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A peirosaurid mandible from the Albian–Cenomanian (Lower Cretaceous) of Algeria and the taxonomic content of *Hamadasuchus* (Crocodylomorpha, Peirosauridae)

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Abstract: Peirosaurids form an extinct clade of terrestrial crocodylomorphs from the Cretaceous of Africa and South America. Here, we describe a new mandibular ramus attributable to *Hamadasuchus* cf. *rebouli* from the Albian–Cenomanian of La Gara Samani (Algeria). We propose an emended diagnosis for this taxon, originally described from a left dentary fragment from the Kem Kem Group of Morocco and discuss the assignment of the specimens currently referred to it. Using ontogenetic series of extant crocodylians, we show that several mandibular characters commonly used to differentiate between close taxa instead record intraspecific or ontogenetic variability.

In contrast, reliable mandibular characters enable us to propose that the current taxonomic content of *Hamadasuchus rebouli* should be reduced to three specimens, pending future description of relatable cranial remains. Finally, we demonstrate the importance of mandibular characters in phylogenies, by recovering the new specimen from La Gara Samani as closely related to North African peirosaurids on the basis of a data matrix designed solely on mandibular characters.

Key words: Algeria, Crocodylomorpha, *Hamadasuchus*, mandible, middle Cretaceous, Peirosauridae.

PEIROSAURIDAE Gasparini, 1982, belonging to Crocodylomorpha, forms an extinct family known from at least the Aptian to the Maastrichtian (Price 1955; Leardi & Pol 2009). Their relationship to other groups of mesoeucrocodylians, as well as the taxonomic content of this group, are highly debated. Some studies place them as closely related to the uruguayasuchids and the mahajangasuchids from the Cretaceous of South America and Africa (Carvalho *et al.* 2004; Turner & Calvo 2005; Turner 2006; Turner & Sertich 2010; Pol *et al.* 2012, 2014; Kellner *et al.* 2014; Sertich & O'Connor 2014; Leardi *et al.* 2015, 2018; Barrios *et al.* 2016; Fiorelli *et al.* 2016; Godoy *et al.* 2016; Martinelli *et al.* 2018; Coria *et al.* 2019; Dumont *et al.* 2020; Nicholl *et al.* 2021); other studies show them as closely related to neosuchians (Serenio *et al.* 2003; Pol & Norell 2004; Company *et al.* 2005; Pol & Apesteguía 2005; Zaher *et al.* 2006; Turner & Buckley 2008; Leardi & Pol 2009; Serenio & Larsson 2009; Nascimento & Zaher 2011; Pol & Powell 2011); they have also been united with sebecids to form the clade Sebecia (Larsson & Sues 2007; Meunier & Larsson 2017; Geroto & Bertini 2019; Ruiz *et al.* 2021). Inside the peirosaurid group, relationships are also poorly defined and, depending on the inclusion of yet imperfectly understood taxa, such as

Stolokrosuchus lapparenti Larsson & Gado, 2000 or *Miadanasuchus oblita* Rasmussen Simons & Buckley, 2009, results do vary.

Several new taxa have been described recently and attributed to Peirosauridae, mostly on the basis of mandibular fragments (Barrios *et al.* 2016; Lio *et al.* 2016; Filippi *et al.* 2018; Coria *et al.* 2019; Lamanna *et al.* 2019; Nicholl *et al.* 2021). Such poor morphological representation could explain why this group is still poorly understood in terms of taxonomy and systematics. Given that phylogenetic matrices are mostly defined on cranial characters (only 13% of mandibular characters in Leardi *et al.* 2018 and Ruiz *et al.* 2021, for example), the unsettled relationships of peirosaurids may partly be explained by this lack of information.

Since the recognition of *Hamadasuchus rebouli* Buffetaut, 1994, from the Kem Kem Group of Morocco, the formation has yielded numerous and far more complete peirosaurid specimens (Rauhut & Lopez-Arbarelo 2005; Larsson & Sues 2007; Ibrahim *et al.* 2020; Nicholl *et al.* 2021). African peirosaurids are also known in East Africa, suggesting a wider distribution during the Cretaceous (Sertich & O'Connor 2014). Because the holotype of *Hamadasuchus* consists of a mandibular fragment,

taxonomic assignment of subsequent cranial discoveries has proven difficult (Cavin *et al.* 2010; Ibrahim *et al.* 2020; Nicholl *et al.* 2021). Moreover, and specifically for the Kem Kem Group of Morocco, the uncertain tracing of commercially acquired specimens and the high number of fossiliferous localities hamper the ability to address the contemporaneity of the various specimens.

Here, we describe a left mandibular ramus (MNHN-SAM 136) from slightly older stratigraphic deposits of the Albian–Cenomanian of Algeria that we attribute to Peirosauridae. We also discuss the taxonomic composition of North African peirosaurids in an attempt to clarify the identity of the taxon *Hamadasuchus rebouli*, propose an emended diagnosis for the species, and refer this fossil to it. Using a new matrix of mandibular characters only, we also attempt to better understand the phylogenetic relationships of peirosaurids from the middle to the Late Cretaceous.

GEOLOGICAL SETTING

The specimen was found at La Gara Samani locality (Algeria), on the north-western border of the Tademaït, between Timimoun and El Menia (Fig. 1; de Lapparent de Broin *et al.* 1971), during a fieldtrip by C. Grenot and R. Vernet in 1970. This locality is part of the Saharan ‘Continental Intercalaire’ and is considered as late Albian to early Cenomanian in age (de Lapparent de Broin *et al.*

1971; Lefranc & Toutin 1971; Lefranc & Guiraud 1990; Busson & Cornée 1991; de Lapparent de Broin 2002; Meunier & Larsson 2017; Benyoucef *et al.* 2022). La Gara Samani has yielded a diverse fauna including crocodylomorphs (de Lapparent de Broin *et al.* 1971; de Lapparent de Broin 2002; Meunier & Larsson 2017), dinosaurs (Taquet & Russell 1998), dipnoi (Busson & Cornée 1991), osteichthyes and turtles (de Lapparent de Broin *et al.* 1971), and molluscs (Busson & Cornée 1991).

MATERIAL AND METHOD

A well-preserved and uncrushed left hemi-mandible (MNHN-SAM 136; Figs 2–4) is described here for the first time. A surface scan of the mandible was obtained using an Artec Space Spider and the software Artec Studio (v.15) and MeshLab (v.2020.07). The 3D surface model is available in Dryad (Pochat-Cottilloux *et al.* 2023a; the video was made and rendered using Blender v.2.91).

Phylogenetic analysis

A matrix of 92 characters and 65 taxa was constructed based on Pol *et al.* (2014) and Geroto & Bertini (2019) (and references therein; Appendices S1, S2; Pochat-Cottilloux *et al.* 2023b) in order to sample as many



FIG. 1. Location of La Gara Samani, Algeria and the Kem Kem Group, Morocco. Cretaceous outcrops are highlighted in green (modified after Choubert *et al.* 1976).

notosuchian taxa as possible. *Dibothrosuchus elaphros* Simmons, 1965 was used as the operational outgroup and *Hamadasuchus rebouli* was separated into two different operational taxonomic units (OTUs) because of the differences observed between the specimens assigned to it (see Discussion and Appendix S1). Given that our aim was to study the impact of mandibular characters, the matrix used here contains only this type of character. We want to clarify here that those analyses are not meant to redefine clades or create new ones, but rather to assess the impact of mandibular characters on the phylogeny of notosuchians, and more precisely of peirosaurids. The results were then compared with those from more 'classic' matrices (Appendix S3). Another set of analyses was then conducted on taxa usually attributed to Peirosauridae only, using *Kaprosuchus saharicus* Sereno & Larson, 2009 as the operational outgroup, to better understand their relationships. Of the 92 equally weighted characters, 2 are continuous and were not discretized because the raw data linked to them did not show clear partitions. The matrix also has 9 ordered characters. Three new characters based on the mandibular symphysis, splenial and diastema were formulated based on personal observation of specimens. The definitions of 13 characters were modified and the coding was evaluated and modified when necessary for the other 76 characters if the data were available (Appendix S1). The matrix is also available in MorphoBank (Pochat-Cottilloux *et al.* 2023b).

The analyses were carried out using parsimony, without phylogenetically uninformative characters, and removing taxa with a significant amount of missing data (more than 80%; see also Appendix S3 for more details).

Analyses were run on TNT v.1.5 (Goloboff & Catalano 2016). New Technology Search was used, enabling all search algorithms (Sectorial Search, Ratchet, Drift and Tree Fusing; Goloboff 1999; Nixon 1999). The default settings for these advanced search methods were changed only to increase the iterations of each method, to 100 sectorial search drifting cycles, 100 ratchet iterations, 100 drift cycles and 100 rounds of tree fusion per replicate. This tree-space search procedure was repeated for five different random start seeds (following the procedure in Jouve 2016) using driven search to find the minimum length 10 times. Otherwise, the default parameters were retained. Extended implied weighting (Goloboff 2014) was not used because its utility remains controversial (Congreve & Lamsdell 2016; Groh *et al.* 2020). Bootstrap scores were then calculated. When necessary, the ACCTRAN optimization was used (accelerated transformation; Farris 1970; Swofford & Maddison 1987).

FigTree v.1.4.4 was used to visualize the phylogenetic trees obtained.

Institutional abbreviations. CPPLIP, Centro de Pesquisas Paleontológicas Llewellyn Ivor Price, Peirópolis, Brazil; DGM, Divisão de Geologia e Mineralogia, Rio de Janeiro, Brazil; MAÑE, Museo de Ciencias de Añelo, Añelo, Argentina; MAU, Museo Municipal Argentino Urquiza, Rincón de los Sauces, Argentina; MC, Canadian Museum of Nature, Ottawa, Canada (now CMN); MCF, Museo Municipal Carmen Funes, Plaza Huincul, Argentina; MCT, Museu de Ciências da Terra, Rio de Janeiro, Brazil; MDE, Musée des Dinosaurés d'Espéraza, Espéraza, France; MN, Museu Nacional, Rio de Janeiro, Brazil; MNHN, Muséum national d'Histoire naturelle, Paris, France; MPMA, Museu de Paleontologia de Monte de Alto, Monte Alto, Brazil; MOZ, Museo Professor J. Olsacher, Zapala, Argentina; ROM, Royal Ontario Museum, Toronto, Canada; UNPSJB-PV, Universidad Nacional de la Patagonia San Juan Bosco-Paleontología de Vertebrados, Comodoro Rivadavia, Argentina.

SYSTEMATIC PALAEOLOGY

CROCODYLIFORMES Hay, 1930

CROCODYLIFORMES Hay, 1930 (*sensu* Benton & Clark 1988)

MESOEUCROCODYLIA Whetstone & Whybrow, 1983

NOTOSUCHIA Gasparini, 1971

PEIROSAURIDAE Gasparini, 1982 (*sensu* Geroto & Bertini 2019)

Genus *HAMADASUCHUS* Buffetaut, 1994

Diagnosis. A crocodylomorph characterized by the following unique combination of features: at least 15 dentary alveoli; all alveoli are very close-set; at least four very small alveoli posterior to the large fourth alveolus; posterior dentary alveoli visible in lateral view; 11 completely involved alveoli in the mandibular symphysis; symphyseal region shallow dorsoventrally and narrow mediolaterally; dorsal and ventral dentary-splenial sutures directed anteromedially to posterolaterally (V-shaped if both hemi-mandibles were assembled); ventrolateral dentary surface anterior to mandibular fenestra transversely compressed; dentary extends posteriorly beneath the mandibular fenestra; anterior alveoli of dentary procumbent; concavity for the reception of the enlarged maxillary tooth lateral to the 7th–8th alveolus of the dentary; surangular overlaps dentary above the external mandibular fenestra.

Locality & horizon. 'Hamada du Guir', near Taouz, southern Morocco, red beds of late Albian to early Cenomanian age; La Gara Samani, Algeria, late Albian to early Cenomanian.

Hamadasuchus cf. rebouli Buffetaut, 1994

Holotype. Incomplete left dentary (MDE C001).

Referred specimens. MNHN-MRS 3110, mandibular symphysis (Ibrahim *et al.* 2020, fig. 82A–C); MNHN-SAM 136 (Figs 2–5).

Revised diagnosis. As for genus + heavily sculpted mandible; seven alveoli completely involved in the dentary part of the symphysis; surangular forms lateral margin of articular fossa; prominent posterolateral ridge on lateral surface of surangular.

Locality & horizon. As for genus.

Description

MNHN-SAM 136 is a left mandibular ramus. Apart from the coronoid and the retroarticular process, all of the bones are preserved and almost complete. The margins of the external mandibular fenestra are imperfect in some places, but the general outline is well-preserved. This fenestra is directed antero-posteriorly and is triangular shaped in lateral view, with the longest side dorsally and parallel to the dorsal edge of the surangular. In lateral view, the mandible is arched anterodorsally. The outer surface of the mandible is ornamented with nutrient foramina in its anterior portion and shallow pits in its posterior area, corresponding to the ventral margin of the surangular and the angular. The mandible is nearly smooth and devoid of ornamentation in the anterior area of the external mandibular fenestra.

Dentary. The mandibular symphysis is extensive and involves completely the first 11 alveoli (Figs 2B, 3B). Both dentaries are firmly sutured to each other along a medial contact until the level of the seventh dentary alveolus (Figs 2B, 3B). The symphyseal region is shallow dorsoventrally and narrow mediolaterally (Fig. 4A). In dorsal view the suture with the splenial is oblique anteriorly (directed posterolaterally to anteromedially) up until the 11th dentary alveolus, then it straightens posteriorly (Figs 2B, 3B). In ventral view the dentary–splenial suture is oblique all the way (Figs 2A, 3A). In medial view it is interdigitated and directed postero-ventrally (Figs 2C, 3C). The dentaries remain uniform in width up to their point of divergence, where they begin to taper off. Posteriorly, in lateral view, the dentary bone divides into a long postero-dorsal process and a shorter posteroventral process (Figs 2D, 3D) that contribute, respectively, to the anterodorsal and the antero-ventral margins of the external mandibular fenestra. The postero-ventral process lies down against the angular. The posterior end of the tooth row seems to connect to one of the anterior processes of the surangular, but it is difficult to assess because the area is damaged. There are 17 alveoli, of which the fourth is the largest. Some alveoli preserve the root of a tooth, namely the 5th, 9th and 11th to 13th, which are laterally moderately and variably compressed (precise measurements of each alveolus are available in Table 1). The first four alveoli are gradually directed anteriorly to anterolaterally, and the dentary narrows medially at the level of the eighth or ninth alveoli. Although this area may be deformed, this anatomical trait is still prominent. In lateral view the mandibular dentition has a sinuous margin, marked by two sets of waves (Figs 2D, 3D). The apex of the first wave culminates at the large fourth alveolus, whereas the second wave culminates at the 12th or 13th alveoli, which are also large. In between, dentary alveoli are distinctly but variably small (Table 1). The fourth alveolus is not dorsally elevated from the first one. The ventral surface of the dentary of

MNHN-SAM 136 is anterolaterally curved dorsally and bears small but deep foramina (Fig. 2A). The ventrolateral margin of the dentary has a very developed prominence, which stretches antero-posteriorly from the fourth alveolus to the ventral margin of the external mandibular fenestra (Figs 2D, 3D). This gives a nearly flat ventral profile to the dentary, as observed in lateral view.

Splenial. The splenial is mostly exposed medially, where it forms a vertical plate that sutures with the dentary. The splenial's anterior portion contributes to the mandibular symphysis and would have sutured medially with the corresponding right splenial (Figs 2A–C; 3A–C). Here, the splenial reaches anteriorly to the level of the seventh alveolus, dorsally and ventrally (Figs 2A, B, 3A, B). The dorsal and ventral exposure of the splenial is strictly triangular shaped and comprises more than one-third of the mandibular symphysis. In posterior view the foramen intermandibularis oralis is displaced laterally, indicating the paired condition for the complete mandibular rami (Figs 2C, 3C). Posteriorly, the splenial becomes thin and plate-like along the medial surface of the dentary and contributes to the medial wall for the last seven dentary alveoli, until it tapers off dorsally and probably contacts the surangular medially. The area of insertion can be seen in medial view (Figs 2C, 3C). The splenial also meets with the angular ventrally (Figs 2A, C; 3A, C). Overall, all of the surfaces of the splenial are smooth.

Angular. The angular is the ventralmost mandibular element, it comprises about two-thirds of the mandibular ramus. In lateral view it is elongated and curved posterodorsally (Figs 2D, 3D). Medially, it is convex with a prominent crest twisting anterodorsally to posteroventrally just ventral to the external mandibular fenestra, which forms the posterodorsal part of the adductor fossa (Figs 2C, 3C). Anteriorly, a long process sutures with the splenial medially and the dentary laterally up to the level of the 16th alveolus. The anterior part of the adductor fossa is formed ventrally and medially by the angular and medially by the splenial, whereas the posterior part of the medial wall of the adductor fossa is missing. The angular forms the ventral margin of the external mandibular fenestra laterally (Figs 2D, 3D). The foramen intermandibularis caudalis is either absent or not preserved on the medial side. Posteriorly to the external mandibular fenestra, and for the rest of its length, the angular sutures with the surangular, reaching ventrally to the articulation surface of the articular as a sharp process and curving inwards and up (Figs 2C, 3C, 4B). The lateral surface of the angular bears the prolongation of the pronounced lateral crest observed on the dentary (Figs 2B, D; 3B, D), which becomes a groove in dorsolateral view, just ventral to the external mandibular fenestra. The posteroventral margin of the angular shows a developed area for the insertion of the musculus pterygoideus, which is visible in lateral and ventral views (Figs 2A, D; 3A, D).

Surangular. This bone is robust and elongated. Anteriorly, the suture with the dentary is complex: the dentary has two posterior processes that interlock with two anterior processes of the surangular (Figs 2B, 3B). In lateral view the surangular curves dorsally at the level of the external mandibular fenestra (Figs 2D, 3D). The surangular forms the posterior and posterodorsal



FIG. 2. MNHN-SAM 136 in: A, ventral; B, dorsal; C medial; D, lateral view. *Abbreviations:* ang, angular; ar, articular; c, crest; d, dentary; fio, foramen intermandibularis oralis; mf, external mandibular fenestra; r, ridge; san, surangular; spl, splenial. Scale bar represents 5 cm.

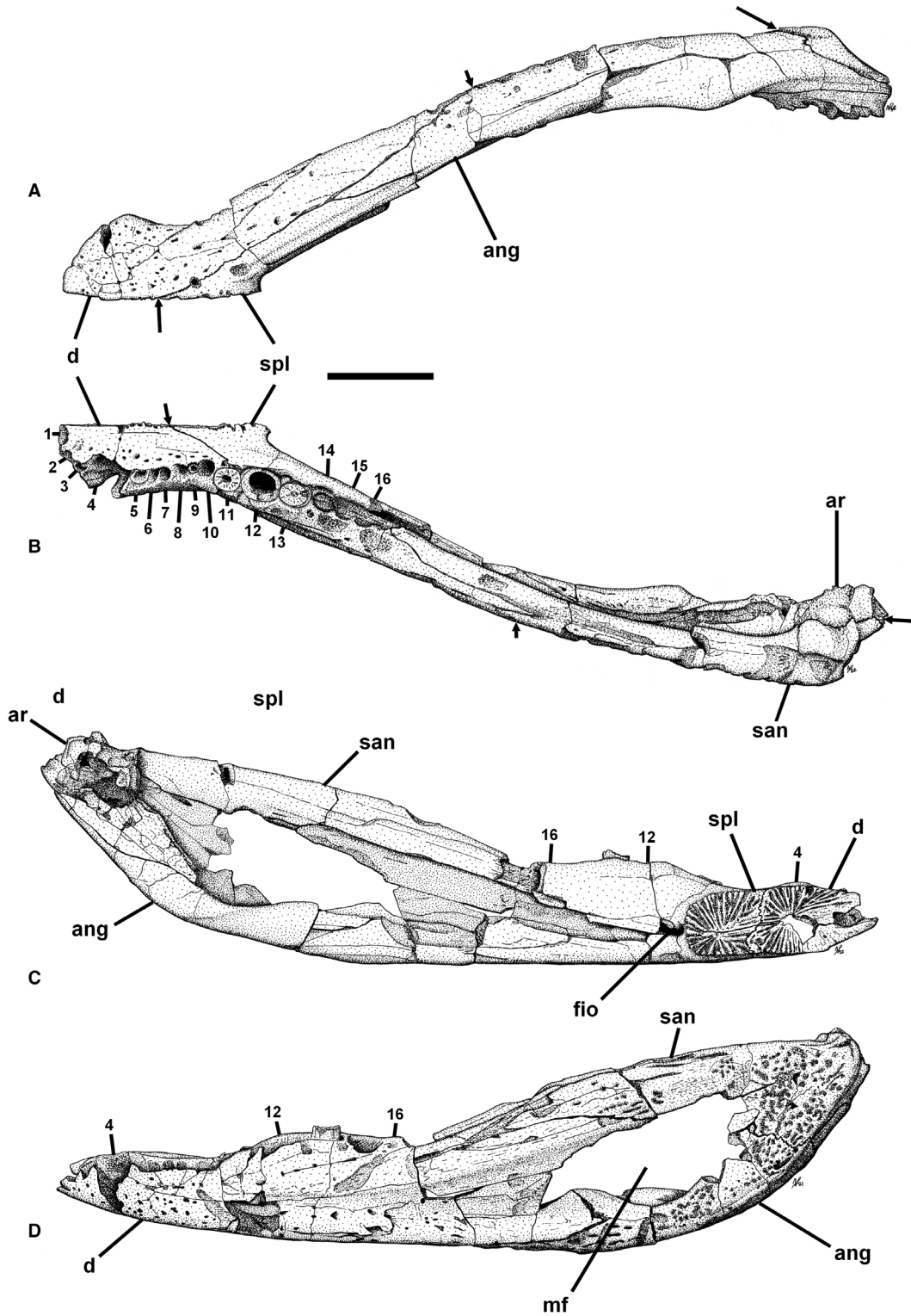


FIG. 3. Interpretative drawings of MNHN-SAM 136 in: A, ventral; B, dorsal; C, medial; D, lateral view. *Abbreviations:* 1–16: alveolus 1–16; an, angular; ar, articular; d, dentary; fio, foramen intermandibularis oralis; mf, external mandibular fenestra; san, surangular; spl, splenial. Arrows indicate bone sutures. Scale bar represents 5 cm.

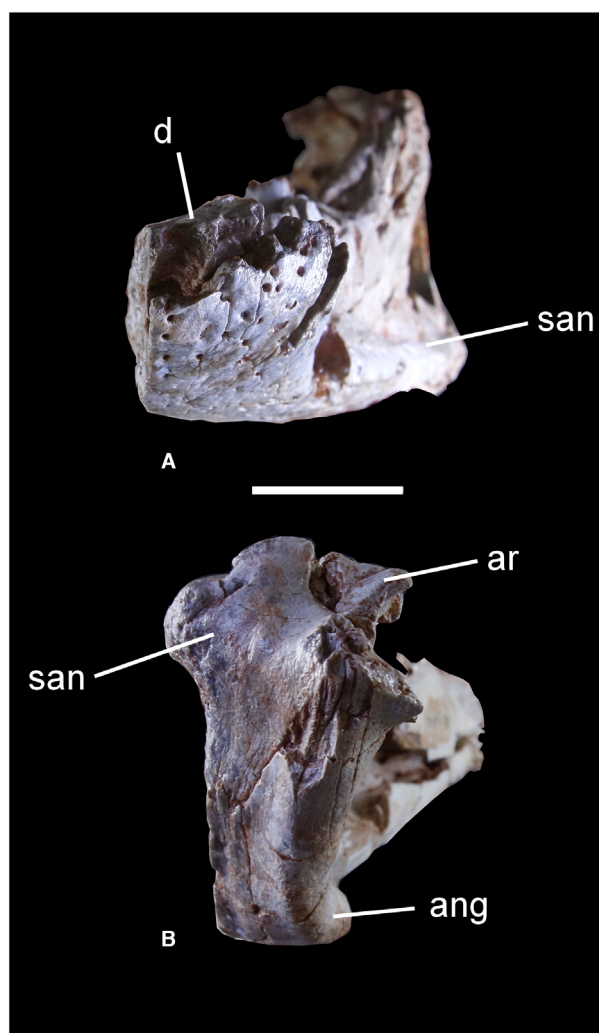


FIG. 4. MNHN-SAM 136 in: A, anterior; B, posterior view. *Abbreviations:* ang, angular; ar, articular; d, dentary; san, surangular. Scale bar represents 2 cm.

margins of the external mandibular fenestra (Figs 2C, D; 3C, D). Posteriorly to this fenestra, the surangular sutures with the angular for the rest of its length and it also becomes thinner mediolaterally and ventrally. The suture is linear anteriorly and curves dorsally toward the posterior end. The bone also curves dorsally and forms the lateral margin of the glenoid fossa (Figs 2B, 3B, 4B, 5A). Laterally to this, there is a tiny ridge followed by a huge depression that is located beneath the level of the glenoid surface, corresponding to the articulation with the quadratojugal condyle, indicating a double mandibular articulation (Figs 2B, 3B). The posteriormost part of the surangular is broken. The dorsal surface is overall convex but flattens considerably just before the glenoid surface with the quadrate. The lateral surface is not as well preserved as the other parts of the mandible, but it bears a prominent posterolateral ridge (Figs 2D, 3D). On the medial surface, the suture with the articular is directed posterodorsally to anteroventrally.

Articular. The articular is contained laterally by the posterior parts of the angular and surangular. Only the anterior portion and part of the dorsal surface are preserved. The anterodorsal surface is separated from the posterodorsal surface by a mediolateral ridge and would have articulated with the quadrate. This ridge is tall and dorsally edged (Figs 2B, C; 3B, C; 4B; 5A). The articular fossa is divided into a lateral and a medial portion separated by a small ridge oriented anteroposteriorly. Both seem to be of the same size; however, the medialmost part is broken (the foramen aërum is not preserved). The preserved part of the posterior surface is concave, curved ventromedially. The retroarticular process is broken but would have been directed posterodorsally. Ventromedially, the articular forms the posterior wall of the adductor chamber. It sutures with the surangular at its lateral margin and with the angular at its ventral margin (Figs 2B, C; 3B, C; 4B; 5A).

Dentition. The best partially preserved root is the 13th (Figs 2B, 3B). It is broken at the exit of the tooth row. The root is compressed laterally (ovoid shape in dorsal view), no carinae can be seen and it bears apicobasal striations (Figs 2D, 3D).

PHYLOGENETIC ANALYSIS

The analysis generated 94 most parsimonious trees and a consensus tree with a length of 436 steps (Fig. 6; consistency index (CI) = 0.33, retention index (RI) = 0.79).

Our results retrieved some of the same groups within Crocodylomorpha as other recent phylogenetic studies (Pol *et al.* 2014; Godoy *et al.* 2016; Leardi *et al.* 2018; Dumont *et al.* 2020; see also Appendix S3; Fig. 6). Here, based on ACCTRAN optimization, Baurusuchidae Price, 1945 are separated from all other notosuchians on the basis of lacking posteroventral symphyseal depressions (char. 42), an anterior portion of the mandibular symphysis with an anteriorly verticalized angle of more than 45° (char. 43), a surangular that does not participate in the quadrate articulation (char. 50), a surangular anterior border clearly bifurcated and divergent (char. 54), a lateral flange of the retroarticular process that is shorter than the mediolateral width of the glenoid facets of the articular (char. 85), a small bulge located proximally on the medial flange of the retroarticular process that is absent (char. 88), and an anteromedial end of the medial flange of the retroarticular process that projects anteroventrally as a deep pendant process (char. 89). Sphagesauridae (and 'advanced' notosuchians or Sphagesauria; Kuhn 1968; Pol *et al.* 2014; Ruiz *et al.* 2021) are monophyletic on the basis of having a posterior region of alveolar margins facing dorsally, forming a broad alveolar shelf that is strongly inset medially from the lateral surface of the dentaries (char. 13), middle and posterior dentary teeth with a transverse circular to subcircular section without significant lateral compression (char. 24), the

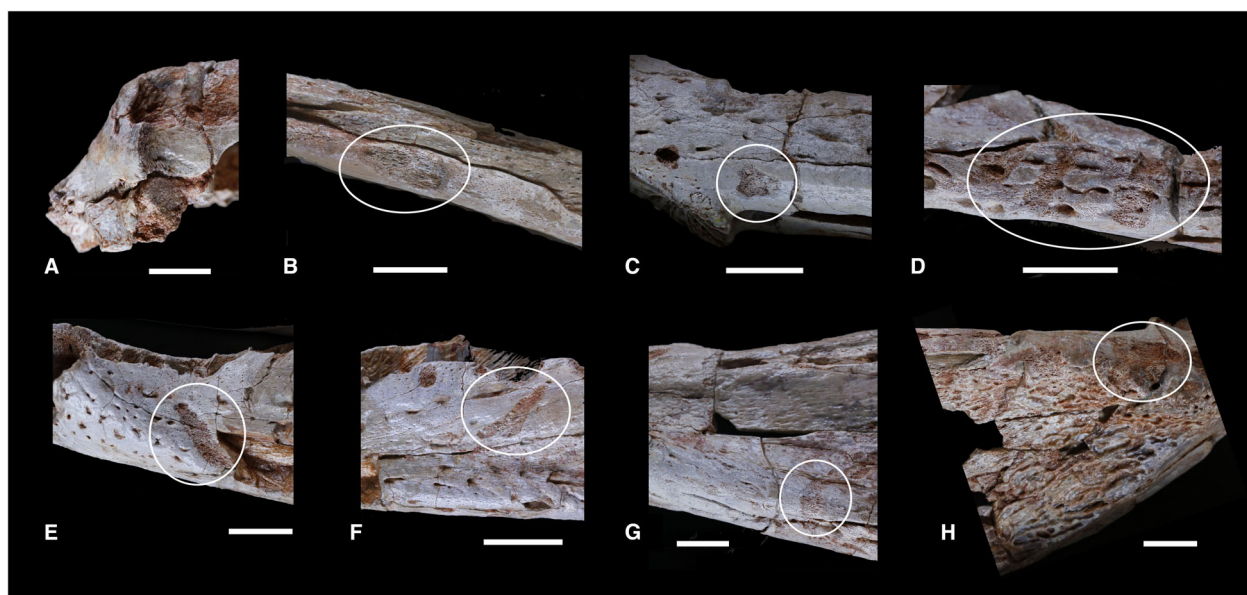


FIG. 5. Close ups of MNHN-SAM 136 in: A–B, dorsal; C–D, ventral; E–H, lateral view. White circles indicate dermestid traces. Scale bars represent 2 cm.

dentary symphysis tapering anteriorly forming an angle (V-shaped; char. 36), and having well developed coronoid tuberosities on the medial surface of the surangular, forming prominent crests (char. 45). Finally, Uruguaysuchidae Gasparini, 1971 (with the inclusion of *Comahuesuchus brachybuccalis*) is retrieved as monophyletic on the basis of an unsculpted region on the dentary below the tooth row (char. 11), a dentary that overlaps the surangular above the external mandibular fenestra (char. 16), middle and posterior dentary teeth with a transverse section circular to subcircular without significant lateral compression (char. 24), a splenial that forms close to 30% of the symphyseal length (char. 29), a straight shape of the splenial–dentary suture adjacent to the dentary tooth row (char. 39), an insertion area for the M. pterygoideus posterior that extends onto the lateral surface of the angular (char. 66), and a retroarticular process that has a rounded surface, is longer than wide, flat, is posteroventrally oriented and facing dorsomedially (char. 84).

Interestingly, the taxa usually attributed to the monophyletic family Peirosauridae Gasparini, 1982 are split into two groups: one is close to sphagesaurids and ‘advanced’ notosuchians and is composed of *Barrosasuchus neuquenianus*, *Bayomesasuchus hernandezi*, *Colluhupisuchus lunai*, *H. rebouli* (*sensu* Buffetaut 1994 and Larsson & Sues 2007), *Kinesuchus overoi*, *Antaeusuchus taouzensis* and MNHN-SAM 136, whereas the other one is closely related to uruguaysuchids and is composed of *Miadanasuchus oblita*, *Montealtosuchus arrudacamposi*, *Patagosuchus anielensis*, *Uberabasuchus terrificus*,

Gasparinisuchus peirosauroides, *Lomasuchus palpebrosus*, *Itasuchus jesuinoi*, *Pepesuchus deiseae* and *Stolokrosuchus lapparenti* (Fig. 6).

The first taxa mentioned are grouped based on having procumbent, anteriorly inclined dentary teeth (char. 14), a surangular that overlaps the dentary above the external mandibular fenestra (char. 16), middle dentary teeth disposed in a groove, originally separated from each other only by soft tissue (char. 23), the surangular participating in the quadrate articulation and forming approximately one-third of the glenoid fossa with the quadratojugal bearing an articular condyle (char. 50), and a surangular–angular suture intersecting with the external mandibular fenestra at the posterodorsal angle (char. 59).

The remaining peirosaurids are related to uruguaysuchids on the basis of having a foramen intermandibularis oralis that is small or absent (char. 4), the posterior portion of the external mandibular fenestra that is sculpted (char. 7), a pattern of mandibular dentition after the fourth dentary teeth that is composed of 3–4 caniniforms, followed by molariforms (char. 22), a mandibular symphysis that is shallow and tapering anteriorly in lateral view (char. 37), a splenial–dentary suture on the ventral surface that is transverse (char. 38), a surangular posterior edge bent downward, forming a convexity (char. 56), a strong pitted pattern on the angular and the posterior part of the surangular (char. 64), a posterior border of the articular glenoid fossa that is well developed, with a ridge limiting the posterior mandibular movement (char. 78), a retroarticular process that is elongated posteriorly,

TABLE 1. Labiolingual and mesiodistal measurements of each mandibular alveolus of peirosaurid taxa (in mm).

Tooth position	<i>Hamadasuchus rebouli</i>		<i>Bayomasasuchus hernandezi</i>		<i>Pepesuchus deiseae</i>		<i>Montealtosuchus arrudacamposi</i>		<i>Barrosasuchus neuquenianus</i>		<i>Kinesuchus overoi</i>	
	ROM 49282		MCF PVPH-822		MN 7005-V		MPMA-16-0007-04		MCF-PVPH-413		MAUV-Pv-CO-583	
	LL	MD	LL	MD	LL	MD	LL	MD	LL	MD	LL	MD
d1	8	9	?	?	?	4.4	4	4	12.6	?	5.9	5.3
d2	5	5.5	?	?	7.6	3.1	3.2	4	8.4	10	6.5	5.3
d3	4.5	5	4.2	?	7.1	4.4	4	4	12.6	11.6	4.7	4.1
d4	9.5	11.5	6	10.1	7.6	11.1	6	6.8	10.5	5.2	8.8	10.6
d5	6	6.5	3.6	4.2	8.9	?	2.6	4	?	?	4.7	6.5
d6	4.5	4.5	3	3.6	?	?	3.2	3.6	10.5	?	5.3	5.9
d7	4	4	3	3.6	3.6	?	2.8	2.8	6.3	5.3	4.1	5.3
d8	4	4	3	4.2	4.4	4.4	3.2	4	5.3	8.4	3.5	5.3
d9	4	4	?	?	6.2	6.7	2.8	4	8.4	8.4	4.7	5.3
d10	5	5.5	?	?	5.3	?	3.2	4	7.4	7.4	?	5.9
d11	5.5	6	?	?	8.9	6.7	3.2	4.8	7.4	11.6	5.9	5.9
d12	7	7.5	?	?	8.9	?	4	6	9.5	12.6	6.5	7.1
d13	7.5	11	?	?	8.9	7.1	4	6	7.4	9.5	7.1	8.8
d14	5	7	?	?	8.9	?	2.4	4	5.3	8.4	5.9	8.2
d15	?	?	?	?	5.3	?	3.6	5.6	5.3	8.4	4.1	8.2
d16	?	?	?	?	8.9	6.2	3.7	4	?	?	3.5	5.9
d17	?	?	?	?	?	4	3.2	4	?	?	4.1	5.9
d18	?	?	?	?	3.1	?	2.8	4.8	?	?	?	?

Tooth position	<i>Lomasuchus palpebrosus</i>		<i>Patagosuchus anielensis</i>		<i>Gasparinisuchus peirosauroides</i>		<i>Itasuchus jesuinoi</i>		<i>Colhuehuapisuchus lunai</i>		New specimen	
	MOZ 4084 PV		MAÑE-PV 1		MOZ 1750 PV		DGM 434-R		UNPSJB-PV 961		MNHN-SAM 136	
	LL	MD	LL	MD	LL	MD	LL	MD	LL	MD	LL	MD
d1	8	?	?	?	?	?	?	12.8	5	7.3	?	16
d2	5	5	4	?	7	8.8	15.3	17.9	5.1	5.5	12	10
d3	8	10	3	?	?	?	12.8	15.3	6	5.4	10	8
d4	?	?	7.7	?	?	14.7	9	12.8	8.3	9.7	19	21
d5	?	?	4.7	4.7	5.9	7.6	7.8	10.2	?	?	11	9
d6	?	?	4	3	4.1	5.9	?	?	3	4.1	8	5
d7	?	?	5	4	5.9	6.5	10.2	?	3	3.9	9	7
d8	?	?	4	4.3	4.1	5.3	12.8	15.3	?	?	8	7
d9	?	?	3	5.7	4.7	3.5	?	16.6	?	?	5	5
d10	?	?	5	4	5.9	5.9	17.9	19.2	?	?	10	11
d11	?	?	5	6	8.2	7.6	11.5	14.1	2.8	4.3	12	14
d12	?	?	?	?	7.6	11.2	15.3	15.3	4.7	6.4	17	24
d13	?	?	?	?	10	14.1	14.1	16.6	?	?	13	15
d14	?	?	?	?	5.3	7.1	12.8	14.1	?	?	11	11
d15	?	?	?	?	4.1	5.9	11.5	12.8	?	?	10	?
d16	?	?	?	?	3.5	7.1	11.5	10.2	?	?	10.5	?
d17	?	?	?	?	4.1	7.6	?	?	?	?	?	?
d18	?	?	?	?	2.9	5.3	?	?	?	?	?	?

LL, labiolingual; MD, mesiodistal.

triangular in shape and facing dorsally (char. 84), and a medial edge of the medial flange of the retroarticular process that is straight or slightly convex (char. 91).

Another set of analyses was conducted using taxa attributed only to Peirosauridae from the complete dataset and

using *Kaprosuchus saharicus* as an outgroup. Here, this enables the inclusion for the first time of *K. overoi*, *P. anielensis* or *C. lunai*. This analysis generated three most parsimonious trees and a consensus tree of 114 steps (Fig. 7; Appendix S3; CI = 0.66, RI = 0.53). The same dichotomy as

in the general analysis is found. Using mandibular characters, the groups *Pepesuchinae* and *Peirosaurinae sensu* Geroto & Bertini (2019) are not retrieved. However, *S. lapparenti* and *M. oblita*, the positions of which have been greatly debated (de Lapparent de Broin 2002; Sereno *et al.* 2003; Carvalho *et al.* 2004; Jouve *et al.* 2006; Larsson & Sues 2007; Turner & Buckley 2008; Sereno & Larsson 2009; Turner & Sertich 2010; Pol & Powell 2011; Bronzati *et al.* 2012; Pol *et al.* 2012, 2014; Adams 2013; Kellner *et al.* 2014; Sertich & O'Connor 2014; Leardi *et al.* 2015; Barrios *et al.* 2016; Fiorelli *et al.* 2016; Meunier & Larsson 2017; Martinelli *et al.* 2018; Geroto & Bertini 2019; Coria *et al.* 2019; Nicholl *et al.* 2021; Ruiz *et al.* 2021) are retrieved here, using mandibular characters, deeply nested within Peirosauridae and, furthermore, the topology presented in Figure 7 does not change if we remove one or both taxa from the analysis. These results on mandibular characters reflect a methodological choice underlining the close relationship of *S. lapparenti*, *M. oblita* and peirosaurids but should be confirmed by other lines of evidence.

DISCUSSION

MNHN-SAM 136 as a peirosaurid

Cretaceous crocodylomorphs from Africa with a long mandibular symphysis to which the splenial contributes, and laterally compressed teeth which are procumbent in the anterior part of the mandible, are restricted to certain notosuchians (de Lapparent de Broin 2002; Sereno & Larsson 2009; Martin & de Lapparent de Broin 2016; Meunier & Larsson 2017; Ibrahim *et al.* 2020). The morphology of MNHN-SAM 136 is very different from that of *Anatosuchus minor* Sereno *et al.*, 2003 and *Laganosuchus* Sereno & Larsson, 2009, because the symphyseal region of the mandible is not generally square-shaped, as it is in those two taxa. The posterior alveoli are visible in lateral view, which enables this specimen to be distinguished from *Araripesuchus wegneri* Buffetaut & Taquet, 1979 (Sereno & Larsson 2009). The medial part of the dentary symphysis does not bear an oval fenestra, therefore this specimen cannot be attributed to *Araripesuchus rattoides* Sereno & Larsson, 2009. Of the remaining taxa, the peirosaurids are characterized by a heavily sculpted mandible and two waves of enlarged dentary teeth (Gasparini 1982; Geroto & Bertini 2019), as reported here in MNHN-SAM 136. Comparisons will thus be made with peirosaurids of similar morphology that preserve comparable elements (for the full list of specimens, see Table 2): *Hamadasuchus rebouli* Buffetaut, 1994 (Larsson & Sues 2007); *Montealtosuchus arrudacamposi* Carvalho *et al.*, 2007; *Uberabasuchus terrificus* Carvalho *et al.*, 2004, which will be treated here as such although it might be a junior

synonym of *Peirosaurus tormini* Price, 1955; *Pepesuchus deiseae* Campos *et al.*, 2011 (Geroto & Bertini 2019); *Itasuchus jesuinoi* Price, 1955; *Patagosuchus anielensis* Lio *et al.*, 2016; *Bayomesasuchus hernandezi* Barrios *et al.*, 2016; *Gasparinisuchus peirosauroides* Martinelli *et al.*, 2012; *Colluhuehuapisuchus lunai* Lamanna *et al.*, 2019; *Barrosasuchus neuquenianus* Coria *et al.*, 2019; *Antaeusuchus taouzensis* Nicholl *et al.*, 2021 and *Kinesuchus overoi* Filippi *et al.*, 2018.

In MNHN-SAM 136 the two dentaries separate dorsally at the level of the seventh dentary alveolus (as in *K. overoi*, *B. neuquenianus*, *G. peirosauroides*, *P. deiseae* and *I. jesuinoi*). The mandibular symphysis extends up to the 12th alveolus, as in *K. overoi* and *A. taouzensis*, whereas it extends only to the 11th alveolus in *H. rebouli*, the 10th alveolus in *B. hernandezi*, *M. arrudacamposi*, *C. lunai* and *P. deiseae*, the ninth alveolus in *P. anielensis* and to the eighth alveolus in *G. peirosauroides* and *B. neuquenianus*. In medial view, the symphyseal region is dorsoventrally shallow and, in dorsal view, it is narrow mediolaterally (as in *B. hernandezi*, *M. arrudacamposi*, *I. jesuinoi*, *H. rebouli* and *K. overoi*).

The first four alveoli are gradually directed anteriorly to anterolaterally and the dentary narrows significantly medially at the level of the 8th/9th alveoli (as in *P. deiseae* and *K. overoi*). In lateral view, the apex of the first wave of enlargement of the tooth row is the large fourth alveolus, whereas the second one is formed by the 12th/13th alveoli, which are also large (as in *B. neuquenianus*, *K. overoi*, *M. arrudacamposi*, *C. lunai*, *A. taouzensis* and *H. rebouli*). The fourth alveolus is not dorsally elevated markedly from the first one (as in *M. arrudacamposi*, *B. neuquenianus*, *K. overoi*, *I. jesuinoi*, *A. taouzensis* and *P. deiseae*). The dorsal and ventral dentary–splenial sutures are directed anteromedially to posterolaterally (V-shaped if both hemi-mandibles were assembled), as in *H. rebouli*, *B. hernandezi*, *K. overoi*, *A. taouzensis* and *P. deiseae*. In posterior view the foramen intermandibularis oralis is displaced laterally, and it thus would have been paired. This is also seen in *A. taouzensis*, and probably in *C. lunai* and *K. overoi*, although the foramen is still close to the splenial symphysis suture in the latter, almost touching it.

The surangular curves dorsally and forms the lateral margin of the articular fossa (as in *B. hernandezi*, *M. arrudacamposi* and *B. neuquenianus*). On the surangular there is a tiny ridge followed by a huge depression that is beneath the level of the articulation surface: this might be for the articulation with the quadratojugal condyle, indicating a double mandibular articulation, as in *M. arrudacamposi*. The lateral surface is not as well preserved as the other parts of the mandible but it bears a prominent posterolateral ridge, as in *B. hernandezi*, *B. neuquenianus* and *U. terrificus*.

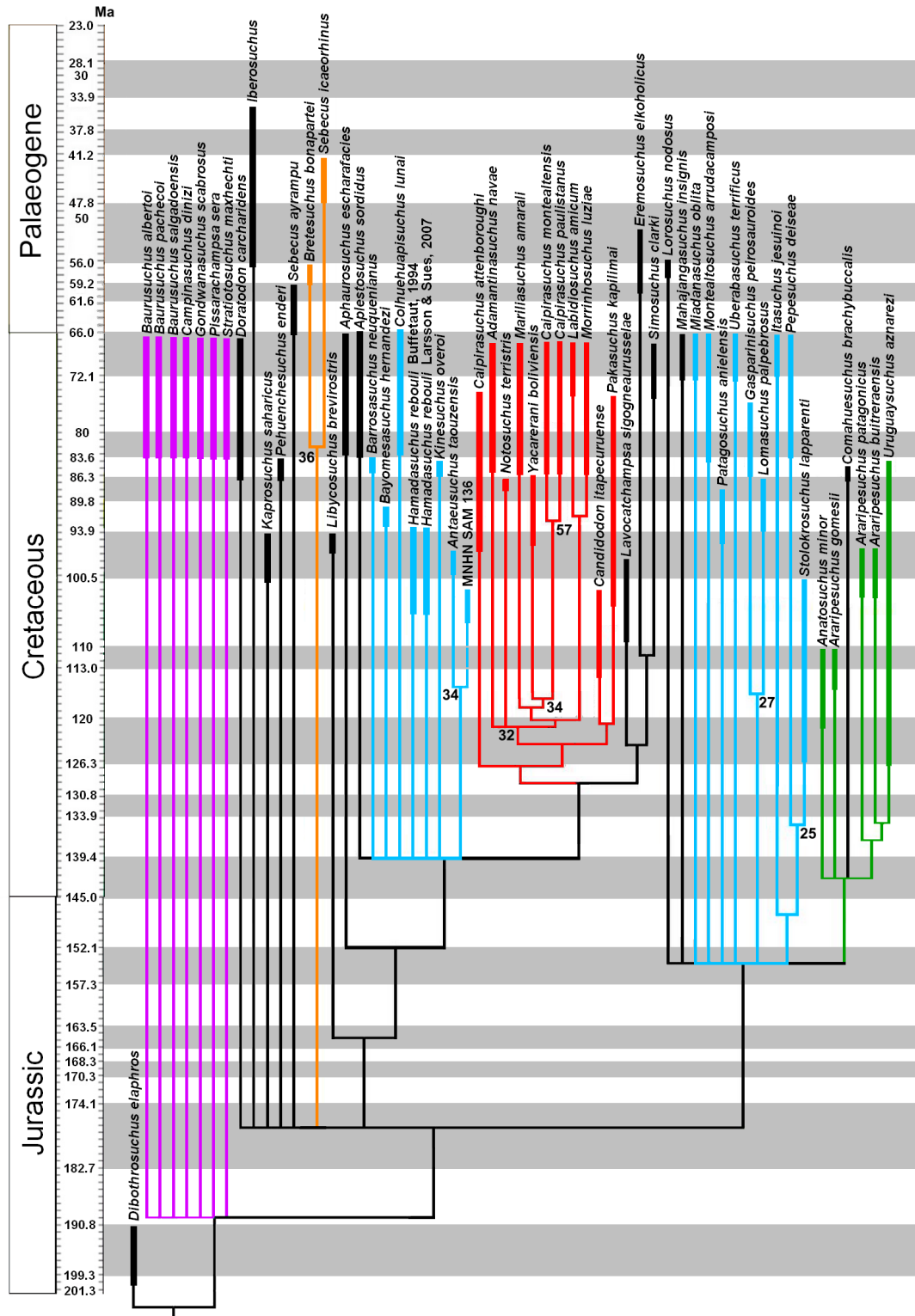


FIG. 6. Time-calibrated phylogenetic tree of the full set of notosuchian taxa sampled here; results obtained using mandibular characters only. Colours represent taxa usually attributed to different clades: purple, Baurusuchidae; orange, Sebecidae; red, Sphagesauridae and ‘advanced’ notosuchians; green, Uruguaysuchidae; blue, Peirosauridae. Bootstrap scores are indicated at nodes when greater than 25%.

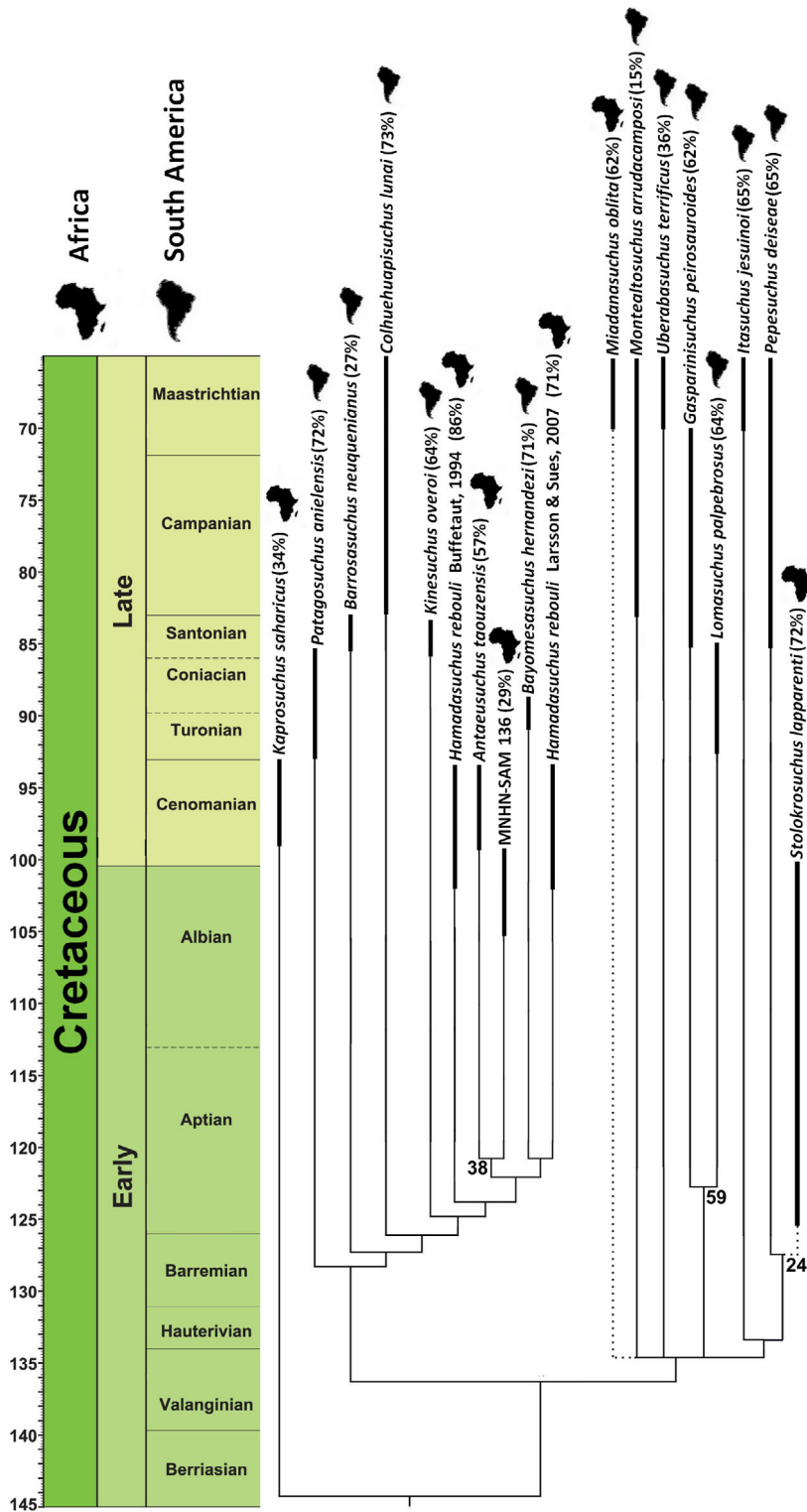


FIG. 7. Time-calibrated phylogenetic tree of the Peirosauridae taxa (*sensu* Geroto & Bertini 2019) sampled here; result obtained using mandibular characters only. Branches with dashed lines indicate taxa that are often retrieved outside Peirosauridae. Bootstrap scores are indicated at nodes when greater than 25%. Silhouettes of South America and Africa indicate the geographical occurrence of each taxon.

TABLE 2. Global mandibular measurements of peirosaurid taxa (in mm).

Taxon	Specimens	Mandibular length*	Mandibular fenestra height	Mandibular fenestra width	Mandibular symphysis width†	References
<i>Hamadasuchus rebouli</i>	ROM 49282	?	?	?	42	Larsson & Sues (2007)
<i>Bayomasuchus hernandezii</i>	MCF PVPH-822	?	?	?	50	Barrios et al. (2016)
<i>Pepesuchus deiseae</i>	MN 7005-V, MCT 1723-R	?	?	?	36	Campos et al. (2011); Geroto & Bertini (2019)
<i>Uberabasuchus terrificus</i>	CPPLIP 630	280	60	20	68	Carvalho et al. (2004)
<i>Montealtosuchus arrudacamposi</i>	MPMA-16-0007-04	220	50	20	57	Carvalho et al. (2007)
<i>Barrosasuchus neuquenianus</i>	MCF-PVPH-413	383	36	9	100	Coria et al. (2019)
<i>Kinesuchus overoi</i>	MAUV-Pv-CO-583	?	?	?	50	Filippi et al. (2018)
<i>Lomasuchus palpebrosus</i>	MOZ 4084 PV	150	?	?	73	Gasparini et al. (1991)
<i>Patagosuchus anielensis</i>	MAÑE-PV 1	?	?	?	60	Lio et al. (2016)
<i>Gasparinisuchus peirosauroides</i>	MOZ 1750 PV	287	?	?	87	Martinelli et al. (2012)
<i>Itasuchus jesuinoi</i>	DGM-434-R	?	?	?	78	Price (1955)
<i>Collhuehuapisuchus lunai</i>	UNPSJB-PV 961	?	?	?	69	Lamanna et al. (2019)
<i>Hamadasuchus rebouli</i>	MNHN-SAM 136	460	100	45	90	This study
<i>Antaeusuchus taouzensis</i>	NHMUK PV R36829	?	?	?	87	Nicholl et al. (2021)

*Distance between the extremities of the articular and the dentary.

†Distance between the lateral extremities of the mandible at the posterior margin of the mandibular symphysis.

Following this comparison and the phylogenetic analysis, MNHN-SAM 136 can be attributed confidently to Peirosauridae *sensu* Geroto & Bertini (2019).

Taxonomic content of North African peirosaurids

In the Cretaceous of North Africa, a peirosaurid taxon of interest is *Hamadasuchus rebouli*. It was originally described by Buffetaut (1994) on the basis of a left anterior part of a dentary (MDE C001; Fig. 8C, D) from the upper Albian to Cenomanian of the Kem Kem Group, Morocco, as a crocodylomorph with at least 15 closely separated alveoli in the dentary. The fourth alveolus is described as huge and the four alveoli posterior to it are small. The teeth posterior to the eighth one are tall, laterally compressed and with denticles on the mesiodistal carinae. Finally, the symphysis between the dentaries reaches the posterior margin of the seventh alveolus.

Other specimens were then described and attributed to *Hamadasuchus rebouli* by Larsson & Sues (2007) on the basis of a complete skull as well as several skull fragments and another left anterior part of a mandible that has more than 15 closely spaced alveoli in the dentary (ROM

49282; Fig. 8G, H). They also come from the Albian–Cenomanian Kem Kem Group of Morocco. Here, the fourth dentary alveolus is the biggest and the four alveoli behind it (at least) are small. Behind the eighth alveolus, only the 13th tooth is preserved and it is laterally compressed. However, the symphysis between the dentaries reaches only the posterior margin of the fifth alveolus. Two other dentaries were mentioned (ROM 52045 and ROM 52047) but were not illustrated.

Of particular interest, another associated skull with a mandible in connection from the Kem Kem Group was briefly illustrated (BSPG 2005 I 83) and attributed to *Hamadasuchus* by Rauhut & Lopez-Arbarello (2005), but awaits a comprehensive description with most of the anatomy of the mandible remaining unknown.

Recently, in their review of the fauna from the Kem Kem Group of Morocco, Ibrahim et al. (2020) illustrated two other mandibular symphyses that they also assigned to *H. rebouli*: MNHN-MRS 3110 (Fig. 8E, F) and NMC 41784 (Fig. 8I, J). However, these authors specify that the current *Hamadasuchus* diagnosis should be refined with the complete description of the skull (BSPG 2005 I 83) illustrated by Rauhut & Lopez-Arbarello (2005). In both cases, the dentaries are broken off before the 15th

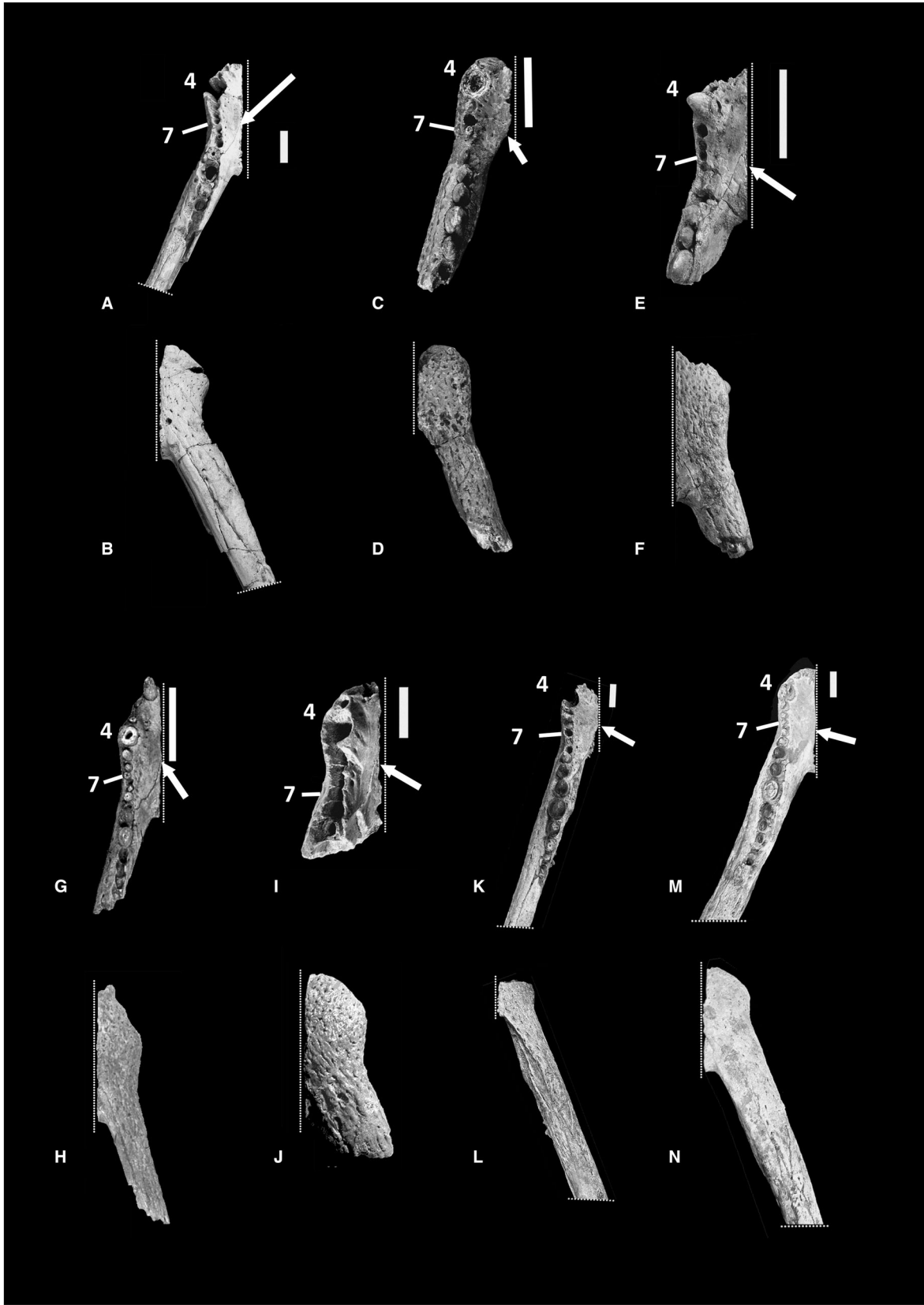


FIG. 8. Comparisons of anterior parts of peirosaurid mandibles. A–B, MNHN-SAM 136 in: A, dorsal; B, ventral view. C–D, MDE C001 in: C, dorsal; D, ventral view. E–F, MNHN-MRS 3110 in: E, dorsal; F, ventral view. G–H, ROM 49282 in: G, dorsal; H, ventral view. I–J, NMC 41784 in: I, dorsal; J, ventral view. K–L, NHMUK PV R36874 in: K, dorsal; L, ventral view. M–N, NHMUK PV R36829 in: M, dorsal; N, ventral view. Numbers indicate respective alveoli. Arrows indicate the suture between the dentary and the splenial in the symphysis. Scale bars represent 3 cm.

alveolus, but the alveoli are closely spaced. The fourth alveolus is the largest in each specimen, however, the four alveoli behind it are small only in MNHN-MRS 3110, not in NMC 41784. In MNHN-MRS 3110, the teeth behind the eighth one are tall and laterally compressed. In MNHN-MRS 3110 the dentary symphysis reaches and completely includes the 7th–8th alveolus (depending on the viewing angle), however, it reaches and completely includes only the 5th–6th alveolus in NMC 41784 (also depending on the viewing angle).

Finally, another peirosaurid taxon from the Cretaceous Kem Kem Group of Morocco, North Africa, was recently erected by Nicholl *et al.* (2021): *Antaeusuchus taouzensis*. This taxon closely resembles the *Hamadasuchus rebouli* holotype mandible and MNHN-SAM 136 but it also differs from them by the following traits: wide divergence angle of the mandibular rami (40–45°); relatively unornamented surface texture of dentary adorned with narrow, shallow ridges; rugose tooth enamel formed by anastomosing grooves and ridges. Two specimens were described: NHMUK PV R36829 (Fig. 8M, N) and NHMUK PV R36874 (Fig. 8K, L). Both have more than 15 alveoli in the dentary, as well as a large fourth alveolus with four small alveoli following posteriorly. In both specimens the teeth posterior to the eighth are tall, laterally compressed and possess denticles. In NHMUK PV R36829 the dentary symphysis reaches the 7th–8th alveolus, whereas it reaches only the 5th–6th one in NHMUK PV R36874. Nicholl *et al.* (2021) also mention that the material described in Larsson & Sues (2007) differs from the type specimen (MDE C001; Buffetaut 1994) and they would assign it to another taxon. However, they justifiably refrained from doing so pending a complete description of BSPG 2005 I 83 (Rauhut & Lopez-Arbarelo 2005).

All of those mandibular characters thus do vary and are summarized in Table 3. Can these anatomical traits concerning the mandible be considered as diagnostic of different taxa or could they be due only to different ontogenetic stages? To assess this, we used ontogenetic series of extant crocodylians, representing different morphotypes (*Alligator mississippiensis*, *Caiman crocodilus*, *Caiman latirostris*, *Gavialis gangeticus*, *Mecistops* sp., *Osteolaemus tetraspis* and *Tomistoma schlegelii*; Table S1 and Figs S1–S3). The total number of alveoli completely involved in the mandibular symphysis as well as the

number of alveoli completely involved in the dentary part of the mandibular symphysis in dorsal view, do not vary throughout the different ontogenetic stages (apart from one specimen of *A. mississippiensis* and one specimen of *O. tetraspis*, showing a variation of only one alveolus). The number of alveoli involved in the ventral extension of the splenial part of the mandibular symphysis does not vary ontogenetically (apart from one alveolus in a specimen of *G. gangeticus*). Finally, the lateral constriction of the dentary at the level of the 6th–10th dentary alveoli does not vary ontogenetically, but this is more subject to caution given that a constriction was not observed in all of the examined specimens of Crocodylia. In contrast, the total number of mandibular alveoli, the number of mandibular alveoli after which the alveoli become confluent, the largest alveolus after the fourth one and the angle of divergence of the mandibular rami do vary significantly throughout ontogeny and we thus recommend against their use as systematic and/or phylogenetic characters. Moreover, it should be stressed that fossil species are represented by a handful of specimens and that ontogenetic series cannot be understood yet. However, these data provide important information that should be considered in future taxonomic studies of mandibular remains in the context of Crocodylomorpha.

As such, following the original diagnosis of Buffetaut (1994), the specimen ROM 49282 cannot be attributed to *H. rebouli* confidently because it has only five alveoli completely involved in the dentary part of the mandibular symphysis rather than seven +/- one. The other (mostly cranial) specimens described by Larsson & Sues (2007) also cannot be attributed to *H. rebouli* because no skull fragment is linked with a mandible. As suggested by Cavin *et al.* (2010), Ibrahim *et al.* (2020) and Nicholl *et al.* (2021), the specimens assigned to *H. rebouli* until now probably belong to at least two different taxa based on mandibular characters. One group would be composed of MDE C001, MNHN-SAM 136 and MNHN-MRS 3110 and another group of ROM 49282 (and probably subsequent material) and NMC 41784, the main point of divergence being the number of alveoli completely involved in the dentary part of the mandibular symphysis. However, we are aware that this hypothesis could be reinforced by diverging cranial or postcranial characters as well. That is why we refrain (for now) from creating a new taxon for the specimens that we here exclude from *H. rebouli*. This is pending

TABLE 3. Specific mandibular characters of specimens close to or assigned to *Hamadasuchus rebouli*.

Specimen	MNHN-SAM 136	<i>Hamadasuchus rebouli sensu</i> Buffetaut, 1994; MDE C001	MNHN-MRS 3110	<i>Hamadasuchus rebouli sensu</i> Larsson & Sues, 2007; ROM 49282	NMC 41784	<i>Antaeusuchus taouzensis</i> NHMUK PV R36829	<i>Antaeusuchus taouzensis</i> NHMUK PV R36874
Reference	This study	Buffetaut (1994)	Ibrahim <i>et al.</i> (2020)	Larsson & Sues (2007)	Ibrahim <i>et al.</i> (2020)	Nicholl <i>et al.</i> (2021)	Nicholl <i>et al.</i> (2021)
Number of alveoli completely involved in the mandibular symphysis	11	?	10/11?	11	?	11	?
Number of alveoli completely involved in the dentary part of the mandibular symphysis in dorsal view	7	7	7	5	5	8	5
Number of alveoli completely involved in the splenial part of the mandibular symphysis in ventral view	3	?	3 / 4?	4	2/3?	3	?
Number of mandibular alveoli	17	?	?	17	?	18	18
Lateral constriction of the dentary at the level of the 6th–10th alveoli	Marked (but may be due to deformation)	Minor	Minor	Minor	Minor	Minor	Minor
Number of mandibular alveoli after which the alveoli become confluent	4	4	5	5	3	10	4
Angle of divergence of mandibular rami (°)	40	26?		29		44	43
Largest alveolus after the 4th one	12	12	?	12/13	?	13	13

a complete description and reassessment of BSPG 2005 I 83, which is the only fossil known in which the mandible is linked to the skull, and would thus enable cranial characters to be linked to the diagnosis of *H. rebouli* (or create a new species of *Hamadasuchus*). One must thus keep in mind that skull parts referred to *H. rebouli* (ROM 52620 for example) cannot be referred to this taxon for now, but they could be in the future.

Concerning the taxonomic status of the two specimens attributed to *Antaeosuchus*, we agree with Nicholl *et al.* (2021) in distinguishing NHMUK PV R36829 from all other specimens discussed above as another taxon, but based solely on the peculiar ornamentation of the dentary and the structure of the tooth enamel (although both characters may be subject to mechanical abrasion). The mandibular angle proposed as diagnostic is most probably ontogenetic in nature. However, the attribution to a new genus is open to debate, given all of the other characteristics that make this taxon close to the holotype mandible and all of the now referred specimens of *H. rebouli*. We would rather interpret this taxon that is composed solely of NHMUK PV R36829 as another species of *Hamadasuchus* and have adapted the emended diagnosis of the genus accordingly. Concerning the second specimen (NHMUK PV R36874), although it also has the peculiar ornamentation of the dentary and the structure of the tooth enamel seen in NHMUK PV R36829, the number of alveoli completely involved in the dentary part of the mandibular symphysis is significantly smaller (5–6 depending on the viewing angle) than in NHMUK PV R36829 (7–8 depending on the viewing angle). This is a crucial difference and makes NHMUK PV R36874 more closely related to some specimens referred to *Hamadasuchus* (ROM 49282 and NMC 41784). As a result, we are casting doubt on the current taxonomic attribution of this specimen, which will hopefully be clarified in future studies.

As for MNHN-SAM 136, the combination of the following characters link this specimen with confidence to the genus *Hamadasuchus*: at least 15 dentary alveoli; all alveoli are very close-set; four very small alveoli posterior to the large fourth alveolus; posterior dentary alveoli visible in lateral view; two waves of enlarged dentary teeth; 11 completely involved alveoli in the mandibular symphysis; symphyseal region shallow dorsoventrally and narrow mediolaterally; dorsal and ventral dentary–splenial sutures directed anteromedially to posterolaterally (V-shaped if both hemi-mandibles were assembled); ventrolateral dentary surface anterior to mandibular fenestra transversely compressed; dentary extends posteriorly beneath the mandibular fenestra; anterior alveoli of dentary procumbent; concavity for the reception of the enlarged maxillary tooth lateral to the seventh alveolus of the dentary; surangular overlaps dentary above the mandibular fenestra (see

revised diagnosis, as well as support from the phylogenetic analyses). Certainly, we observe little morphological differences between the type specimen and the specimen from La Gara Samani. Nevertheless, the type specimen is of very limited completeness, hence we refer MNHN-SAM 136 to *Hamadasuchus cf. rebouli*.

Palaeobiogeography and methodological implications

During the Cretaceous the Gondwanan landmass separated, and the South Atlantic Ocean formed (Granot & Dymont 2015). The two future continents (South America and Africa) were still connected at least until the late Aptian, as highlighted by studies on other crocodylomorphs genera: *Araripesuchus* and *Sarcosuchus* (Buffetaut & Taquet 1977; Ortega *et al.* 2000) and then separated, effectively creating a vicariance effect (Turner 2004). As seen in the phylogenetic results, the peirosaurid taxa studied here form two different groups (Fig. 7). However, these two groups do not represent a geographical separation, suggesting a Gondwanan distribution of peirosaurids during the Cretaceous (Sertich & O'Connor 2014; Barrios *et al.* 2016), which will of course need to be confirmed by more detailed studies involving cranial remains as well.

Terrestrial taxa (like peirosaurids) are of particular interest when studying those hypotheses because they are constrained by land, and thus in theory cannot disperse in water, rendering biogeographic assumptions stronger. Another interesting question resulting from this relates to the origin of peirosaurids: this clade would seem to have originated in Africa, given that the oldest known fossils come from this continent (Larsson & Gado 2000; this study). However, although there is a continental fossil record from the Lower Cretaceous in South America (Gallina *et al.* 2014), the absence of peirosaurid specimens in these strata does not mean that the clade did not originate on that continent (for example, *Amargasuchus minor* Chiappe, 1988 could very well be a South American peirosaurid from the Hauterivian). Furthermore, the repartition of notosuchian taxa has also been shown to be related to climate (Carvalho *et al.* 2010). This question must thus remain open and will hopefully be answered in future studies.

We have also shown that, for Peirosauridae, mandibular characters bear a phylogenetic signal on their own and are important for better resolution of phylogenetic relationships. Thus, they are of interest when studying the relationships of groups for which the remains are fragmentary. As a result, we were able here to assess the phylogenetic relationships of some poorly known taxa, such as *K. overoi*, *P. anielensis* or *C. lunai*. However, as can be seen on the full Crocodylomorpha analysis, the results

should be taken with caution, given that some groups are retrieved in unexpected positions, and it is also probably linked to our character sampling: cranial characters remain important and must be included with the mandibular and postcranial characters when looking at such a large-scale taxonomic sample. Furthermore, the study of ontogenetic series of extant specimens has enabled us to validate some characters for use in taxonomic/phylogenetic work while invalidating others (Table S1; Figs S1–S3). This is very important and should be widened whenever possible when dealing with fragmentary fossil remains that still have close extant representatives.

Taphonomy and palaeoenvironmental implications

The external surface of MNHN-SAM 136 preserves at least seven instances of traces of bioerosion characterized by shallow gouges affecting the surface of the cortical bone (Fig. 5B–H). These structures are straight to ovoid and centimetric in size. They can be attributed to dermestid traces and imply arid conditions with pupae developing on drying carcasses (Höpner & Bertling 2017). Given that these structures occur only in fresh bone that was adjacent to dried tissues, they imply an absence of water of several weeks or months, which allows the development of such larvae (Martin & West 1995). The subsequent erosion of the bone occurs after the infestation and removes the surface containing the pupation chamber, which explains those hollowed-out structures. These observations are consistent with a hot environment (Russell & Paesler 2003; Holz 2015), albeit with access to water (presence of aquatic taxa; de Lapparent de Broin *et al.* 1971; Busson & Cornée 1991; de Lapparent de Broin 2002; Meunier & Larsson 2017).

CONCLUSION

A new peirosaurid mandibular ramus (MNHN-SAM 136) from the Albian–Cenomanian of North Africa is described and compared with other closely related taxa. It is referable to *Hamadasuchus* cf. *rebouli*, of which an emended diagnosis is proposed, on the basis of the unique combination of several mandibular characters. The taxonomic content of this taxon is reviewed and, using ontogenetic series of extant crocodylians, we propose some mandibular characters as suitable for taxonomic differentiation between specimens, whereas we argue against the use of others. As a result, several specimens currently attributed to *H. rebouli* are not congruent with the holotype mandible and probably represent a new peirosaurid taxon from the Cretaceous of North Africa. This will be confirmed by the future study of cranial

remains attributable to *Hamadasuchus* and the erection of a new taxon if necessary. Based on these considerations, we studied the phylogenetic relationships of MNHN-SAM 136 using a mandibular character-only matrix. We found that those data bear a phylogenetic signal and are of particular interest in the case of a group mainly composed of taxa defined on fragmentary mandibular remains, clustering the fossil studied here with *Hamadasuchus rebouli sensu* Buffetaut (1994).

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DATA ARCHIVING STATEMENT

Data for this study (including 3D surface models of MNHN-SAM 136) are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.prr4xgxp4>) and MorphoBank (<http://morphobank.org/permalink?P4104>).

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1002/spp2.1485>):

Appendix S1. Character list and taxonomic sample.

Appendix S2. Phylogenetic matrix (TNT format; see also Pochat-Cottilloux *et al.* 2023b).

Appendix S3. Phylogenetic analysis.

Table S1. Mandibular characters on ontogenetic series of extant crocodylians.

Figure S1. An example of the variation (or not) of mandibular characters in an ontogenetic series of *Caiman latirostris*.

Figure S2. An example of the variation (or not) of mandibular characters in an ontogenetic series of *Alligator mississippiensis*.

Figure S3. An example of the variation (or not) of mandibular characters in an ontogenetic series of *Mecistops*.

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