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Systematic revision of *Sarcosuchus hartti* (Crocodyliformes) from the Recôncavo Basin (Early Cretaceous) of Bahia, north-eastern Brazil

RAFAEL G. SOUZA[1*], RODRIGO G. FIGUEIREDO[2], SÉRGIO A. K. AZEVEDO[3], DOUGLAS RIFF[4] and ALEXANDER W. A. KELLNER[1]

[1]*Laboratório de Sistemática e Tafonomia de Vertebrados Fósseis, Setor de Paleovertebrados, Departamento de Geologia e Paleontologia, Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista s/n, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brazil*
[2]*Departamento de Biologia, Universidade Federal do Espírito Santo, Alto Universitário s/n, Guararema, 29500-000, Alegre, ES, Brazil*
[3]*Laboratório de Processamento de Imagem Digital, Setor de Paleovertebrados, Departamento de Geologia e Paleontologia, Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista s/n, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brazil*
[4]*Laboratório de Paleontologia, Instituto de Biologia, Universidade Federal de Uberlândia, Rua Ceará s/n, Umuarama, 38400-902, Uberlândia, MG, Brazil*

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Sarcosuchus hartti was a top predator that inhabited the fluvial and coastal areas of north-eastern Brazil during the Early Cretaceous. Several fossil remains were recovered during the late 19th and early 20th centuries from strata that outcrop in the Recôncavo Basin in the state of Bahia. A re-analysis of this material shows that *S. hartti* is a valid species. The Brazilian taxon differs from the African *Sarcosuchus imperator* in the unique pattern of anastomosing ornamentation observed on the enamel surface. The inclusion of *S. hartti* in a novel phylogenetic analysis recovered it inside Tethysuchia, a large clade comprising South and North American pholidosaurids along Elosuchidae and Dyrosauridae. The evolutionary origin of *Sarcosuchus* is likely related to a cladogenesis event that resulted from the break-up of Gondwana.

ADDITIONAL KEYWORDS: Gondwana – Neosuchia – Recôncavo Basin.

INTRODUCTION

Tethysuchians are aquatic crocodyliforms that occurred in both fluvial and marine environments (e.g. Buffetaut & Hutt, 1980), which are usually characterized by a long and tubular rostrum with a large number of teeth (e.g. Wu *et al.*, 2001; Barbosa *et al.*, 2008; Fortier *et al.*, 2011). Most of the clade occured during the Mesozoic, but with dyrosaurids surviving to the end of the Cretaceous mass-extinction event and being recovered from Palaeocene to Eocene rocks (e.g. Buffetaut, 1976, 1978, 1982; Jouve, 2005, 2007; Jouve *et al.*, 2005a, b, 2006, 2008; Barbosa *et al.*, 2008; Hill *et al.*, 2008; Hastings *et al.*, 2010, 2014). In terms of geographical distribution, species have been recovered from formations in Africa (e.g. de Broin & Taquet, 1966), Asia (e.g. Martin *et al.*, 2013), Europe (e.g. Buffetaut & Hutt, 1980; Hua *et al.*, 2007), North America (e.g. Wu *et al.*, 2001) and South America (e.g. Marsh, 1869; Barbosa *et al.*, 2008; Fortier *et al.*, 2011).

TAXONOMIC HISTORY

The best known genus of Tethysuchia is *Sarcosuchus*, the giant crocodylian dubbed ‘supercroc’ in popular science (Sloam, 2002), and counts two species: the African *S. imperator* de Broin & Taquet, 1966 and the South American *S. hartti* (Marsh, 1869). *Sarcosuchus hartti* has a history dating back to the 1860s, when several vertebrate fossil remains were recovered

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*Corresponding author. E-mail: rafelsouz@gmail.com

from Early Cretaceous rocks in the state of Bahia, Brazil. One of the earliest discoveries was made by Mr Samuel Allport, who reported the presence of fossils in the localities of Fort Mont Serrat and Plataforma, both within the city limits of Salvador (Allport, 1860). Naturalists Louis Agassiz and Charles F. Hartt coordinated the Thayer Expedition (1864–65), which led to the discovery of more fossils from new localities in Bahia. Marsh (1869) studied those remains and named two reptilian species based on some isolated teeth. The features that Marsh (1869) used to diagnose the new species followed the teeth morphotypes originally proposed by Allport (1860). The first morphotype comprises teeth with strong and continuous striae and 'coarse riblets' (Allport, 1860: pl. XV, fig. 5; pl. XVI, figs 4, 6–8). These teeth were assigned to *Thoracosaurus bahiensis* Marsh, 1869. However, this species is now considered a *nomen dubium* (Souza *et al.*, 2015). A second morphotype comprising teeth with a 'delicate wrinkled surface' (Allport, 1860: pl. XVI, figs 1–3, 5) was regarded as belonging to *Crocodylus hartti* Marsh, 1869.

Mawson & Woodward (1907) described new specimens that were collected by Mawson during several years of field work in Bahia. This material was deposited in the 'Mawson collection' in the British Museum of Natural History, London. In this same study the authors assigned a large lower jaw (BMNH R3423), a dorsal osteoderm (BMNH R3224) and two teeth (BMNH R3079, BMNH R2983) to *Crocodylus hartti* and allocated the species to the genus *Goniopholis* based on the presence of a peg on the dorsal osteoderm (Mawson & Woodward, 1907). Buffetaut & Taquet (1977) revisited this material and pointed out their affinities with the African genus *Sarcosuchus*. Their decision was based on features like the presence of a long mandibular symphysis (unlike *Goniopholis*), the spatulated shape of the anterior extremity of the mandible, the smaller dentary alveoli being the first and the second ones, while the larger ones are the third and the fourth, the presence of coarse ornamentation of the ventral surface of the dentary bone and teeth that bear fine sinuous wrinkles. Buffetaut & Taquet (1977) also observed the presence of a peg on dorsal osteoderms, which is a characteristic shared with *Goniopholis*, but not restricted to it. However, the absence of well-defined autapomorphies and characters that clearly distinguishes the type specimens of both *Sarcosuchus* species was noted by them, indicating that they could be potentially synonymized. This latter approach was followed by, Turner & Buckley (2008), Pol *et al.* (2009), Fortier *et al.* (2011), Martin *et al.* (2013, 2016) and Young *et al.* (2017) without further discussions (*contra* Andrade *et al.*, 2011, which considered them as two distinct species).

In the present paper we describe new specimens of *S. hartti* from Bahia and discuss the systematic status of the genus *Sarcosuchus*, showing that the Brazilian species belongs to this genus, but differs from the African one.

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York; BMNH, Natural History Museum, London; CAS, Sirindhorn Museum, Kalasin Province, Sahatsakhan, Thailand; DMR, Department of Mineral Resources, Bangkok, Thailand; MCT, Museu de Ciências da Terra, CPRM – Serviço Geológico do Brasil, Rio de Janeiro; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; MN, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro; ONM, Museu of Geology, Office National des Mines, Tunisia; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow; PRC, Palaeontological Research and Education Centre, Mahasarakham University, Thailand; SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas; TF, Texas Memorial Museum, University of Texas, Texas; YPM, Yale Peabody Museum, Yale University, New Haven.

GEOLOGY

The first specimens assigned to *Sarcosuchus hartti* were collected at Fort Mont Serrat and Plataforma (BMNH R 3079) with additional material from Setúbal (BMNH R 3224, BMNH R 3423), Itacaranha (BMNH R 3079) and Aratu (MN 7459-V, MN 7460-V, MN 7461-V). Today, all localities lie within the city limits of Salvador (Fig. 1). The outcrops comprise a succession of conglomerates, sandstones and high fossiliferous shales (see further information in: Allport, 1860; Fig. 2).

The era inferred for those outcrops is the Lower Cretaceous (Allport, 1860; Mawson & Woodward, 1907). Buffetaut & Taquet (1977) suggested an age slightly older than Aptian, based on the similarities between fossils from the Recôncavo, Gabon and Tegama basins. Andrade *et al.* (2011) referred the specimens described by Mawson & Woodward (1907) as coming from the Aptian–Albian Ilhas Formation of the Recôncavo Basin. However, some authors elevated the Ilhas Formation to Ilhas Group and proposed the older age of Late Barresian to Early Valaginian, based on the study of microfossils (Viana *et al.*, 1971; for a more complete historical and geological perspective of the Ilhas Group and the Recôncavo Basin, see: Lima *et al.*, 1981).

The outcrops presented by Allport (1860) and Mawson & Woodward (1907) are attributed by Rodrigues & Kellner (2010) to the Recôncavo Basin, Bahia Supergroup. The succession of conglomerates, sandstones and shales observed in those outcrops suggest that they are part of prograding deltaic rocks of the Ilhas Group, within the Bahia Supergroup (Souza *et al.*, 2015). They comprise the Sequence K30 of the Rift Supersequence and, therefore, they would have a Late Hauterivian to Early Barremian age (Silva *et al.*, 2000, 2007). However, the high urbanization, together with the poorly refined stratigraphy of the outcrops in this region, make a confident positioning of the fossil and the establishment of their age difficult. Further studies on the stratigraphy and geology of those outcrops are in need.

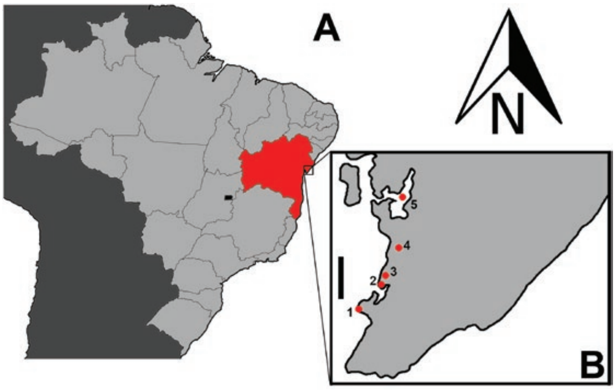

Figure 1. Map showing the fossil localities of *Sarcosuchus hartii*. A, Brazil (light grey) and Bahia State (red). B, Recôncavo baiano region. Red dots show the localities where the studied fossil were collected: 1, Fort Mont Serrat (BMNH R 3079); 2, Plataforma (BMNH R 3079); 3, Itacaranha (BMNH R 3079); 4, Setúbal (BMNH R 3224, BMNH R 3423); 5, Aratu (MN 7459-V, MN 7460-V, MN 7461-V). The black box delimitates the area in B where light grey represents the landmasses and white the sea. Scale bar: 6 km.

MATERIAL AND METHODS

SPECIMENS AND SPECIES

The most relevant specimens attributed to *Sarcosuchus hartti* are revised, which include the supposed holotype material (YPM 516, *sensu* Norell & Storrs, 1989) and the specimens referred to by Mawson & Woodward (1907), consisting of a large-sized and incomplete mandible with some preserved teeth (BMNH R3423), a fragment of a right mandibular ramus with a few cross-sectioned teeth bases inside the alveoli (MN 7459-V), three isolated teeth crowns with anastomosed enamel (BMNH R 3079, MN 7460-V, MN 7461-V) and a single broken osteoderm from the right side of the dorsal dermal shield (BMNH R3224). The new specimens described here are a partially preserved jaw (MN 7459-V) and two associated teeth (MN 7460-V and MN 7461-V) housed at the palaeovertebrate collection of the Museu Nacional, Universidade Federal do Rio de Janeiro (MN/UFRJ), Brazil. These fossils were collected by Mr Roberto Tinoco at the locality of Aratu and donated to the museum in the 1980s. Dr Fausto L. S. Cunha was one of the museum palaeontologists at the time and received the specimens together with photographs of the outcrops (Fig. 2), but no precise geographic and stratigraphic information on those fossils was recorded. On 2 September 2018, the main buildings of Museu Nacional, including the palaeontological collections, were caught in a devastating fire leading

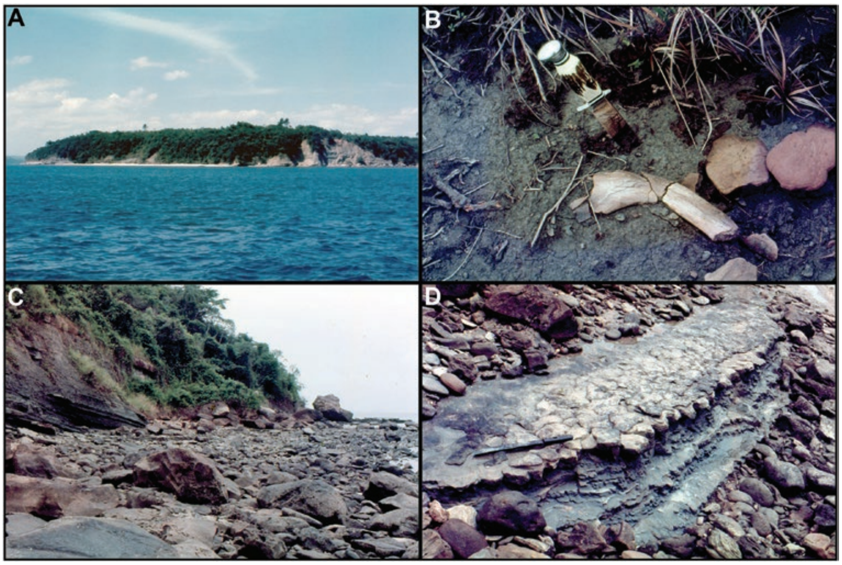

Figure 2. Aratu locality (Bahia) in the 1970s. A, an unspecified view of Aratu Bay. B, fossil fragments. C, outcrops (left) and Aratu bay at the horizon (right corner). D, an unspecified outcrop of the Recôncavo Basin. All pictures by Roberto Tinoco.

Table 1. List of species and its specimens used on anatomical comparisons. The species column will present the species name and its author while the specimens and references column provide the list of specimens and references consulted regarding each species

Species	Specimens and reference
Chalawan thailandicus (Buffetaut & Ingavat, 1980)	CAS42-20 (formerly TF 1370) from Buffetaut & Ingavat (1980); Buffetaut & Ingavat (1984); PRC102-143 from Martin *et al.* (2013)
Elosuchus cherifiensis (Lavocat, 1955)	de Broin, 2002; Meunier & Larsson, 2016
Fortignathus felixi (de Broin, 2002)	de Broin (2002); Young *et al.* (2017)
Meridiosaurus vallisparadisi Mones, 1980	Fortier *et al.* (2011)
Oceanosuchus boecensis Hua *et al.*, 2007	Hua *et al.* (2007)
Pholidosaurus purbeckensis (Mansel-Pleydell, 1888)	Martin *et al.* (2016)
Sarcosuchus imperator de Broin & Taquet, 1966	de Broin & Taquet (1966); Sereno *et al.* (2001)
Sarcosuchus hartti (Marsh, 1869)	YPM 516; BMNH R3423; BMNH R 3079; BMNH R3224; MN 7459-V; MN 7460-V, MN 7461-V; Allport (1860); Marsh (1869); Mawson & Woodward (1907); Buffetaut & Taquet (1977); Norell & Storrs (1989)
Sunosuchus junggariensis Wu *et al.*, 1996	Wu *et al.* (1996)
Sunosuchus miaoi Young, 1948	Young (1948)
Sunosuchus phuwiangensis (Buffetaut & Ingavat, 1983)	Buffetaut & Ingavat (1983)
Sunosuchus shartegensis Efimov, 1988	PIN 4174-1 from Halliday *et al.* (2015)
Terminonaris robusta Mook, 1934	Wu *et al.* (2001); SMU 76590 from Adams *et al.* (2011)
Turanosuchus aralensis Efimov, 1988	Halliday *et al.* (2015)

to the destruction of the museum. Despite the efforts of the rescue team, the materials MN 7459-V, MN 7460-V and MN 7461-V remain lost. We here document these specimens, based on measurements before the fire, in case they are found in the future. The new specimens are compared with comparable material of other crocodyliform species. The species and its specimens are summarized in Table 1.

PHYLOGENETIC ANALYSIS

A new data matrix is compiled to infer the phylogenetic relationships of *Sarcosuchus hartti*. The complete dataset includes 50 ingroup taxa, all neosuchian species, and one outgroup species, a notosuchian. The present work considers Thalattosuchia as a non-neosuchian clade and hence they were not included in the analysis (e.g. Young & Andrade, 2009; Parrilla-Bel *et al.*, 2013; Wilberg, 2015). Character sampling was based on previously published papers with the addition of one novel character (see Supporting Information, Supplementary Information 1). A nexus file was created using MESQUITE v.3.03 (Maddison & Maddison, 2015). The analysis was performed under parsimony with heuristic search algorithms on Tree analysis using New Technology – TNT v. 1.5 (Goloboff & Catalano, 2016). A Traditional Search was conducted with starting random seeds set at zero and performing 5000 replicates of Wagner trees (using random additional sequences) followed by TBR branch swapping (holding ten trees per replicate). Zero-length branches were collapsed (*sensu* Coddington & Scharff, 1994). All characters were left 'unweighted', and 'multistate' characters were treated as unordered. A strict consensus tree was obtained with the command Strict Consensus (Nelsen). The consistence index (CI) and retention index (RI) were calculated using the TNT script 'stats.run'. More details about the parameters used in the analysis are present in Supporting Information, Supplementary Information.

RESULTS

SYSTEMATICS

CROCODYLOMORPHA WALKER, 1970

CROCODYLIFORMES HAY, 1930 (*SENSU* CLARK IN BENTON & CLARK, 1988)

NEOSUCHIA BENTON & CLARK, 1988

TETHYSUCHIA BUFFETAUT 1982 (*SENSU* ANDRADE *ET AL.*, 2011)

TETHYSUCHOIDEA NEW CLADE

Definition: Stem-based on all species that share a more recent common ancestor with *Meridiosaurus valliparadisi* and *Dyrosaurus phosphaticus* than to *Pholidosaurus purbeckensis*.

Diagnosis: Posterodorsal process of premaxilla extends anterior to the third maxillary alveolous (Char. 53: 1 -> 0); the ventral margins of premaxilla and maxilla are at the same level (Char. 56: 2 -> 1); occlusion pits for the first dentary teeth at the palatal surface of premaxilla (Char. 58: 0 -> 1); no lacrimal process beneath the orbits (Char. 85: 1 -> 0); upper temporal bar is oblique (Char. 127: 0 -> 1); pterygoid participates at the posterior, lateral and parts of the anterior margin of the choana (Char. 208: 1 -> 2); and, posterodorsal-directed retroarticular process in lateral view (Char. 241: 1 -> 2).

SARCOSUCHUS DE BROIN & TAQUET, 1966

Type species: Sarcosuchus imperator de Broin & Taquet, 1966

Emended diagnosis for the genus: Sarcosuchus is diagnosed by the following combination of characters: large-sized crocodyliforms with longirostrine snout; mandibles with straight margins in lateral view; flared anterior tip of mandibular symphysis; teeth 1–4 at the anteriormost region of the symphysis; enamel of mid-posterior teeth with many basi-apical low ridges, feeble and set close to each other, poorly anastomosed, with anastomosis stronger apically; premaxillary alveoli are transversally aligned; highly procumbent dentary teeth 1 and 2; confluent dentary alveoli 1 and 2; dentary teeth 3 medial relative to dentary teeth 4; dentary teeth 5 occluding at the premaxilla–maxilla contact. Also, the synapomorphies from the phylogenetic analysis are: the posterior dentition of maxillary and dentary present a weak-developed ridges on the enamel surface (Char. 268: 1 -> 0); the maxilla–dentary anterior dentition has bulbous crown shape (Char. 270: 0 -> 1); the dentary alveoli have a transitional morphology from circular to oval (Char. 272: 0 -> 1); the dentary alveoli 1 and 2 are close to each other (Char. 276: 0 -> 1); and the third dentary alveolus is medial in relation to the fourth (Char. 279: 2 -> 0).

Comments: In the original diagnosis of the genus, de Broin & Taquet (1966: 2328) based it on some general cranial features that today we known to be synapomorphies of more general groups or homoplastic, such as the relation between the orbits and supratemporal fenestrae and the participation of the frontal on the supratemporal fenestrae. Later, Buffetaut & Taquet (1977) provided some potential mandibular features to define *Sarcosuchus*, such as the lateral expansion of the anterior end of the mandible and a general teeth ornamentation description (‘fine sinuous wrinkles’), but still they did not provide a revision or expansion of the diagnosis. However, both features are known to be shared with other crocodyliform genera such as *Chalawan* and *Elosuchus*. The most recent work on *Sarcosuchus* was made by Sereno *et al.* (2001), but no diagnosis was provided for the genus.

SARCOSUCHUS HARTTI (MARSH, 1869)
(FIGS 3–7, 10A)

Basionym: Crocodylus hartti Marsh, 1869.

Synonym: Goniopholis hartti (Marsh, 1869) Mawson & Woodward, 1907.

Lectotype (designated here): YPM 516.

Comments: The syntypes are the teeth listed by Marsh (1869), but he did not present the collection numbers of those teeth and only referred to those described and illustrated by Allport (1860: pl. XVI, figs 1–3, 5). The tooth YPM 516 mistakenly designated as holotype by Norell & Storrs (1989) must be treated as the lectotype and all other teeth studied by Marsh are paralectotypes.

Referred material: A large-sized and incomplete mandible with some preserved teeth (BMNH R3423), a fragment of a right mandibular ramus with a few cross-sectioned teeth bases inside the alveoli (MN 7459-V), three isolated teeth crowns with anastomosing enamel (BMNH R 3079, MN 7460-V, MN 7461-V).

Horizon and locality: The type specimens and referred material were recovered from strata of the Lower Cretaceous Recôncavo Basin, Bahia Supergroup, Ilhas Group (Late Hauterivian–Early Barremian). No further details are available.

Revised diagnosis: Sarcosuchus hartti is diagnosed by the following combination of characters (autapomorphies indicated by *): false ziphodont teeth; heterodont dentition with large and tall anterior caniniforms and circular and blunt posterior teeth; smooth crenulations on both carinae; delicate longitudinal and oblique lines forming an anastomosed enamel surface*; elliptic dentary alveoli; ventral depressed and sculptured area between the mandibular symphysis and the medial alveolar margin*; double festooned mandible with the first concavity being the deeper one and located between the fourth and tenth alveoli, while the second one is shallow and is placed between the 13th and the 21st alveoli*. Based on the phylogenetic inference, two characters are considered autapomorphies in all trees: the dorsal margin of dentary in lateral view is double festooned (Char. 224: 0 -> 4) and the posterior dentitions of maxilla and dentary are elliptical (Char. 265: 1 -> 0).

SARCOSUCHUS SP. (DE BROIN & TAQUET, 1966)

Referred material: A single broken osteoderm from the right side of the dorsal dermal shield (BMNH R3224).

Horizon and locality: Setúbal locality, Lower Cretaceous Recôncavo Basin, Bahia Supergroup, Ilhas Group (Late Hauterivian–Early Barremian) with no more refinements.

TAXONOMIC DECISIONS

There is a common error in the literature about the type specimens of *Sarcosuchus hartti*. Some authors treat the specimen BMNH R3423 described by Mawson & Woodward (1907) as the holotype of this species (e.g. Andrade *et al.*, 2011). Also, Norell & Storrs (1989) designated the specimen YPM 516 as its holotype, which is a single tooth said to be originally studied by Marsh (1869). However, those assignments are not in agreement with the rules of the ICZN (1999). In Marsh's (1869) original description, he did not designate a holotype, nor did he provide the identity of the teeth he studied. He only mentioned the teeth illustrated by Allport (1860) and the teeth collected by Hartt. Therefore, the three teeth from Allport (1860, pl. XVI, figs 1–3, 5) plus the teeth collected by Hartt, must be treated as part of the type series of *Sarcosuchus hartti*. This is the case even with those teeth being lost at the present time, as recommended in articles 72.1.1 and 72.4 of the ICZN (1999). Based on the articles 72.2 and 74 of the ICZN (1999), we propose that the specimen YPM 516 should not be treated as the holotype, but as a lectotype of *Sarcosuchus hartti*. This is justified, because the specimen belongs to the type series of Marsh (1869) and was designated as type material by Norell & Storrs (1989). Also, the remaining specimens of the type series (e.g. Allport's specimens) must be treated as paralectotypes based on articles 72.1.3 and 74.1.3 of the ICZN (1999). The referral of the specimens described by Mawson & Woodward (1907) to *Sarcosuchus hartti*, which were latter discussed by Buffetaut & Taquet (1977), should be regarded with caution, being recognized as referred materials only.

The large tooth BMNH R2983 (Fig. 3B, C), described by Mawson & Woodward (1907), was also referred to *Sarcosuchus hartti*. However, this material has lost all the enamel and, therefore, cannot be properly assignated to this species due to the absence of autapomorphic features; but, based on the overall morphology, this specimen can be considered a crocodyliform.

The discovery of the mandible (BMNH R3423) with *in situ* teeth presenting 'delicate wrinkled surface' suggests that the teeth from Bahia State (Recôncavo Basin) belong to *Sarcosuchus hartti*. Even though the specimen BMNH R3224 (an osteoderm) came from the same locality as the mandible (BMNH R3423), Mawson & Woodward (1907) gave no detailed taphonomic information about this specimen, thus the assignment of the osteoderm to the same species of the other material from Bahia (both the mandible and teeth) is hampered. Therefore, based on the morphological features properly described below, the specimen BMNH R3224 can only be assigned to *Sarcosuchus* sp.

The final Brazilian material referred to *Sarcosuchus* is a procoelous centrum of a dorsal vertebra collected and classified by Owen, which described the reptilian material in Allport (1860), as a 'dinosaurian reptile' with affinities to *Megalosaurus*. Mawson & Woodward (1907) described this material as Megalosauridae. Later it was referred to a 'carnosaur' dinosaur by Buffetaut & Taquet (1977). More recent works suggested, first, that this vertebra could belong to *Sarcosuchus hartti* (Campos & Kellner, 1991), and was further assigned as an indeterminate crocodyliform (Kellner & Campos, 2000). Unfortunately, this specimen is lost and it is, therefore, not certain which crocodyliform species it represents.

FULL DESCRIPTION

Dentition

The teeth illustrated by Allport (1860: pl. XVI, figs 1–3, 5) are described as having a 'delicate wrinkled surface' (not the same used for Theropoda teeth, see: Brusatte *et al.*, 2007). Marsh (1869) complements that description, stating that they show cutting edges and refines Allport's (1860) definition of wrinkles as a peculiar striate pattern that was not seen in other specimens before.

YPM 516 is 70 mm in height with the crown alone comprising 60 mm (Fig. 3A). Only a small portion of the root is preserved. The tooth is almost straight with a very gentle curvature to the lingual face. The enamel presents many delicate longitudinal and oblique lines forming an anastomosing surface along the entire crown (Fig. 4A). The anterior and posterior carinae are composed of well-marked longitudinal ridges with smooth crenulations on them (Figs 3A, 4A). Therefore, this tooth can be described as false-ziphodont in

Figure 3. *Sarcosuchus hartti*, teeth. A, YPM 516, Lectotype, in mesial view. B, BMNH R2983, in mesial (?) view. C, BMNH R2983, in distal (?) view. D, BMNH R3079, in mesial (?) view. E, BMNH R3079, in distal (?) view. F, MN 7460-V, in distal (?) view. G, MN 7460-V, in apical view. H, MN 7461-V, in distal (?) view. I, MN 7461-V, in apical view. Scale bar: 1 cm.

morphology (*sensu* Prasad & de Broin, 2002). The carinae do not touch the basal margin of the tooth, presenting a progressive growing until the apex (Fig. 3A). The tooth is subcircular in cross-section. Based on the general morphology of *Sarcosuchus imperator*, YPM 516 is probably a 'caniniform' anterior tooth (*sensu* D' Amore *et al.*, 2019) in having a straight, tall and sharp crown.

Here we present a more refined description of the paralectotypes based on Allport's (1860: pl. XVI, figs 1–3, 5) illustrations. The teeth illustrated in Allport's figures 1, 2, 3 and 5, are referred to here as teeth one, two, three and four, respectively. Tooth one presents most of the characteristics described for YPM 516. It differs only in the longitudinal ridge on the carinae, which goes all the way long from the base to the apex of tooth one. Tooth two is apicobasally short, being smaller and stouter in comparison with YPM 516 and tooth one. The enamel is badly preserved, being restricted to the extreme convex apex. The labial face is slightly curved lingually, while the lingual face is straight. The enamel anastomosing surface is inferred based on Allport's (1860) classification of teeth morphotypes. Tooth three has a well-preserved anastomosing enamel surface. Like tooth two, it is also apicobasally short, but tooth three differs from tooth four in having a more acute apex, the result of the stronger curvature on the lingual surface. Tooth four slightly resembles YPM 516 and tooth one, but it differs in being less robust and presenting a sigmoid curvature in the labial face. The illustration just enables us to infer a subcircular cross-section for teeth two, three and four. Also, the longitudinal ridges on the carinae can only be observed in tooth one.

The two teeth studied by Mawson & Woodward (1907) and Buffetaut & Taquet (1977) are BMNH R2983 (Fig. 3B, C) and BMNH R3079 (Fig. 3D, E). The specimen BMNH R 2983 is 54 mm in height, with a straight lingual margin and a slightly curved labial margin (Fig. 3B, C). It is subcircular in cross-section with a major axis of 33 mm. The enamel is badly preserved and does not show the longitudinal and oblique lines, but some deep, parallel scratches are present on the surface of the tooth (Fig. 3B, C). The carinae are also not preserved and the apex presents a well-marked wear facet (Fig. 3B, C). Due to the absence of the diagnostic features, this tooth cannot be assigned to *Sarcosuchus hartti*. BMNH R3079 is 88 mm in height, with both lingual and labial margins slightly curved lingually (Fig. 3D, E). This tooth shows a subcircular cross-section with a major length of 40 mm. The enamel is partially preserved, mainly at the apex and on the lingual margin. It presents the characteristic delicate longitudinal striation that forms the anastomosing surface of the tooth (Fig. 4C). This pattern is particularly well-preserved at the tooth apex. The longitudinal ridges on the carinae are preserved on both sides of the apex, being slightly developed. The apex is concave without any wear facets.

The specimen MN 7460-V is 25 mm in height (Fig. 3F, G). The labial margin is slightly convex and the lingual margin is gently concave, thus the apex assumes a more lingual-oriented position (Fig. 3F, G). The enamel shows the characteristic delicate longitudinal and oblique lines that form the anastomosed surface (Fig. 4B). The tooth apex is concave and the enamel was lost, what could be a wear facet (Fig. 3F, G). The cross-section is circular. Both carinae have well-marked longitudinal ridges, being completely absent next to the base (Fig. 3F, G). The specimen MN 7461-V (Fig. 3H, I) is shorter in height than the first one, with a total length of 22 mm. Both lingual and labial facets are convex with a more rounded than pointed apex ('molariform' *sensu* D' Amore *et al.*, 2019; Fig. 3H, I). The cross-section is circular. The enamel and the carinae have the same characteristics observed in MN 7460-V (Fig. 4D).

Mandible

In the anterior portion, specimen BMNH R3423 consists of an incomplete mandible (Figs 5, 6). The dentary is only preserved bone, but it is possible to observe the region where the splenial would contact it. The maximum preserved length of the mandible is 430 mm, but the total length of the lower jaw could reach at least twice this length. The mandibular symphysis is elongated (Figs 5B, D, 6B, D) and dorsoventrally flattened (Figs 5A, C, 6A, C). The

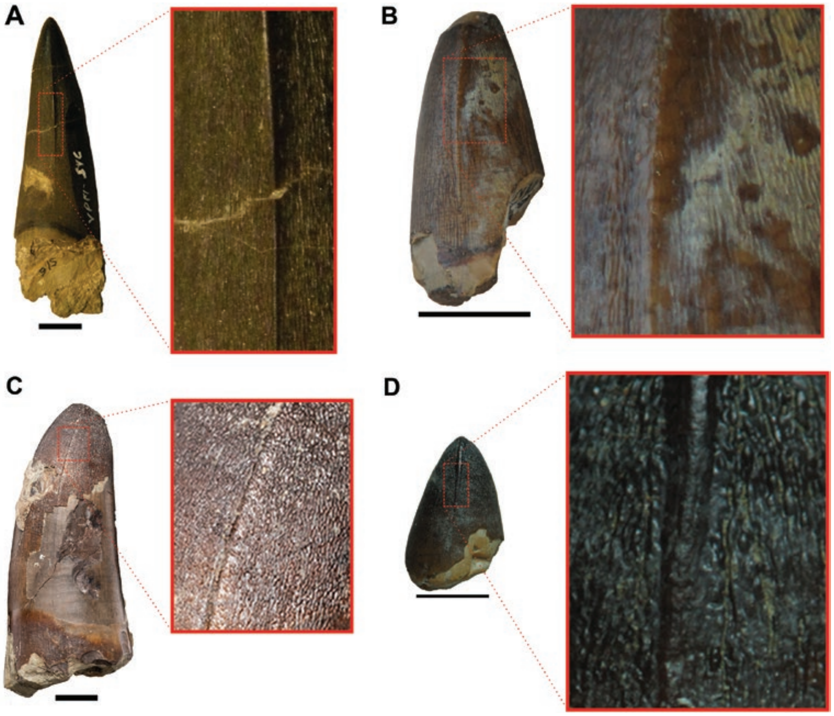

Figure 4. *Sarcosuchus hartti*, teeth in detail. The enamel structures are shown in the red boxes. A, YPM 516, Lectotype, in mesial view. B, MN 7460-V, in distal (?) view. C, BMNH R3079, in distal (?) view. D, MN 7461-V, in distal (?) view. Scale bar: 1 cm.

anteriormost region is spatulated in shape due to the lateral expansion of the dentaries (Figs 5D, 6D). It flares up at the level of the fifth alveolus and reaches its maximum width at the level of the fourth alveolus (Figs 5D, 6D). In this region, the dorsal surface has a shallow concavity, which is more rugose than the remaining surface of the mandible (Figs 5D, 6D). The dorsal surface going from the region next to the final portion of the anterior splenial process to the eighth alveolus is rugose (Figs 5D, 6D). The dorsal surface posterior to the anterior flared region shows a low median sagittal keel, with the syphysis between the dentaries comprising its apex (Figs 5D, 6D). There are depressions on each side of the sagittal keel, between the midline and the medial alveolar margins (Fig. 5D). There is no participation of the splenials in the medial margins of the posterior alveoli that are preserved (Fig. 5D). The ventral surface of the dentary has a coarse ornamentation with shallow interconnected grooves (Fig. 5B). In lateral view, the mandible shows a linear ventral margin up to the posterior border of the fourth alveolus and from this point beyond it slopes anterodorsally (Figs 5A, 6A). The laterodorsal profile of the mandible is double festooned (i.e. two distinct concave regions), the first and deeper concavity is located between the fourth and tenth alveoli, while the second one is shallow and is placed between the 13th and the 21st alveoli (Figs 5A, 6A). There are 22 dentary alveoli on the left side of the mandible and 11 on the right side. The first two pairs of teeth are transversally aligned in the anterior margin of the dentary (Figs 5D, 6D). They are procumbent and smaller in comparison with all other teeth (Figs 5D, 6D). The third and fourth pair of alveoli are similar in size, but the fourth ones are the largest teeth in the dentary (Figs 5D, 6D). These teeth are lateroposteriorly tilted relative to the second pair of alveoli, being the third pair more medially than the fourth (Figs 5D, 6D). There is a diastema between the fourth and fifth alveoli, being the diastema similar in width to the size of the fourth alveoli (Figs 5D, 6D). A depressed region is present close to the diastema and probably represents a notch for an enlarged tooth at the premaxilla–maxilla (Figs 5D, 6D). Starting from the fifth pair of alveoli, all

Figure 5. *Sarcosuchus hartti*, mandible (BMNH R 3423). A, left lateral view. B, ventral view. C, anterior view. D, dorsal view. Scale bar: 10 cm.

others are anteroposteriorly aligned (Figs 5D, 6D). They are similar in size, but show different shapes from subcircular to labiolingually elliptic outlines (Figs 5D, 6D). The posterior series of teeth are packed together, separated by thin bone bars between each alveolus (Figs 5D, 6D). The only exceptions are the last four sockets, which are confluent and form a dental groove (Figs 5D, 6D).

Specimen BMNH R3423 shows seven complete teeth preserved *in situ* (Fig. 5A, D), all of them present the autapomorphic ornamentation of the enamel, allowing us to assign this material to *Sarcosuchus hartti*. There is one 'caniniform' tooth partially erupted on the third alveolus of the right dentary, which is similar in morphology to the lectotype specimen YPM 516. The remaining teeth are on the left side of the dentary from the 12th to the 17th, and the morphology exhibited by them is like those observed in MN 7460-V and MN 7461-V. Therefore, the dentition has a heterodont pattern, with at least the third teeth being a tall caniniform, while the posterior ones are blunter and shorter. The mandible shows occlusion marks (Fig. 5D), with the anterior ones visible in lateral view and the posterior ones in dorsal view, near the lateral margins of the alveoli. The distribution pattern of those toothmarks indicates overbite occlusion.

The new specimen MN 7459-V consists of a fragment of the right ramus of the mandibular symphysis (Fig. 7). There are 14 preserved alveoli and two associated teeth (specimens MN 7460-V and MN 7461-V). The alveoli are similar in size with two different outlines: subcircular and labiolingually elliptical (Fig. 7A). The interalveolar space is smaller than the anteroposterior length of the alveoli (Fig. 7A). There are several tooth marks in the interalveolar spaces posterior to the seventh alveolus (Fig. 7A). The first two marks are placed near the lateral margin of the alveoli and the posterior ones are displaced medially

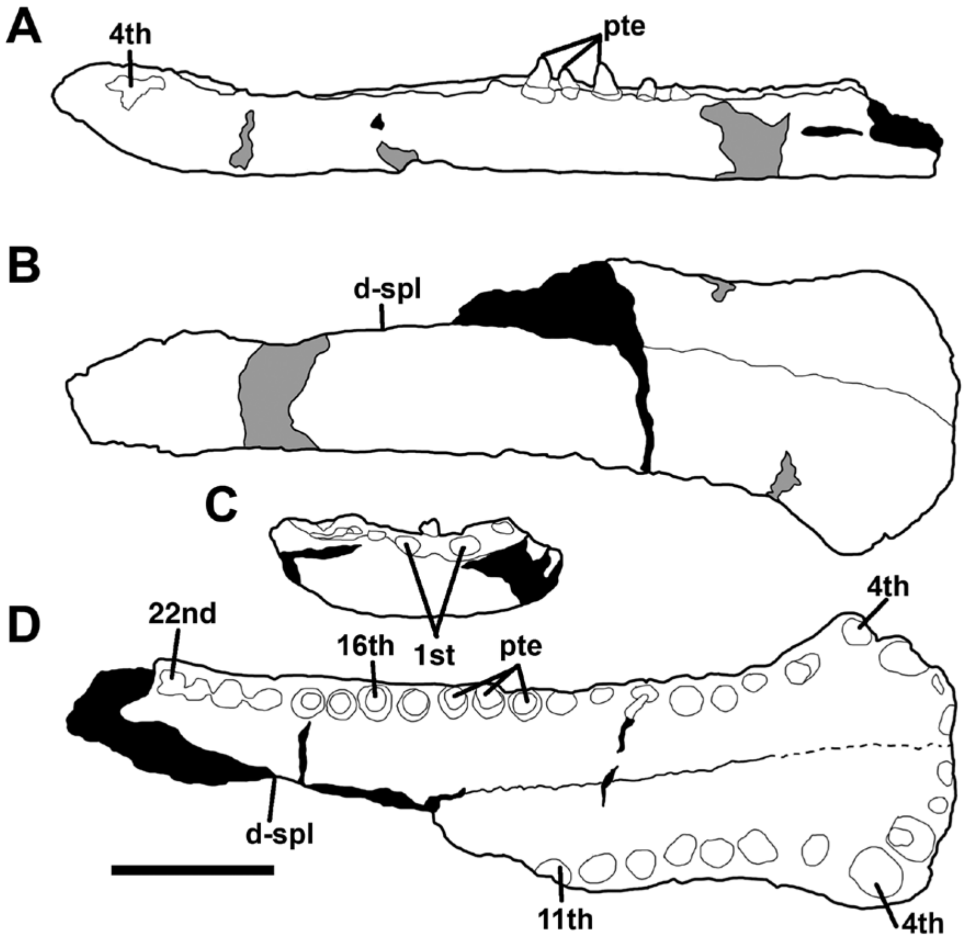

Figure 6. *Sarcosuchus hartti*, schematic drawing of the mandible (BMNH R 3423). A, left lateral view. B, ventral view. C, anterior view. D, dorsal view. Abbreviations: 1st, first dentary alveolus; 4th, fourth dentary alveolus; pte, preserved teeth; 11th, eleventh dentary alveolus; 16th, sixteenth dentary alveolus; 22nd, twenty-second dentary alveolus; d-spl, suture between dentary and splenial. Scale bar: 10 cm.

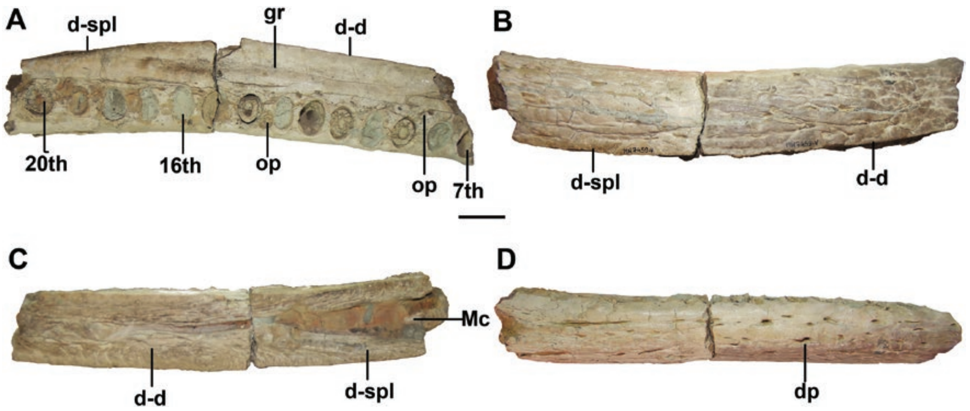

Figure 7. *Sarcosuchus hartti*, right hemimandible (MN 7459-V). A, dorsal view. B, ventral view. C, medial view. D, left lateral view. Abbreviations: 7th, seventh dentary alveoli; 16th, sixteenth dentary alveoli; 20th, twentieth dentary alveoli; d-spl, suture between dentary and splenial; d-d, suture between dentary bones; Mc, Meckel's Canal; dp, dentary pits of the ventral ornamentation; op, occlusion pits; gr, groove region. Scale bar: 3 cm.

in relation with each other. The last toothmark is preserved near the medial margin of the bone, immediately posterior to the last preserved alveolus. There are also some small aligned foramina close to the medial margin of the alveoli (Fig. 7A). The ornamentation in the ventral surface is more tenuous and with more sparse pits than that observed in BMNH R3423 (Fig. 7B, D). In dorsal view, it is possible to see the sutural region between the splenial and the dentary (Fig. 7A). Also, it is possible to observe the dentary–dentary symphysis in medial view (Fig. 7C) and the dentary–splenial contact posteriorly, with a concavity between the dorsal and ventral articular regions (Fig. 7C). The posterior portion of the dentary flares laterally to receive the anterior process of the splenial that wedges anteriorly to the level of the sixth alveolus (Fig. 7A). A low median sagittal keel is observed in the mid-palatal region of the mandible, where the dentaries contact each other (Fig. 7A). Located between this keel and the medial alveolar margin there is a rugs area that ends near the anterior process of the splenial (Fig. 7A).

Osteoderm

The specimen BMNH R3224 is a partially preserved osteoderm (Fig. 8). It is subrectangular in shape and has a straight, smooth and vertical anterior margin for articulation with the anterior osteoderm (Fig. 8A). There is a short and robust anterior process, which is placed at the lateral margin of the osteoderm (Fig. 8A). The bony process is smooth on its surface like the anterior and lateral margins and is slightly directed medially (Fig. 8A). There is a low keel separating the large dorsomedial surface of the osteoderm from the smaller lateral region (Fig. 8A). The keel runs obliquely following the orientation of the anterior bony process. The lateral area is convex and follows the same orientation of the anterior process (Fig. 8A). Because of such orientation, it is possible to infer that the posterior margin was wider than the anterior one, giving a trapezoidal shape for the complete osteoderm. The dorsal surface of the osteoderm is ornamented with a great number of large, deep and isolated pits that varies in shape (Fig. 8A). The ventral facet is smooth with no muscular scars (Fig. 8B). The osteoderm is thick in lateral view proportionally to the other surfaces (Fig. 8B). The broken region allows the observation of two different kinds of bone tissue; a more compact bone that composes the dorsal, ventral and lateral regions of the osteoderm, and a spongy tissue located in the inner region (Fig. 8B). Based on comparisons with the specimen MNN 607 of *Sarcosuchus imperator*, it is possible to suggest that this osteoderm would be a more anterior element of the dermal shield.

PHYLOGENY

The phylogenetic analysis resulted in 12 minimum-length trees (see Supporting Information, Supplementary Information X for the graphical representation of those trees), with 1287 steps (CI: 0.327 and RI: 0.610). The topological hypotheses are summarized and presented on the resulting strict consensus tree (Fig. 9).

The first lineage of Neosuchia, sister to all other species, is the clade uniting *Batrachomimus* and *Fortignathus*. This relationship is supported by the share of an elongated symphyseal region, which is based on the proportion between length and width (Char. 222: 1 -> 2; i.e. the ancestor species has the condition 1, while the descendent species hereditary acquired the modified condition 2). Its sister-clade is formed by

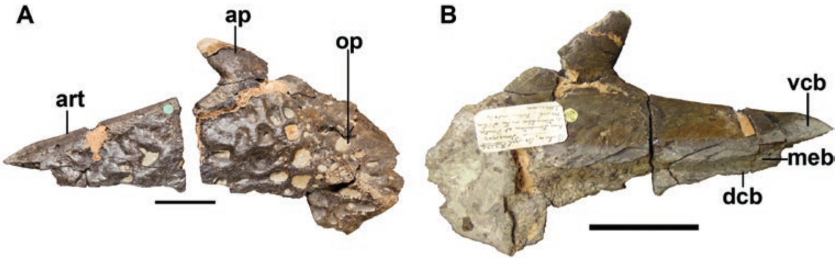

Figure 8. *Sarcosuchus* sp., osteoderm (BMNH R3224). A, dorsal view. B, ventral view. Abbreviations: art, articular facet; ap, anterior projection; op, ornamentation pit; vcb, ventral compact bone tissue; meb, medial spongiest bone tissue; dcb, dorsal compact bone tissue. Scale bar: 3 cm.

the remaining neosuchian species, and is supported by the following synapomorphies: ornamented region below the dental groove of the dentary (Char. 18: 1 -> 0); anteriormost end of the frontal acute (Char. 98: 0 -> 1); presence of the spina quadratojugalis at the posterior margin of the lower temporal fenestra (Char. 145: 0 -> 1); flat symphyseal region at the dorsal surface of mandible (Char. 221: 1 -> 0); and an aligned occlusion pattern of the premaxilla–dentary (Char. 246: 1 -> 0). Also, in some of the minimum length trees, the lateral margin of the upper temporal bar, postorbital–squamosal, being convex (Char. 128: 1 -> 0) is recovered as a synapomorphy.

The clade ((Susisuchidae + Eusuchia) (*Rugosuchus* ((*Bernissartia* (*Theriosuchus*)) (Coelognathosuchia))) is supported by the following synapomorphies: external nares opens dorsally (Char. 40: 0 -> 3); double festooning at the lateroventral margin of the maxilla (Char. 64: 2 -> 3); the quadrate condyles are at the same level as the occipital condyle (Char. 155: 0 -> 1); rounded choana (Char. 187: 3 -> 1); laminar neural spines at the posterior series of cervical vertebrae (Char. 318: 1 -> 0); and absence of a rounded fossa between the base of the neural spine and the postzygapophyses in dorsal vertebrae (Char. 325: 1 -> 0).

The clade composed by (Susisuchidae + Eusuchia) is supported by the following synapomorphies: absence of a perinarial fossa in the premaxilla (Char. 49: 1-> 0); absence of a notch in the lateral surface of premaxilla–maxilla contact (Char. 59: 1 -> 0); premaxilla–maxilla contact with sinusoid orientation at the palatal surface (Char. 61: 0 -> 1); a narrow rectangular frontal (Char. 97: 01 -> 2); a subequal proportion between anteroposterior and lateromedial axes of choana (Char. 188: 0 -> 1); anterior margin of choana posterior to the suborbital fenestrae (Char. 192: 1 -> 2); choana completely enclosed within the pterygoid (Char. 208: 12 -> 3); the proximal end of the scapular blade is wider than the distal end (Char. 291: 1 -> 0); presence of a notch at the dorsal margin of the iliac blade (Char. 307: 0 -> 1); procoelous centra in cervical vertebrae (Char. 320: 0 -> 1); biconvex articulation in the first caudal vertebrae (Char. 333: 0 -> 1); procoelous centra in caudal vertebrae (Char. 334: 0 -> 1); and the cervical osteoderms differs morphologically from the dorsal ones (Char. 346: 0 -> 1).

The sister-group of (Susisuchidae + Eusuchia) is the clade (*Rugosuchus* ((*Bernissartia* (*Theriosuchus*)) (Coelognathosuchia)), which is supported by three synapomorphies: absence of occipital exposition of the cranioquadrate passage (Char. 122: 0 -> 1); absence of supraoccipital exposure at the skull roof (Char. 162: 1 -> 0); and choana anteriorly positioned in relation to the anterior margin of the pterygoid (Char. 193: 1 -> 0).

A shared recent ancestrality between *Tomistoma* and *Gavialis* is not supported here by any unambiguous character transformation. The phylogenetic position of true-gharials (*Gavialis*) and false-gharial (*Tomistoma*) have been a subject of continuous scientific debate for almost forty years, and it is now a classic case of phylogenetic conflict in the literature (Buffetaut, 1982, 1985; Norell 1989; Brochu 1997; Gatesy *et al.* 2003; Piras *et al.* 2010; Iijima &, Kobayashi, 2019). Usually molecular analyses consider both lineages as sister taxa diverging each other during Eocene or mid-Miocene, whereas morphology-based analyses set *Gavialis* apart from *Tomistoma* and other crocodylian species, and the stratigraphic data imply that the split of the Gavialoidea lineage occurred by the Late Cretaceous. The oldest gavialoid remains are from Upper Cretaceous and Paleocene deposits of North America, Europe and Africa (Hua & Jouve, 2004). Today, the critically endangered *Gavialis* is limited to the northern part of the Indian subcontinent. However, the zenith of gavialoid diversity is in the South American Miocene (Riff *et al.* 2010; Scheyer *et al.*, 2013; Cidade *et al.* 2019). Contradicting the results presented here in this respect, previous studies including the morphologically varied South American Neogene gavialoids strongly supported the monophyly of Gavialoidea and its basal-most position within Crocodylia (e.g. Brochu & Rincón 2004; Vélez-Juarbe *et al.* 2007; Riff & Aguilera, 2008; Bona *et al.*, 2017; Salas-Gismondi *et al.* 2017).

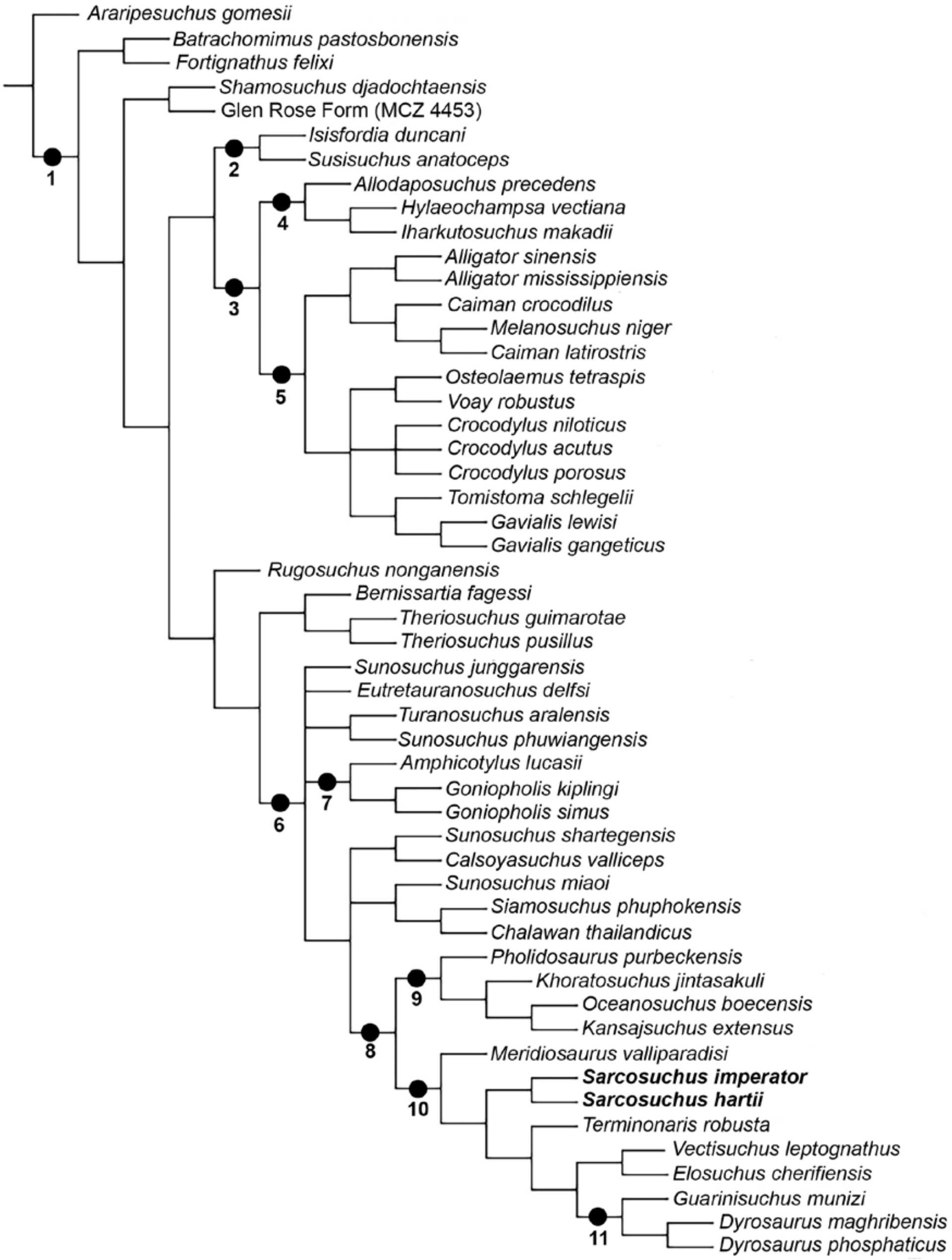

Figure 9. Consensus cladogram resulted from 12 minimum-length trees with 1287 steps (CI: 0.327 and RI: 0.610). The numbered nodes are the following clades: 1, Neosuchia; 2, Susisuchidae; 3, Eusuchia; 4, Allodaposuchidae; 5, Crocodylia; 6, Coelognathosuchia; 7, Goniopholididae; 8, Tethysuchia; 9, Pholidosauridae; 10, Tethysuchoidea; 11, Dyrosauridae.

Clade ((*Bernissartia* (*Therioschus*)) (Coelognathosuchia)) is supported by: the external nares are anterodorsal oriented (Char. 40: 3 -> 2); the anterior and posterior processes of jugal are subequal (Char. 133: 2 -> 1); triangular choana (Char. 187: 1 -> 2); dentary tooth medially located in relation to the premaxilla–maxilla contact (Char. 282: 0 -> 1); and dorsal osteoderms wider than long (Char. 337: 1 -> 2). In some minimum-length trees, the squamosal posterior processes are parallel (Char. 113: 1 -> 0).

The clade Coelognathosuchia shows a polytomy of several smaller clades ((*Sunosuchus junggarensis*) (*Eutretauranosuchus*) (*Turanosuchus* + *Sunosuchus phuwiangensis*) (*Amphicotylus* + *Goniopholis*) (node 64)). Coelognathosuchia itself is well supported by the following synapomorphies: nasal does not participate in the borders of the external nares (Char. 76: 0 -> 1); the frontal is wide in the region between the orbits (Char. 95: 0 -> 1); the frontal posterior margin is positioned at the postorbital bar in the skull roof (Char. 103: 1 -> 0); the quadrate posterior ramus are at the same level of the maxillary teeth row (Char. 154: 2 -> 1); elliptic mandibular fenestra (Char. 214: 1 -> 0); the posterior teeth of maxilla–dentary are circular in cross-section (Char. 265: 0 -> 1); dentary alveoli 3 and 4 are close to each other (Char. 277: 0 -> 1); the third dentary alveoli are anterior to the fourth ones (Char. 279: 1 -> 2); and absence of a longitudinal keel at dorsal osteoderms (Char. 340: 0 -> 1). Some of the minimum-length trees present the following features as synapomorphies: presence of a non-ornamented region below the dental groove of dentary (Char. 18: 0 -> 1); lacrimal present a long length in relation to the width (Char. 84: 0 -> 1); robust postorbital bar (Char. 131: 0 -> 1); and robust splenial posterior to the mandibular symphysis (Char. 238: 0 -> 1).

The polytomy results from two diverging hypotheses found in the minimum-length trees. The first hypothesis is observed on minimum-length trees 1, 9, 10 and 11 and consists of ((*Eutretauranosuchus* (*Amphicotylus* + *Goniopholis*)) (*Sunosuchus junggarensis* ((*Turanosuchus* + *Sunosuchus phuwiangensis*) (node 64)))).

Clade ((*Eutretauranosuchus* (*Amphicotylus* + *Goniopholis*)) is supported by all minimum length-trees by follow features: the anteromedial region of the orbits present a transversal crest (Char. 8: 0 -> 1); there is no ornamentation in the surface below the dental groove (Char. 18: 0 -> 1); the posterior margin of the nasals are between the anterior margins of the orbits (Char. 80: 0 -> 1); the squamosal present an elongated posterior process (Char. 112: 0 -> 1); the temporo-orbital opening does not expose dorsally (Char. 115: 0 -> 1); the mandibular fenestra is horizontal at its anteroposterior axis (Char. 215: 1 -> 0); and the last premaxillary tooth is anteromedial in relation with the first maxillary tooth (Char. 256: 1 -> 2).

Clade (*Amphicotylus* + *Goniopholis*) accounts for the following characters: perinarinal crest present in the premaxilla (Char. 1: 0 -> 1); preorbital crest present in the anterior region of the orbits (Char. 5: 0 -> 1); the postnarial fossa on premaxilla is present (Char. 51: 0 -> 1); the premaxilla has a hatchet-like shape in dorsal view (Char. 55: 0 -> 4); there are paired maxillary depressions at the laterodorsal surface of maxilla (Char. 71: 0 -> 1); the posterior ramus of prefrontal is long reaching the median region of the orbits (Char. 90: 0 -> 1); the frontal is wide (Char. 94: 0 -> 1); the frontal has two unlevelled surfaces (Char. 99: 0 -> 1); and, at the skull table the parietal-squamosal suture is grooved (Char. 108: 0 -> 1).

The (*Sunosuchus junggarensis* ((*Turanosuchus* + *Sunosuchus phuwiangensis*) (node 64))) lineage has some particular features recovered in all minimum length-trees, which are: small anterior palpebrals (Char. 35: 1 -> 0); the incisive foramen is small (Char. 45: 0 -> 1); premaxilla has a paddle-like shape in dorsal view (Char. 55: 0 -> 3); and there are vascular openings at the dorsolateral surface of posterorbital bar (Char. 126: 0 -> 1).

The node ((*Turanosuchus* + *Sunosuchus phuwiangensis*) (node 64))) is supported by only one character that is the premaxilla overbiting the mandible in occlusion (Char. 246: 0 -> 1). While (*Turanosuchus* + *Sunosuchus phuwiangensis*) has the following synapomorphies: wedge-shaped mandible (Char. 211: 1 -> 0); the anterior region of the symphyseal portion, in lateral view, is acute (Char. 216: 1 -> 0); and the symphyseal region has the anterior width smaller than the posterior (Char. 218: 2 -> 0).

The second hypothesis is observed in minimum-length trees 2, 3, 4, 5, 6, 7, 8 and 12, and consists of ((*Amphicotylus* + *Goniopholis*) ((*Eutretauranosuchus* (*Sunosuchus junggarensis* (*Turanosuchus* + *Sunosuchus phuwiangensis*))) (node 64))). The (*Amphicotylus* + *Goniopholis*) is well supported by several features in all minimum length-trees, which are: perinarinal crests present in external nares (Char. 1: 0 -> 1); preorbital crest present (Char. 5: 0 -> 1); there is a transversal crest in the anteromedial region to the orbits (Char. 8: 0 -> 1); there is a postnarial fossa (Char. 51: 0 -> 1); there are paired maxillary depressions in the laterodorsal surface of maxilla (Char. 71: 0 -> 1); the prefrontal posterior ramus is long (Char. 90: 0 -> 1); the region between orbits is wide (Char. 94: 0 -> 1); the frontal has two unlevelled surfaces (Char. 99: 0 -> 1); the parietal–squamosal extends over the occipital surface (Char. 108: 0 -> 1); the temporo-orbital opening is not exposed dorsally (Char. 115: 0 -> 1); the maxillary teeth row is in the same level of the occipital condyle (Char. 178: 0 -> 1); the last premaxillary tooth is anteromedial located in relation to the first maxillary tooth (Char. 256: 1 -> 2); there is a paradistal rotation of the dentition in relation to the medial sagittal axis (Char. 262: 0 -> 1); and the crown of anterior dentition is bulbous (Char. 270: 0 -> 1).

Clade((*Eutretauranosuchus*(*Sunosuchusjunggarensis* (*Turanosuchus* + *Sunosuchus phuwiangensis*))) (node 64))) is supported by: the anterior palpebrals are small in size (Char. 35: 1 -> 0); the incisive foramen is small (Char. 45: 0 -> 1); in the lateral surface of the premaxilla–maxilla there is an indentation (Char. 60: 1 -> 0); there is a fossa close to the alveolar margin in the maxilla (Char. 70: 0 -> 1); the premaxilla overbites the dentary (Char. 246: 0 -> 1); and the first two alveoli pairs from mandible are smaller than the third and fourth ones (Char. 278: 2 -> 0).

The clade (*Eutretauranosuchus* (*Sunosuchus junggarensis* (*Turanosuchus* + *Sunosuchus phuwiangensis*))) has the following characters supporting it: there is a single festooning at the lateroventral margin of maxilla (Char. 64: 3 -> 2); the maxilla–prefrontal suture is present (Char. 73: 0 -> 1); and the first pair of dentary alveoli are anterior in relation to alveoli three and four (Char. 275: 0 -> 1). The inner clade (*Sunosuchus junggarensis* (*Turanosuchus* + *Sunosuchus phuwiangensis*)) accounts for only one character: that is the surface below the dental groove is ornamented (Char. 18: 1 -> 0). The (*Turanosuchus* + *Sunosuchus phuwiangensis*) clade is supported by: wedge-shaped mandible (Char. 211: 1 -> 0); the anterior width of the symphyseal region is smaller in relation to the posterior one (Char. 218: 2 -> 0); and there is a hypertrophied tooth adjacent to premaxilla–maxilla suture (Char. 281: 0 -> 1).

The polytomy ((*Sunosuchus shartegensis* + *Calsoyasuchus*) (*Sunosuchus miaoi* (*Siamosuchus* + *Chalawan*))) (Tethysuchia)), node 64 in the consensus tree (see Supporting Information, Supplementary Information X), is the result of two competing topological hypotheses present in the minimum-length trees. This polytomy is supported by the following features as synapomorphies: the surface below the dental groove is non-ornamented (Char. 18: 0 -> 1); the posterodorsal process of the premaxilla extends posterior to the third maxillary alveolus (Char. 53: 0 -> 1); there is no spina quadratojugalis in the lower temporal fenestra (Char. 145: 1 -> 0); there are lateral openings to the main Eustachian tube (Char. 159: 0 -> 1); the choana is rectangular (Char. 187: 2 -> 3); the symphyseal region is extremely long (Char. 222: 2 -> 3); the splenial has a long participation in the mandibular symphysis (Char. 237: 1 -> 2); and there are no hypertrophied teeth in the anterior dentition of the maxilla (Char. 257: 0 -> 1).

The first competing hypothesis of the aforementioned polytomy is observed in minimum-length trees 1, 3, 5, 6, 7, 9 and 11 and consists of ((*Sunosuchus miaoi* (*Siamosuchus* + *Chalawan*)) ((*Sunosuchus shartegensis* + *Calsoyasuchus*) (Tethysuchia))). The clade (*Sunosuchus miaoi* (*Siamosuchus* + *Chalawan*)) has the following features to support it: the preorbital bones are elevated laterodorsally (Char. 26: 0 -> 1); the surangular participates in the glenoid fossa (Char. 228: 0 -> 1); and the surangular extends to the posterior region of the retroarticular process (Char. 232: 0 -> 1). The (*Siamosuchus* + *Chalawan*) clade is supported by two features: the quadrate medial condyle is hypertrophied (Char. 156: 0 -> 1); and supraoccipital exposes on skull roof (Char. 162: 0 -> 1). The clade (*Sunosuchus shartegensis* + *Calsoyasuchus*) (Tethysuchia)) accounts for: the premaxilla does not taper between maxilla and nasal (Char. 52: 1 -> 0); the maximum width of the premaxilla is wider than the maxilla (Char. 54: 0 -> 1); the external auditory meatus is large (Char. 117: 1 -> 0); and the mandible symphyseal region is parallel to the horizontal plane (Char. 217: 0 -> 1). Finally, the clade (*Sunosuchus shartegensis* + *Calsoyasuchus*) is supported by: the narrow platyrostral rostrum (Char. 30: 4 -> 3); the snout has an external antorbital fenestra (Char. 43: 0 -> 1); and, the premaxilla–maxilla suture is sinusoid in palatal surface (Char. 61: 0 -> 1).

The second hypothesis is based on the topological relationship observed in the minimum-length trees 2, 4, 8, 10 and 12, which is (((*Sunosuchus shartegensis* + *Calsoyasuchus*) (*Sunosuchus miaoi* (*Siamosuchus* + *Chalawan*))) (Tethysuchia)). The ((*Sunosuchus shartegensis* + *Calsoyasuchus*) (*Sunosuchus miaoi* (*Siamosuchus* + *Chalawan*))) lineage accounts for: the absence of incisive foramen (Char. 44: 0 -> 1); the frontal–parietal suture rests on skull roof (Char. 104: 2 -> 0); the mandibular fenestra is large in relation to the orbit (Char. 213: 0 -> 1); and the mandibular fenestra is oblique at its anteroposterior axis (Char. 215: 0 -> 1). The (*Sunosuchus shartegensis* + *Calsoyasuchus*) clade is supported by two characters: a narrow platyrostral rostrum (Char. 30: 4 -> 3); and the snout present an external antorbital fenestra (Char. 43: 0 -> 1). The clade (*Sunosuchus miaoi* (*Siamosuchus* + *Chalawan*)) is supported by: the periorbital bones are laterodorsally elevated (Char. 26: 0 -> 1); the maxillopalatal fenestra is present (Char. 74: 0 -> 1); the postorbital bar is thin (Char. 131: 1 -> 0); the surangular participates on the glenoid fossa (Char. 228: 0 -> 1); and the surangular extend to the posterior region of the retroarticular process (Char. 232: 0 -> 1). Finally, the (*Siamosuchus* + *Chalawan*) clade is united by two characters: the quadrate medial condyle is hypertrophied (Char. 156: 0 -> 1) and the supraoccipital is exposed on the skull roof (Char. 162: 0 -> 1).

The Tethysuchia is supported in all minimum length-trees by the following characters: the premaxilla ventral margin is ventral in relation to the maxillary ventral margin (Char. 56: 1 -> 2); the maxilla lateroventral margin is straight (Char. 64: 3 -> 0); the lateral border posterior to the external narial opening of nasal is oblique to the sagittal axis (Char. 78: 1 -> 0); the postorbital bar is elliptic in cross-section (Char. 130: 1 -> 0); and the dentary does not extend below the mandibular fenestra (Char. 223: 1 -> 0). In some trees it is also united by: there being a posteroventral process of lacrimal beneath the orbits (Char. 85: 0 -> 1).

Within Tethysuchia there is a new clade Tethysuchoidea, which consists of (*Meridiosaurus* ((*Sarcosuchus*) (*Terminonaris* ((*Elosuchus* + *Vectisuchus*) (Dyrosauridae)))), being supported by: posterodorsal process of premaxilla extends anterior to the third maxillary alveolous (Char. 53: 1 -> 0); the ventral margin of premaxilla and maxilla are at the same level (Char. 56: 2 -> 1); occlusion pits for the first dentary teeth at the palatal surface of premaxilla (Char. 58: 0 -> 1); no lacrimal process beneath the orbits (Char. 85: 1 -> 0); upper temporal bar is oblique (Char. 127: 0 -> 1); pterygoid participates at the posterior, lateral and parts of the anterior margin of the choana (Char. 208: 1 -> 2); and posterodorsal-directed retroarticular process in lateral view (Char. 241: 1 -> 2).

The genus *Sarcosuchus* shows the following characters: the posterior dentition of maxillary and dentary present a weak-developed ridges on the enamel surface (Char. 268: 1 -> 0); the maxilla–dentary anterior dentition has a bulbous crown shape (Char. 270: 0 -> 1); the dentary alveoli have a transitional morphology from circular to oval (Char. 272: 0 -> 1); the dentary alveoli one and two are close to each other (Char. 276: 0 -> 1); and the third dentary alveolus is medial in relation to the fourth (Char. 279: 2 -> 0). Clade (*Terminonaris* ((*Elosuchus* + *Vectisuchus*) (Dyrosauridae)) is supported by the following features: the surface below the dental groove is ornamented (Char. 18: 1 -> 0); the rostrum is subequal (Char. 30: 4 -> 2); the frontal surpass the anterior portion of the prefrontals (Char. 96: 1 -> 0); the parietal–postorbital suture is outside the supratemporal fossa (Char. 107: 1 -> 0); the retroarticular process is long (Char. 240: 0 -> 2); the premaxilla–dentary has an aligned occlusion pattern (Char. 246: 1 -> 0); the ulna is shorter than the humerus (Char. 297: 0 -> 1); and the centrum of dorsal vertebrae is spool-shaped (Char. 330: 0 -> 1). The ((*Elosuchus* + *Vectisuchus*) (Dyrosauridae)) lineage is united by: the posterodorsal process of the premaxilla is anterior to the third maxillary alveolus (Char. 53: 1 -> 0); the ventral margins of maxilla and premaxilla are at the same level (Char. 56: 2 -> 1); there are occlusion pits for first dentary teeth in the premaxilla (Char. 58: 0 -> 1); there is no lacrimal posteroventral process beneath the orbits (Char. 85: 1 -> 0); the upper temporal bar is oblique in relation to the median sagittal axis (Char. 127: 0 -> 1); and the pterygoid composes the posterior, lateral and partially the anterior margins of choana (Char. 208: 1 -> 2). Finally, the (*Elosuchus* + *Vectisuchus*) clade has the following synapomorphies: the periorbital bones are laterodorsally elevated (Char. 26: 0 -> 1); the orbits are anteriorly inclined (Char. 34: 0 -> 1); the mandibular fenestra is larger than the orbits (Char. 213: 0 -> 1); the crown shape of maxilla–dentary anterior dentition is bulbous (Char. 270: 0 -> 1); and the dorsal osteoderms has a longitudinal keel (Char. 340: 1 -> 0). The features that support Dyrosauridae are available from the Supporting Information, Supplementary Information X.

DISCUSSION

COMPARATIVE ANATOMY

The dentition of *Sarcosuchus hartti* is like that of *Sarcosuchus imperator* in having some degree of heterodonty, with larger caniniform-like anterior teeth and short, rounded and robust posterior teeth. Both species have carinae with well-marked anterior and posterior longitudinal ridges and smooth crenulations on them, i.e. a false ziphodont condition (*sensu* Prasad & de Broin, 2002). The enamel has the same pattern of delicate longitudinal lines in both species. However, *S. hartti* differs from *S. imperator* in having some additional oblique lines that form an anastomosing ornamentation on the enamel surface (Fig. 4). This is considered here as an autapomorphy of the species *S. hartti*. More recently, Dridi (2018) described some *Sarcosuchus* teeth (ONM KAM 1 and ONM KAM 2) from Tunisia with a well-distinct enamel pattern of apicobasal ridges and grooves that are different from other species.

'Pholidosaurid' crocodyliforms show several different patterns in dental anatomy. The Laurasian species *Terminonaris robusta* Mook, 1934 shows tooth crowns that are asymmetrical and divided by weakly developed carinae (Wu *et al.*, 2001). The teeth have concave lingual surfaces with vertical striae (Wu *et al.*, 2001). The specimen SMU 76590 (= *Terminonaris* cf. *T. robusta*) shows homodont dentition with conical teeth that are slightly recurved mesially and labially (Adams *et al.*, 2011). The carinae are well marked on both lingual and labial surfaces, and the enamel is generally smooth with fine vertical striations (Adams *et al.*, 2011). Another important northern hemisphere taxon is *Pholidosaurus purbeckensis* Mansel-Pleydell, 1888. This British species has homodont dentition with slender crowns that are medially bent. The enamel is ornamented with well-marked longitudinal ridges that can barely be differentiated from the carinae (Martin *et al.*, 2016). The French *Oceanosuchus boecensis* Hua *et al.*, 2007 shows slim and delicate conical anterior teeth that are subcircular in cross-section, but the posterior mandibular teeth are blunter (Hua *et al.*, 2007). There are longitudinal striations along the surface of the enamel with anteroposterior carinae perpendicular to the tooth crowns (Hua *et al.*, 2007). *Sunosuchus miaoi* Young, 1948 differs from *Sarcosuchus hartti* in presenting only pointing circular to subcircular teeth, with well-marked longitudinal striations along the entire crown (Young, 1948). Also, some of the smaller teeth are triangular, while the large ones have a straight posterior margin (Young, 1948).

Important comparisons on teeth morphology must be made with *Chalawan thailandicus* (Martin *et al.*, 2013) and *Elosuchus cherifiensis* (Lavocat, 1955), once these species also show a similar mandibular morphology relative to *Sarcosuchus* (see below). *Chalawan thailandicus* is described as having robust, conical teeth with circular cross-sections. The enamel shows wrinkles, but no further details are given about their morphology (Martin *et al.*, 2013). In this way, *C. thailandicus* is similar to *S. hartti*, but differs in the presence of false ziphodont dentition and an anastomosing enamel surface. *Elosuchus cherifiensis* has robust and conical teeth with a subcircular outline in cross-section (de Broin, 2002). The crowns have a small degree of curvature and the carinae are well-marked, reaching the base of the tooth (de Broin, 2002). This taxon is like *S. hartii* in the presence of false ziphodont dentition and the anastomosing surface of the enamel, although in the former species it is more evident and restricted to the apex of the tooth (de Broin, 2002). In *S. hartti* the anastomosing surface is smooth and distributed along the entire surface of the crowns.

The only other South American pholidosaurid is *Meridiosaurus vallisparadisi* Mones, 1980 from Uruguay. This species has homodont dentition with subcircular and conical teeth (Fortier *et al.*, 2011). The carinae form longitudinal ridges that run parallel to the vertical striations along the enamel (Fortier *et al.*, 2011). The teeth of *S. hartti* differ from all previously described species in having well-marked anterior and posterior carinae, which do not reach the base in the posterior teeth, the presence of a small curvature on the crowns and the presence of additional oblique lines that form an anastomosed pattern on the enamel surface.

The lower jaws of *S. hartti* (BMNH R3423 and MN 7459-V) differ from *S. imperator* in several features. In the Brazilian species, there is a low, median sagittal keel on the dorsal surface of the mandible, which is bordered by depressed and rugose lateral areas (Figs 4, 6). The same surface is completely smooth in the African taxon. Another important difference is the presence of a double festooned lateral profile in the mandible of *S. hartii*, which is an exclusive feature among longirostrine forms observed on BMNH R3423. The anterior region is deeper and confined between the fourth and the tenth alveoli, whereas the posterior one comprises a shallow region between the 13th and the 21st alveoli. In contrast, *S. imperator* has a rather straight laterodorsal outline that slopes dorsally only in its posteriormost region. The interalveolar space in the dentary of *S. hartii* is smaller than the length of the alveoli and, therefore, differs from the condition observed in *S. imperator*, which shows similar length between alveolar length and interalveolar space. On the other hand, there are also many similarities between both *Sarcosuchus* species. The dentaries have well-marked ornamentation on their ventral surface, a feature that is similar to what is observed on some neosuchians (e.g. Atoposauridae, Goniopholididade). The first four alveoli are aligned and form an arch in which the first two pairs are placed more anteriorly relative to the other two. Also, the first two pairs of alveoli are smaller than the third and fourth ones. In both species, a diastema is observed between the fourth and fifth alveolus.

The mandibular morphology of *S. hartti* differs from that of *O. boecensis* in having an anterior process of the splenial that extends itself for more than three alveoli and by the presence of small interalveolar spaces (Hua *et al.*, 2007). *Terminonaris robusta* (Mook, 1934) have a dentary with parallel margins and without the spatulated anterior end. As a consequence, only the first pair of alveoli is at a more anterior position, therefore contrasting with the condition observed in *S. hartti* where the first three pairs of alveoli are at an anterior position (Wu *et al.*, 2001). A similar morphology of the anterior portion of the jaw is observed in *Fortignathus felixi* (de Broin, 2002) (Young *et al.*, 2017). The latter species also has a single concavity on the lateral profile of the mandible, between the fourth and the 13th alveoli (Young *et al.*, 2017).

Sunosuchus phuwiangensis (Buffetaut & Ingavat, 1983) differs from the genus *Sarcosuchus* in having a relatively short dentary symphysis with six alveoli, and a short anterior process of the splenial with two alveoli. Also, *Sunosuchus phuwiangensis* has a lateral expansion on the dentary, which is restricted to the region of the third and fourth alveoli (Buffetaut & Ingavat, 1983). Despite the size proportion between the first four dentary alveoli being the same in *Sunosuchus phuwiangensis* and *Sarcosuchus*, the disposition of the alveoli is different. In *Sunosuchus phuwiangensis* the second to sixth alveoli are anteroposteriorly aligned and the seventh and the remaining posterior ones, slope laterally (Buffetaut & Ingavat, 1983).

Halliday *et al.* (2015) proposed that *Sunosuchus shartegensis* Efimov, 1988 (specimen PIN 4174-1) is synonymous with '*Sunosuchus*' *thailandicus* (Buffetaut & Ingavat, 1980), amd questioned the presence of '*Sunosuchus*' *thailandicus* in the genus *Sunosuchus*, which agrees with the new genus allocation, *Chalawan*, proposed by Martin *et al.* (2013). This will be further discussed later. The proposed synonymization must be taken with caution due to some anatomical differences between the specimens: the mandibular ramus opens lateroposteriorly after the symphysis creating a 'V' pattern in *Sunosuchus shartegensis* (PIN 4174-1), while *Chalawan thailandicus* presents a 'U' pattern. Also, PIN 4174-1 presents a slenderer mandible in comparison with *Chalawan thailandicus*. Therefore, we consider *Sunosuchus shartegensis* as a valid species. This species differs from *Sarcosuchus hartti* in presenting a short anterior splenial process and a slender mandible (Halliday *et al.*, 2015).

Turanosuchus aralensis Efimov, 1988, considered by Halliday *et al.* (2015) as '?Goniopholididae gen. et sp. indet.' differs from *Sarcosuchus hartti* in presenting a lateral expansion at the fourth alveolus, which grows gradually from the first to the fourth alveoli. After the fourth alveolus, there is a constriction where the fifth and posterior alveoli are located. Also, it differs in presenting the first three alveoli with the same size, whereas the fourth is the larger one. About the displacement of the alveoli, the first four ones form a closed arch, with the first three opening more laterally than the fourth, which is more medial and dorsal.

Pholidosaurus purbeckensis differs from *Sarcosuchus hartti* in having a slender mandible with an anterior splenial process reaching the 14th alveolus (Martin *et al.*, 2016). The dentary alveoli have the same size, with the first alveolus being more medially displaced than the others, while the second and posterior ones are linearly aligned with its medial margin passing the lateral margin of the first alveolus. The third and fourth alveoli are confluent with their margin being elevated dorsally above the level of the other margins (Martin *et al.*, 2016).

Chalawan thailandicus and *Elosuchus cherifiensis* share the presence of a spatulated anterior margin of the dentary with both *Sarcosuchus* species. The specimen CAS42-20 (formerly TF 1370 in DMR, Bangkok, see: Martin *et al.*, 2013), which is the holotype of *C. thailandicus* (Buffetaut & Ingavat, 1980, 1984), has the first four alveoli similar, but it differs from *Sarcosuchus* by the fourth alveolus being distal to the third, by the presence of a short space between the fourth and fifth alveoli, by the anterolateral displacement of the fifth and 6th alveoli in relation to the posterior ones and by the interalveolar spacing, which is similar to the length of the alveoli (Buffetaut & Ingavat, 1984). The specimen PRC102-143 referred to *C. thailandicus* has a few differences in alveolar morphology in comparison to both *Sarcosuchus* species. It has the first three alveoli similar in size and a fourth larger one, the fourth alveoli are posterior to the third, and there is a short spacing between the fourth and fifth alveoli (Martin *et al.*, 2013). In this specimen, the ventral ornamentation and the distance between the dentary alveoli are all similar to what is observed in *S. hartti*. *Elosuchus cherifiensis* differs from *Sarcosuchus* species in having the first two alveoli as the larger and the third is the smaller one in the anterior portion of the mandible. The first, fourth and all posterior alveoli are mesial-distally aligned, contrasting with the second and third ones that are laterally projected and aligned between them (de Broin, 2002). Therefore, in *E. cherifiensis* only, the first three alveoli take part in the construction of the spatulated portion of the mandible. Also, the interalveolar spacing is like that observed in *S. hartti*.

The anterior region of the mandible has features that can be considered as homologues among different specimens (Fig. 10), such as the disposition and size of the alveoli and the expansions on the anterior portion of the dentary. Regarding the size of the first four alveoli in *Sarcosuchus* spp., *Sunosuchus phuwiangensis* and *Chalawan thailandicus*, they have the first two pairs of alveoli smaller than the third and fourth ones. In *Pholidosaurus purbeckensis* and *Fortignathus felixi*, the first four alveoli are the same size. *Turanosuchus aralensis* and PRC102-143 (referred to *C. thailandicus*) present the first three alveoli with similar size and a fourth one that is the larger. Finally, among the analysed species, *Elosuchus cherifiensis* has the first two alveoli as the larger ones and the third one is smaller in comparison to the others.

The positioning of the first four alveoli shows variations that are shared among the analysed species. *Sarcosuchus* and the specimen PRC102-143 (referred to *C. thailandicus*) have aligned alveoli that form an arch, in which the first two pairs are more anteriorly relative to the other two, and show a diastema between the fourth and fifth alveoli. *Sunosuchus phuwiangensis*, *Fortignathus felixi* and *Pholidosaurus purbeckensis* have the first alveoli that are more medially displaced than the others, while the second and posterior ones linearly displaced passing the lateral margin of the first alveoli. In *Turanosuchus aralensis* the first four alveoli aligned in the form of a closed arch (Fig. 10I) in relation with specimen CAS42-20 (Fig. 10H). The holotype of *Chalawan thailandicus* (CAS42-20) has the first four dentary alveoli forming an arch (Fig. 10H), while the referred specimen PRC102-143 of *Chalawan thailandicus* has the first three alveoli forming an open arch, with the fourth alveolus aligned with the lateral margin of the third one (Fig. 10C). *Elosuchus cherifiensis* has the second and third alveoli laterally displaced in relation to the first and fourth ones, which are mesiodistally aligned.

Regarding the lateral expansion on the anterior portion of the mandible, it is possible to observe important variation. The genus *Sarcosuchus* and the species *Chalawan thailandicus* (observed in CAS42-20 and PRC102-143) have a lateral expansion restricted to the region of first four alveoli. *Sunosuchus phuwiangensis* has a lateral expansion that is restricted to the third and fourth alveoli and in *Turanosuchus aralensis* the lateral expansion is placed at the fourth alveolus, which grows gradually from the first to the fourth alveoli. On the other hand, *Pholidosaurus purbeckensis* has a lateral linear margin on the dentary. *Fortignathus felixi* has only a slight expansion on the lateral margin of the dentary, which ranges from the fourth to sixth alveoli.

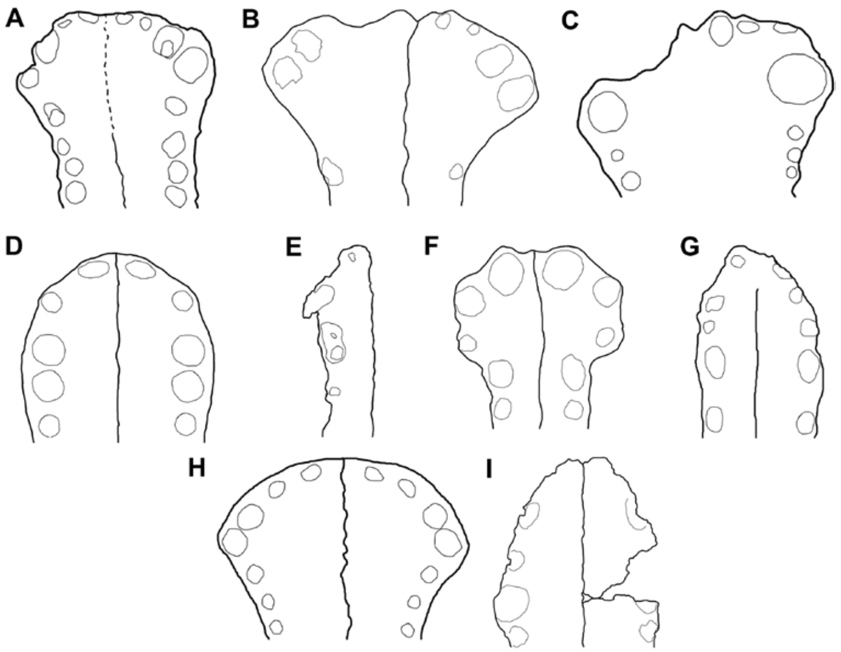

Figure 10. Schematic drawings of the anterior end of the mandible in selected pholidosaurids. All drawings in dorsal view. A, *Sarcosuchus hartti* (BMNH R3423). B, *Sarcosuchus imperator* from Buffetaut & Taquet (1977). C, PRC102-143 referred to *C. thailandicus* from Martin *et al.* (2013). D, *Sunosuchus phuwiangensis* from Buffetaut & Ingavat (1983). E, *Pholidosaurus purbeckensis* from Martin *et al.* (2016). F, *Elosuchus cherifiensis* from de Broin (2002). G, *Fortignathus felixi* from Young *et al.* (2017). H, CAS42-20 holotype of *Chalawan thailandicus* from Buffetaut & Ingavat (1984). I, *Turanosuchus aralensis* from Halliday *et al.* (2015). Not to scale.

Elosuchus cherifiensis has a lateral expansion that is restricted to the first three alveoli.

The morphology of the osteoderm (BMNH R3224) suggests that this element comes from the anterior portion of the dermal shield. The osteological features described for this bone allows its assignment to the genus *Sarcosuchus*. However, based on indirect evidence, like species distribution, it is reasonable to suggest that it belongs to *Sarcosuchus hartti*, but for now the material will remain identified as *Sarcosuchus* sp. until new *S. hartii* material is recovered. Also, there are important features that distinguish this osteoderm from those described for *Sarcosuchus imperator* (Sereno *et al.*, 2001). The Brazilian species shows straighter articular margins, lateral margins that are medially inclined and slightly convex, and an anterolateral process that follows this orientation, a smooth dorsal crest that is aligned with the anterior process. The crest does not have the lateral inclination observed in *Sarcosuchus imperator*. Those features also differentiate this osteoderm from those described for *Elosuchus cherifiensis* (de Broin, 2002) and *Fortignathus felixi* (de Broin, 2002; Martin *et al.*, 2016), which have the crest more medially displaced and no anterior process developed. The mid-dorsal osteoderms described for *Sunosuchus junggariensis* Wu *et al.*, 1996 differ from *S. hartti* in having a rectangular shape with a bowed lateral margin, the ornamentation is more regularly composed by circular pits, and only the anterior articular surface is smooth, which forms a straight platform that ends on a spine-like anterior smooth projection (Wu *et al.*, 1996). The osteoderms referred as *Sunosuchus* (in Averianov, 2000 and Maisch *et al.*, 2003) differs from *S. hartti* in being thin bone structures with a square shape with regular and deep pits in its ornamentation. Despite *Terminonaris robusta* osteoderms being rectangular in shape and having the anterolateral process, those osteoderms differ from BMNH R3224 mainly in the dorsal smooth surface without any pits. As presented by Souza & Campos (2018), BMNH R3224 differs from the newly described osteoderm (MCT 1860-R) recovered from Tucano Sul Sub-basin (Bahia). The osteoderm ONM NG K 3 attributed to *Sarcosuchus* from Early Cretaceous of Tunisia (Dridi, 2018) is similar to BMNH R3224 in all described features.

SARCOSUCHUS PALAEOECOLOGY

Sarcosuchus species are gigantic semi-aquatic crocodyliforms that inhabited fluvial environments during the Early Cretaceous of what is today known as

South America and Africa (Buffetaut & Taquet, 1977; Sereno *et al.*, 2001; Dridi, 2018). The two *Sarcosuchus* species share the same general rostral and mandibular morphology. They have long and wide snouts that are dorsoventrally compressed and, at least in adult specimens, also show well-marked lateral expansions of the anterior ends. The dentition is heterodont on both the upper and lower jaws, with anterior caniniform teeth and small, rounded and robust posterior teeth. A general overbite occlusion pattern is inferred for both species, with interlocking teeth from the premaxilla to at least the level of the seventh alveoli. An interocclusal pattern on the posterior region is suggested by the presence of tooth-marks on the space between the alveoli. Sereno *et al.* (2001) pointed out that despite some morphological adaptations that are traditionally related to primary ichthyophagy feeding in extant Crocodylia, *Sarcosuchus imperator* may have had a more generalized diet, including large terrestrial prey, such as dinosaurs. A similar predatory behaviour is observed in *Crocodylus niloticus* Laurenti, 1768, which feeds on large mammals. Despite the several morphological similarities shared with *Sarcosuchus hartti*, this feeding behaviour was never directly proposed for the Brazilian species. However, some complementary comments are necessary to refine the Sereno *et al.* (2001) proposition and construct a more robust palaeoecological hypothesis for the behaviour of *Sarcosuchus* species. *Crocodylus niloticus* is a large-sized extant Crocodylia that in adult life ambushes big mammals, dragging them underwater to drown and then tears them apart by a 'death roll' movement (Pooley & Gans, 1976). Blanco *et al.* (2015) analysed the allometry and skull strength of several extant Crocodylia and other fossil species. Their results suggest that *Sarcosuchus imperator* was not able to perform the 'death roll' movement, contra to what was proposed by Sereno *et al.* (2001). So, the feeding strategy of preying on large-sized dinosaurs, larger than *Sarcosuchus* itself, is unlikely if the 'death roll' movement is a requirement for that strategy (Blanco *et al.*, 2015; and references therein). Nevertheless, smaller dinosaurs would still be a potential prey for *Sarcosuchus* species. The feeding behaviour of these extinct animals is probably more like that observed in *Tomistoma schlegelii* (Müller, 1838) or *Mecistops cataphractus* (Cuvier, 1825), which prey on animals smaller than themselves, swallowing them completely without the need of applying a 'death roll' movement (Blanco *et al.*, 2015).

There are some features in both *Sarcosuchus* species that could support other interesting behaviours. The heterodont dentition suggests a facultative durophagy, as observed among large-sized Alligatoroidea, such as *Alligator mississippiensis* (Daudin, 1802) and the extinct *Deinosuchus riograndensis* (Colbert & Bird, 1954) (Pooley, 1989; Schwimmer, 2002). In this way, *Sarcosuchus* could be able to prey on turtles and crush large bones of carcasses. Another interesting feature shared by both species of *Sarcosuchus* is the ontogenetic modifications observed on the lateral projections of both the dentary and the premaxilla, which was illustrated by Buffetaut & Taquet (1977), and probably imply in a differential dentition pattern observed among juveniles and adults specimens (e.g. Erickson *et al.*, 2003). The ontogenetic changes suggest the presence of niche partitioning, a well-known phenomenon observed in extant Crocodylia, with juveniles preying on insects, crustaceans, mollusks and small fish, while adults prey on large terrestrial and aquatic animals, such as mammals, turtles and big fish, but also carcasses (e.g. Blanco *et al.*, 2015).

The development of different kinds of long snouts in the evolutionary history of Crocodyliformes and other vertebrates remains an undergoing field of research to understand the real natural pressures that positively select for those modifications (see: Walmsley *et al.*, 2013). Also, the adult modifications on the rostrum of *Sarcosuchus* are a feature in need of explanation and that requires more specific morphometrics and strength analyses.

PHYLOGENETIC AFFINITIES

The phylogenetic relationships of Neosuchia is one of the most important issues regarding the evolution of crocodylomorphs, yet much of the effort in understanding the morphological variation within the major clades is still in progress (Pol *et al.*, 2009; Turner, 2015). One classic example is the 'longirostrine problem', i.e. the close affinities of Thalattosuchia with other long-snouted crocodylomorphs, such as the dyrosaurids and pholidosaurids, within the clade of Mesoeucrocodylia (Clark, 1994). The derived position of the group is far from being considered a consensus in the literature and several phylogenetic analyses place them either as basal mesoeucrocodylians or outside Crocodyliformes (e.g. Sereno *et al.*, 2001; Young & Andrade, 2009; Parrilla-Bel *et al.*, 2013; Wilberg, 2015). The 'neosuchian hypothesis' for the positioning of thalattosuchians seems to be largely an effect of taxon and character sampling, which also influences the interpretation of character evolution in other species (Wilberg, 2015). For this reason, the alternate 'non-neosuchian hypothesis' is used in the present study with the a priori exclusion of Thalattosuchia from the phylogenetic analysis. This scenario provides new insights in the evolution and biogeography of 'pholidosaurids' and closely related taxa like the dyrosaurids and 'goniopholidids' (Fig. 9).

There are three main competing hypotheses for the higher relationships of Pholidosauridae. The first one supports a closer affinity with the Dyrosauridae (e.g. Sereno *et al.*, 2001; Pol *et al.*, 2009; Fortier *et al.*, 2011; Montefeltro *et al.*, 2013; Halliday *et al.*, 2015; Turner, 2015; Young *et al.*, 2017; Adams *et al.*, 2017; Schwarz *et al.*, 2017). Andrade *et al.* (2011) proposed a redefinition of the name Tethysuchia for this clade, which was composed of *Pholidosaurus purbeckensis* and *Dyrosaurus phosphaticus* (Thomas, 1839), their common ancestor and all its descendants. Tethysuchia was originally created by Buffetaut (1982) as an infraorder comprising a single family, the Dyrosauridae. This arrangement recognized the anatomical distinctiveness of dyrosaurids in comparison to other longirostrine taxa, especially teleosaurids and pholidosaurids (Buffetaut, 1982). Goniopholidids are usually recovered as more closely related to Eusuchia in this 'pholidosaurid-dyrosaurid' hypothesis (e.g. Jouve, 2009; Pol *et al.*, 2009).

The second hypothesis favours a relationship between Pholidosauridae and a paraphyletic arrangement of 'goniopholidids' (Martin & Buffetaut, 2012). This clade was named Coelognathosuchia by Martin *et al.* (2014), but as observed by Young *et al.* (2014) the absence of dyrosaurid taxa in the analyses of Martin & Buffetaut (2012) and Martin *et al.* (2014) means that the monophyly of Pholidosauridae was not properly assessed in the light of all evidence. More than that, the exclusion of dyrosaurids shows that there is no support for a Coelognathosuchia clade as originally proposed by Martin *et al.* (2014). Rather the phylogenetic analyses performed by Martin *et al.* (2016) also supports the Tethysuchia hypothesis when dyrosaurids are included in the analysis (Martin *et al.*, 2016: fig. 10A). The Coelognathosuchia hypothesis is only recovered with the exclusion of Dyrosauridae from the dataset (Martin *et al.*, 2016: fig. 10D).

A third hypothesis shows a sister-taxon position between Pholidosauridae and Thalattosuchia (Lauprasert *et al.*, 2009), but it is important to notice that *Pholidosaurus* is the only pholidosaurid taxon included in this analysis. The Goniopholididae is monophyletic in this scenario, but the inclusion of a few derived taxa shows that the higher affinities inside Neosuchia are poorly resolved (Lauprasert *et al.*, 2009: fig. 3a, b). In any case, despite this arrangement was new at that time, the authors did not extensively discuss this hypothesis.

The results of the current analysis recovered the Tethysuchia hypothesis (Fig. 9; node 8). Dyrosauridae is a less inclusive clade nested in several 'pholidosaurid' lineages, being sister to the Elosuchidae. Goniopholididae is paraphyletic in its traditional sense. There are several smaller groups that are usually recognized as 'goniopholidids', and all of them are more closely related to Tethysuchia than to Eusuchia. This large clade, comprising tethysuchians and 'goniopholidids', was also recovered by Sereno *et al.* (2001) and Martin *et al.* (2016). These groups of animals have been classified together in the past, but in a gradist scheme. Nopcsa (1928) grouped the subfamilies Congosaurinae, Hyposaurinae, Goniopholinae, Pholidosaurinae and Bernissartinae in the family Goniopholidae. While most analyses find *Bernissartia* as more closely related to the Eusuchia (e.g. Sereno *et al.*, 2001; Halliday *et al.*, 2015; Turner, 2015; Adams *et al.*, 2017), that is not the case for the present hypothesis. *Bernissartia* together with *Theriosuchus* (i.e. Atoposauridae) is the sister-taxon of this large unnamed clade of 'goniopholidids' and tethysuchians. Hay (1930) recognizes the Goniopholidiformes as the group including both the Goniopholididae and the Pholidosauridae, which also encompassed the dyrosaurids. This name would be suitable in case the clade proves to be stable with time, especially after the inclusion of more dyrosaurid taxa in the analysis.

The phylogenetic hypothesis presented here shows important results regarding the relationships among pholidosaurids, because it includes the higher number of such taxa (nine species), together with that of Young *et al.* (2017). Other relevant hypotheses are those of Fortier *et al.* (2011) and Turner (2015), each with six species. All those more complete analyses recovered a paraphyletic 'Pholidosauridae', except for Fortier *et al.* (2011). There are two sister-clades of pholidosaurids in this latter hypothesis: the first unites *Pholidosaurus* and *Sarcosuchus* + *Terminonaris* and the second *Meridiosaurus* and *Elosuchus* + *Oceanosuchus*. Most phylogenetic hypotheses show *Pholidosaurus purbeckensis* as more distantly related to the other 'pholidosaurids', which usually are the sister-taxon of the dyrosaurids (e.g. Sereno *et al.*, 2001; Halliday *et al.*, 2015; Turner, 2015; Young *et al.*, 2016; Adams *et al.*, 2017). In the current hypothesis, *P. purbeckensis* comprises a clade with *Khoratosuchus jintasakuli* Lauprasert *et al.*, 2009 (a putative 'advanced neosuchian'), *Oceanosuchus boecensis* and *Kansajsuchus extensus* Efimov, 1975 (a putative 'goniopholidid'). This latter clade, which is sister to the other tethysuchians (i.e. the other 'pholidosaurids' and Dyrosauridae) is considered here to be Pholidosauridae *sensu stricto* (Fig. 9; node 9). Interestingly, the genus *Pholidosaurus* is paraphyletic in the analysis of Young *et al.* (2017).

Our novel analysis shows a second large clade inside Tethysuchia with *Meridiosaurus valliparadisi* as the sister-species of the *Sarcosuchus* spp., plus the group of *Terminonaris robusta*, which is sister to Elosuchidae plus Dyrosauridae. This new clade is here named Tethysuchoidea (Fig. 9; node 10). In some hypotheses, *M. valliparadisi* shows close affinities with *Elosuchus*

(Fortier *et al.*, 2011; Turner, 2015; Adams *et al.*, 2017). However, as observed on the current analysis and others (e.g. Halliday *et al.*, 2015; Young *et al.*, 2017), this is only correct when *Vectisuchus leptognathus* is absent. Also the close affinities between Elosuchidae and Dyrosauridae is shown here. Regarding the relationship of the *Sarcosuchus* species, there is little doubt that both species are sister-taxa, even though the inclusion of *S. hartii* in phylogenetic analysis is rare (e.g., Andrade *et al.*, 2011). Most analyses show *T. robusta* as the sister-taxon of *S. imperator* when it is the sole species of the genus in an analysis (Sereno *et al.*, 2001; Fortier *et al.*, 2011; Turner, 2015; Martin *et al.*, 2016, Adams *et al.*, 2017). Notable exceptions are close relationships with *Chalawan thailandicus* (Young *et al.*, 2017) or Elosuchidae (Halliday *et al.*, 2015). However, *S. hartii* is missing from both analyses.

As discussed above, Elosuchidae was found to be the sister-taxon of the Dyrosauridae. *Chalawan thailandicus* is the only putative 'pholidosaurid' that is recovered outside Tethysuchia in the current phylogenetic analysis. It is sister to another Thai taxon, *Siamosuchus phuphokensis* Lauprasert *et al.*, 2007, and together they form a clade with the Chinese *Sunosuchus miaoi*. The affinities of the several 'goniopholidid' taxa are complex, but there are certain groups that are more closely related to the tethysuchians than others.

BIOGEOGRAPHY

Regarding the biogeography of the genus *Sarcosuchus* and the related species, some hypotheses are proposed. The phylogenetic inference made by Fortier *et al.* (2011) resulted in the following topology for the group: (Thalattosuchia (Dyrosauridae ((*Pholidosaurus* (*Sarcosuchus*, *Terminonaris*)) (*Oceanosuchus* (*Meridiosaurus, Elosuchus*))))). Based on this result, together with the occurrence of *Anglosuchus geofroyi* (Owen, 1884) and *A. laticeps* (Owen, 1884) from the Bathonian of England (both in Mook, 1942), and *Crocodilaemus robustus* Jourdan, 1857 from the Kimmeridgian of France, Fortier *et al.* (2011) defends that the common ancestor of Dyrosauridae and Pholidosauridae is from the Middle Jurassic of Europe. However, the oldest known fossil record for Pholidosauridae (e.g. Caroll, 1988; Fortier *et al.*, 2011) are species in need of redescriptions to elucidate their relationship with Pholidosauridae. Therefore, those species were not included in the phylogenetic and biogeographical discussions. Also, Fortier *et al.* (2011) defends that Pholidosauridae remained in Europe until the Late Cenomanian with *Terminonaris* (Buffetaut & Wellnhofer, 1980) and points out three dispersion routes for the clade: (1) a dispersion for North Africa and eastern South America during Toarcian–Kimmeridgian, which results on the occurrence of *Sarcosuchus* species, (2) a second dispersion for Africa and South America during Kimmeridgian–Late Albian explaining, respectively, the species *Elosuchus* and *Meridiosaurus* and (3) the last dispersion proposed was between the *Terminonaris* species from Europe to North America during the Late Cenomanian–Early Turonian, being North America the last place inhabited by Pholidosauridae.

The phylogenetic inference made by Martin *et al.* (2014) resulted in the following relationship of Pholidosauridae and its sister-group: (*Siamosuchus phuphokensis*, *Goniopholis simus*, *Goniopholis baryglyphaeus* (*Pholidosaurus* sp. (*Sarcosuchus imperator*, *Chalawan thailandicus*, *Elosuchus cherifiensis*))). Based on this result, Martin *et al.* (2014) proposed a worldwide distribution for the group in the Late Jurassic–Early Cretaceous interval, probably resulting from the conquest of north and south portions of the Tethys Ocean, which connect these regions. Also, they observe the relationship of *Chalawan thailandicus* from Thailand with South America and Africa as an exception for the region due to dispersal events during the Jurassic–Aptian, because all other strata and crocodilian records from Thailand are more closely related to the Asian fauna (Fernandez *et al.*, 2010).

Both analyses discussed above include species that are not present in the phylogenetic inference (e.g. *Sarcosuchus hartti*), which weakens the methodology of inferring biogeographical hypotheses from topology in a consensus cladogram. Based on the present topology hypotheses (Fig. 11), and in the calibration of the specimens analysed, a new biogeographical hypothesis with be proposed based on new evidence to better explain the distribution of *Sarcosuchus* and its allies.

The present phylogenetic analysis results in two biogeographical hypotheses for the species in the clade ((*Sunosuchus shartegensis* + *Calsoyasuchus*) (*Sunosuchus miaoi* (*Siamosuchus* + *Chalawan*))) (Tethysuchia)). The first hypothesis is observed in minimum-length trees 1, 3, 5, 6, 7, 9 and 11 (Fig. 11A), which presents the following topological relationship ((*Sunosuchus miaoi* (*Siamosuchus* + *Chalawan*)) ((*Sunosuchus shartegensis* + *Calsoyasuchus*) (Tethysuchia))). In this phylogenetic scenario, the clade (*Sunosuchus miaoi* (*Siamosuchus* + *Chalawan*) is composed of Asiatic fluvial species from the Late Jurassic to the Early Cretaceous, with the Thai species the sister to the Chinese species. The clade ((*Sunosuchus shartegensis* + *Calsoyasuchus*) (Tethysuchia)) has a more complex biogeographic scenario where two fluvial species from the Jurassic of Mongolia and North America are sister species. This phylogenetic context is difficult to explain in a

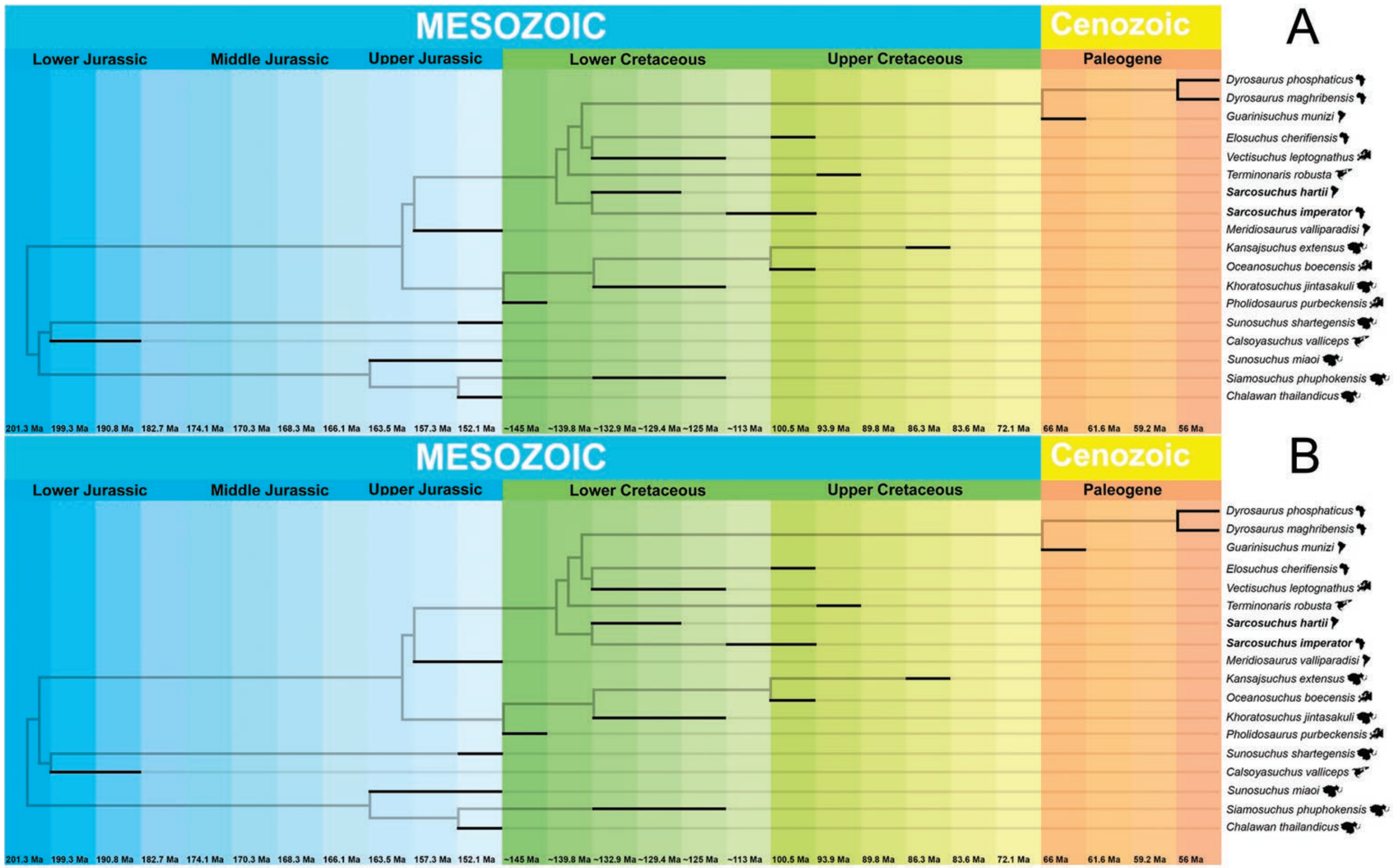

Figure 11. Detail of the Tethysuchia clade and their sister-clade from the consensus cladogram. The two phylogenetic hypotheses that originated the polytomy in the consensus cladogram: A, hypothesis two: *Sunosuchus shartegensis*, *Calsoyasuchus*, *Sunosuchus miaoi*, *Siamosuchus phuphokensis* and *Chalawan thailandicus* as a clade sister to Tethysuchia. B, hypothesis one: *Sunosuchus shartegensis* and *Calsoyasuchus* as sister-group of Tethysuchia.

biogeographical scenario for the common ancestor of Tethysuchia.

The second hypothesis is based on the topological relationship observed in the minimum-length trees 2, 4, 8, 10 and 12 (Fig. 11B), which is (((*Sunosuchus shartegensis* + *Calsoyasuchus*) (*Sunosuchus miaoi* (*Siamosuchus* + *Chalawan*))) (Tethysuchia)). The biogeographical hypothesis for the common ancestor of Tethysuchia remains doubtful. However, the main difference from the first hypothesis is the clade ((*Sunosuchus shartegensis* + *Calsoyasuchus*) (*Sunosuchus miaoi* (*Siamosuchus* + *Chalawan*))) representing an Asian clade with probably a posterior colonization of North America.

Even though it is complex to infer a biogeographical hypothesis for the common ancestor of Tethysuchia, its two clades have much less complicated scenarios. The Pholidosauridae clade contains species from the Early Cretaceous of Asia and Europe, with the European species related to marine environments and the Asian species related to fluvial/terrestrial environments. However, there is no evidences to infer if the common ancestor of this clade lived in Europe or Asia, nor if it was a marine or terrestrial species. On the other hand, the other clade of Tethysuchia includes both marine and fluvial species from the Late Jurassic to the Early Cretaceous of the Americas and Africa. The first species to diverge is the marine *Meridiosaurus* from the Late Jurassic of Uruguay, which is the sister-species of a clade that includes the genus *Sarcosuchus* and a clade of Elosuchidae + Dyrosauridae. In this context both fluvial *Sarcosuchus* species are from the Early Cretaceous of South America and Africa, being its cladogenesis, probably related with the early events of the break-up of Gondwana, as already proposed in earlier literature. The marine North American species of *Terminonaris* seems to be related to the North African taxa, such the ancestors of *Elosuchus*.

This new phylogenetic hypotheses enables the discussion of some interesting biogeographical scenarios, but further work is needed to provide better supported biogeographical hypotheses and to test these properly. This study is merely a contribution to future, more complete biogeographical studies.

CONCLUSION

Sarcosuchus hartii was a top predator that inhabited the fluvial areas near the continental edges of north-east Brazil during the Early Cretaceous. The fossil remains recovered from the Recôncavo Basin show that this is a taxonomically valid species. A unique pattern of anastomosed ornamentation on the enamel surface separates it morphologically from the African relative *Sarcosuchus imperator*. The inclusion of *S. hartii* in phylogenetic analyses is rare. It is included here where it is recovered as part of Tethysuchia, a large clade comprising of *Meridiosaurus* as the sister-species of *Sarcosuchus* plus the group of *Terminonaris*, which is sister to Elosuchidae and Dyrosauridae. The origin of *Sarcosuchus* species is likely related to a cladogenesis event that resulted from the break-up of Gondwana.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Supplemenatry Information 1. Systematic revision of the giant pholidosaurid *Sarcosuchus hartti* (Marsh, 1869) from the Recôncavo Basin (Early Cretaceous) of Bahia, northeastern Brazil.