of the largest tooth (the apex of the  
25 posterior wave) also varies amongst peirosaurids (Pol et al. 2014). The apex of this  
26 posterior wave corresponds to the 13<sup>th</sup> tooth position in *Antaeusuchus*,  
27 *Barrosasuchus*, *Gasparinisuchus*, and *Kinesuchus overoi* (Martinelli et al., 2012;  
28 Filippi et al. 2018; Coria et al. 2019), whereas it occurs at the level of the 12<sup>th</sup> tooth in  
29 *Hamadasuchus* and *Montealtosuchus* (Carvalho et al. 2007; Larsson & Sues 2007).  
30 In *Stolokrosuchus*, the jaw gradually increases in dorsoventral height posteriorly,  
31 corresponding with a progressively larger tooth size towards the posterior region of  
32 the dentary (Larsson & Gado 2000). In lateral view, the dorsoventrally expanded  
33 posterior region of the mandible of *Antaeusuchus* more closely resembles that of  
34 *Hamadasuchus*, *Montealtosuchus*, and *Uberabasuchus* (Carvalho et al. 2004, 2007;  
35 Larsson & Sues 2007) than it does in taxa such as *Barrosasuchus* and *Kinesuchus*  
36 (and potentially *Pepesuchus deiseae*) (Campos et al., 2011; Filippi et al. 2018; Coria  
37 et al. 2019), in which the region is more dorsoventrally compressed.  
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45 All peirosaurid taxa, except for the longirostrine-snouted *Stolokrosuchus* (Larsson &  
46 Gado 2000), are characterised by a mediolaterally broad mandibular symphysis (Fig.  
47 9). This is most prominent in *Colhuehuapisuchus lunai*, *Barrosasuchus*, and  
48 *Gasparinisuchus* (Martinelli et al. 2012; Coria et al. 2019; Lamanna et al. 2019), in  
49 which the anteroposterior length to mediolateral width ratio of the symphyseal dorsal  
50 surface is less than 1.0 (values range from 0.8–0.9). Although still broad in  
51 comparison with many other notosuchian taxa, such as sphagesaurians (Ruiz et al.  
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2021), which often have length to width ratios exceeding 2.0 (Pol et al. 2014), *Antaeosuchus*, as well as *Hamadasuchus*, possess some of the anteroposteriorly longest mandibular symphyses amongst Peirosauridae, with a ratio of 1.4 and 1.5 for *Antaeosuchus* 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 *Antaeosuchus* participate in the mandibular symphysis, although the extent to which this is the case varies between peirosaurids (Fig. 9). The splenial of *Antaeosuchus* 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 *Antaeosuchus*, 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 *Antaeosuchus*.

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

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

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46 In numerous peirosaurids, including *Antaeusuchus*, *Hamadasuchus*,  
47 *Uberabasuchus*, *Montealtosuchus*, *Pepesuchus*, *Stolokrosuchus*, and *Lomasuchus*,  
48 an anteroposteriorly elongate groove runs parallel to the dentary toothrow, just  
49 ventral to the dorsal margin of the lateral surface of the mandible (Gasparini et al.  
50 1991; Larsson & Gado 2000; Carvalho et al. 2004; Carvalho et al. 2007; Larsson &  
51 Sues 2007; Campos et al. 2011). The lateral surface of the dentary is also typically  
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10 sculpted with pits and/or grooves in peirosaurids; however, there is interspecific  
11 variation in the degree to which this sculpting continues over the entire surface. In  
12 *Antaeusuchus*, the lateral surface of the dentary is similar in its texture and sculpting  
13 both above and below the groove. In this regard, the morphology is similar to that of  
14 *Uberabasuchus*, *Barrosasuchus*, and *Kinesuchus* (Carvalho et al. 2004; Filippi et al.  
15 2018; Coria et al. 2019). In *Hamadasuchus*, *Montealtosuchus*, *Pepesuchus*, and  
16 *Patagosuchus*, the region above the groove is smooth, differing markedly from the  
17 remainder of the highly sculpted lateral dentary surface (Carvalho et al. 2007;  
18 Larsson & Sues 2007; Campos et al. 2011; Lio et al. 2016). Although *Stolokrosuchus*  
19 shows no difference in bone surface texture above and below the anteroposterior  
20 groove (Larsson & Gado 2002), it differs from *Antaeusuchus* in that the majority of  
21 the lateral dentary surface is smooth and unornamented.  
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27 The degree of sculpting on the lateral surface of the dentary varies across  
28 notosuchian taxa, including within Peirosauridae. Whereas the surface is covered in  
29 deep pits in *Hamadasuchus*, *Uberabasuchus*, *Montealtosuchus*, *Patagosuchus*,  
30 *Bayomesasuchus*, and *Miadasuchus* (Carvalho et al. 2004; 2007; Larsson & Sues  
31 2007; Rasmusson Simons & Buckley 2009; Barrios et al. 2016; Lio et al. 2016), the  
32 surface of *Antaeusuchus* is considerably smoother and is textured with narrow,  
33 shallow grooves.  
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37 Unlike *Montealtosuchus*, *Gasparinisuchus*, *Bayomesasuchus*, *Stolokrosuchus*,  
38 *Patagosuchus*, *Pepesuchus*, and *Colhuehuapisuchus* (Buckley & Brochu 1999;  
39 Larsson & Gado 2000; Carvalho et al. 2007; Campos et al. 2011; Martinelli et al.  
40 2012; Lamanna et al. 2019), the lateral surface of the dentary adjacent to the 5<sup>th</sup>–8<sup>th</sup>  
41 teeth forms a distinct anteroposteriorly elongate concavity in *Antaeusuchus*. This is  
42 otherwise known only in *Hamadasuchus* (Larsson & Sues 2007), although a  
43 shallower concavity also characterizes *Barrosasuchus* (Coria et al. 2019). This  
44 depression would likely have functioned to receive an enlarged premaxillary tooth  
45 during occlusion.  
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50 Although incompletely preserved, the mandibular fenestra in *Antaeusuchus* is almost  
51 certainly large and anteroposteriorly elongate, as is the case in *Hamadasuchus*,  
52 *Montealtosuchus*, and *Uberabasuchus* (Carvalho et al. 2004; Carvalho et al. 2007;  
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10 Ibrahim et al. 2020), but differing from *Barrosasuchus* in which the fenestra is greatly  
11 reduced (Coria et al. 2019). However, *Montealtosuchus* and *Uberabasuchus* differ  
12 from the dentaries of *Antaeusuchus* and *Hamadasuchus* (Ibrahim et al. 2020) in that  
13 the latter two have a small posterior process that extends ventral to the mandibular  
14 fenestra. This process is absent in *Montealtosuchus* and *Uberabasuchus*, in which  
15 the dentary-angular contact is entirely anterior to the mandibular fenestra instead  
16 (Carvalho et al. 2004; Carvalho et al. 2007). The dentary-surangular contact is  
17 similar in *Antaeusuchus*, *Hamadasuchus*, *Montealtosuchus*, and *Uberabasuchus*,  
18 with the surangular contacted by two posterior processes: the dorsal process  
19 intrudes entirely into the surangular, whereas the second process forms the ventral  
20 margin of the surangular and the anterodorsal margin of the mandibular fenestra  
21 (Carvalho et al. 2004; Carvalho et al. 2007; Larsson & Sues 2007). This feature  
22 cannot be assessed in other peirosaurid taxa, in which the relevant region of the  
23 mandible is not preserved.  
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30 When complete, each dentary of *Antaeusuchus* has 18 tooth positions. This count is  
31 common amongst peirosaurids, e.g. *Montealtosuchus*, *Gasparinisuchus*,  
32 *Kinesuchus*, *Pepesuchus*, and possibly *Barrosasuchus* (Carvalho et al. 2007;  
33 Campos et al. 2011; Martinelli et al. 2012; Filippi et al. 2018; Coria et al. 2019), but  
34 differs from *Stolokrosuchus*, in which there are at least 30 dentary alveoli (Larsson &  
35 Gado 2000). As in all peirosaurids (Pol et al. 2014), the first two dentary teeth of  
36 *Antaeusuchus* are strongly procumbent.  
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40 The dentary teeth posterior to the 5<sup>th</sup> alveolus are closely spaced and are mostly  
41 situated in a continuous groove in *Antaeusuchus*, *Hamadasuchus* (Larsson & Sues  
42 2007), *Gasparinisuchus* (Martinelli et al. 2012), and *Barrosasuchus* (Coria et al.  
43 2019). This differs from the condition in *Kinesuchus* (Filippi et al. 2018) and  
44 *Patagosuchus* (Lio et al. 2016), in which the teeth are separated by distinct septa  
45 that extend fully to the dorsal margin of the dentary.  
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## 49 **5.2. Detailed comparisons with *Hamadasuchus rebouli***

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51 Although several crocodyliform taxa, including notosuchians, have been identified  
52 from the Kem Kem Group (Ibrahim et al. 2020), only one peirosaurid species is  
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10 currently recognised from these beds: *Hamadasuchus rebouli* (Buffetaut 1994;  
11 Larsson & Sues 2007). Since the original description of the holotype dentary by  
12 Buffetaut (1994), several specimens have been referred to *Hamadasuchus* (Larsson  
13 & Sidor 1999; Rauhut & López-Arbarelo 2006; Larsson & Sues 2007; Ibrahim et al.  
14 2020). In our CTM (and previous iterations), the OTU of *Hamadasuchus* comprises  
15 the holotype mandibular fragment, MDEC001, plus the cranial material, ROM 52620,  
16 referred by Larsson & Sues (2007). Almost all characters that could be assessed for  
17 *Antaeusuchus* received the same score as *Hamadasuchus*, resulting in their  
18 consistent recovery as sister taxa in our phylogenetic analyses. The only differences  
19 in scores are present in characters 77 (scored as 2 and 1&2 for *Antaeusuchus* and  
20 *Hamadasuchus*, respectively), 155 (scored as 1 and 0&1 for *Antaeusuchus* and  
21 *Hamadasuchus*, respectively), and 393 (scored as 0 and 0&1 for *Antaeusuchus* and  
22 *Hamadasuchus*, respectively). The score of 1&2 for character 77 reflects the  
23 fragmentary nature of the *Hamadasuchus* type specimen and uncertainty of the  
24 precise length of the splenial contribution to the mandibular symphysis, rather than  
25 representing a polymorphism, whereas the score of 0&1 for characters 155 and 393  
26 represents the definite presence of both states in this OTU. Given the similarity of  
27 the scores of both Kem Kem specimens, and that those provided for the mandible of  
28 *Hamadasuchus* are based only on the holotype specimen and not any referred  
29 material, we provide more detailed comparisons in the following section.

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36 *Antaeusuchus* is compared to several anatomically overlapping specimens currently  
37 assigned to *Hamadasuchus*, namely the holotype dentary (MDEC001), several  
38 partial mandibles (ROM 49282, 52045, and 52047) described by Larsson & Sues  
39 (2007), a complete skull and lower jaws (BSPG 2005 I 83) figured by Rauhut &  
40 López-Arbarelo (2006), and two mandibular symphyses (MNHN-MRS 3110 & NMC  
41 41784) illustrated in Ibrahim et al. (2020). Despite being largely similar in overall  
42 morphology, *Antaeusuchus* differs in several respects from all specimens assigned  
43 to *Hamadasuchus* (Fig. 10).

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48 Although only one dentary is preserved in the holotype (MDEC001), the angle of  
49 divergence of the mandibular rami can be inferred by measuring the angle of  
50 deviation of one dentary from the exposed symphyseal suture. Estimated mandibular  
51 rami divergence angles of ~20° for ROM 52047, ~25° for MDEC001 and ~30° for  
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10 ROM 49282, 52045, are much narrower than that of *Antaeosuchus* (43–44°). This  
11 suggests that *Hamadasuchus* had a slenderer rostrum than that of *Antaeosuchus*.  
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14 The surface texture of the *Antaeosuchus* dentary differs from all three specimens  
15 referred to *Hamadasuchus* in that it is not covered in deep pits and grooves. Instead,  
16 it is ornamented with relatively narrow and shallow grooves. *Antaeosuchus* also  
17 differs from these specimens in the dorsal region of the dentary lateral surface. In  
18 MDEC001, the area just ventral to the toothrow is smooth and lacks pits, differing  
19 from the remainder of the lateral surface (Buffetaut 1994). Instead, this dorsal region  
20 has a corrugated morphology, with broad, shallow dorsoventral grooves that do not  
21 correspond to the position of the dentary teeth (Fig. 10). A similar morphology  
22 characterizes ROM 49282, BSPG 2005 I 83, and NMC 41784, although it is not as  
23 prominent in those specimens. In *Antaeosuchus*, the degree of ornamentation is  
24 much the same across the lateral surface of the dentary and a fluted dorsal region is  
25 absent.  
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31 The apex of the second mandibular wave is marked by the position of the 13<sup>th</sup> tooth  
32 in *Antaeosuchus*, as well as ROM 49282, BSPG 2005 I 83, and probably MNHN-  
33 MRS 3110. By contrast, the tip of the second dentary wave is most likely marked by  
34 the 12<sup>th</sup> tooth in the holotype MDEC001, which is significantly larger than the 13<sup>th</sup>  
35 tooth (Buffetaut 1994).  
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39 Posterior to the 7<sup>th</sup> dentary tooth, the teeth of MDEC001 are strongly labiolingually  
40 compressed, and possess serrated carinae on their anterior and posterior cutting  
41 edges. A similar morphology is also present in *Antaeosuchus*, as well as MNHN-  
42 MRS 3110, but not in ROM 49282, in which the teeth are compressed only from the  
43 10<sup>th</sup> tooth. The 5<sup>th</sup> to 9<sup>th</sup> teeth are damaged in BSPG 2005 I 83 and so it is unclear at  
44 which tooth position the compression commences. The posterior teeth in MDEC001  
45 have a lanceolate shape (Buffetaut 1994) that is not present in *Antaeosuchus*, but  
46 which is most reminiscent of the morphology in MNHN-MRS 3110. In NHMUK PV  
47 R36829, teeth 11, 12, 14, and 15 are the only ones which are fully preserved; the  
48 anterior two of these have rounded crowns that do not form an angular tip. Although  
49 the 14<sup>th</sup> and 15<sup>th</sup> teeth of NHMUK PV R36829 are slightly pointed at their apices,  
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10 they are not comparable to the almost triangular shape of those in the holotype  
11 MDEC001 (Buffetaut 1994). In NHMUK PV R36874, the 10<sup>th</sup>–14<sup>th</sup> teeth are slightly  
12 more angular in appearance, but their anterior and posterior margins are parallel for  
13 most of their length, converging to a point only at the crown apex (Fig. 10).  
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17 The only fully preserved tooth in the ROM 49282 dentary is the 13<sup>th</sup> one (Larsson &  
18 Sues 2007). Comparing the broad morphology, it is most similar to the teeth at a  
19 similar dentary position in *Antaeosuchus*, in that its apical margin is rounded.  
20 However, the tooth enamel of ROM 49282 is essentially smooth. By contrast, the  
21 enamel in *Antaeosuchus* is wrinkled into anastomosing apicobasal ridges  
22 (approximately 2–3 ridges per mm) (Fig. 10). Both morphologies differ from that of  
23 the teeth of MDEC001, in which the enamel is textured, but has an irregular, globular  
24 pattern towards its base, and anastomosing ridges towards the apex of the crown  
25 (Buffetaut 1994). ROM 49282 also displays a unique condition in which the tooth  
26 enamel is fluted with broad apicobasal ridges around its circumference.  
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31 The teeth of all specimens assigned to *Hamadasuchus*, as well as those of  
32 *Antaeosuchus*, have very finely serrated carinae on their anterior and posterior  
33 cutting edges, with individual serrations spaced at approximately 3–5 per mm.  
34 Although most prominent in MDEC001, vertical fluting on the anterior and posterior  
35 regions of the crowns is visible in the posterior dentary teeth of all the specimens  
36 discussed in this section.  
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40 Finally, *Antaeosuchus* is significantly larger than all *Hamadasuchus* specimens, such  
41 that it is almost double the size of MDEC001, ROM 49282, and BSPG 2005 I 83.  
42 Although the size of the specimen alone should not be a reason to erect a new species  
43 (e.g. Griffin et al. 2021), we believe it to be a valid morphological difference as part of  
44 a large, unique combination of features. Furthermore, *Hamadasuchus* is already  
45 known from an ontogenetic series, including specimens considered 'adult' (Larsson &  
46 Sues 2007); as such, it is difficult to reconcile the numerous anatomical differences  
47 merely as a result of *Antaeosuchus* being an even older individual of *Hamadasuchus*.  
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## 51 **6. Discussion**

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### 6.1. Taxonomic affinities of NHMUK PV R36829 and R36874

In all of our analyses, the NHMUK PV R36829 + R36874 OTU (i.e. *Antaeosuchus*) is recovered as the sister taxon of *Hamadasuchus*. This relationship is supported by a single unambiguous synapomorphy (a distinct concavity adjacent to the 5<sup>th</sup> to 10<sup>th</sup> 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 *Antaeosuchus*, 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), *Antaeosuchus* 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 *Antaeosuchus* 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 *Antaeosuchus* 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 *Antaeosuchus*, 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 R36874 are not referable 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

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10 curved apex; (5) minor labiolingual compression of the posterior dentary teeth; (6) a  
11 lack of fluting on the dorsal region of the lateral dentary surface; (7) a relatively  
12 unornamented surface texture of the dentary adorned with narrow, shallow ridges  
13 rather than deep pits or grooves; and (8) dentary teeth more widely spaced at their  
14 base.  
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18 As such, it seems clear that NHMUK PV R36829 + R3687 represents a second  
19 peirosaurid in the Kem Kem Group, and thus supports our erection of *Antaeusuchus*  
20 *taouzensis* n. gen. n. sp. In addition, material currently referred to *Hamadasuchus*  
21 also differs from the type specimen (MDEC001), as well as *Antaeusuchus*. In  
22 particular, the partial mandible, ROM 49282, described by Larsson & Sues (2007),  
23 differs from both taxa in several features, including: (1) distinctive apicobasal fluting  
24 on the 13<sup>th</sup> tooth; (2) a highly elongate contribution of the splenial to the mandibular  
25 fenestra; (3) a mandibular rami divergence of approximately 30°; and (4) possession  
26 of relatively smooth tooth enamel. The unique combination of characters in each of  
27 MDEC001, ROM 49282, and NHMUK PV R36829 + R36874, therefore suggests the  
28 presence of at least three separate, albeit closely related, peirosaurid species from  
29 the Kem Kem Group. Although we erect a new name for NHMUK PV R36829 +  
30 R3687, we refrain from naming a new taxon for ROM 49282 pending the description  
31 and assessment of additional materials currently assigned to *Hamadasuchus rebouli*  
32 (namely BSPG 2005 I 83 and additional ROM specimens).  
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## 38 **6.2. Implications for peirosaurid relationships**

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40 Peirosauridae was erected by Gasparini (1982) to accommodate *Peirosaurus*  
41 *torminni* (Price 1955) from the late Maastrichtian Marília Formation of Brazil. This  
42 family was subsequently expanded by Gasparini et al. (1991) to include *Lomasuchus*  
43 from the late Turonian–early Coniacian of Argentina. Geroto & Bertini (2019 p. 328)  
44 provided a phylogenetic definition for Peirosauridae as “the least inclusive clade  
45 containing *P. tormini* [sic] Price, 1955, *Itasuchus jesuinoi* Price, 1955,  
46 and *Stolokrosuchus lapparenti* Larsson & Gado, 2000, but not including *Notosuchus*  
47 *terrestris* Woodward, 1896, *Baurusuchus pachecoi* Price, 1945, *Sphagesaurus*  
48 *huenei* Price, 1950, *Araripesuchus gomesii* Price, 1959, *Sebecus*  
49 *icaeorhinus* Simpson, 1937, *Mariliasuchus amarali* Carvalho & Bertini, 1999,  
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10 and *Crocodylus niloticus* Laurent, 1768". Although a phylogenetic definition based on  
11 two well-nested and stable species-level specifiers would be preferable (e.g. Sereno  
12 1998, 2005; Lee 2005), we follow the definition of Geroto & Bertini (2019) here,  
13 pending a detailed re-evaluation of the interrelationships of this part of the  
14 notosuchian tree.  
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18 Following Geroto & Bertini's (2019) definition, Peirosauridae comprises a  
19 taxonomically rich array of crocodyliforms from across the Cretaceous of South  
20 America, Africa, and Madagascar (e.g. Price 1955; Carvalho et al. 2004; Carvalho et  
21 al. 2007; Larsson & Sues 2007; Leardi & Pol 2009; Sertich O'Connor 2014; Campos  
22 et al. 2011; Martinelli et al. 2012; Lio et al. 2016; Barrios et al. 2016; Filippi et al.  
23 2018; Coria et al. 2019). However, there is little consensus regarding the position of  
24 Peirosauridae. A number of analyses have recovered Peirosauridae within  
25 Notosuchia, as the sister taxon to Mahajangasuchidae (i.e. *Kaprosuchus* +  
26 *Mahajangasuchus*), with these lineages forming a clade with Uruguaysuchidae that  
27 is the sister taxon to all other notosuchians (e.g. Pol et al. 2014; Sertich & O'Connor  
28 2014; Coria et al. 2019). Others have recovered Peirosauridae as part of Sebecia,  
29 forming a clade with Sebecidae (e.g. Larsson & Sues 2007; Sereno & Larsson  
30 2009), and sometimes also including Mahajangasuchidae (e.g. Geroto & Bertini  
31 2019; Ruiz et al. 2021). Whereas some of these analyses place Sebecia as the  
32 sister taxon to all other notosuchians (e.g. Geroto & Bertini 2019; Ruiz et al. 2021),  
33 others recover Sebecia within Neosuchia (e.g. Larsson & Sues 2007; Sereno &  
34 Larsson 2009). Peirosauridae has also been recovered as an early diverging  
35 neosuchian clade in some studies (e.g. Pol & Apesteguía 2005; Gasparini 2006;  
36 Turner & Buckley 2008; Leardi & Pol 2009).  
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45 In several recent phylogenetic analyses (e.g. Pol et al. 2014; Geroto & Bertini 2019;  
46 Coria et al. 2019), *Hamadasuchus* has been recovered as the sister taxon to a group  
47 of exclusively South American Cretaceous peirosaurids (comprising various  
48 combinations of *Montealtosuchus*, *Uberabasuchus*, *Lomasuchus*, *Gasparinisuchus*,  
49 and *Barcinosuchus*). Similarly, Barrios et al. (2016) recovered *Hamadasuchus* in a  
50 polytomy with most of these taxa, along with *Bayomesasuchus* from the Turonian  
51 (Late Cretaceous) of Argentina. Sertich & O'Connor (2014) recovered  
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10 *Hamadasuchus* in an unresolved trichotomy with *Rukwasuchus* and *Stolokrosuchus*,  
11 forming a clade of African peirosaurids.  
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14 Here, under both equal and extended implied weighting schemes, the position of  
15 Peirosauridae is consistent with the results of Pol et al. (2014) and subsequent  
16 studies based on this dataset (e.g. Leardi et al. 2015; Fiorelli et al. 2016; Iori et al.  
17 2018; Leardi et al. 2018; Martinelli et al. 2018; Coria et al. 2019). Under its  
18 broadened taxonomic content, following the phylogenetic definition of Geroto &  
19 Bertini (2019), Peirosauridae includes Mahajangasuchidae in our EIW analyses (Fig.  
20 8). This occurs because *Stolokrosuchus* is recovered as more closely related to  
21 Mahajangasuchidae than to other peirosaurids in the EIW topology. Our equal  
22 weights analysis recovers *Stolokrosuchus* as the most 'basal' member of  
23 Peirosauridae instead, with Mahajangasuchidae outside of this clade (Fig. 7). In both  
24 cases, our peirosaurid + mahajangasuchid grouping is the sister taxon of  
25 Uruguaysuchidae, with this clade the sister taxon to all other notosuchians.  
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31 In our strict consensus trees, the clade comprising *Antaeusuchus* and  
32 *Hamadasuchus* is most closely related to *Bayomesasuchus*. This grouping is the  
33 sister taxon to other peirosaurids (excluding *Stolokrosuchus* and  
34 Mahajangasuchidae) (Fig. 7). The remaining South American taxa are grouped in a  
35 polytomy with the African taxon *Rukwasuchus*, with this recovered as the sister  
36 taxon of a clade comprising the Malagasy taxon *Miadasuchus* and the  
37 Argentinean species *Barrosasuchus*. The aforementioned polytomy can be resolved  
38 via *a posteriori* pruning of *Gasparinisuchus*, resulting in *Rukwasuchus* as the sister  
39 taxon of (*Uberabasuchus* + (*Lomasuchus* + *Montealtosuchus*)).  
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44 The fact that our analyses produce topologies more consistent with those derived  
45 from the data matrix of Pol et al. (2014) than alternative matrices is not surprising  
46 given that this is the underlying dataset for our study. As such, the interrelationships  
47 of Peirosauridae within Metasuchia will require further testing, ideally merging  
48 characters and taxa from across studies with competing hypotheses. However, the  
49 recovery of Peirosauridae as an early diverging metasuchian clade outside of the  
50 ziphosuchian notosuchian radiation is consistent across analyses, regardless of the  
51 underlying dataset.  
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11 One of the notable results of our analyses is the placement of *Miadanasuchus* within  
12 Peirosauridae, which was independently recovered in this clade by Geroto and  
13 Bertini (2019). This species from the Maastrichtian of Madagascar was originally  
14 described as *Trematochampsia oblita* (Buffetaut & Taquet 1979), before being  
15 assigned to a new genus by Rasmusson Simons & Buckley (2009). The type species  
16 of *Trematochampsia*, *T. taqueti*, is based on fragmentary remains from the  
17 Coniacian–Santonian In Beceten Formation of Niger (Buffetaut 1974; 1976a, b), for  
18 which the family Trematochampsidae was also erected (Buffetaut 1974). Several  
19 additional crocodyliform taxa have been assigned to Trematochampsidae (e.g.  
20 *Amargasuchus minor* [Chiappe 1988], *Barreirosuchus franciscoi* [Iori et al. 2012],  
21 *Hamadasuchus*, *Itasuchus*, *Mahajangasuchus*), spanning the Cretaceous of Africa,  
22 Europe, Madagascar, and South America, with most of these known from  
23 fragmentary remains (see review in Meunier & Larsson 2018). Buffetaut  
24 (1988, 1989) also included *Peirosaurus torminni* as a member of  
25 Trematochampsidae, which would therefore have priority over Peirosauridae.  
26 However, multiple authors have questioned or rejected the monophyly of  
27 Trematochampsidae, which appears to have become a wastebasket taxon (e.g.  
28 Gasparini et al. 1991; Ortega et al. 1996; Buckley & Brochu 1999; Turner & Calvo  
29 2005; Larsson & Sues 2007; Rasmusson Simons et al. 2009; Meunier & Larsson  
30 2018). Furthermore, Meunier & Larsson (2018) demonstrated that *Trematochampsia*  
31 *taqueti* is a nomen dubium, based on non-diagnostic, chimeric remains, with some of  
32 these displaying peirosaurid affinities. Our analyses provide further evidence that  
33 most, if not all, Cretaceous taxa previously assigned to Trematochampsidae belong  
34 to Peirosauridae, and confirm the presence of this latter clade in the Maastrichtian of  
35 Madagascar. Given the lack of diagnostic features in the type remains of  
36 '*Trematochampsia taqueti*' and the absence of a formal definition for  
37 'Trematochampsidae', coupled with its approximate synonymy with the formally  
38 defined and widely used Peirosauridae, we support the proposal of Meunier &  
39 Larsson (2018) to abandon the name *Trematochampsia* and its coordinated rank  
40 taxa.  
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### 51 **6.3. Gondwanan notosuchian diversity outside of South America**

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10 During the Mesozoic, notosuchians (*sensu* Pol et al. 2014) were the most diverse  
11 clade of Gondwanan crocodyliforms (Turner & Sertich 2010), although this high  
12 species richness varied through both time and space (Pol & Leardi 2015; De Celis et  
13 al. 2020). At least 70% of known notosuchian diversity is found on Gondwanan  
14 continents (Pol & Leardi 2015), with a small number of species recognised from  
15 Europe (Kuhn 1968; Antunes 1975; Rossman et al. 2000; Company et al. 2005;  
16 Dalla Vecchia & Cau 2011; Rabi & Sebök 2015; Martin 2016; Sellés et al. 2020) and  
17 Asia (Wu et al. 1995; Wu & Sues 1996). Though most numerous in South America,  
18 Gondwanan notosuchian occurrences are also known from mainland Africa,  
19 Madagascar, India, and Pakistan, as well as possibly the Arabian Peninsula.  
20 Currently no notosuchians are known from Australasia or Antarctica, although it  
21 remains unclear whether this represents a genuine absence, perhaps pertaining to a  
22 high-latitude environmental dispersal barrier, or it reflects a sampling bias (e.g. see  
23 Poropat et al. 2021). Here, we provide a critical reappraisal of the Gondwanan  
24 record of notosuchians outside of South America.  
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### 30 **6.3.1. Jurassic**

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32 The stratigraphically oldest known notosuchian is *Razanandrongobe sakalavae*  
33 (Maganuco et al. 2006) from the Bathonian (Middle Jurassic) Isalo IIIb Formation in  
34 northwestern Madagascar. Originally named as an archosaur of uncertain affinities  
35 on the basis of teeth and a fragmentary maxilla (Maganuco et al. 2006), several  
36 more skull fragments, including a right premaxilla and an incomplete left dentary,  
37 have since been assigned to the taxon, enabling its identification as a large-bodied  
38 notosuchian (Dal Sasso et al. 2017). Considering that the next stratigraphically  
39 oldest notosuchians are from the Aptian (late Early Cretaceous), resulting in a ~40  
40 million-year ghost lineage, *Razanandrongobe* is a stratigraphic outlier and its  
41 affinities might seem doubtful. However, based on the sister taxon relationship of  
42 Notosuchia and Neosuchia, with the latter clade known from the Early Jurassic  
43 (Tykoski et al., 2002), *Razanandrongobe* instead partly fills the inferred ghost lineage  
44 of notosuchians, which otherwise would extend back approximately 65–75 million  
45 years (Dal Sasso et al. 2017; Mannion et al. 2019). In the small number of  
46 phylogenetic analyses to have incorporated it (Dal Sasso et al. 2017; Sellés et al.  
47 2020), including ours, *Razanandrongobe* is recovered in a position close to the  
48 'base' of Sebecosuchia. This nested position within Notosuchia for such a  
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10 stratigraphically early species necessitates the extension of multiple unsampled  
11 lineages back into the Jurassic (Fig. 11). As such, the phylogenetic affinities of  
12 *Razanandrongobe* require further evaluation to test whether this poor stratigraphic fit  
13 is genuine.  
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### 16 **6.3.2. Early Cretaceous**

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18 In southeastern Africa, the Aptian Dinosaur Beds of northern Malawi (Fig. 12) have  
19 yielded numerous remains of *Malawisuchus mwakasyungutiensis*, preserving most  
20 of the skeleton (Gomani 1997). Recognised in part for its unusual mammal-like  
21 multicuspid teeth, some analyses have placed *Malawisuchus* in a nested position  
22 within Sphagesauria (e.g. Gomani 1997; Sereno & Larsson 2009; O'Connor et al.  
23 2010). However, most recent analyses typically recover *Malawisuchus* as an early  
24 diverging ziphosuchian, with sphagesaurians currently restricted to South America  
25 (e.g. Pol et al. 2014; Ruiz et al. 2021; this study). Unlike the topology of Martin and  
26 Lapparent de Broin (2016), *Malawisuchus* is not recovered within Candidodontidae  
27 in our analyses (Fig. 7).  
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33 The Aptian–Albian Elrhaz Formation exposed at Gadoufaoua, central Niger (Fig. 12),  
34 has yielded the remains of three morphologically diverse notosuchian species  
35 (*Anatosuchus minor*, *Araripesuchus wegneri*, and *Stolokrosuchus lapparenti*). The  
36 bizarre, 'duck-billed' *Anatosuchus* is known from several individuals, including a skull  
37 and associated partial postcranial skeleton, as well as a skull of a juvenile animal  
38 (Sereno et al. 2003; Sereno & Larsson 2009). *Anatosuchus* has often been  
39 recovered as a member of Uruguaysuchidae (e.g. Sereno & Larsson 2009; Pol et al.  
40 2014); some analyses have placed it outside of this clade, although these tend to  
41 recover it as a 'basal' member of Notosuchia. The small and gracile species  
42 *Araripesuchus wegneri* was erected from the anterior region of an articulated upper  
43 and lower snout (Buffetaut & Taquet 1979). Multiple remains have since been  
44 assigned to the taxon, including a block preserving at least five separate individuals,  
45 three of which are essentially complete, partially articulated skeletons (Sereno &  
46 Larsson 2009). In our analyses, *Araripesuchus wegneri* and *Anatosuchus* are  
47 recovered as sister taxa within Uruguaysuchidae, further questioning the monophyly  
48 of *Araripesuchus* (see Sereno & Larsson 2009: p. 31). The longirostrine-snouted  
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10 *Stolokrosuchus* is known from an almost complete skull (Larsson & Gado 2000).  
11 Originally referred to Peirosauridae (Larsson & Gado 2000; see also Larsson & Sues  
12 2007; Sereno & Larsson 2009; Geroto & Bertini 2019), subsequent analyses have  
13 shown the position of *Stolokrosuchus* to be highly labile, such that it has also been  
14 placed as an early diverging member of both Notosuchia (e.g. Dal Sasso et al. 2017)  
15 and Neosuchia (e.g. Turner & Sertich 2010; Andrade et al. 2011). Following the  
16 definition of Peirosauridae provided by Geroto & Bertini (2019), our analyses recover  
17 *Stolokrosuchus* as the earliest diverging member of this clade, which is consistent  
18 with previous analyses that have continued to place it close to the 'base' of  
19 Metasuchia.  
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24 Several isolated teeth from the Aptian–Albian Koum Formation of northeastern  
25 Cameroon (Fig. 12) were reported by Flynn et al. (1988) and Congleton (1990), who  
26 recognised their possible affinities with *Araripesuchus*, especially *A. wegeneri*.  
27 Kellner (1994 p. 618) questioned this referral, suggesting that these strongly  
28 serrated, laterally compressed, leaf-shaped teeth differed from those in the posterior  
29 toothrow of *Araripesuchus gomesii*, which he described as “weakly serrated” and  
30 “less leaf-shaped”. It is unclear why Kellner (1994) limited comparisons to  
31 *Araripesuchus gomesii*; nonetheless, the description of additional specimens of  
32 *Araripesuchus wegeneri* from Niger (Sereno & Larsson 2009), along with other  
33 species of this genus (e.g. Pol & Apesteguia 2005; Ortega et al. 2000; Turner 2006;  
34 Sereno & Larsson 2009; Dumont et al. 2020; Ibrahim et al. 2020), allows for more  
35 thorough comparisons with the teeth from Cameroon. Given that none of the South  
36 American *Araripesuchus* species, nor *Araripesuchus tsangatsangana*, have  
37 denticles, the labiolingually compressed, lanceolate shape of these teeth, with  
38 serrated carinae along their posteriormost and anteriormost margins, is supportive of  
39 a referral to either *Araripesuchus wegeneri* or *Araripesuchus rattoides* (the latter  
40 comparison is based on referred material, BSPG 2008 I 41, rather than the holotype  
41 specimen [Ibrahim et al. 2020]). However, because of variation in crown morphology  
42 along the toothrow in all species of *Araripesuchus*, and given that teeth in the  
43 middle-to-posterior toothrow are either absent or poorly preserved in *Araripesuchus*  
44 *rattoides*, it is not currently possible to provide a species-level referral.  
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10 The Albian Aïn el Guettar Formation in southern Tunisia (Fig. 12) has yielded  
11 numerous crocodyliform remains, including teeth assigned to *Araripesuchus*  
12 *wegeneri*, *Araripesuchus* sp., and aff. *Hamadasuchus* sp. (Le Loeuff et al. 2000;  
13 Cuny et al. 2010; Fanti et al. 2012). The specimens assigned to *Araripesuchus*  
14 (Cuny et al. 2010, fig. 4.7; Fanti et al. 2012, fig. 12U–X) are labiolingually  
15 compressed and triangular, with serrated carinae and relatively smooth enamel.  
16 Based on the slightly dorsoventrally constricted lanceolate shape of the teeth in  
17 lateral view, it is likely that they come from the middle region of the toothrow. All of  
18 these features support their referral to *Araripesuchus*, widening the spatial  
19 distribution of the genus to north-central Africa. Although serrated tooth margins are  
20 known to be present in *Araripesuchus wegeneri* and a referred specimen of  
21 *Araripesuchus rattoides* (Ibrahim et al. 2020), we refrain from assigning these  
22 specimens beyond generic level as was “cautiously” proposed by Cuny et al. (2010:  
23 p. 625) for the same reasons outlined in the preceding paragraph. A single tooth  
24 referred to aff. *Hamadasuchus* sp. is labiolingually compressed and approximately  
25 triangular in lateral view, with “remnants of clear serration” (Cuny et al. 2010: fig. 4.8,  
26 p. 625). Although the more extreme labiolingual compression towards the anterior  
27 and posterior margins of the tooth is reminiscent of *Hamadasuchus*, the apparent  
28 lack of rugose enamel is unusual given its presence in all teeth associated with the  
29 holotype specimen of *Hamadasuchus*. The only other named crocodyliforms from  
30 the Early Cretaceous of Africa to possess serrated carinae are *Araripesuchus*  
31 *wegeneri* and referred material of *Araripesuchus rattoides*, both of which possess  
32 dentition more similar in size to the tooth reported in Cuny et al. (2010). However,  
33 given that the Tunisian specimen is clearly well-worn and is not dissimilar in broad  
34 morphology from either *Hamadasuchus* or *Araripesuchus*, we regard this specimen  
35 as an indeterminate notosuchian. Re-evaluation and full description of specimens  
36 referred to *Hamadasuchus* that have teeth with smooth enamel (e.g. BSPG 2005 I  
37 83) might enable referral to a particular genus.

### 48 **6.3.3. Late Cretaceous**

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50 In northwestern Africa, the Cenomanian Kem Kem Group of Morocco has yielded  
51 three previously named notosuchian species (*Araripesuchus rattoides*,  
52 *Hamadasuchus rebouli*, *Lavocatchampsia sigogneaurussellae*), in addition to the new  
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10 species, *Antaeosuchus taouzensis*, described herein (Fig. 12). *Araripesuchus*  
11 *rattoides* is known from the holotypic partial dentary, as well as several referred  
12 dentary fragments (Sereno & Larsson 2009; Ibrahim et al 2020). It differs from *A.*  
13 *wegereri* in several features, including its possession of a narrower and deeper  
14 snout, highly procumbent teeth, and potentially a greater number of teeth. Though  
15 not included in our phylogenetic analyses because of its fragmentary nature,  
16 *Araripesuchus rattoides* was recovered by Sereno & Larsson (2009) in a polytomy  
17 with three *Araripesuchus* species (*A. gomesii* and *A. patagonicus* from South  
18 America, and *A. tsangatsangana* from Madagascar), with this the sister group to a  
19 clade comprising the remaining uruguaysuchids (including *A. wegeneri*).  
20 *Lavocatchampsa sigogneaurussellae* was erected based on a small anterior snout  
21 region, which displays unusually heterodont teeth that are convergent with those of  
22 mammals (Martin & Lapparent de Broin 2016). Using the data matrix of Pol et al.  
23 (2014), Martin & Lapparent de Broin (2016) recovered *Lavocatchampsa* as a 'basal'  
24 ziphosuchian within Candidodontidae, a small clade otherwise known only from the  
25 Cretaceous of South America (Carvalho et al. 2004, Montefeltro et al. 2009).

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32 As discussed in detail above, the peirosaurid *Hamadasuchus rebouli* was erected  
33 based on a single dentary fragment from the Kem Kem Group (Buffetaut 1994), but  
34 numerous cranial and mandibular remains have since been referred to this species  
35 from this stratigraphic unit (Larsson & Sues 2007; Ibrahim et al., 2020), including a  
36 skull table previously assigned to *Libykosuchus* sp. (Buffetaut 1976a, b). Although  
37 we do not disagree with referral of these remains to Peirosauridae, it is currently  
38 unclear if all of them are attributable to *Hamadasuchus rebouli*. Isolated teeth  
39 described by Larsson & Sidor (1999) were also referred to this species. One tooth,  
40 inferred to be from the middle of the toothrow (Larsson & Sidor 1999: fig. 1B), is very  
41 reminiscent of those preserved in the holotype of *Hamadasuchus rebouli*, based on  
42 its triangular shape in lateral view, its labiolingual compression, and the density of  
43 serrations. A second tooth shares the globular texture of the enamel towards the  
44 base of the crown, which transitions into more linear ridges towards the apex  
45 (Larsson & Sidor 1999: fig. 1C), which is again consistent with a referral to  
46 *Hamadasuchus rebouli*. However, a conical, retro-curved caniniform tooth shows  
47 distinctive fluting (Larsson & Sidor 1999: fig. 1A), which is absent from the holotypic  
48 specimen, but present in some of the specimens previously referred to the species  
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10 (ROM 49282 and 52620, BSPG 2005 I 83, and possibly NMC 41892 [Ibrahim et al.  
11 2020]).  
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14 Larsson & Sidor (1999) described several additional crocodyliform teeth from the  
15 Kem Kem Group that have been suggested to represent additional notosuchian taxa  
16 (Ibrahim et al., 2020). Material referred to “Indet. crocodyliform 1” (Larsson & Sidor  
17 1999 p. 398) is represented by two small, subtriangular crowns (SGM-Rep 4, SGM-  
18 Rep 5) in labiolingual view, each with three approximately parallel rows of relatively  
19 large cuspids that terminate in angular apices towards the anteroposterior midpoint  
20 of the tooth (Larsson & Sidor 1999, fig. 2 A–D). On one of these teeth, a large  
21 planar wear facet bisects the rows of cusps on the buccal surface. A third tooth  
22 (SGM-Rep 6) referred to by Larsson & Sidor (1999 p. 399) as “Indet. crocodyliform  
23 2” is more elliptical in dorsal view, and has a central, anteroposterior row of cuspids  
24 surrounded labially and lingually by two less dorsally raised rows of smaller cusps  
25 (Larsson & Sidor 1999, fig. 3). The outer two rows merge at the anteriormost and  
26 posteriormost margins of the tooth, forming a cingulum. Unlike the other multicuspids  
27 teeth, the rows of cusps in this third tooth are much closer to horizontal in their  
28 orientation, forming a less acute apex. Furthermore, the cusps of the central row are  
29 relatively larger in comparison to the tooth size and are fewer in number, forming an  
30 apex either mesially or distally (depending on tooth orientation in the jaw) rather than  
31 centrally. *Lavocatchampsa sigogneaurussellae* is the only crocodyliform from the  
32 Kem Kem Group that exhibits a multicuspids tooth morphology (Martin & Lapparent  
33 de Broin 2016); however, we agree with the observations of Ibrahim et al. (2020) that  
34 both morphologies are distinct from this taxon. We do note that the less acute tooth  
35 described as ‘Indet. crocodyliform 2’ is most similar in its morphology to the taxon  
36 described by Martin & de Lapparent de Broin (2016) based on its elliptical shape in  
37 occlusal view, and the presence of a cingulum bearing multiple cusps that surround  
38 a central carina formed of a relatively small number (four) of cusps.  
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47 In summary, the Kem Kem Group seems to record the presence of at least seven  
48 potential notosuchians, represented by three peirosaurids (*Hamadasuchus rebouli*,  
49 *Antaeusuchus taouzensis*, and at least one unnamed species), *Araripesuchus*  
50 *rattoides*, and three species with multicuspids teeth (*Lavocatchampsa*  
51 *sigogneaurussellae* and two unnamed species). However, given poor stratigraphic  
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10 constraints for many of these species, it remains possible that these were not all  
11 contemporaneous.  
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14 The Cenomanian Bahariya Formation of north-central Egypt has yielded just a single  
15 notosuchian species (Fig. 12), with *Libycosuchus brevirostris* represented by a  
16 complete skull and lower jaws, as well as several isolated vertebrae (Stromer 1914;  
17 Buffetaut 1976). *Libycosuchus* has an anteroposteriorly short skull and is fairly  
18 consistently recovered as an early diverging ziphosuchian (e.g. Sertich & O'Connor  
19 2014; Pol et al. 2014; Martin & Lapparent de Broin 2016; Geroto & Bertini 2019), as  
20 is also the case in our analyses.  
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24 The large-bodied species *Kaprosuchus saharicus* is the only published notosuchian  
25 currently known from the Cenomanian Echkar Formation of northwestern Niger  
26 (Sereno & Larsson 2009) (Fig. 12). This species is based on an essentially complete  
27 skull and mandible and has been informally referred to as the “boar croc” due to its  
28 enlarged caniniform teeth. *Kaprosuchus* has been consistently recovered as the sister  
29 taxon to *Mahajangasuchus insignis* from the Maastrichtian of Madagascar (see  
30 below), and is thus a member of Mahajangasuchidae (e.g. Sereno & Larsson, 2009;  
31 Pol et al. 2014, Geroto & Bertini 2019; this analysis) (Fig. 6). Sereno & Pol (2019)  
32 reported an undescribed partial skeleton from the Echkar Formation that appears to  
33 be most closely related to the Maastrichtian Malagasy species, *Araripesuchus*  
34 *tsangatsangana*.  
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40 In the southeastern region of Africa, two notosuchian taxa are known from the Namba  
41 Member of the Galula Formation of western Tanzania (Fig. 12). Originally thought to  
42 be Aptian–Cenomanian (O'Connor et al. 2010; Roberts et al. 2010), new dates  
43 indicate either a Cenomanian–Santonian or more likely a Campanian age for this  
44 stratigraphic unit (Widlansky et al. 2018). Represented by the posterior region of the  
45 skull, the medium-to large-bodied *Rukwasuchus yajabalijekundu* was recovered by  
46 Sertich & O'Connor (2014) as a peirosaurid. It had not been included in a subsequent  
47 phylogenetic analysis prior to ours, which provides further support for a peirosaurid  
48 placement (Figs 6 & 7). Known from an essentially complete skeleton, *Pakasuchus*  
49 *kapilimai* is one of several small notosuchians with multicuspid teeth from the  
50 Cretaceous of Gondwana that appears to fill an ecological niche that would later be  
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10 occupied by mammals (O'Connor et al. 2010; Sertich & O'Connor 2014). As is the  
11 case in several previous studies (e.g. O'Connor et al. 2010; Pol et al. 2014; Sertich &  
12 O'Connor 2014; Martin and Lapparent de Broin 2016), our analyses recover  
13 *Pakasuchus* as an early diverging member of Ziphosuchia, closely related to  
14 *Malawisuchus* (Fig. 7).  
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18 The Coniacian–Santonian In Beceten Formation of Niger (Fig. 12) has yielded the  
19 type material (an incomplete lacrimal) of *Trematochampsia taqueti* (Buffetaut 1974).  
20 As discussed in Section 6.2, Meunier & Larsson (2018) demonstrated that  
21 *Trematochampsia taqueti* is a nomen dubium, and suggested that isolated bones and  
22 teeth informally referred to the taxon represent at least three different small-medium  
23 sized crocodyliform species. They noted that many of these specimens show  
24 potential affinities to peirosaurids (especially *Hamadasuchus*), uruguaysuchids  
25 (especially *Araripesuchus wegeneri* and *Anatosuchus minor*), ziphosuchians, and/or  
26 neosuchians, which we follow here.  
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31 The Wadi Milk Formation of northern Sudan (Fig. 12) has traditionally been regarded  
32 as Cenomanian (e.g. Buffetaut et al. 1990; Rage & Werner 1999), but more recent  
33 work indicates that it should be assigned to the Campanian–Maastrichtian (Owusu  
34 Agyemang et al. 2019). An undescribed peirosaurid has been briefly reported,  
35 consisting of partial mandibles and part of the skull roof, and which is notable for its  
36 large size (Evans et al. 2014).  
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40 Putative notosuchian remains from the Maastrichtian Dukamaje Formation in  
41 western Niger have been mentioned in the literature, but not described. Moody and  
42 Sutcliffe (1991: table 2) listed the presence of *Trematochampsia taqueti* and  
43 *Libycosuchus* sp. in this formation, but they provided no further details. We suspect  
44 that that this was a mistake, with the In Beceten faunal list accidentally incorporated,  
45 but this cannot currently be confirmed.  
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49 A mandibular fragment preserving the middle portion of a right dentary could  
50 potentially represent the only occurrence of a notosuchian from the Arabian  
51 Peninsula (Buscalioni et al. 2004). Buscalioni et al. (2004) tentatively assigned the  
52 specimen from the Maastrichtian Al-Khod Conglomerate Formation of northern  
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10 Oman as cf. *Trematochampsia* indet. and noted similarities with *Miadanosuchus*  
11 (*'Trematochampsia'*) *oblita* from the Maastrichtian of Madagascar. These similarities  
12 included the presence of an enlarged tooth in the 10<sup>th</sup> alveolus, and a morphology  
13 indicative of a long and wide mandibular symphysis (despite this region not being  
14 preserved). Our analyses recover *Miadanosuchus* within Peirosauridae, a clade  
15 characterised by two distinct waves on the dorsal margin of the dentary. The very  
16 straight, only slightly inclined dorsal edge of the dentary in the Oman specimen is  
17 therefore not indicative of a specimen belonging to this clade, especially as the  
18 presence of an enlarged tooth would be expected to be accompanied by the  
19 dorsoventral expansion of the dentary. Furthermore, the dentary of *Miadanosuchus*  
20 maintains its mediolateral width posterior to the enlarged tooth for at least the  
21 distance of two alveoli. The Oman specimen shows gradual, but distinct narrowing  
22 posterior to the enlarged tooth. Given the highly fragmentary nature of the specimen,  
23 and the few preserved anatomical features of phylogenetic relevance, we suggest  
24 that the material can only be assigned to an indeterminate crocodyliform.  
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31 The Maastrichtian Maevarano Formation that outcrops in northwestern Madagascar  
32 has thus far yielded four notosuchian taxa (Fig. 12). The bizarre “pug-nosed”  
33 *Simosuchus clarki* is represented by multiple individuals preserving most of the  
34 skeleton (Buckley et al. 2000; Georgi & Krause 2010; Hill 2010; Kley et al. 2010;  
35 Sertich & Groenke 2010). Most analyses recover *Simosuchus* as an early diverging  
36 ziphosuchian (e.g. Turner & Sertich 2010; Pol & Powell 2011; Pol et al. 2014; Geroto  
37 & Bertini 2019; this study). The large-bodied *Mahajangasuchus insignis* is known  
38 from an almost complete skull and much of the postcranial skeleton (Buckley &  
39 Brochu 1999; Turner & Buckley 2008). Initially thought to have affinities with  
40 ‘*Trematochampsidae*’, the taxon has since been recovered as a peirosaurid (e.g.  
41 Turner & Calvo 2005), or just outside of this clade (e.g. Pol et al. 2014). It is now the  
42 clade specifier for Mahajangasuchidae (Serenó & Larsson 2009), with our analyses  
43 providing evidence for a position both within (EIW) and just outside (equal weighting)  
44 of Peirosauridae. *Araripesuchus tsangatsangana* is represented by a nearly  
45 complete skull, as well as a second individual preserving a nearly complete skeleton  
46 (Turner 2006). *Miadanosuchus ('Trematochampsia') oblita* is known from partial  
47 dentaries, part of the skull roof, and a vertebra (Buffetaut & Taquet 1979;  
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10 Rasmusson Simons & Buckley 2009), and it appears to represent a peirosaurid  
11 (Geroto & Bertini (2019; this study).  
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14 *Pabwehshi pakistanensis*, recovered from the Maastrichtian Pab Formation of  
15 southwestern Pakistan (Fig. 12), is known from fragmentary specimens, which  
16 preserve the anterior region of the snout and the associated section of the mandible  
17 of two individuals (Wilson et al. 2001). The limited remains of *Pabwehshi* mean that  
18 its phylogenetic position is labile (Pol et al. 2014), although most authors have  
19 supported a close relationship with Baurusuchidae (e.g. Wilson et al. 2001; Turner &  
20 Calvo 2005; Nascimento & Hussam 2010; Turner & Sertich 2010; Pol & Powell 2011;  
21 Carvalho et al. 2011; Dal Sasso et al. 2017; Geroto & Bertini 2019; Coria et al.  
22 2019), which is otherwise known only from South America (e.g. Montefeltro et al.  
23 2020; Darlim et al. 2021). By contrast, Larsson & Sues (2007) recovered *Pabwehshi*  
24 as the most 'basal' member of Sebecia, i.e. as the sister taxon to a clade comprising  
25 Peirosauridae and Sebecidae. *Pabwehshi pakistanensis* was excluded from our  
26 analyses because of its labile position, but more complete material will ultimately be  
27 needed to robustly resolve its phylogenetic position.  
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34 An isolated tooth from the Maastrichtian Kallamedu Formation of southern India (Fig.  
35 12) was described by Prasad et al. (2013), who identified it as cf. *Simosuchus* sp.  
36 Based on comparisons with *Simosuchus clarki*, Prasad et al. (2013) suggested that  
37 the tooth is probably from the posterior region of the dentary. We fully agree with the  
38 evaluation and assignment of this specimen.  
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#### 40 41 **6.3.4. Paleogene** 42

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44 Buffetaut (1989) erected *Eremosuchus elkoholicus* from the El Kohol Formation of  
45 southwest Algeria (Fig. 12), which is dated to the Ypresian, early Eocene (Coster et  
46 al. 2012). This species is known from a partial mandible, teeth, vertebrae, and a  
47 fibula. When initially described, *Eremosuchus* was placed in the family  
48 Trematochampsidae (Buffetaut 1989), but more recently it has been included in  
49 Sebecosuchia by several authors (e.g. Gasparini et al. 1991; Ortega et al. 1996;  
50 Turner & Calvo 2005). However, it has not been included in most phylogenetic  
51 analyses, presumably because of its incomplete nature, and has largely been  
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10 neglected in treatments of crocodyliform evolutionary history. A detailed  
11 redescription and analysis of the phylogenetic relationships of *Eremosuchus* is  
12 needed to establish its systematic and biogeographic affinities.  
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15 Finally, the late Eocene Birket Qarun Formation (Seiffert 2006) in northeastern Egypt  
16 (Fig. 12) has yielded a fragmentary right dentary with ziphodont dentition (Stefanic et  
17 al. 2020). Though not assigned to a genus, the specimen clearly has sebecosuchian  
18 affinities and extends the temporal range of Notosuchia in Africa (Stefanic et al.  
19 2020).  
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### 23 **6.3.5. Summary**

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26 Our review of the Gondwanan record of notosuchians outside of South America  
27 demonstrates their spatiotemporal distribution in the Middle Jurassic, from the  
28 Aptian–Maastrichtian, and in the Eocene, with their remains known from Africa and  
29 Indo-Madagascar. A possible occurrence from the latest Cretaceous of Oman  
30 (Buscalioni et al. 2004) cannot be confidently referred to Notosuchia. The African  
31 and Indo-Madagascan Cretaceous record indicates the presence of several  
32 lineages, all with close ties to South American clades, with many faunas  
33 demonstrating multiple sympatric species. Given that notosuchians only first  
34 appeared in the Aptian in South America (and Asia), coupled with palaeogeographic  
35 reconstructions documenting the increasing fragmentation of Gondwana at this time  
36 (e.g. Seton et al. 2012), this diverse record supports previous suggestions regarding  
37 an undocumented pre-Aptian radiation of Notosuchia (e.g. Martin and Lapparent de  
38 Broin 2016; Mannion et al. 2019). By contrast, their Gondwanan Paleogene record  
39 outside of South America is currently limited to just two occurrences, both from the  
40 Eocene of north Africa and both belonging to Sebecosuchia. No stratigraphically  
41 younger remains have been assigned to Notosuchia from this region, with their last  
42 Laurasian occurrences from the middle Eocene of western Europe (e.g. Martin  
43 2016), indicating their extirpation outside of South America by the end of the Eocene.  
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### 50 **7. Conclusions**

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10 Two new crocodyliform specimens from the Cenomanian Kem Kem Group of  
11 Morocco are described and incorporated into a phylogenetic analysis. Both  
12 specimens are referable to *Antaeosuchus taouzensis* n. gen. n. sp., which is  
13 recovered within the notosuchian clade Peirosauridae, as the sister taxon to the  
14 contemporaneous *Hamadasuchus rebouli*. Comparisons of materials previously  
15 assigned to *Hamadasuchus* indicate the presence of at least three distinct  
16 peirosaurid species from the same spatiotemporal interval. Coupled with a critical  
17 reappraisal of the non-South American Gondwanan record of Notosuchia, we  
18 recognise a much greater taxonomic and ecomorphological diversity within this clade  
19 during the Cretaceous.  
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26  
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45 Data accessibility. The datasets supporting this article have been uploaded as part of  
46 the electronic supplementary material.  
47

48  
49 Authors' contributions. C.S.C.N and P.D.M. conceived of the study and interpreted  
50 the results. All authors contributed to the design of the study and to the drafting of  
51 the manuscript. Analyses were conducted by C.S.C.N. Figures were produced by  
52 C.S.C.N. and E.S.E.H. All authors approved the final version of the manuscript.  
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10 **Tables**

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13 **Table 1**

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

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27 **Table 2**

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

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

<i>Rukwasuchus yajabalijekundu</i>	Galula Fm., Tanzania	Cenomanian–Campanian, Late Cretaceous	Peirosauridae	Sertich and O'Connor, 2014
<i>Pakasuchus kapilimai</i>	Galula Fm., Tanzania	Cenomanian–Campanian, Late Cretaceous	Basal Ziphosuchia	O'Connor et al., 2010
<i>Araripesuchus tsangatsangana</i>	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Uruguaysuchidae	Turner, 2006
<i>Simosuchus clarki</i>	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Basal Ziphosuchia	Buckley et al., 2000
<i>Mahajangasuchus insignis</i>	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Mahajangasuchidae	Buckley and Brochu, 1999
<i>Miadanosuchus oblita</i>	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Peirosauridae	Rasmusson Simons and Buckley, 2009
<i>Pabwehshi pakistanensis</i>	Pab Fm., Pakistan	Maastrichtian, Late Cretaceous	Sebecosuchia?	Wilson et al., 2001
<i>Eremosuchus elkoholicus</i>	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 *Antaeosuchus taouzensis* n. gen. n. sp. (NHMUK PV R36829 and R36874) within the Kem Kem Group of Morocco.

### Figure 2

Line drawings and photographs of *Antaeosuchus 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 *Antaeosuchus 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 *Antaeosuchus 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 *Antaeosuchus 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 *Antaeosuchus 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, *Antaeosuchus taouzensis* n. gen. n. sp. (NHMUK PV 36829\*); B, *Antaeosuchus 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,

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*Bayomesasuchus hernandezii* (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 (*Antaeosuchus taouzensis* n. gen. n. sp. holotype); B, NHMUK PV R36874 (*Antaeosuchus 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/>).



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10 **Appendix**  
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13 Character scores modified from the respective matrices of Martínez et al. (2018) and  
14 are listed below:  
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16 *Hamadasuchus rebouli*:

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19 **103 ? -> 0; 363 ? -> 0; 365 ? -> 0; 383 ? -> 0; 384 ? -> 0; 388 ? -> 0; 389 ? -> 0; 392**  
20 **? -> 1; 393 ? -> 0&1; 394 ? -> 0; 443 0 -> 1**  
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23 *Gasparinisuchus peirosauroides*:

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26 **443 0 -> 0&1**  
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28 *Montealtosuchus arrudacamposi*:

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31 **443 0 -> 1**  
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33 *Libycosuchus brevirostris*:

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36 **441 ? -> 0**  
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38 *Malawisuchus mwakasyungutiensis*:

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40 **441 ? -> 0**  
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42 *Caipirasuchus stenognathus*:

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45 **441 ? -> 0**  
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47 *Caipirasuchus montealtensis*:

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50 **441 ? -> 0**  
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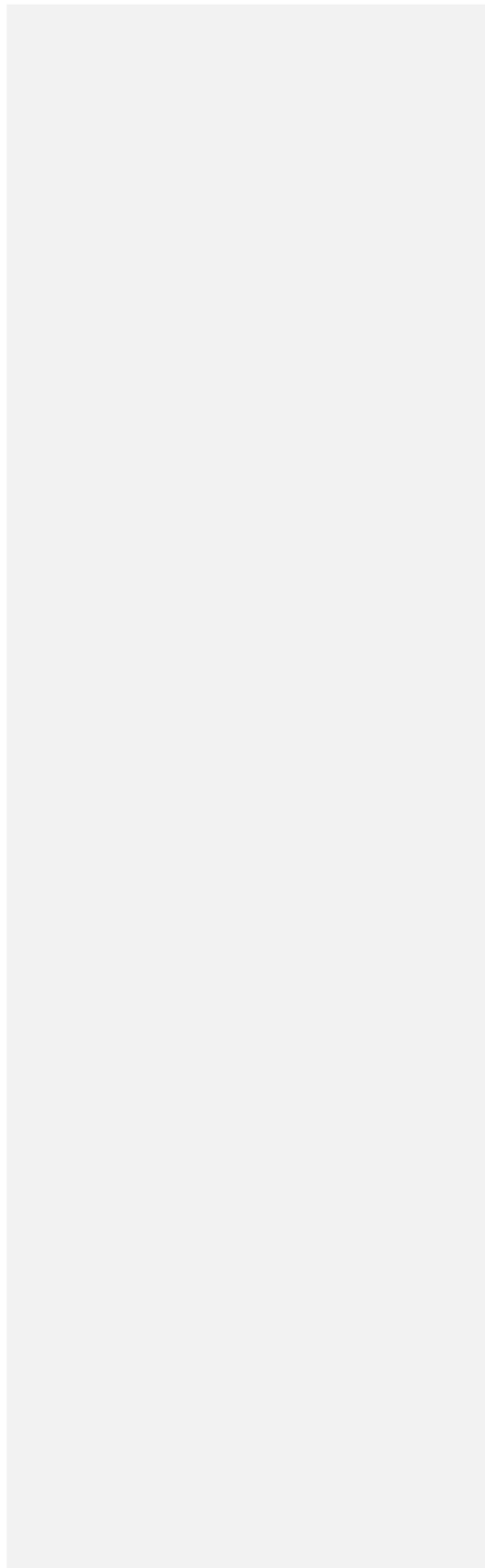
52 *Baurusuchus salgadoensis*:  
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441 ? -> 0

*Stolokrosuchus lapparenti*:

441 ? -> 0



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

Tooth position	Apicobasal length (mm)	Alveolar dimension (mm)			
		Left mandible, anteroposterior length	Right mandible, anteroposterior length	Left mandible, Mediolateral width	Right mandible, Mediolateral width
<b>1</b>	-	11.0	11.5	14.1	14.1
<b>2</b>	-	7.4	7.0	8.7	8.4
<b>3</b>	-	5.0	5.0	5.0	5.4
<b>4</b>	12.1	17.5	12.5	16.0	12.0
<b>5</b>	-	10.0	10.0	10.0	9.5
<b>6</b>	-	5.6	5.5	6.5	7.0
<b>7</b>	-	4.6	5.2	6.8	6.1
<b>8</b>	-		5.1		6.0
<b>9</b>	-	6.6	5.4	6.5	6.2
<b>10</b>	11.0	11.2	11.1	10.5	10.0
<b>11</b>	18.0	14.2	-	13.0	-
<b>12</b>	19.0	15.6	-	12.2	-
<b>13</b>	16.0	23.1	-	16.2	-
<b>14</b>	10.0	14.4	-	11.5	-
<b>15</b>	13.0	13.0	-	8.5	-
<b>16</b>	8.0	10.0	-	7.0	-
<b>17</b>	-	7.0	-	6.0	-
<b>18</b>	-	8.0	-	7.0	-

<b>Taxon</b>	<b>Stratigraphic and geographic provenance</b>	<b>Age</b>	<b>Phylogenetic position</b>	<b>Reference</b>
<i>Razanandrongobe sakalavae</i>	Isalo IIIB Fm., Madagascar	Bathonian, Middle Jurassic	Sebecosuchia?	Maganuco et al., 2006
<i>Malawisuchus mwakasyungutiensis</i>	Dinosaur Beds Fm., Malawi	Aptian, Early Cretaceous	Basal Ziphosuchia	Gomani, 1997
<i>Stolokrosuchus lapparenti</i>	Elrhaz Fm., Niger	Aptian–Albian, Early Cretaceous	Peirosauridae	Larsson and Gado, 2000
<i>Araripesuchus wegeneri</i>	Elrhaz Fm., Niger	Aptian–Albian, Early Cretaceous	Uruguaysuchidae	Buffetaut, 1981
<i>Anatosuchus minor</i>	Elrhaz Fm., Niger	Aptian–Albian, Early Cretaceous	Uruguaysuchidae	Sereno et al., 2003
<i>Hamadasuchus rebouli</i>	Kem Kem Group, Morocco	Cenomanian, Late Cretaceous	Peirosauridae	Buffetaut, 1994
<i>Lavocatchampsia sigogneaurusselae</i>	Kem Kem Group, Morocco	Cenomanian, Late Cretaceous	Basal Ziphosuchia	Martin and Lapparent de Broin, 2016
<i>Araripesuchus rattoides</i>	Kem Kem Group, Morocco	Cenomanian, Late Cretaceous	Uruguaysuchidae	Sereno and Larsson, 2009
<i>Libycosuchus brevirostris</i>	Bahariya Fm., Egypt	Cenomanian, Late Cretaceous	Basal Ziphosuchia	Stromer, 1914
<i>Kaprosuchus saharicus</i>	Echkar Fm., Niger	Cenomanian, Late Cretaceous	Mahajangasuchidae	Sereno and Larsson, 2009
<i>Rukwasuchus yajabalijekundu</i>	Galula Fm., Tanzania	Cenomanian–Campanian, Late Cretaceous	Peirosauridae	Sertich and O'Connor, 2014
<i>Pakasuchus kapilimai</i>	Galula Fm., Tanzania	Cenomanian–Campanian, Late Cretaceous	Basal Ziphosuchia	O'Connor et al., 2010
<i>Araripesuchus tsangatsangana</i>	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Uruguaysuchidae	Turner, 2006
<i>Simosuchus clarki</i>	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Basal Ziphosuchia	Buckley et al., 2000
<i>Mahajangasuchus insignis</i>	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Mahajangasuchidae	Buckley and Brochu, 1999
<i>Miadanosuchus oblita</i>	Maevarano Fm., Madagascar	Maastrichtian, Late Cretaceous	Peirosauridae	Rasmusson Simons and Buckley, 2009

<i>Pabwehshi pakistanensis</i>	Pab Fm., Pakistan	Maastrichtian, Late Cretaceous	Sebecosuchia?	Wilson et al., 2001
<i>Eremosucus elkoholicus</i>	El Kohol Fm., Algeria	Ypresian, early Eocene	Sebecosuchia?	Buffetaut, 1989

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## Figure captions

### Figure 1

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

### Figure 2

Line drawings and photographs of *Antaeosuchus 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 *Antaeosuchus 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 *Antaeosuchus 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 *Antaeosuchus 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 *Antaeosuchus 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; re, ridged rugose enamel. Scale bar represents 10 mm.

### Figure 7

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3 Strict consensus tree showing the relationships of notosuchians using equal  
4 weighting of characters. Numbers at the nodes indicate Bremer support values.  
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### 8 **Figure 8**

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10 Strict consensus tree showing the relationships of notosuchians using extended  
11 implied weighting at  $k$ -values of 8 and 12. Some clades (Uruguaysuchidae and  
12 Ziphosuchia) have been condensed.  
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### 16 **Figure 9**

17 Comparison of the dorsal mandibular surfaces of several notosuchians: A,  
18 *Antaeusuchus taouzensis* n. gen. n. sp. (NHMUK PV 36829\*); B, *Antaeusuchus*  
19 *taouzensis* (NHMUK PV R36874); C, *Montealtosuchus arrudacamposi* (MPMA 16-  
20 0007-04\*); D, *Gasparinisuchus peirosauroides* (MOZ 1750 PV\*); E, *Hamadasuchus*  
21 *rebouli* (ROM 49282); F, *Hamadasuchus rebouli* (MDE C001\*); G, *Barrosasuchus*  
22 *neuquenianus* (MCF-PVPH-413\*); H, *Araripesuchus rattoides* (CMN 41893\*); I,  
23 *Bayomesasuchus hernandezi* (MCF PVPH-822). Asterisk indicates a holotype  
24 specimen.  
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### 34 **Figure 10**

35 Comparison of peirosaurid mandibles from the Kem Kem Group in lateral view: A,  
36 NHMUK PV 36829 (*Antaeusuchus taouzensis* n. gen. n. sp. holotype); B, NHMUK  
37 PV R36874 (*Antaeusuchus taouzensis* paratype); C, MDEC001 (*Hamadasuchus*  
38 *rebouli* holotype); D, ROM 49282; E, BSPG 2005 I 83. A1–E1 show close-up images  
39 of the teeth of each respective taxon. Image B is reversed. Scale bars represent 50  
40 mm.  
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### 48 **Figure 11**

49 Time-calibrated phylogenetic topology showing the agreement subtree of  
50 notosuchians using equal weighting of characters. Some clades are condensed and  
51 the polytomy including *Razanandrongo* *sakalavae* is shown despite being pruned  
52 from the agreement subtree.  
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### 58 **Figure 12**



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

### 20 **Table 1**

21  
22  
23 Mandibular measurements of the holotypic specimen (NHMUK PV R36829) of  
24 *Antaeusuchus taouzensis* n. gen. n. sp.  
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### 29 **Table 2**

30  
31 Tooth and alveolus measurements of the holotypic specimen (NHMUK PV R36829)  
32 of *Antaeusuchus taouzensis* n. gen. n. sp.  
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### 35 **Table 3**

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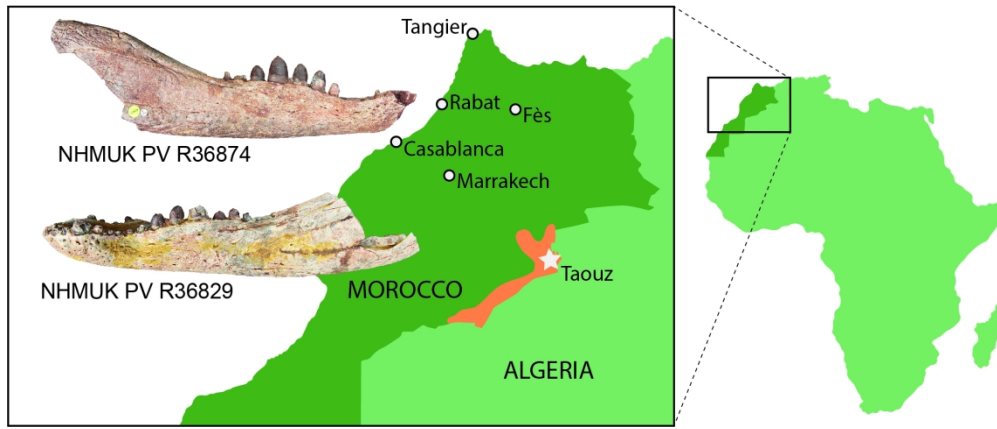


Figure 1 Map showing locality of the new fossil remains. White star indicates the approximate geographic position of *Antaeusuchus taouzensis* n. gen. n. sp. (NHMUK PV R36829 and R36874) within the Kem Kem Group of Morocco.

189x83mm (300 x 300 DPI)

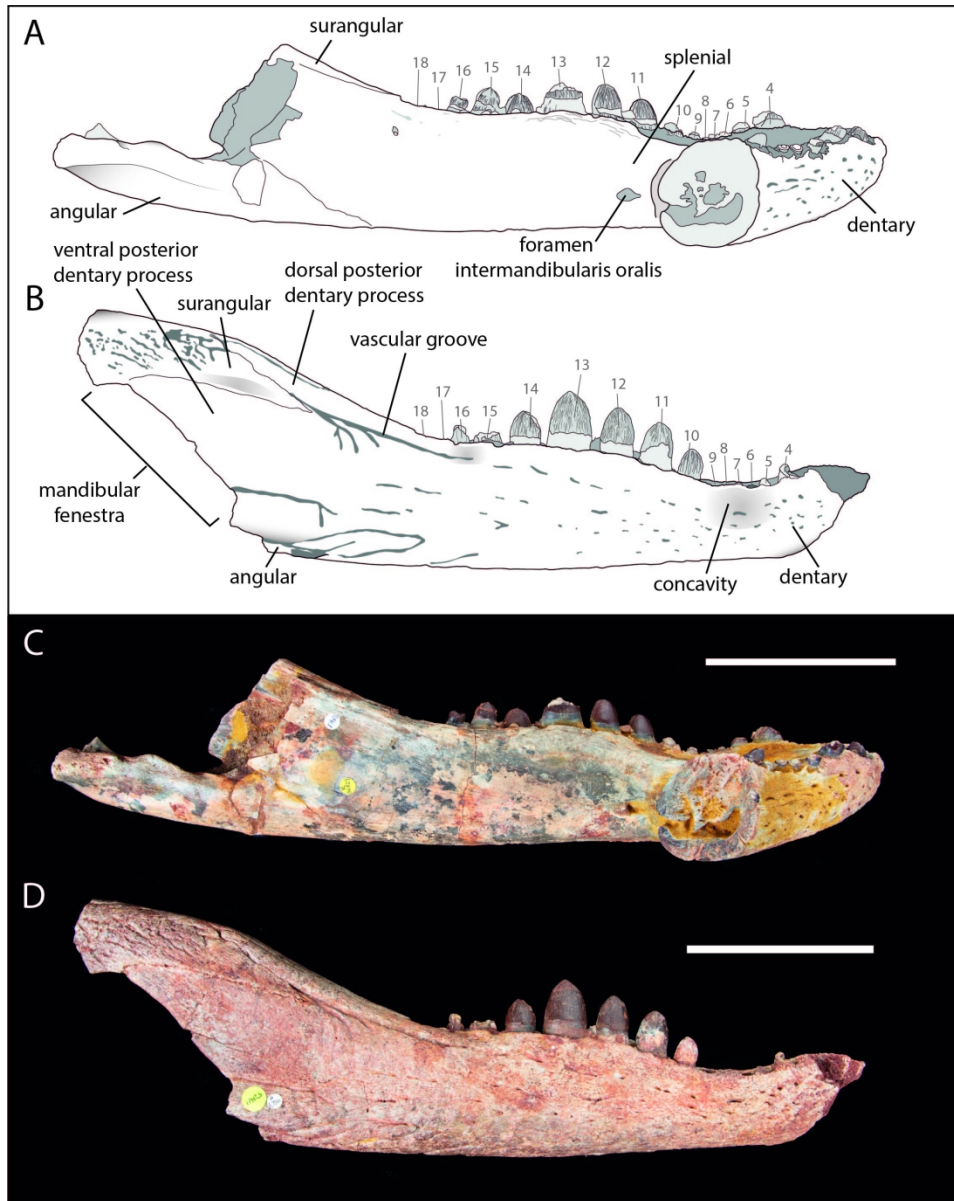


Figure 2 Line drawings and photographs of *Antaeosuchus taouzensis* n. gen. n. sp. (NHMUK PV R36829 [A&C] and NHMUK PV R36874 [B&D]) in right lateral view. Scale bar represents 100 mm.

193x241mm (300 x 300 DPI)

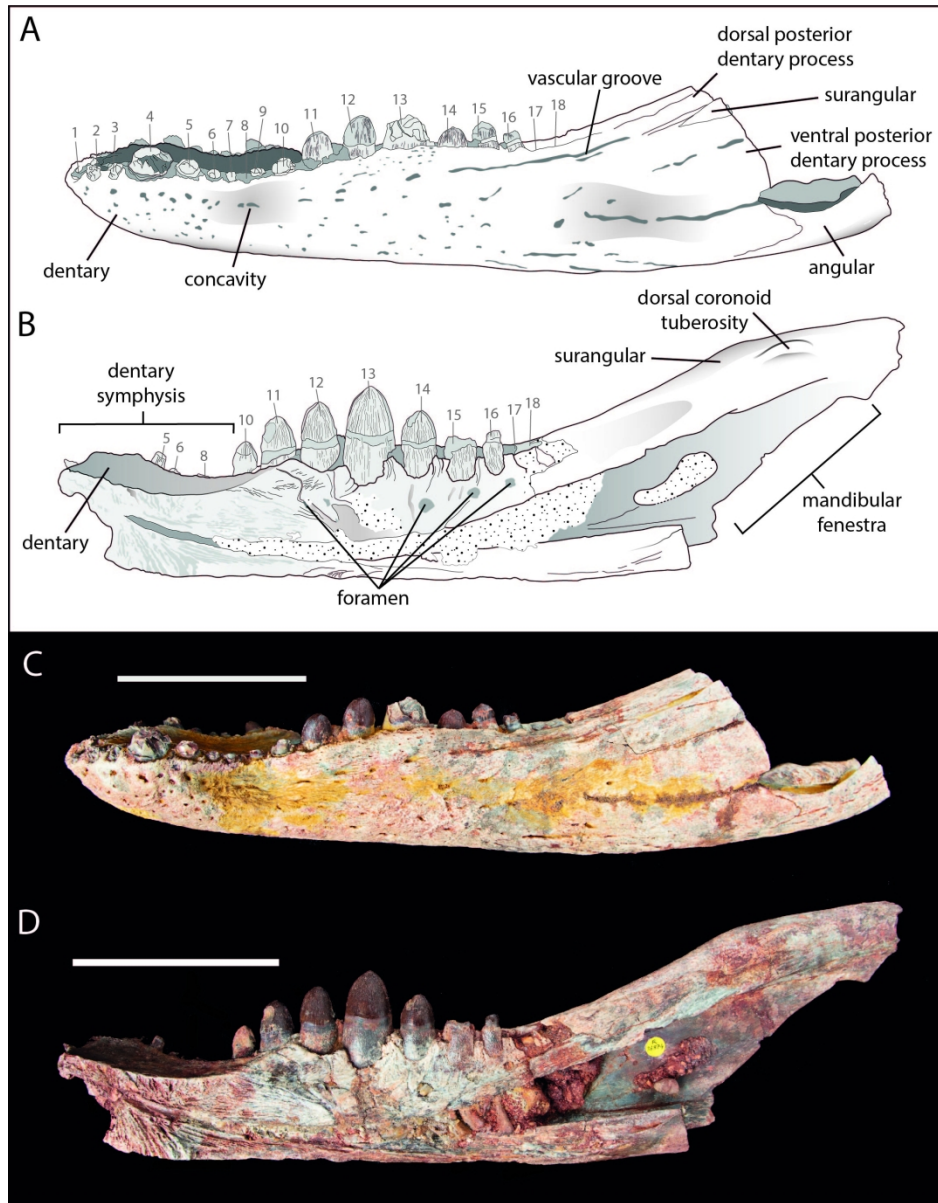


Figure 3  
 Line drawings and photographs of *Antaeosuchus taouzensis* n. gen. n. sp. (NHMUK PV R36829 [A&C] and NHMUK PV R36874 [B&D]) in left lateral view. Scale bar represents 100 mm.

193x246mm (300 x 300 DPI)

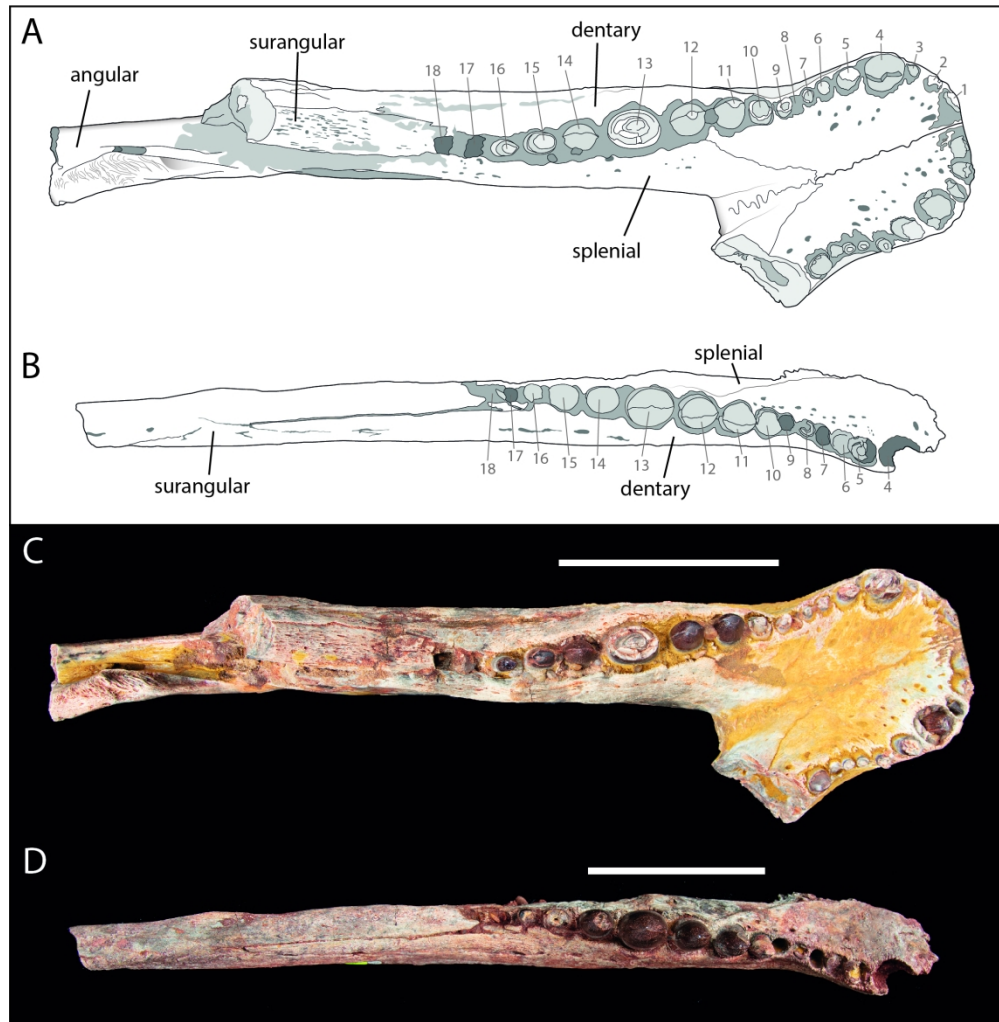


Figure 4

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

197x200mm (300 x 300 DPI)

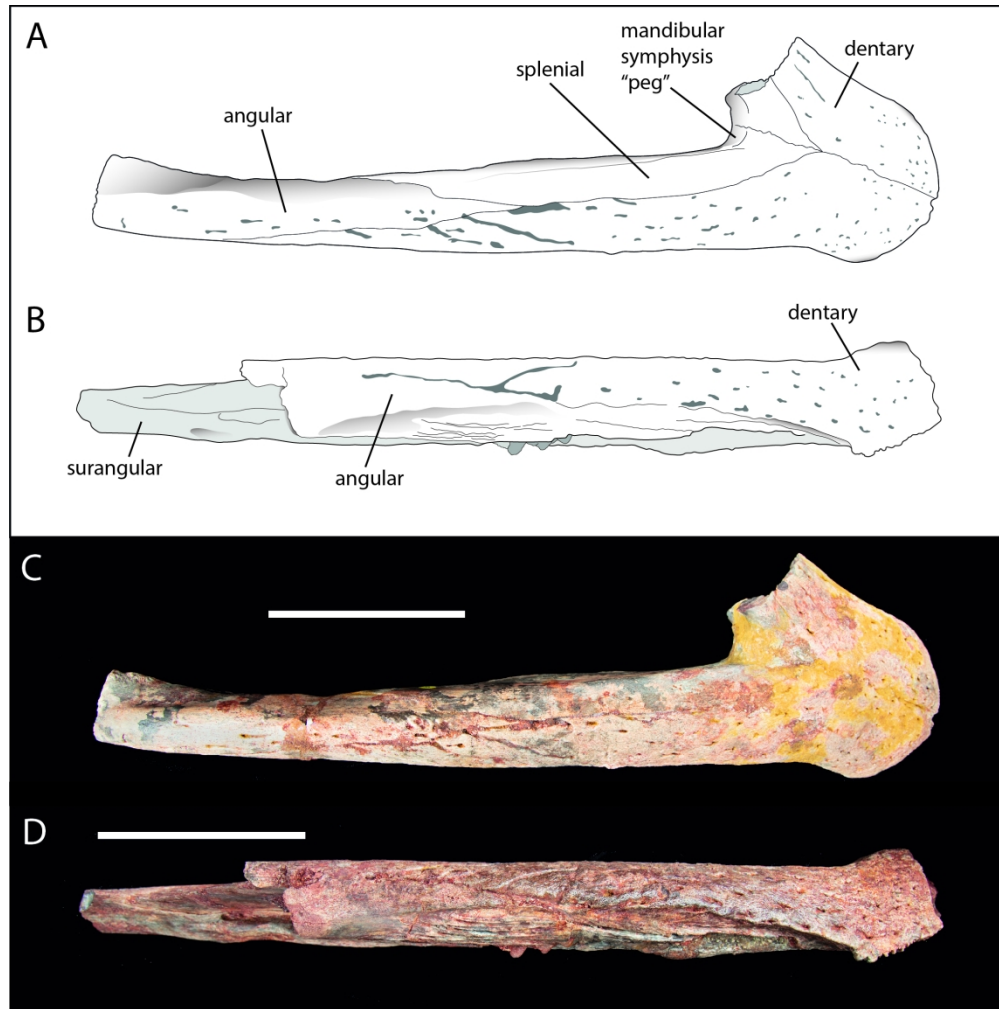


Figure 5

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

196x197mm (300 x 300 DPI)

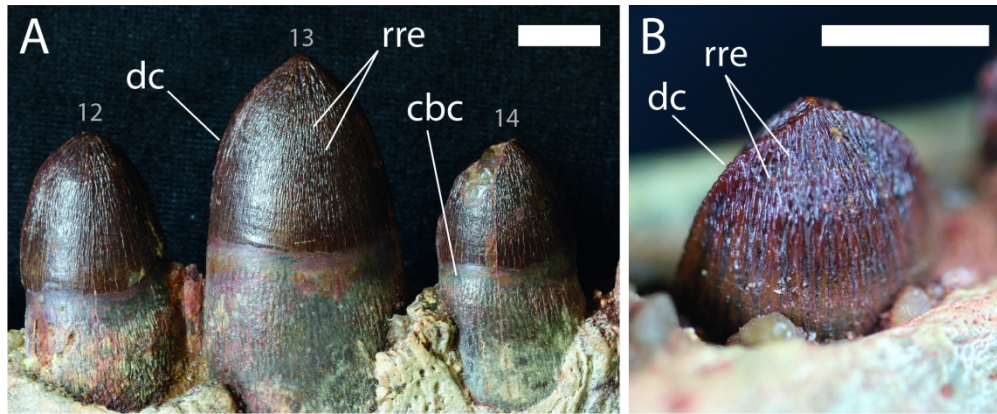


Figure 6

Teeth of *Antaeosuchus 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.

188x77mm (300 x 300 DPI)

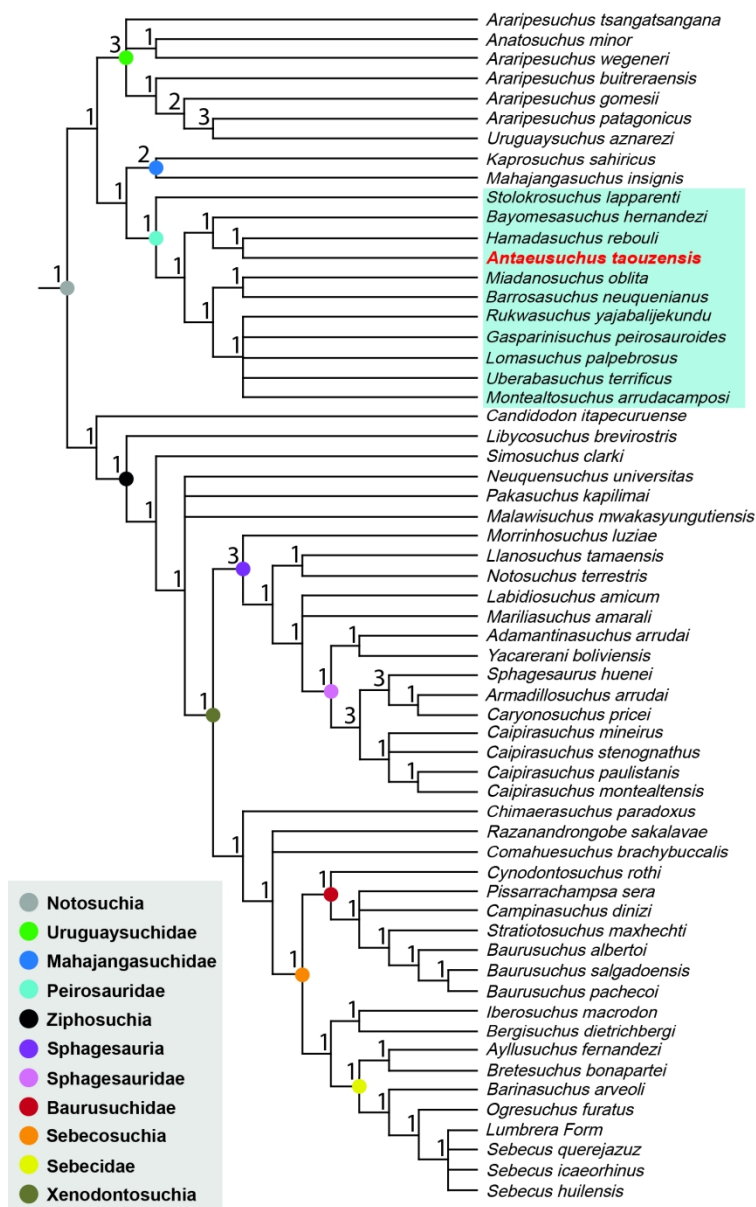


Figure 7

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

147x236mm (300 x 300 DPI)



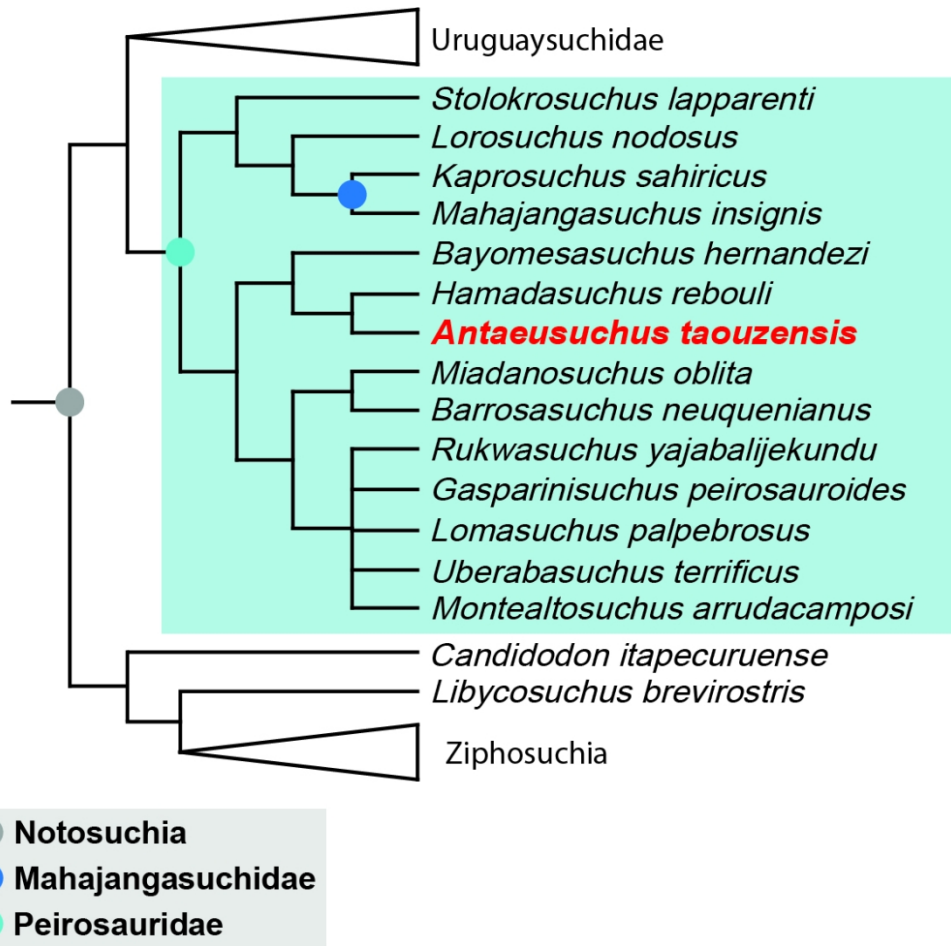


Figure 8

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.

99x93mm (300 x 300 DPI)

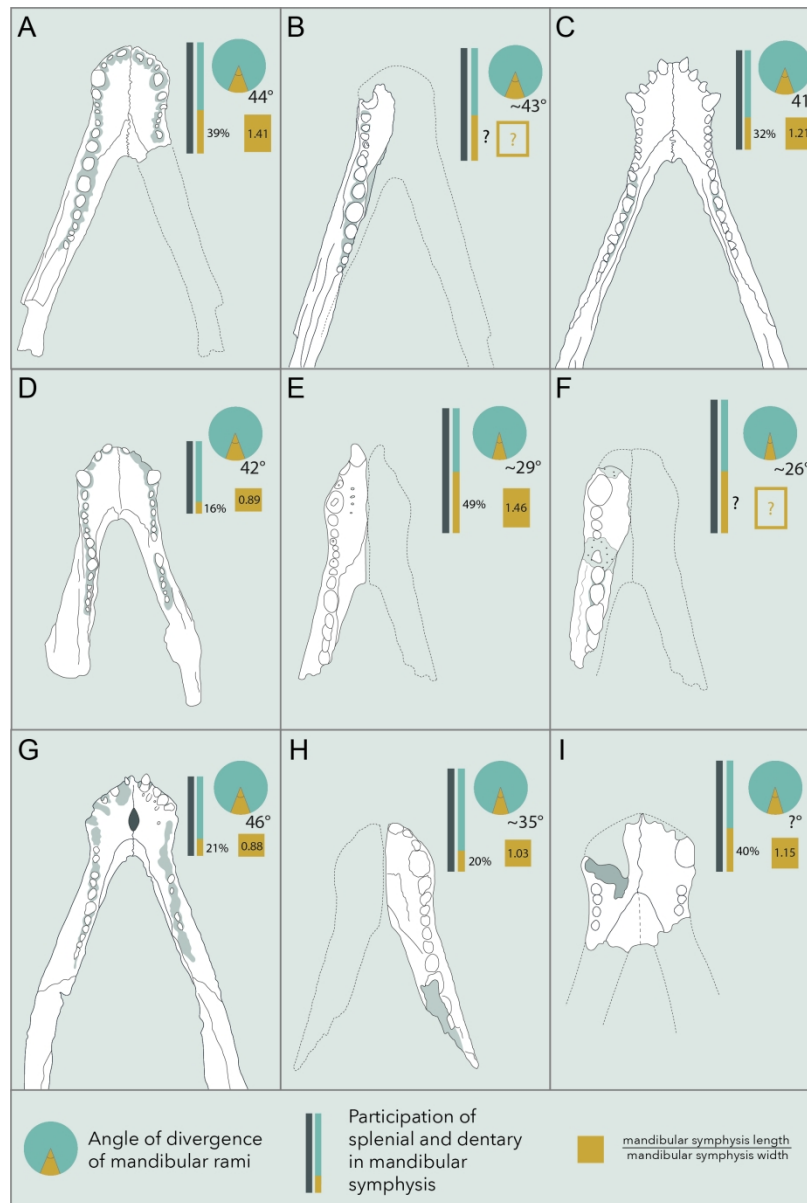


Figure 9

Comparison of the dorsal mandibular surfaces of several notosuchians: A, *Antaeosuchus taouzensis* n. gen. n. sp. (NHMUK PV 36829\*); B, *Antaeosuchus 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)

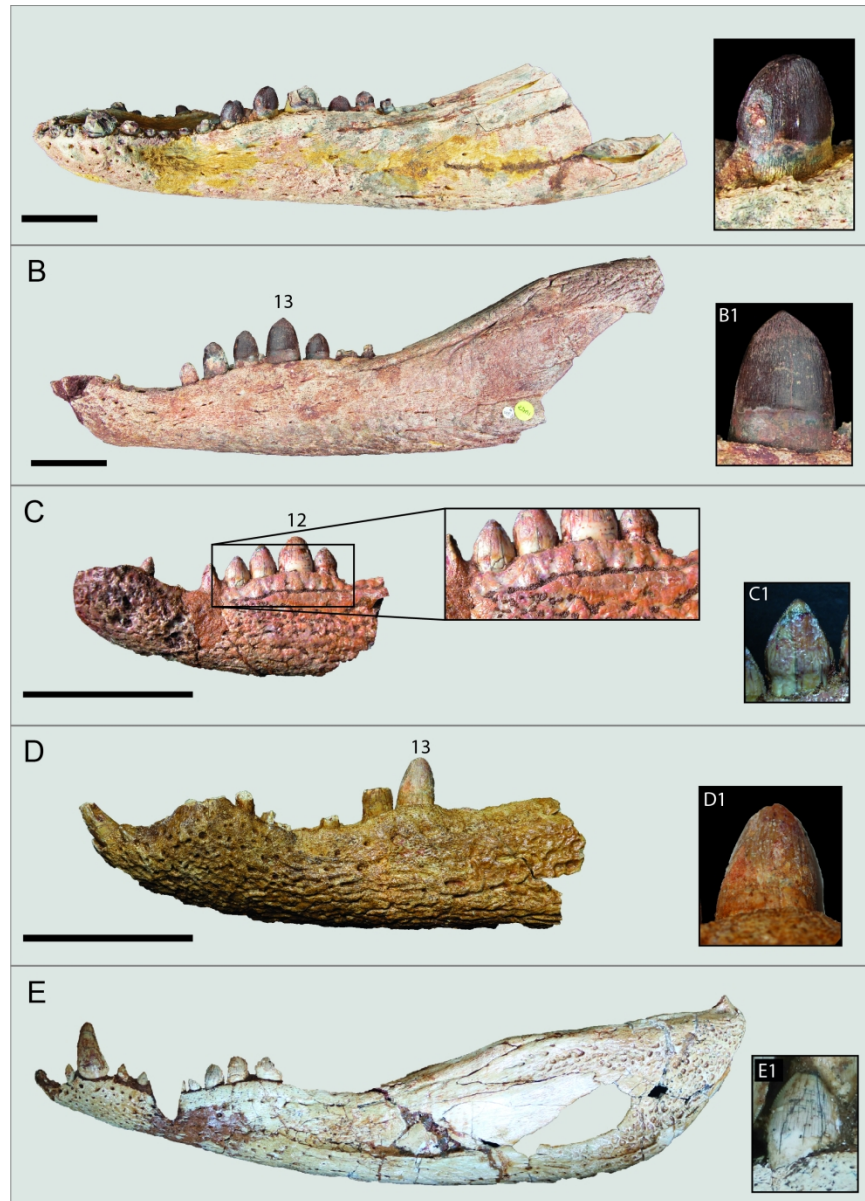


Figure 10

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)

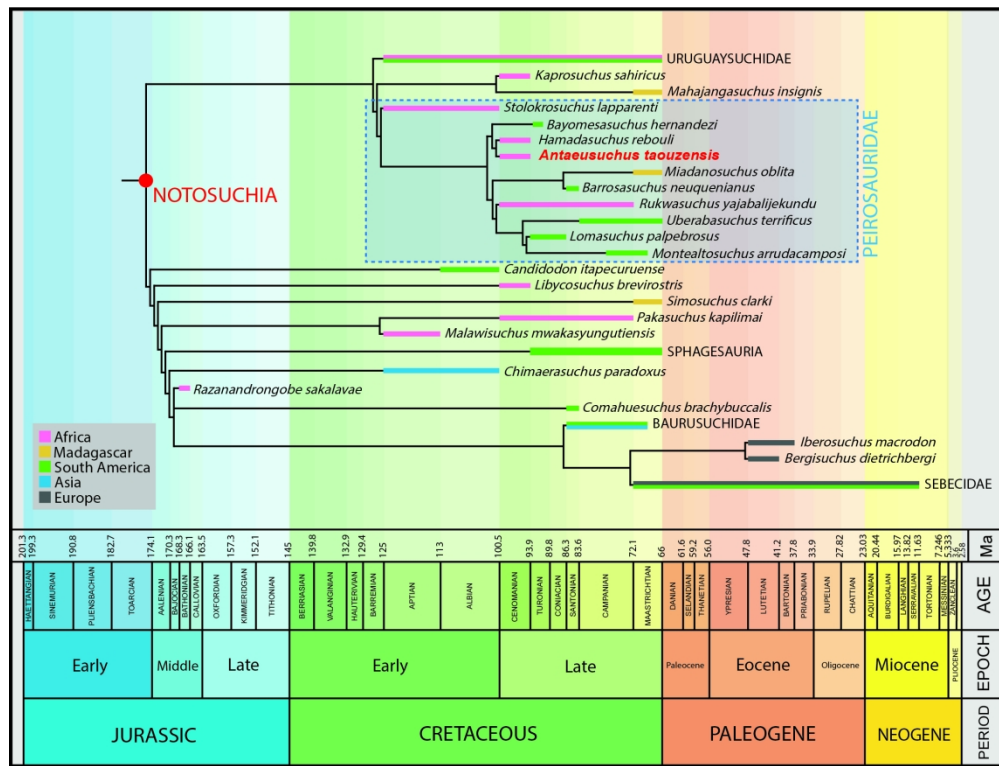


Figure 11  
 Time-calibrated phylogenetic topology showing the agreement subtree of notosuchians using equal weighting of characters. Some clades are condensed and the polytomy including Razanandrongobe sakalavae is shown despite being pruned from the agreement subtree.

198x150mm (300 x 300 DPI)

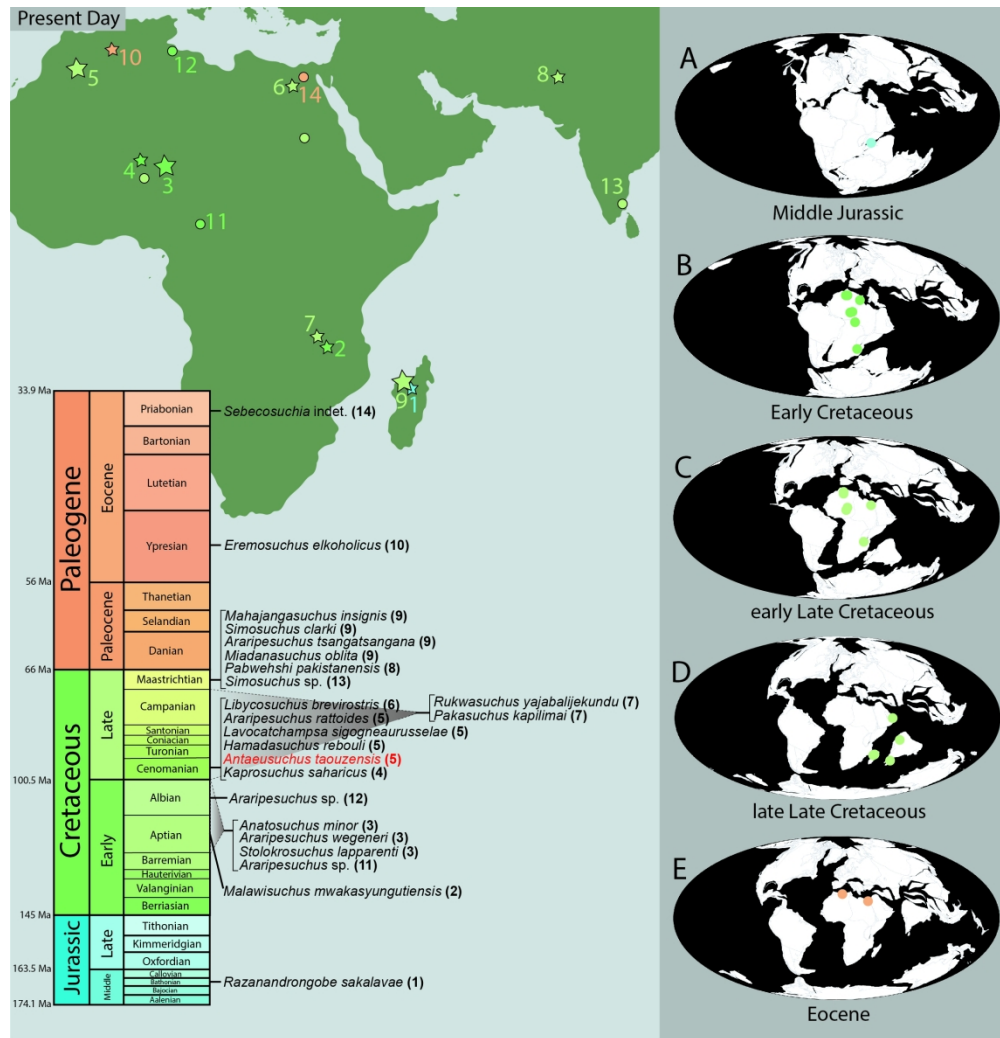


Figure 12

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)