

Evolutionary relationships and systematics of Atoposauridae (Crocodylomorpha: Neosuchia): implications for the rise of Eusuchia

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Atoposaurids are a group of small-bodied, extinct crocodyliforms, regarded as an important component of Jurassic and Cretaceous Laurasian semi-aquatic ecosystems. Despite the group being known for over 150 years, the taxonomic composition of Atoposauridae and its position within Crocodyliformes are unresolved. Uncertainty revolves around their placement within Neosuchia, in which they have been found to occupy a range of positions from the most basal neosuchian clade to more crownward eusuchians. This problem stems from a lack of adequate taxonomic treatment of specimens assigned to Atoposauridae, and key taxa such as *Theriosuchus* have become taxonomic ‘waste baskets’. Here, we incorporate all putative atoposaurid species into a new phylogenetic data matrix comprising 24 taxa scored for 329 characters. Many of our characters are heavily revised or novel to this study, and several ingroup taxa have never previously been included in a phylogenetic analysis. Parsimony and Bayesian approaches both recover Atoposauridae as a basal clade within Neosuchia, more stemward than coelognathosuchians, bernissartiids, and paralligatorids. Atoposauridae is a much more exclusive clade than previously recognized, comprising just three genera (*Alligatorellus*, *Alligatorium*, and *Atoposaurus*) that were restricted to the Late Jurassic of western Europe, and went extinct at the Jurassic/Cretaceous boundary. A putative Gondwanan atoposaurid (*Brillanceausuchus*) is recovered as a paralligatorid. Our results exclude both *Montsecosuchus* and *Theriosuchus* from Atoposauridae. *Theriosuchus* is polyphyletic, forming two groupings of advanced neosuchians. *Theriosuchus* (restricted to *Theriosuchus pusillus*, *Theriosuchus guimarotae*, and *Theriosuchus grandinaris*) spanned the Middle Jurassic to early Late Cretaceous, and is known from Eurasia and North Africa. Two Cretaceous species previously assigned to *Theriosuchus* (*Theriosuchus ibericus* and *Theriosuchus sympiestodon*) are shown to be nested within Paralligatoridae, and we assign them to the new genus *Sabresuchus*. The revised phylogenetic placement of *Theriosuchus* has several implications for our understanding of eusuchian evolution. Firstly, the presence of fully pterygoidean choanae, previously regarded as a defining characteristic of Eusuchia, is not found in some basal members of Eusuchia. However, eusuchians can be distinguished from *Theriosuchus* and other basal neosuchians in that their choanae are posteriorly positioned, with an anterior margin medial to the posterior edge of the suborbital fenestra. This feature distinguishes eusuchians from *Theriosuchus* and more basal neosuchians. Secondly, our refined understanding of *Theriosuchus* implies that this taxon possessed only amphicoelous presacral vertebrae, and therefore fully developed vertebral procœly is likely to have evolved only once in Crocodylomorpha, on the lineage leading to Eusuchia. These and other findings presented herein will provide an important framework for understanding the neosuchian–eusuchian transition.

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INTRODUCTION

Atoposaurids comprise a clade of extinct neosuchian crocodyliforms, often characterized by their differentiated dentition and diminutive body size (Owen, 1879; Joffe, 1967; Buscalioni & Sanz, 1990a). This group has a long history of study, with specimens first identified from Late Jurassic deposits in France and Germany in the mid-19th century (von Meyer, 1850, 1851). The current view is that atoposaurids were an important and diverse component of Eurasian Late Jurassic and Cretaceous terrestrial to semi-aquatic ecosystems, often with multiple sympatric lineages (e.g. Wellnhofer, 1971; Thies, Windolf & Mudroch, 1997; Martin, Rabi & Csiki, 2010; Lauprasert *et al.*, 2011; Tennant & Mannion, 2014). A number of discoveries indicate that atoposaurids might also have been present in the Jurassic and Cretaceous of Africa (Michard *et al.*, 1990; Flynn *et al.*, 2006; Haddoumi *et al.*, 2016) and North America (e.g. Cifelli *et al.*, 1999; Eaton *et al.*, 1999; Fiorillo, 1999).

TAXONOMIC COMPOSITION

Despite their long history of study, the taxonomic composition of Atoposauridae remains uncertain and many putative atoposaurid species have never been incorporated into a phylogenetic analysis. In an extensive revision of the taxonomy of atoposaurids, Wellnhofer (1971) recognized three genera from the Late Jurassic of continental western Europe (*Alligatorellus*, *Alligatorium*, and *Atoposaurus*), and followed previous authors by including *Theriosuchus* from the UK (Joffe, 1967), *Shantungosuchus* from China (Young, 1961), and *Hoplosuchus* from North America (Gilmore, 1926), in Atoposauridae (see also Steel, 1973). *Alligatorium* comprises the type species *Alligatorium meyeri* (Gervais, 1871), and Wellnhofer (1971) also considered the referred species *Alligatorium depereti* (Vidal, 1915), *Alligatorium franconicum* (Ammon, 1906), and *Alligatorium paintenense* (Kuhn, 1961) to be valid, although all specimens of the latter two species were lost or destroyed during the Second World War. Subsequently, the Spanish species *Alligatorium depereti* was considered to be distinct enough to warrant its own genus, *Montsecosuchus* (Buscalioni & Sanz, 1988, 1990a,b). Efimov (1976) described the putative atoposaurid *Karatausuchus* from Kazakhstan, but Buscalioni & Sanz (1988) subsequently removed this taxon, as well as *Hoplosuchus* and *Shantungosuchus*, from Atoposauridae. Benton & Clark (1988) considered only *Alligatorium* to be valid amongst atoposaurid taxa from the Late Jurassic of France and Germany, regarding *Alligatorellus* and *Atoposaurus* as juvenile individuals of

this taxon. Benton & Clark (1988) also followed Joffe (1967) in considering *Theriosuchus* to represent an atoposaurid. Buscalioni & Sanz (1990a,b) largely followed Benton & Clark (1988), also accepting *Alligatorellus*, but not *Atoposaurus*, as valid. Most recently, Tennant & Mannion (2014) argued that *Alligatorellus*, *Alligatorium*, and *Atoposaurus* all represent valid atoposaurid genera, with each comprising two species. These authors also suggested that *Alligatorium paintenense* is likely to be a junior synonym of *Alligatorium franconicum*. In addition to the type species of *Theriosuchus* (*Theriosuchus pusillus*; Owen, 1878a, 1879), four additional species have subsequently been named: *Theriosuchus guimarotae* (Schwarz & Salisbury, 2005), *Theriosuchus grandinaris* (Lauprasert *et al.*, 2011), *Theriosuchus ibericus* (Brinkmann, 1989), and *Theriosuchus sympiestodon* (Martin *et al.*, 2010, 2014a). Some authors have further taken the view that *Theriosuchus* is distinct enough from all other atoposaurids to constitute its own clade, Theriosuchidae (Kälin, 1955; Buffetaut, 1982, 1983), but this taxonomic assignment has not been widely adopted. Two additional taxa have also been referred to Atoposauridae, with Michard *et al.* (1990) describing the first putative Gondwanan atoposaurid (*Brillanceausuchus babouriensis*) from Cameroon, and *Pachycheilosuchus trinquei* described from North America (Rogers, 2003). However, subsequent studies have placed *Pachycheilosuchus* outside of Atoposauridae, and it is likely to be a member of Hylaeochampsidae (e.g. Buscalioni *et al.*, 2011).

ATOPOSAURIDS IN TIME AND SPACE

Based on our current understanding of Atoposauridae, the oldest diagnostic remains are: (1) a partial dentary from the Middle Jurassic (late Bajocian–Bathonian) of the Isle of Skye, UK (Young *et al.*, 2016), ascribed to *Theriosuchus* sp.; (2) isolated tooth crowns from the late Bathonian of France and the UK (Evans & Milner, 1994; Kriwet, Rauhut & Gloy, 1997; Knoll *et al.*, 2013); (3) crocodyliform teeth, possibly referable to an atoposaurid, from the Bathonian Grand Causses of France (Knoll *et al.*, 2013; Knoll & López-Antoñanzas, 2014); and (4) teeth and mandibular and postcranial remains from the Bathonian of Madagascar (Flynn *et al.*, 2006) and Morocco (Haddoumi *et al.*, 2016) (Fig. 1). These remains indicate that atoposaurids had attained their characteristic small body size and heterodont dentition, along with a broad geographical distribution, by the Middle Jurassic.

In addition to the presence of *Alligatorellus*, *Alligatorium*, *Atoposaurus*, and *Montsecosuchus* in the Late Jurassic and Early Cretaceous of western Europe, *Theriosuchus* is known from a number of Late

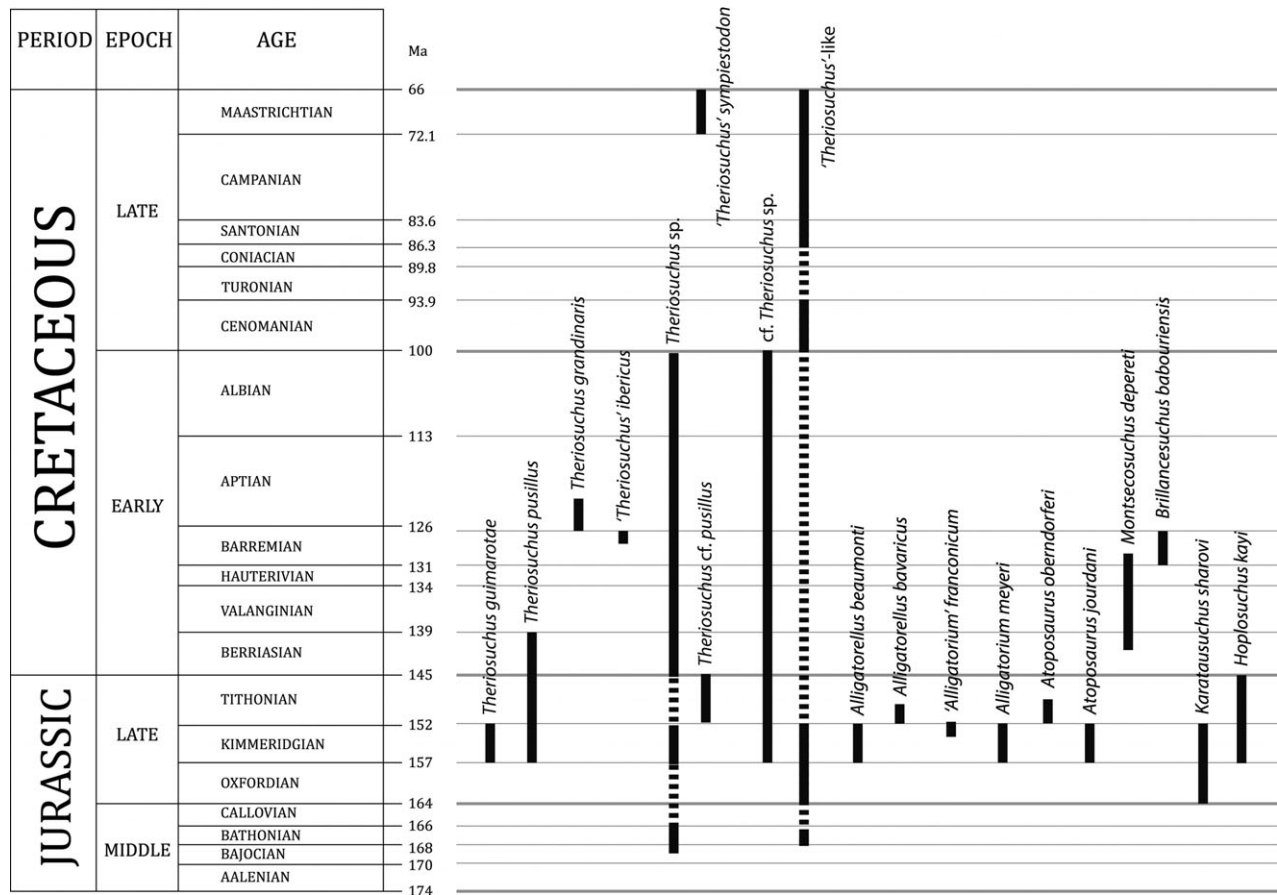


Figure 1. Stratigraphic ranges for taxa previously attributed to Atoposauridae. The dashed lines represent the inferred presence of lineages.

Jurassic and Cretaceous localities in Europe (e.g. Owen, 1879; Buscalioni & Sanz, 1984, 1987a,b; Buscalioni, 1986; Salisbury, 2002; Martin *et al.*, 2010, 2014a; Salisbury & Naish, 2011; Tennant & Mannion, 2014; Young *et al.*, 2016). Reports based on isolated teeth also place *Theriosuchus* in the middle Cretaceous of North America (Pomes, 1990; Winkler *et al.*, 1990; Cifelli *et al.*, 1999; Eaton *et al.*, 1999; Fiorillo, 1999), alongside the putative atoposaurid *Pachycheilosuchus* (Rogers, 2003). Remains of *Theriosuchus* are also found in the latest Jurassic to Early Cretaceous of Thailand (Lauprasert *et al.*, 2011) and China (Wu, Brinkmann & Russell, 1996). In addition, *Brillancesuchus* from western Africa (Michard *et al.*, 1990) is the only putative Cretaceous Gondwanan occurrence of Atoposauridae, along with the fragmentary and poorly known Middle Jurassic remains mentioned by Flynn *et al.* (2006) and Hadoumi *et al.* (2016). Finally, fragmentary putative atoposaurid remains from the Eocene of Yemen would mean that Atoposauridae passed through the end-Cretaceous mass extinction (Stevens *et al.*, 2013).

EVOLUTIONARY RELATIONSHIPS

The monophyly of Atoposauridae has not been tested at a low taxonomic level since Buscalioni & Sanz (1990a), and even species attributed to *Theriosuchus* have not been conclusively demonstrated to form a monophyletic genus. This is partly because of the taphonomy and preservation of these specimens, whereby incompleteness and the mode of preservation (i.e. dorsal flattening) restricts assessment of important characters. Furthermore, the generally small body size of atoposaurids has led to an overall lack of clarity in distinguishing amongst plesiomorphic, juvenile, and paedomorphic characteristics (Joffe, 1967; Buffetaut, 1982; Clark, 1986; Buscalioni & Sanz, 1988; Tennant & Mannion, 2014), although the ontogeny of *Theriosuchus* is reasonably well understood (Joffe, 1967; Schwarz & Salisbury, 2005; Martin *et al.*, 2014a).

Most phylogenetic analyses recover atoposaurids as non-eusuchian neosuchians, part of the important crocodyliform lineage that includes living crocodiles (e.g. Benton & Clark, 1988; Buscalioni & Sanz, 1990a,b; Salisbury *et al.*, 2006; Brochu *et al.*, 2009;

Pol & Gasparini, 2009; Martin *et al.*, 2010; Adams, 2013, 2014; Sertich & O'Connor, 2014). Whereas some analyses have found Atoposauridae to be outside of Neosuchia (e.g. Sereno *et al.*, 2003), this has not gained support from more recent studies. Recent analyses consider atoposaurids to be within Neosuchia, but their position differs greatly, varying amongst: (1) basal to Goniopholididae and other neosuchians when investigating higher neosuchian or eusuchian relationships (e.g. Pol & Norell, 2004a; Gasparini, Pol & Spalletti, 2006; Turner, 2006; Fortier & Schultz, 2009; Pol, Turner & Norell, 2009; Figueiredo *et al.*, 2011; Adams, 2014) (Fig. 2A); (2) in an uncertain position within basal Neosuchia (Pol & Apesteguía, 2005; Larsson & Sues, 2007; Turner & Buckley, 2008; Lauprasert *et al.*, 2009; Martin *et al.*, 2010); (3) just outside of Eusuchia (Rogers, 2003; Salisbury *et al.*, 2006; Fig. 2B); or (4) as the sister group to Paralligatoridae within Eusuchia (Fig. 2C) that, together with Hylaeochampsidae, comprises the sister group to crown Crocodylia (Turner, 2015; Turner & Pritchard, 2015).

The first analysis of atoposaurid inter-relationships recovered two subclades comprising (*Montsecosuchus* + *Theriosuchus*) and (*Alligatorium* + *Alligatorellus*) (Buscalioni & Sanz, 1988; Fig. 3A), although the position of *Montsecosuchus* was unstable. Karl *et al.* (2006) recovered the same topology, but also included *Atoposaurus*, which they placed as the most basal atoposaurid. However, these two studies predated the identification of several new species of *Theriosuchus*. Bronzati, Montefeltro & Langer (2012) constructed a crocodyliform supertree that included *Alligatorium*, *Alligatorellus*, *Atoposaurus*, *Montsecosuchus*, *Pachycheilosuchus*, and *T. guimarotae*, *T. pusillus*, and *T. sympiestodon*, placing them all within Atoposauridae, as the sister group to Goniopholididae and more advanced neosuchians (Fig. 3B). However, they were unable to fully resolve the internal relationships of the group beyond finding *Alligatorellus* and *Atoposaurus* to be sister taxa, and that the three *Theriosuchus* species formed a clade. Turner (2015) included *T. guimarotae*, *T. pusillus*, and *T. sympiestodon*, finding them to be paraphyletic with respect to *Alligatorium* (Fig. 3C).

Consequently, the full plethora of putative atoposaurid species has never previously been included in any phylogenetic analysis. In studies that have included atoposaurids, *Montsecosuchus* and the putative atoposaurids *Brillianceausuchus* and *Karatausuchus* have been almost completely disregarded. As a result, neither the phylogenetic position of Atoposauridae within Neosuchia, nor its intrarelationships are clear at present.

Here, we undertake a full systematic reassessment of all species previously assigned to Atoposauridae,

determining the composition and internal relationships of the group, as well as its position within Neosuchia. We present a new phylogenetic character matrix, analysed using parsimony and Bayesian approaches. Revised diagnoses are provided for all genera and species assigned to Atoposauridae, as well as the first phylogenetic definition for the clade, and we discuss the taxonomic and phylogenetic status of putative atoposaurids. Lastly, we discuss the implications of our results for the evolution of Eusuchia.

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York City, New York, USA; BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; CHE, Cherves-de-Cognac Collection, Musée d'Angoulême, France; CM, Carnegie Museum, Pittsburgh, Pennsylvania, USA; DFMMh, Dinosaurier-Freilichtmuseum Münchshagen, Germany; FGGUB, Faculty of Geology and Geophysics, University of Bucharest, Bucharest, Romania (LPB, Laboratory of Paleontology); GZG, Geowissenschaftliches Museum, Georg-August-Universität, Göttingen, Germany (BA, Max Ballerstedt collection; STR, stratigraphic collection); IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MCDRD, Muzeul Civilizatxiei Dacice si Romane, Deva, Romania; MfN, Museum für Naturkunde, Berlin, Germany (MB.R, Reptile Collection); MGB, Museo de Geologia del Ayuntamiento de Barcelona, Barcelona, Spain; MHNL,* Muséum d'Histoire Naturelle, Lyon, France; MO, Musée de l'île d'Oléron, Saint-Pierre-d'Oléron, France; MTM, Hungarian Natural History Museum, Budapest, Hungary; NHMUK, Natural History Museum, London, UK; NMS, National Museums Scotland, Edinburgh, UK; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; PMC, Laboratoire de Paléontologie des Vertébrés de l'Université Pierre et Marie Curie; PRC, Palaeontological Research and Education Centre, Mahasarakham University, Thailand; SMU, Southern Methodist University, Dallas, Texas, USA; TM, Teyler's Museum, Haarlem, Netherlands; UP, Université de Poitiers, Poitiers, France; UT, University of Texas, Austin, Texas, USA.

MATERIAL AND METHODS

TAXON SAMPLING

All previously identified atoposaurid species were included (Table 1), with the exception of *Karatausuchus sharovi* (Efimov, 1976), which we were not able

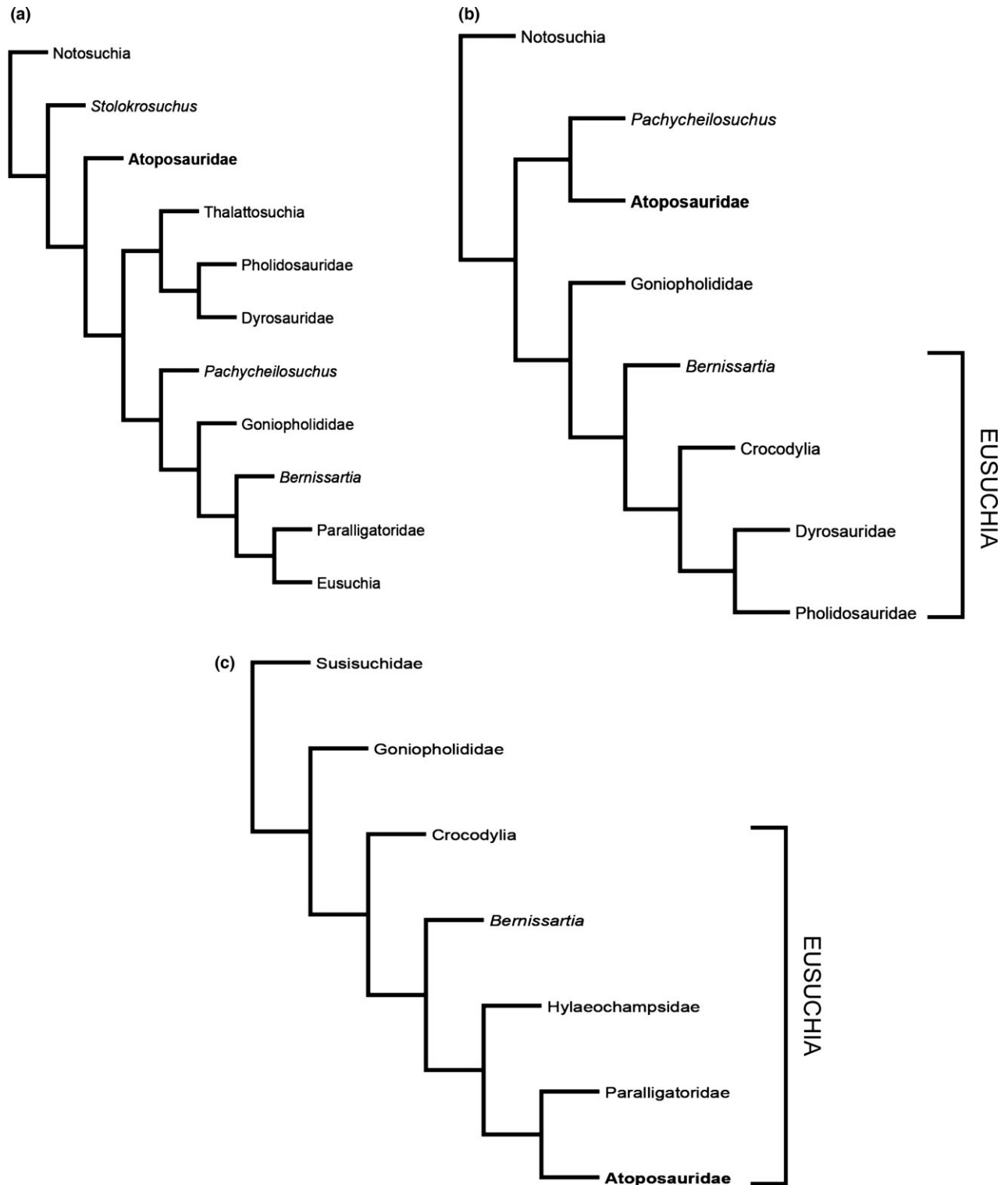


Figure 2. Previously recovered inter-relationships between Atoposauridae and other major crocodyliform clades: (A) Adams (2014); (B) Rogers (2003); (C) Turner & Pritchard (2015).

to observe directly, and for which there is insufficient morphological data published to adequately score it from the literature. We also excluded

Shantungosuchus chuhsienensis (Young, 1961) for similar reasons, and because this taxon is likely to be either a protosuchian-grade crocodyliform

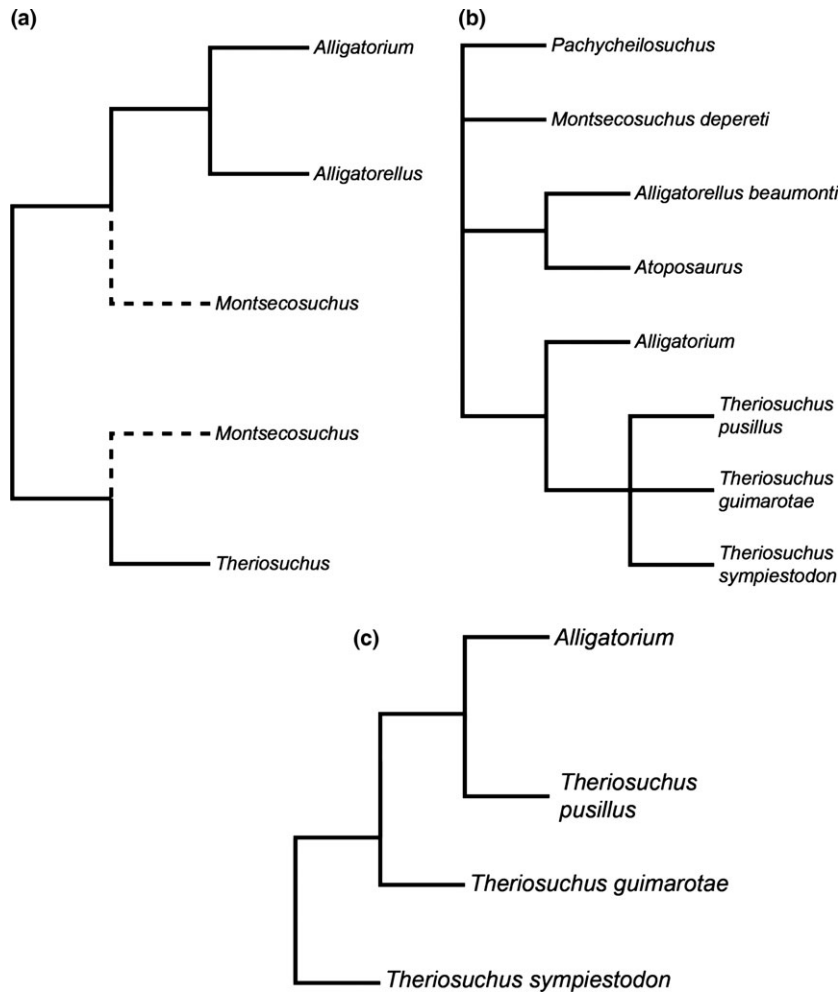


Figure 3. Previously recovered intrarelationships within Atoposauridae. (A) Buscalioni & Sanz (1988); (B) Bronzati *et al.* (2012); (C) Turner (2015).

(Wu, Brinkmann & Lu, 1994) or member of Shartegosuchidae (Clark, 2011). All personal observations of specimens were made by J. P. T. Measurements and ratios of key morphological characteristics are provided in Tables 2 and 3, respectively. For specimens not personally observed, measurements were acquired using reported values and via ImageJ (<http://imagej.nih.gov/ij/>; Schneider, Rasband & Eliceiri, 2012) from published photographs of specimens. Most measurements and ratios provided are given to two decimal places and based on the holotype specimens, as opposed to multiple specimens. As such, we do not provide ratio ranges for species. In all cases, measurements represent the maximum distance for each element measured between the proximal-most and distal-most points.

We included both species of *Atoposaurus* (*Atoposaurus jourdani* and *Atoposaurus oberndorferi*) and *Alligatorellus* (*Alligatorellus bavaricus* and

Alligatorellus beaumonti), as well as *Alligatorium meyeri*, and *Alligatorium franconicum* was scored based on figures and illustrations in Wellnhofer (1971). We included all species of *Theriosuchus*, with *T. pusillus*, *T. ibericus*, and *T. sympiestodon* (supplemented by new material described by Martin *et al.*, 2014a) and scored *T. guimarotae* and *T. grandinaris* based on Schwarz & Salisbury (2005) and Lauprasert *et al.* (2011), respectively. Scoring for *Montsecosuchus depereti* was based on the holotype specimen, and specimens described as *Alligatorellus* sp. (MB.R.3632, from the Late Jurassic of Germany; Schwarz-Wings *et al.*, 2011), and *Theriosuchus* sp. (NMS G. 2014.52.1, from the Middle Jurassic of the Isle of Skye, UK; Young *et al.*, 2016) were both incorporated to test their generic assignment. In addition, *Brillianceausuchus babouriensis* (Michard *et al.*, 1990) and *Pachycheilosuchus trinquei* (Rogers, 2003) were also included as previously identified putative atoposaurids.

Table 1. Details of the atoposaurid and non-atoposaurid taxa used for the present study

Taxon	Age	Numerical age (Mya)	Distribution	References/sources	Personally observed	This study	Parent taxon
<i>Ingroups</i>							
<i>Alligatorium meyeri</i>	Kimmeridgian	157.3–152.1	Cerin, France	Wellnhofer (1971)	Yes	<i>Alligatorium meyeri</i>	Atoposauridae
<i>Alligatorium francoicum</i>	Late Kimmeridgian	154.75–152.1	Kelheim, Germany	Wellnhofer (1971)	No	' <i>Alligatorium francoicum</i>	Neosuchia
<i>Atoposaurus jourdani</i>	Kimmeridgian	157.3–152.1	Cerin, France	Wellnhofer (1971)	Yes	<i>Atoposaurus jourdani</i>	Atoposauridae
<i>Atoposaurus oberndorferi</i>	Early Tithonian	152.1–148.55	Kelheim, Germany	Wellnhofer (1971)	Yes	<i>Atoposaurus oberndorferi</i>	Atoposauridae
<i>Alligatorellus bavaricus</i>	Early Tithonian	152.1–148.55	Eichstätt, Germany	Wellnhofer (1971), Tennant & Mannion (2014)	Yes	<i>Alligatorellus bavaricus</i>	Atoposauridae
<i>Alligatorellus beaumonti</i>	Kimmeridgian	157.3–152.1	Cerin, France	Wellnhofer (1971), Tennant & Mannion (2014)	Yes	<i>Alligatorellus beaumonti</i>	Atoposauridae
<i>Alligatorellus</i> sp.	Early Tithonian	152.1–148.55	Kelheim, Germany	Schwarz-Wings <i>et al.</i> (2011)	Yes	<i>Alligatorellus</i> sp.	Atoposauridae
<i>Montsecosuchus depereti</i>	Late Berriasian–Early Valanginian	142.4–136.35	Montsec, Spain	Buscalioni & Sanz (1990a)	Yes	<i>Montsecosuchus depereti</i>	Neosuchia
<i>Theriosuchus pusillus</i>	Berriasian	145–139.8	Dorset, England	Owen (1879), Clark (1986)	Yes	<i>Theriosuchus pusillus</i>	Neosuchia
<i>Theriosuchus guimarotae</i>	Kimmeridgian	157.3–152.1	Guimarota, Portugal	Schwarz & Salisbury (2005)	No	<i>Theriosuchus guimarotae</i>	Neosuchia
<i>Theriosuchus grandinaris ibericus</i>	Early Aptian	125–118	Sakon Nakhon, Thailand	Lauprasert <i>et al.</i> (2011)	No	<i>Theriosuchus grandinaris ibericus</i>	Neosuchia
<i>Theriosuchus sympiestodon</i>	Barremian	129.4–125	Serrania de Cuenca, Spain	Brinkmann (1989)	Yes	<i>Sabresuchus sympiestodon</i>	Paralligatoridae
<i>Theriosuchus</i> sp.	Maastrichtian	72.1–66	Hateg, Romania	Martin <i>et al.</i> (2010)	Yes	<i>Sabresuchus sympiestodon</i>	Paralligatoridae
<i>Brillianceausuchus babouriensis</i>	Late Bajocian–Bathonian	169.3–166.1	Isle of Skye, Scotland	Young <i>et al.</i> (2016)	No	<i>Theriosuchus</i> sp.	Neosuchia
<i>Outgroups</i>	Barremian	145–139.8	Babouri-Figuil, Cameroon	Michard <i>et al.</i> (1990)	Yes	<i>Brillianceausuchus babouriensis</i>	Paralligatoridae
<i>Pachycheilosuchus trinqueti</i>	Early Albian	113–106.75	Texas, USA	Rogers (2003)	Yes	<i>Pachycheilosuchus trinqueti</i>	Hylaeochampsidae
<i>Wannchampsus kirpachi</i>	Aptian	125–114	Texas, USA	Adams (2014)	Yes	<i>Wannchampsus kirpachi</i>	Paralligatoridae

<i>Karatausuchus sharovi</i>	Oxfordian	163.5–157.3	Karatau, Kazakhstan	Storrs & Efimov (2000)	No	<i>Karatausuchus sharovi</i>	Neosuchia
<i>Hoplosuchus kayi</i>	Early Tithonian	152.1–148.55	Utah, USA	Gilmore (1926)	Yes	<i>Hoplosuchus kayi</i>	Protosuchia
<i>Koumpiodontosuchus aprosdokiti</i>	Barremian	129.4–125	Isle of Wight, England	Sweetman <i>et al.</i> (2015)	No	<i>Koumpiodontosuchus aprosdokiti</i>	Bernissartiidae
<i>Eutretauranosuchus delfsi</i>	Kimmeridgian–Early Tithonian	157.3–148.55	Colorado and Wyoming, USA	Pritchard <i>et al.</i> (2012)	No	<i>Eutretauranosuchus delfsi</i>	Goniopholididae
<i>Amphicotylus lucasii</i>	Kimmeridgian	157.3–152.1	Colorado, USA	Mook (1942)	Yes	<i>Amphicotylus lucasii</i>	Goniopholididae
<i>Protosuchus richardsoni</i>	Hettangian	201.3–199.3	Arizona, USA	Colbert & Mook (1951)	Yes	<i>Protosuchus richardsoni</i>	Protosuchia
<i>Pholidosaurus purbeckensis</i>	Berriasian	145–139.8	Swanage, England	Salisbury (2002)	No	<i>Pholidosaurus purbeckensis</i>	Pholidosauridae
<i>Shamosuchus djadochtaensis</i>	Late Campanian	77.85–72.1	Omnogov, Mongolia	Pol <i>et al.</i> (2009)	No	<i>Shamosuchus djadochtaensis</i>	Paralligatoridae

We selected several basal ‘protosuchian’-grade taxa, and a range of neosuchian taxa for outgroups. We incorporated *Protosuchus richardsoni* (Colbert & Mook, 1951) and *Hoplosuchus kayi* scored from (Gilmore (1926) as protosuchians. Within Neosuchia, we selected the goniopholidids *Amphicotylus lucasii* scored from Mook (1942) and *Eutretauranosuchus delfsi*, scored from Smith *et al.* (2010) and Pritchard *et al.* (2013), as these both preserve highly complete cranial material. In addition to these goniopholidids, we also included *Pholidosaurus purbeckensis* (Salisbury, 2002) as a further representative of ‘coelognathosuchian’ crocodyliforms (*sensu* Martin *et al.*, 2014b). We included *Koumpiodontosuchus aprosdokiti* to represent Bernissartiidae (Sweetman, Pedreira-Segade & Vidovic, 2015). We also included the advanced neosuchians *Wannchampsus kirpachi* (Adams, 2014) and *Shamosuchus djadochtaensis*, based on Pol *et al.* (2009), both of which are likely to belong to Paralligatoridae (e.g. Turner, 2015). *Protosuchus* was constrained as the ultimate outgroup taxon in each analysis.

DATA MATRIX

We constructed a new character matrix (Appendix S1) based on a range of primary sources, with the majority of characters derived from Clark (1994), Ortega *et al.* (2000), Pol *et al.* (2009), and Andrade *et al.* (2011). Ninety-two novel characters were also incorporated, following an extensive review of the literature, as well as via personal observations of specimens. Some of these were created by the splitting of previous characters. We formatted all characters to a standardized notation, and many characters were revised, quantified, and/or clarified to remove ambiguity, including removal of problematic gaps between plesiomorphic and derived character states (see Appendix 1 and Appendix S2). Our final data set comprises 329 characters (including autapomorphies – see ‘Bayesian inference’ below) scored for 24 operational taxonomic units (OTUs; 15 ingroup and nine outgroup taxa; Table 1). As with the majority of fossil crocodyliform data matrices, ours is dominated by cranial, mandibular, and dental characters (263), augmented with 16 axial, 24 appendicular, and 26 osteoderm characters (Appendix 1). We opted to use a reductive (contingent) coding approach, which treats non-applicable character states as missing data when there is no logical basis for interpreting the character for any given OTU (Strong & Lipscomb, 1999). The advantage of this approach is that it facilitates the capture of grouping information between successive transformations between particular characters and state values (Brazeau, 2011).

PHYLOGENETIC ANALYSIS

Parsimony analysis

We used TNT v. 1.1 (Goloboff, Farris & Nixon, 2000) to perform a series of parsimony analyses. Importantly, we wanted to test the effect of removal of taxa and combinations of taxa to test the stability of resulting topologies. We treated 47 multistate characters as ordered (additive; Appendix 1). Starting with a random seed, we employed 50 iterations of a ratchet search strategy, which is a repeated pseudo-sampling protocol that uses character reweighting to search tree space more effectively. No more than 20 substitutions were accepted during each phase of perturbation, and we did not auto-constrain cycles. An equal probability was used for both up-weighting and down-weighting of characters in each cycle. The ratchet search function uses the tree bisection and reconnection (TBR) branch swapping algorithm to search for the most parsimonious trees (MPTs), which we repeated 1000 times. The MPTs were then subjected to a final exhaustive search for all remaining topologies of equal length, again using the TBR algorithm. All trees reported are the strict consensus topologies of all MPTs for each analysis, and zero-length branches were collapsed by default. We also calculated the absolute Bremer branch support value (or decay index) for each node, which is a measure of the extra number of steps required to collapse a branch in the consensus topology (Bremer, 1994). We performed an additional analysis (with all OTUs included) utilizing implied weighting, using a weighting exponent (k) of 3, as a method for favouring characters that are more likely to be homologous and penalizing those more likely to be homoplastic and therefore producing a more 'reliable' topology (Goloboff, 1993; Goloboff *et al.*, 2003). Finally, to test for the effects of unstable taxa or characters, we employed the *iterpcr* script of Pol & Escapa (2009).

Bayesian inference

In addition, we used Bayesian inference to test for topological congruence with our parsimony results using a different methodology, following the approach described by Lewis (2001). We used MrBayes v. 3.2.5 (Ronquist & Huelsenbeck, 2003), set to perform 10 000 000 generations running four simultaneous Markov chains, sampling every 1000 chains, and setting a burn-in fraction of 0.25. The Markov Chain process started at a random seed, and fixed the states and rate frequencies to vary with an equal probability. Our data matrix includes characters with states that are locally, ambiguously, or unambiguously resolved as autapomorphic characters. These are not informative for our parsimony

analyses, in which it is the shortest number of character state transformations (steps) leading to clades based on synapomorphies that is most important, but they can have the effect of increasing terminal branch lengths for trees obtained using Bayesian inference (Lewis, 2001). We elected to include autapomorphies in agreement with Müller & Reisz (2006), amongst others, who suggested that inclusion of all available data is important for yielding new insights, as well as having an effect on deeper node support values. Ordered characters were treated in the same way as for the parsimony analyses, using the '*ctype ordered:*' command.

RESULTS

PARSIMONY ANALYSES

Unordered analysis

A complete analysis involving all OTUs and all characters defined as unordered resulted in seven MPTs, with a total length of 802 steps (Fig. 4A). In this topology, Atoposauridae comprises all species of *Alligatorium*, *Alligatorellus*, and *Atoposaurus*, with the two species of *Alligatorium* (*Alligatorium meyeri* and *Alligatorium franconicum*) occupying an unresolved basal position. *Atoposaurus* and *Alligatorellus* are sister taxa, with each comprising two constituent species. Atoposauridae is in a more stemward position than a clade comprising *Koumpiodontosuchus* and coelognathosuchians. MB.R.3632 (Schwarz-Wings *et al.*, 2011) does not group with other *Alligatorellus* species, supporting the conclusions of Tennant & Mannion (2014), but instead clusters with *Montsecosuchus*, forming a basal clade with *Pachycheilosuchus*. *Theriosuchus* is resolved as polyphyletic, with a clade of (*T. ibericus* + *T. sympiestodon*) nested within Paralligatoridae, along with *Brillanceausuchus*, *Shamosuchus*, and *Wannchampsus*. The remaining *Theriosuchus* species fall outside of this clade, with (*T. guimarotae* + *T. pusillus*) and (*T. grandinaris* + *Theriosuchus* sp.) forming clades.

Ordered analyses

When all taxa are included and 47 characters are treated as ordered (Appendix 1), we recover a largely unresolved polytomy (Fig. 4B) for the strict consensus of 11 MPTs of length 830 steps. *Theriosuchus* remains polyphyletic, forming the same clades as in the unordered analysis, and *Atoposaurus* and *Alligatorellus* are monophyletic genera.

The *iterpcr* function of Pol & Escapa (2009) found '*Alligatorellus*' sp. (MB.R.3632) and *Alligatorium franconicum* to be the most unstable taxa. The instability of the former taxon is most likely to be a result of a high proportion of missing data, whereas for the

Table 2. Primary cranial and postcranial measurements and counts for all OTUs analysed. All measurements in millimeters

Taxon	Total length	Tail length	Skull length	Skull width	Snout length	Orbit length	Orbit width	Supratemporal fenestra length	Supratemporal fenestra width	Symphysis length	Intermandibular angle
<i>Alligatorellus</i> sp.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>Alligatorellus bavaricus</i>	288	165	40.9	18.5	13.7	13.1	9.3	5.7	4	7	45
<i>Alligatorellus beaumonti</i>	193.4	165	35.5	17.2	13.6	9.2	8	5.7	3.6	7	43
<i>Alligatorium franconicum</i>	NA	NA	77	27.8	42.6	14.6	11	11.4	5.4	NA	36
<i>Alligatorium meyeri</i>	NA	NA	65.6	29	25.3	18	12.5	10.2	6.1	NA	45
<i>Amphicotylus lucasii</i>	NA	NA	480	288	320	48	40	56	40	NA	34
<i>Atoposaurus jourdani</i>	188	111	20	15.6	8.3	8.6	5.8	NA	NA	NA	55
<i>Atoposaurus oberndorferi</i>	130	96	26	13.1	NA	9.1	5.6	NA	NA	4	NA
<i>Brillanceausuchus babourensis</i>	800	NA	75	42	34	11	12	14	6	NA	42
<i>Eutretauranosuchus delfsi</i>	NA	NA	416.6	211.9	251.8	58	39.9	53.2	31.8	NA	33
<i>Hoplosuchus kayi</i>	NA	NA	31	23	9.5	10	6.8	NA	NA	5	45
<i>Karatausuchus sharovi</i>	186	116.4	26.9	NA	10.4	8	5.6	3.2	1.7	NA	NA
<i>Koumpiodontosuchus aprosdokii</i>	NA	NA	112	55	70	20	15	14	10	15	32
<i>Montsecosuchus depereti</i>	NA	NA	53.4	29.7	20	13.2	9.3	6	5.7	6	61
<i>Pachycheilosuchus trinquei</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	6	NA
<i>Pholidosaurus purbeckensis</i>	NA	NA	NA	117	NA	33	33	41.7	41.7	NA	NA
<i>Protosuchus richardsoni</i>	NA	133	113	86	44	25	5	17	14	NA	48
<i>Shamosuchus djadochtaensis</i>	NA	NA	128	86	64	21	18	20	15	NA	42
<i>Theriosuchus</i> sp.	NA	NA	NA	NA	NA	NA	NA	NA	NA	12	NA
<i>Theriosuchus grandinaris</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	12	NA
<i>Theriosuchus guimarotae</i>	NA	NA	74.2	40.8	34.9	14.9	13.6	11.4	8.8	4	44
<i>Theriosuchus ibericus</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	12	NA
<i>Theriosuchus pusillus</i>	NA	NA	84.3	55.7	35.7	22	16.1	12.9	11.6	12	45
<i>Theriosuchus sympiestodon</i>	NA	NA	NA	NA	NA	NA	NA	12	10	11	NA
<i>Wannchampsus kirpachi</i>	NA	NA	64	44.8	24.6	17.2	16.2	8.5	8.7	17.3	40

Taxon	Radiale length	MC I	MC II	MC III	MC IV	MC V	Manus length	Forelimb length	Ilium length	Pubis length	Ischium length	Femur length
<i>Alligatorellus</i> sp.	15.7	11.1	11.2	8.6	10.7	5.5	NA	NA	NA	NA	NA	74.7
<i>Alligatorellus bavaricus</i>	5	NA	NA	NA	NA	NA	21.5	63.1	12	10.2	10.8	27.6
<i>Alligatorellus beaumonti</i>	6.5	3.8	4.5	4.6	4.1	3	19	56.1	11	9.3	NA	26.3
<i>Alligatorium franconicum</i>	6.8	6.8	8.1	7.7	5.5	NA	31.7	94.1	22	24	23	42.3
<i>Alligatorium meyeri</i>	10.3	4.9	6.6	6.7	6.5	4.2	29.5	NA	NA	NA	NA	42
<i>Amphicotylus lucasii</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>Atoposaurus jourdani</i>	3.8	4.1	4.8	5.7	4.4	NA	10.2	31.3	NA	NA	NA	16.7
<i>Atoposaurus oberndorferi</i>	3	2.2	2.5	2.6	2.6	1.6	10.5	39.1	NA	5	NA	17.7
<i>Brillanceausuchus babourensis</i>	9	NA	9	11	9	5	35	123	NA	NA	NA	45
<i>Eutretauranosuchus delfsi</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>Hoplosuchus kayi</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	25
<i>Karatausuchus sharovi</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	12.1
<i>Koumpiodontosuchus aprosdokii</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>Montsecosuchus depereti</i>	7.5	4.3	5.3	5.3	5	0	23.3	71.5	20.1	NA	NA	38.5
<i>Pachycheilosuchus trinquei</i>	11.1	NA	NA	NA	NA	NA	NA	NA	40.9	38.5	35.6	75.1
<i>Pholidosaurus purbeckensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>Protosuchus richardsoni</i>	14	11	11	12	11	8	52	170	51	56	30	100
<i>Shamosuchus djadochtaensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	48	NA
<i>Theriosuchus</i> sp.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>Theriosuchus grandinaris</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>Theriosuchus guimarotae</i>	NA	NA	NA	NA	NA	NA	NA	NA	13.7	NA	20	25.2
<i>Theriosuchus ibericus</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>Theriosuchus pusillus</i>	10.3	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	53.3
<i>Theriosuchus sympiestodon</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>Wannchampsus kirpachi</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

NA, non-applicable.

Premaxillary teeth	Maxillary teeth	Cervical vertebrae	Dorsal vertebrae	Sacral vertebrae	Caudal vertebrae	Coracoid length	Scapula length	Humerus length	Ulna length	Radius length	Ulnare length
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NA	NA	7	15	3	40	NA	9.3	24.6	17	16.9	5
NA	9	7	17	2	40	5.8	13	19.6	17.5	16.7	5.5
NA	NA	7	15	2	NA	NA	NA	35	27.4	24	5.4
NA	11	7	17	NA	NA	8.9	NA	NA	29.9	28.9	8.7
5	15	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NA	NA	6	17	2	50	2.2	4.2	11.2	9.9	9.5	5.3
NA	NA	7	16	2	50	NA	7	15.6	13	13.1	3
NA	15	7	19	NA	NA	NA	24	50	38	38	10
NA	17	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NA	14	11	13	2	NA	NA	12.8	19.3	17.5	17.5	NA
NA	NA	8	NA	NA	46	NA	NA	8.8	6.1	6.1	NA
4	19	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NA	NA	7	15	3	21	NA	35	27.1	21.1	19.6	3
NA	15	7	15	2	18	36.7	41.9	81.8	49.3	47.6	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
4	13	9	15	2	39	25	48	66	52	52	11
NA	12	NA	NA	NA	NA	NA	NA	65	57	50	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5	14	NA	NA	2	NA	18.6	NA	24.8	NA	NA	NA
NA	14	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5	14	NA	NA	NA	NA	NA	NA	40.3	32.2	29.6	8.6
NA	11	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NA	11	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Tibia length	Fibula length	MT I	MT II	MT III	MT IV	MT V	Pes length	Hindlimb length	Personally observed	Specimen	Sources
68.3	61.9	NA	37.9	32.6	33.8	NA	NA	NA	Yes	Ref. spec.	Schwarz-Wings <i>et al.</i> (2011)
26.6	24.9	10	13	14.5	13	NA	29.2	83.4	Yes	Holotype	Wellnhofer (1971), Tennant & Mannion (2014)
23.6	24.2	11.5	14.5	14.5	13	3.5	19	68.9	Yes	Holotype	Wellnhofer (1971), Tennant & Mannion (2014)
26.9	34.8	25	29	30	28	8	60	129.2	No	Holotype of <i>A. paintenense</i>	Wellnhofer (1971), Tennant & Mannion (2014)
39.1	40.6	21.1	17.7	NA	NA	NA	42.6	123.7	Yes	Holotype	Wellnhofer (1971), Tennant & Mannion (2014)
NA	NA	NA	NA	NA	NA	NA	NA	NA	Yes	Ref. spec.	Smith <i>et al.</i> (2010)
15.7	13.9	12.6	15.9	16.1	14.8	NA	17	49.4	Yes	Holotype, ref. spec.	Wellnhofer (1971), Tennant & Mannion (2014)
17.6	15.8	6.7	7.1	7	7.5	1.3	15	50.3	Yes	Holotype	Wellnhofer (1971), Tennant & Mannion (2014)
43	43	NA	NA	NA	NA	NA	NA	NA	Yes	Holotype	Michard <i>et al.</i> (1990)
NA	NA	NA	NA	NA	NA	NA	NA	NA	Yes	Holotype	Pritchard <i>et al.</i> (2013)
23	23	NA	NA	NA	NA	NA	NA	NA	Yes	Holotype	Gilmore (1926)
13.1	13.1	NA	NA	NA	NA	NA	NA	NA	No	Holotype	Storrs & Efimov (2000)
NA	NA	NA	NA	NA	NA	NA	NA	NA	No	Holotype	Sweetman <i>et al.</i> (2015)
30.7	31.7	13.2	17.6	18.8	14.3	NA	44	113.2	Yes	Holotype	Buscalioni & Sanz (1990a,b)
74	72.3	41.5	45.6	0.1	NA	NA	NA	NA	Yes	Holotype, ref. spec.	Rogers (2003)
NA	NA	NA	NA	NA	NA	NA	NA	NA	Yes	Holotype	Salisbury (2002)
83	83	37	40	39	37	15	80	263	Yes	Holotype	Colbert & Mook (1951)
69	71	NA	NA	41	38	NA	NA	NA	No	Holotype, ref. spec.	Pol <i>et al.</i> (2009)
NA	NA	NA	NA	NA	NA	NA	NA	NA	Yes	Holotype	Young <i>et al.</i> (2016)
NA	NA	NA	NA	NA	NA	NA	NA	NA	No	Holotype	Lauprasert <i>et al.</i> (2011)
31.2	NA	NA	NA	NA	NA	NA	NA	NA	No	Holotype	Schwarz & Salisbury (2005)
NA	NA	NA	NA	NA	NA	NA	NA	NA	Yes	Holotype	Brinkmann (1992)
53.6	51.7	31.9	28	31.5	28.4	NA	59	165.9	Yes	Holotype, paratype	Owen (1879)
NA	NA	NA	NA	NA	NA	NA	NA	NA	Yes	Holotype	Martin <i>et al.</i> (2010, 2014a,b)
NA	NA	NA	NA	NA	NA	NA	NA	NA	Yes	Holotype	Adams (2014)

Ref. spec., Referred specimen

Table 3. Ratios between primary measurements (Table 2) for all OTUs used for phylogenetic analysis

Taxon	Skull length: skull width	Skull length: snout length	Skull length: orbit length	Skull length: STF length	Skull width: orbit width	Skull width: STF width	Radius length: humerus length	Tibia length: femur length	Humerus length: femur length	Radius length: tibia length	Forelimb length: hindlimb length
<i>Alligatorellus</i> sp.	NA	NA	NA	NA	NA	NA	NA	0.91	NA	NA	NA
<i>Alligatorellus bavaricus</i>	2.21	2.99	3.12	7.18	1.99	4.63	0.69	0.96	0.89	0.64	0.76
<i>Alligatorellus beaumonti</i>	2.06	2.61	3.86	6.23	2.15	4.78	0.85	0.90	0.75	0.71	0.81
<i>Alligatorium franconicum</i>	2.77	1.81	5.27	6.75	2.53	5.15	0.69	0.64	0.83	0.89	0.73
<i>Alligatorium meyeri</i>	2.26	2.59	3.64	6.43	2.32	4.75	NA	0.93	NA	0.74	NA
<i>Amphicotylus lucasii</i>	1.67	1.50	10.00	8.57	7.20	7.20	NA	NA	NA	NA	NA
<i>Atoposaurus jourdani</i>	1.28	2.41	2.33	NA	2.69	NA	0.85	0.94	0.67	0.61	0.63
<i>Atoposaurus oberndorferi</i>	1.98	NA	2.86	NA	2.34	NA	0.84	0.99	0.88	0.74	0.78
<i>Brillanceausuchus babourensis</i>	1.79	2.21	6.82	5.36	3.50	7.00	0.76	0.96	1.11	0.88	NA
<i>Eutretauranosuchus delfsi</i>	1.97	1.65	7.18	7.83	5.31	6.66	NA	NA	NA	NA	NA
<i>Hoplosuchus kayi</i>	1.35	3.26	3.10	NA	3.38	NA	0.91	0.92	0.77	0.76	NA
<i>Karatausuchus sharovi</i>	NA	2.59	3.36	8.41	NA	NA	0.69	1.08	0.73	0.47	NA
<i>Koumpiodontosuchus aprosdokii</i>	2.04	1.60	5.60	8.00	3.67	5.50	NA	NA	NA	NA	NA
<i>Montsecosuchus depereti</i>	1.80	2.67	4.05	8.90	3.19	5.21	0.72	0.80	0.70	0.64	0.63
<i>Pachycheilosuchus trinquei</i>	NA	NA	NA	NA	NA	NA	0.58	0.99	1.09	0.64	NA
<i>Pholidosaurus purbeckensis</i>	NA	NA	NA	NA	3.55	2.81	NA	NA	NA	NA	NA
<i>Protosuchus richardsoni</i>	1.31	2.57	4.52	6.65	17.20	6.14	0.79	0.83	0.66	0.63	0.65
<i>Shamosuchus djadochtaensis</i>	1.49	2.00	6.10	6.40	4.78	5.73	0.77	NA	NA	0.72	NA
<i>Theriosuchus</i> sp.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>Theriosuchus grandinaris</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>Theriosuchus guimarotae</i>	1.82	2.13	4.98	6.51	3.00	4.64	NA	1.24	0.98	NA	NA
<i>Theriosuchus ibericus</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>Theriosuchus pusillus</i>	1.51	2.36	3.83	6.53	3.46	4.80	0.73	1.01	0.76	0.55	NA
<i>Theriosuchus sympiestodon</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>Wannchampsus kirpachi</i>	1.43	2.60	3.72	7.53	2.77	5.15	NA	NA	NA	NA	NA

NA, non-applicable; STF, supratemporal fenestra.

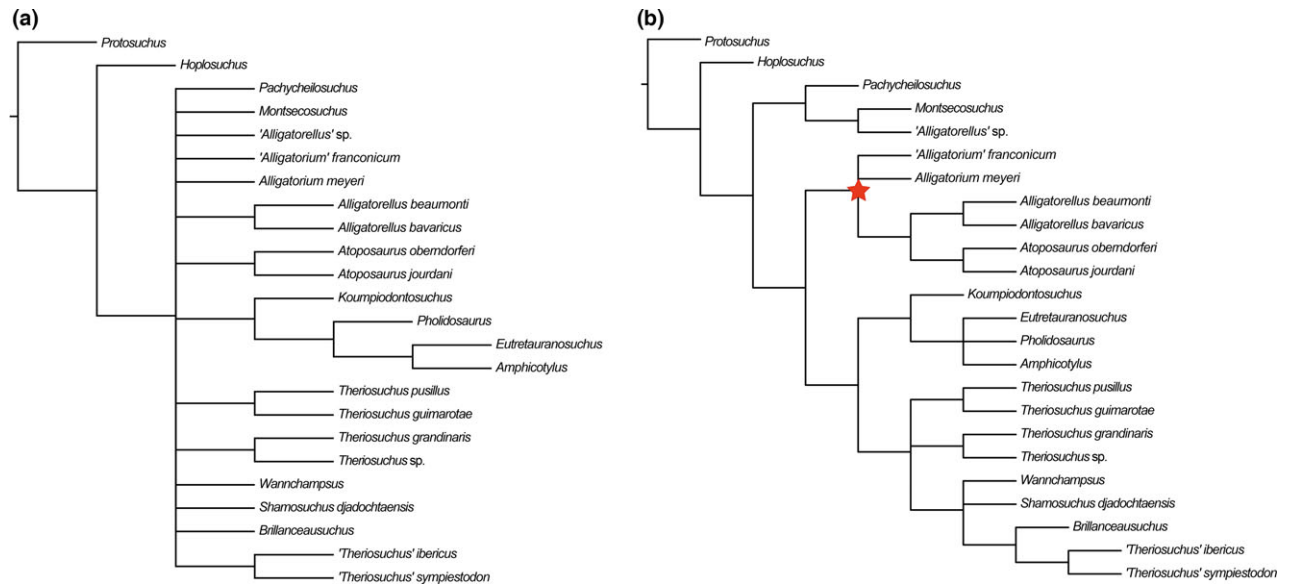


Figure 4. (A) Strict consensus topology for phylogenetic analysis when all taxa are included, and all characters are considered to be unordered (i.e., non-additive). Atoposauridae is marked with a red star. (B) Strict consensus for phylogenetic analysis when all taxa are included, and selected characters are considered to be ordered (see Appendix 1).

latter this is more likely to be a result of character conflict, coupled with our inability to study the specimen first-hand. When these taxa are removed *a priori*, the topology is almost completely resolved (Fig. 5A), producing 11 MPTs of length 805 steps.

The strict consensus identifies the remaining source of conflict to be the relationship amongst *Brillianceausuchus*, *Shamosuchus*, and *Wannchampsus* (Fig. 5A). Atoposauridae comprises *Alligatorium meyeri*, *Alligatorellus*, and *Atoposaurus*. *Montsecosuchus*

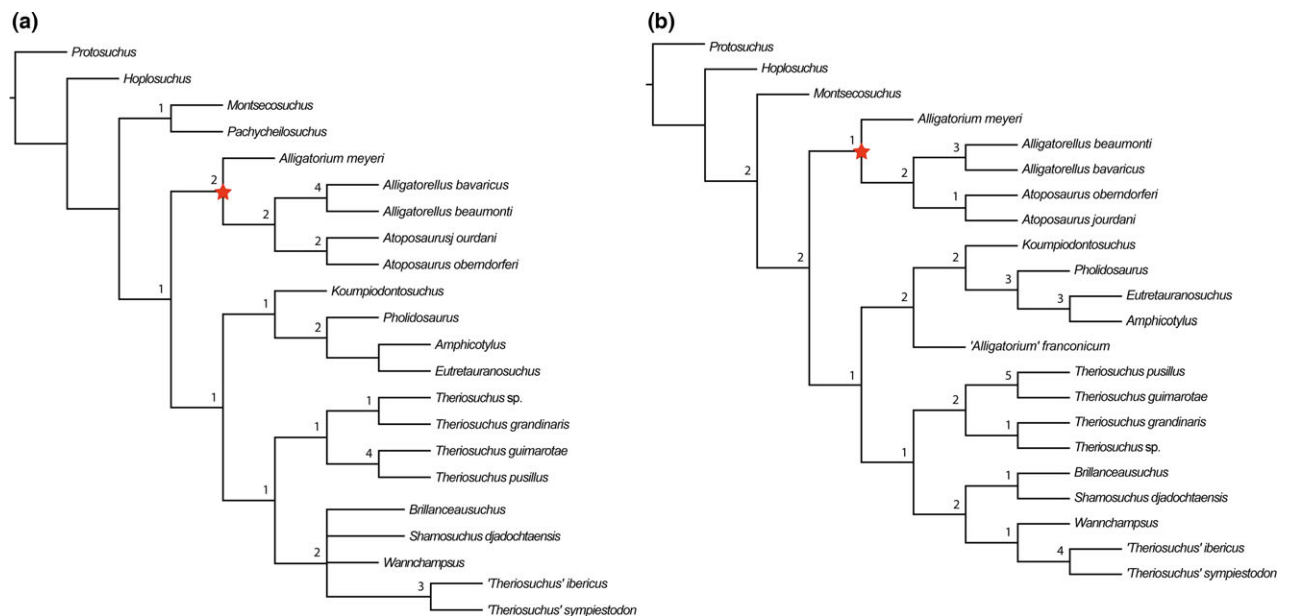


Figure 5. (A) Strict consensus topology for phylogenetic analysis when iterpcr script is employed, and *Alligatorium franconicum* and '*Alligatorellus*' sp. are excluded *a priori*. (B) Single most parsimonious tree for phylogenetic analysis when *Pachycheilosuchus trinquei* and '*Alligatorellus*' sp. (MB.R.3632) are excluded *a priori*. Absolute Bremer support values are provided adjacent to nodes. Atoposauridae is marked with a red star.

is allied with *Pachycheilosuchus*, with this clade outside of all other neosuchian taxa. Bremer support values show that Atoposauridae is moderately well supported with a node value of 2. The two species of *Alligatorellus* are strongly supported with a node value of 4, and the relationship between *Alligatorellus* and *Atoposaurus* is supported by a node value of 2. The clade comprising (*T. pusillus* + *T. guimarotae*) is strongly resolved with a node support value of 4, and (*T. sympiestodon* + *T. ibericus*) has a node support value of 3.

We performed one final analysis that excluded *Pachycheilosuchus* along with MB.R.3632 *a priori*, but included *Alligatorium franconicum*. This was because of the unexpected placement of *Pachycheilosuchus* in our topologies, given the more derived position it usually occupies (e.g. Buscalioni *et al.*, 2011; Adams, 2014; Turner, 2015). This resulted in a single MPT of length 792 steps (Fig. 5B). *Alligatorium franconicum* shifts to a position at the base of the clade comprising *Koumpiodontosuchus* and coelognathosuchians, with no other changes to the topology. Bremer support values show that Atoposauridae is overall only weakly supported (Fig. 5B), with a node value of 1. The sister-taxon relationship between *T. pusillus* and *T. guimarotae* is the most

strongly supported node on the tree, with a Bremer support value of 5, followed by (*T. sympiestodon* + *T. ibericus*), with a support value of 4. Most other nodes have a support value of 1.

Implied weighting

Application of implied weighting on our ordered data set similarly recovers a monophyletic Atoposauridae, but one that also includes *Montsecosuchus* and MB.R.3632 (Fig. 6). *Alligatorium meyeri* remains the most basal member of this clade, followed by *Montsecosuchus*, and MB.R.3632 groups with the two species of *Alligatorellus*. *Theriosuchus* still remains polyphyletic, but there are now three groupings, with the clade comprising (*T. grandinaris* + *Theriosuchus* sp.) shifting to a more basal position (Fig. 6). This possibly reflects the incompleteness of the specimens of both of these taxa. *Alligatorium franconicum* remains as the basal-most member of the clade comprising *Koumpiodontosuchus* and coelognathosuchians. The Bremer node support for Atoposauridae is 0.23 (note that support values are non-integers owing to changes to character weights during the implied weighting procedure), with internal support values of 0.15–0.23. The clade comprising (*T. pusillus* + *T. guimarotae*) remains the

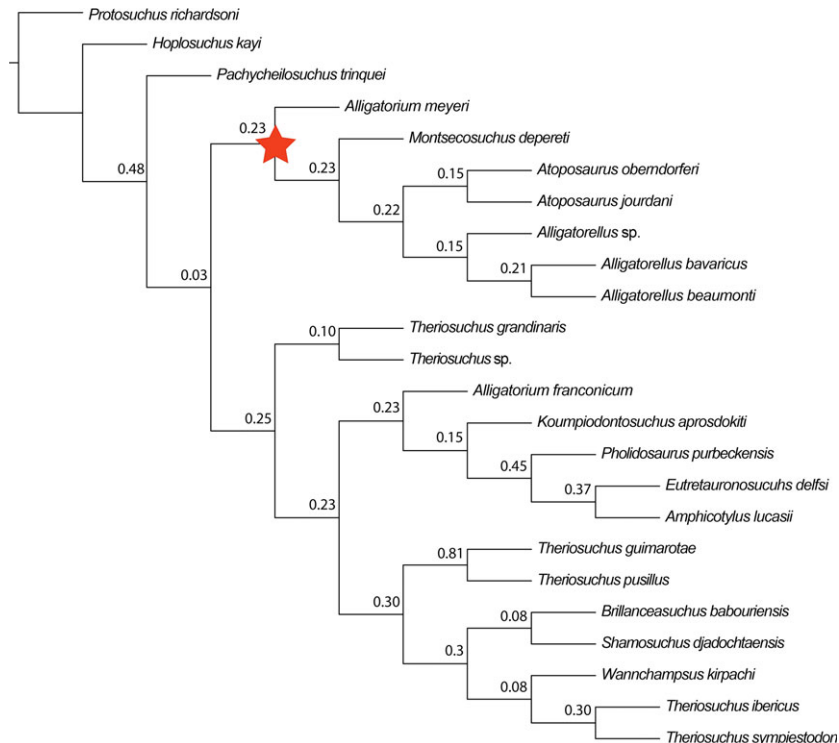


Figure 6. Single most parsimonious tree for phylogenetic analysis when implied weighting is employed with a weighting exponent of $k = 3$. Selected characters are considered to be ordered, and no taxa were excluded *a priori*. Absolute Bremer support values are provided adjacent to nodes.

most strongly supported clade, with a node support value of 0.81.

BAYESIAN ANALYSES

When all taxa are included, the results of the Bayesian analysis produce a largely unresolved topology (Fig. 7A). *Protosuchus* and *Hoplosuchus* are basal crocodyliforms, and *Pachycheilosuchus* retains a position basal to all other remaining taxa. The inter-relationships of MB.R.3632 (*Alligatorellus* sp.), NMS G. 2014.52.1 (*Theriosuchus* sp.), *Alligatorium*, *Montsecosuchus*, and *Koumpiodontosuchus* are all unresolved. Only *Alligatorellus* and *Atoposaurus* are definitely members of Atoposauridae, with a posterior node support value of 0.71. *Theriosuchus* is polyphyletic, as before in our parsimony analyses, with one group within Paralligatoridae, and the other group just outside of this clade. These groups are the most strongly supported nodes across the tree, with the clades (*T. sympiestodon* + *T. ibericus*) and (*T. guimarotae* + *T. pusillus*) both having a posterior node support value of 0.98.

When MB.R.3632 and NMS G. 2014.52.1 are both excluded *a priori* from analyses, then the topology changes, with a clade comprising *Koumpiodontosuchus* and coelognathosuchians nested within Paralligatoridae (Fig. 7B), a result not supported by any previous crocodyliform analysis. *Alligatorium meyeri*

is excluded from Atoposauridae, in a slightly more crownward position at the base of a clade comprising *Theriosuchus* and all other higher neosuchians. *Pachycheilosuchus* and *Montsecosuchus* retain their basal positions.

RESULTS SUMMARY

Our analyses demonstrate that Atoposauridae is a much more restricted clade than previously considered, comprising only *Alligatorellus bavaricus*, *Alligatorellus beaumonti*, *Atoposaurus jourdani*, *Atoposaurus oberndorferi*, and *Alligatorium meyeri*. However, this inclusion of *Alligatorium meyeri* is not supported by our Bayesian results. Based on this restricted taxonomic inclusion, Atoposauridae is recovered in a basal position within Neosuchia. *Theriosuchus* is consistently shown to be a polyphyletic taxon, comprising one set of species (*T. guimarotae* + (*T. pusillus* + *T. grandinaris*)) closely related to paralligatorids, and one clade (*T. ibericus* + *T. sympiestodon*) within Paralligatoridae. NMS G. 2014.52.1 (*Theriosuchus* sp.) is likely to be referable to the more basal group of *Theriosuchus* species. The position of MB.R.3632 (*Alligatorellus* sp.) cannot be conclusively determined, with an atoposaurid and a basal neosuchian placement supported in different analyses. *Montsecosuchus* is recovered outside of Atoposauridae in almost all of our analyses, and might

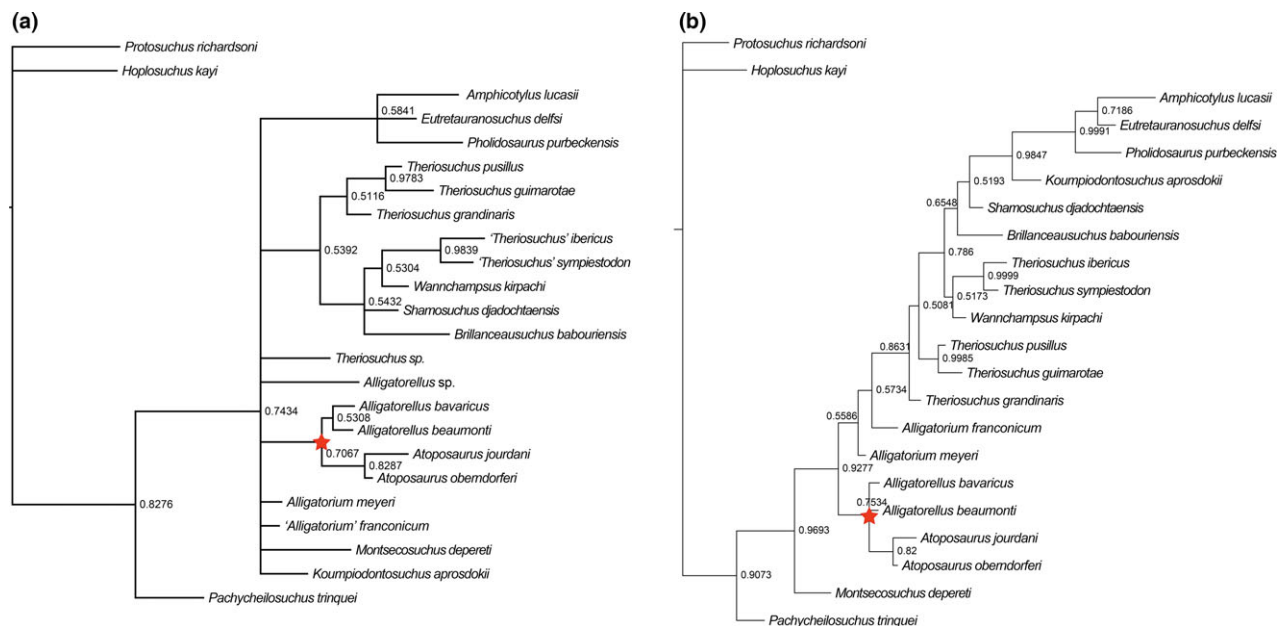


Figure 7. (A) Results of phylogenetic analysis using Bayesian inference, when all OTUs are active and selected characters are considered to be ordered (see Appendix 1). (B) Results of phylogenetic analysis using Bayesian inference, when '*Alligatorellus*' sp. (MB.R.3632) and *Theriosuchus* sp. (NMS G. 2014.52.1) and selected characters are considered to be ordered (see Appendix 1).

be more closely related to *Pachycheilosuchus* and other hylaeochampsids, although we cannot conclusively determine the position of these taxa. *Alligatorium franconicum* is shown to be a non-atoposaurid taxon that is more closely related to bernissartiids and coelognathosuchians. *Brillanceausuchus* occupies a position within Paralligatoridae. Below, we provide revised diagnoses for each of these taxa, along with a discussion of the character states that support the revised systematic positions for all atoposaurid and non-atoposaurid taxa that we analysed.

SYSTEMATIC PALAEONTOLOGY

CROCODYLOMORPHA WALKER, 1970

CROCODYLIFORMES HAY, 1930

NEOSUCHIA BENTON & CLARK, 1988

ATOPOSAURIDAE GERVAIS, 1871

Previous diagnoses and comments

Atoposauridae was originally named as 'Atoposauridés' by Gervais (1871). Since its genesis, there have been few attempts at providing a group diagnosis based on morphology and, to our knowledge, no phylogenetic definition has ever been proposed.

Romer (1956) provided the first morphological definition for Atoposauridae: (1) small, with a broad head and short, pointed snout; (2) external nares sometimes divided; (3) postorbital bar moderately inwardly displaced; (4) large orbits and small supratemporal fenestrae; (5) two rows of flattened dorsal osteoderms; (6) long and slender limbs; and (7) platycoelous vertebrae. However, this assessment was based exclusively on taxa known at the time from the Late Jurassic, comprising *Atoposaurus*, *Alligatorellus*, and *Alligatorium*, as well as *Hoplosuchus*. Kuhn (1960) largely followed this diagnosis, but omitted several characteristics, whereas Steel (1973) subsequently re-incorporated them, and noted that there were at least some cases of atoposaurids with procoelous vertebrae, presumably referring to their inferred presence in *T. pusillus* (Joffe, 1967; see below). Although some of these characteristics, such as the relative sizes of the orbit and supratemporal fenestra, are known to occur in juvenile crocodyliform specimens (e.g. Joffe, 1967; Schwarz & Salisbury, 2005), it is noteworthy that even specimens of adult atoposaurids possess this feature. Therefore, this condition indicates that atoposaurids might consistently retain pedomorphic characteristics into adulthood, a factor that has probably contributed to difficulties in resolving their phylogenetic affinities.

Buscalioni & Sanz (1988) presented several hypotheses of atoposaurid inter-relationships by treating cranial, postcranial, and metric characters independently. They regarded several taxa as *nomina dubia*, including '*Alligatorium*' *franconicum* and '*Alligatorium*' *paintenense*', and non-atoposaurids, including *Karatausuchus*, *Shantungosuchus*, and *Hoplosuchus*, but without explicit statements regarding their morphology to support these taxonomic opinions. Buscalioni & Sanz (1988) concluded that Atoposauridae could be diagnosed based on: (1) enlarged anterior maxillary teeth; (2) loss of the external mandibular fenestra; (3) reduction or loss of the antorbital fenestra; (4) squamosals not ventrally depressed; and (5) lack of dental hypertrophy. They also considered the possession of five premaxillary teeth and between 12 and 18 maxillary teeth as additional ambiguous synapomorphies for Atoposauridae, as these characteristics are not visible in either *Atoposaurus* or *Alligatorium*. However, almost all of these characteristics are more widespread in Neosuchia, or variably present within *Theriosuchus* and other putative atoposaurids. Furthermore, their recovery as atoposaurid synapomorphies might largely have been a product of limited sampling of outgroups.

The most recent diagnosis for Atoposauridae was provided by Martin *et al.* (2010), who analysed several atoposaurids to resolve the position of *T. sympiestodon*, based largely upon the Pol *et al.* (2009) data matrix, which focussed on early eusuchian relationships and their morphological transformation from Neosuchia. Martin *et al.* (2010) diagnosis of Atoposauridae consisted of the following synapomorphies: (1) external nares facing dorsally and not separated by a premaxillary bar from anterior edge of rostrum; (2) antorbital fenestra much smaller than the orbit; (3) five premaxillary teeth; (4) basioccipital and ventral part of otoccipital facing posteriorly; (5) unsculpted region in the dentary below the tooth row absent; and (6) lateral surface of dentaries below alveolar margins at middle to posterior region of tooth row vertically orientated, continuous with rest of lateral surface of dentaries. However, this diagnosis was based only on information provided by three species of *Theriosuchus* and one of *Alligatorium*.

All of these aforementioned putative synapomorphies are included as characters in our new data matrix and below we provide a revised diagnosis for Atoposauridae, as well as defining the group as a phylogenetic clade for the first time. Numbers in parentheses refer to characters and states (e.g. C159.1 means character 159, state 1).

Phylogenetic definition

Atoposauridae is a stem-based clade comprising all taxa more closely related to *Atoposaurus jourdani* von Meyer, 1850, than *Crocodylus Laurenti*, 1768

Included taxa

ALLIGATORIUM MEYERI (JOURDAN, 1862),
ALLIGATORELLUS BEAUMONTI (GERVAIS, 1871),
ALLIGATORELLUS BAVARICUS (WELLNHOFER, 1971),
ATOPOSAURUS JOURDANI (VON MEYER, 1850),
ATOPOSAURUS OBERNDORFERI (VON MEYER, 1850)

Distribution

Late Jurassic of France and Germany.

Revised diagnosis and discussion

Many of the synapomorphies below represent the quantification and demarcation of state boundaries from previously proposed characters. They also diagnose a more exclusive set of taxa, as we no longer consider features shared between *Theriosuchus* and definitive atoposaurids to be diagnostic for a united clade. Measurements and ratios pertaining to synapomorphies for taxa are provided in Tables 2 and 3, respectively. Atoposauridae can be diagnosed based on the following unique combination of character states (synapomorphies, S; Figs 8, 9):

- (S1) *Complete division of the external nares dorsally by anterior projection of the nasals (C10.0)*: This feature is only known for Atoposauridae (Figs 8, 9A), *T. guimarotae*, and *T. pusillus* (Fig. 9B). In '*Alligatorium*' *franconicum*, the external nares are completely opened and undivided, based on the reconstruction presented by Wellnhofer (1971), and similar to *T. grandinaris* (Lauprasert *et al.*, 2011), *Amphicotylus* (Mook, 1942), *Brillanceausuchus*, and some notosuchians (*sensu* Pol *et al.*, 2014), including the baurusuchid *Campinasuchus dinizi* (Carvalho *et al.*, 2011). This division of the external nares by the anterior-most extent of the nasals was considered by Salisbury & Naish (2011) to be diagnostic for *Theriosuchus*, but we consider it to be independently acquired in this genus and atoposaurids. Some other taxa, such as the notosuchian *Araripesuchus*, also share this division, but the external nares are more anteriorly placed and face anteriorly (Buffetaut, 1981).
- (S2) *Skull anteroposterior length to orbit length ratio <4.0 (C27.0-1)*: This synapomorphy is also shared by other neosuchian taxa, including

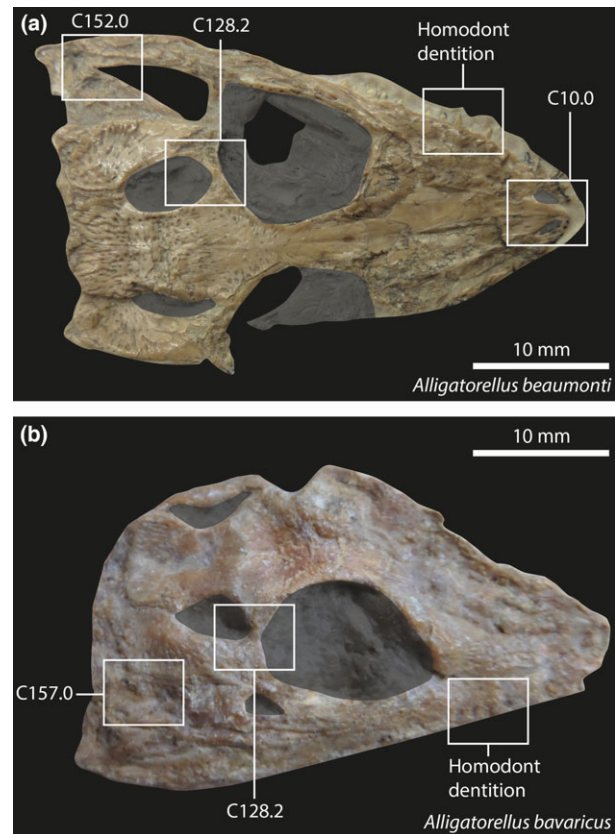


Figure 8. (A) Skull of the holotype of *Alligatorellus beaumonti* (MNHL 15639) in dorsal view. See text for details. (B) Skull of the holotype of *Alligatorellus bavaricus* (BSPG 1937 I 26) in dorsolateral view. Synapomorphies for Atoposauridae indicated (see text for details).

T. pusillus, *Wannchampsus* (Adams, 2014), the 'protosuchian' *Hoplosuchus* (Gilmore, 1926), and possibly *Karatausuchus* (Efimov, 1976). *Atoposaurus* displays an extreme version of this morphology, possessing a relatively longer orbit, giving a ratio of <3.0 for both species. *Montsecosuchus* falls just outside of this range, with a ratio of 4.05. Although the latter value is similar in orbital dimensions to atoposaurids, we chose to set the state boundaries for this character at regular intervals, as opposed to selecting them towards creating inclusive groupings *a priori*, and therefore *Montsecosuchus* is distinct from atoposaurids in this respect. Longirostrine taxa, as expected, have a much higher ratio, with *Amphicotylus* possessing an extreme of this with a value of 10.0. *Shamosuchus* and *Brillanceausuchus*, although brevirostrine, have intermediate ratio values (6.1 and 6.8, respectively), reflecting the smaller dimensions of the orbits.

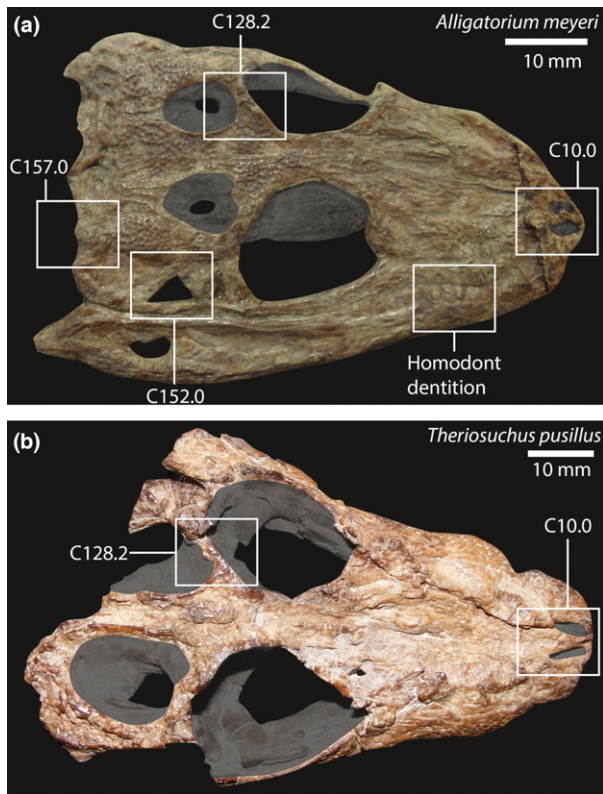


Figure 9. (A) Skull of the holotype of *Alligatorium meyeri* (MNHL 15646) in dorsal view. Synapomorphies for Atoposauridae are indicated (see text for details). (B) Skull of the paratype of *Theriosuchus pusillus* (NHMUK PV R48330) in dorsal view. Shared characteristics with atoposaurids are indicated (see text for details).

- (S3) *Skull mediolateral width to orbit width ratio of <2.5 (C28.0)*: Amongst atoposaurids, only *Atoposaurus jourdani* differs in having a smaller orbital width, giving a ratio of 2.69. '*Alligatorium*' *franconicum* is also just outside this state boundary with a value of 2.53. This ratio is unknown for most specimens attributed to *Theriosuchus*, but the ratios are 3.0 and 3.46 for *T. guimarotae* and *T. pusillus*, respectively. *Montsecosuchus* falls between these two species, with a ratio of 3.19. The relatively large size of the orbits in atoposaurids, as quantified here, might relate to retention of the paedomorphic state, as it appears to also be possessed by mature representatives of species (e.g. *Theriosuchus*).
- (S4) *Skull mediolateral width to external supratemporal fenestra width between 3.0 and 5.0 (C30.1)*: This feature, similar to the proportionally large orbits, also possibly relates to the relatively small body sizes of these taxa. This state is unknown in *Atoposaurus* because it is not possible to assess the morphology of

the supratemporal fenestrae owing to their preservation. Both *T. guimarotae* and *T. pusillus* share this character state with atoposaurids, with ratios of 4.64 and 4.8, respectively. The only taxon in our data matrix that has a proportionally larger supratemporal fenestra is *Pholidosaurus* (Salisbury, 2002), which has a ratio of 2.81. Both '*Alligatorium*' *franconicum* and *Montsecosuchus* have proportionally smaller supratemporal fenestrae, with ratio values of 5.15 and 5.21, respectively.

- (S5) *Dorsal surface of the premaxilla internarial bar projects anteriorly to main body of premaxilla (C35.1)*: This feature is diagnostic for atoposaurids, and possibly only shared outside the group with '*Alligatorium*' *franconicum* (Wellnhofer, 1971). In all other taxa we sampled, the internarial bar of the premaxilla does not project anteriorly to the main body of the premaxilla and the external nares. This morphology is also different to that seen in goniopholidids, in which there is a distinct mediolateral constriction and an anteriorly spatulate morphology.
- (S6) *Ventral depression on dorsal margin of postorbital, sometimes developing into a shallow sulcus (C128.2)*: Wu *et al.* (1996) considered the inwardly displaced (ventrally depressed) postorbital bar between the supratemporal fenestra to be diagnostic for *Theriosuchus*, but this appears to be absent in *T. pusillus* and its presence is questionable in *T. guimarotae*. It is clearly present in *Alligatorellus* (Fig. 8), and perhaps *Alligatorium meyeri* too, and therefore we consider it to be diagnostic for Atoposauridae. However, this feature might have also been acquired by the 'Glen Rose Form' [Turner, 2015 (probably referable to *Wannchampsus*; Adams, 2014)], and is similar to the condition observed in more basal crocodyliforms, including the shartgeosuchid *Fruitachampsia callisoni* (Clark, 2011), in which the postorbital bar is relatively poorly developed. *Paralligator gradilifrons* (Turner, 2015) also possesses this supratemporal-orbital groove, but the postorbital bar is well developed and robust, distinct from *Alligatorellus*.
- (S7) *Quadratojugal contributes extensively to the ventral and posterior margins of the lateral temporal (infratemporal) fenestra (C152.0)*: This feature is present in all atoposaurids (Figs 8, 9A), but cannot be assessed in *Atoposaurus* owing to the preservation of the skull. It is also shared by *T. pusillus*. In some crocodyliforms, including goniopholidids, *Protosuchus*, and *T. guimarotae* (Schwarz &

Salisbury, 2005), the quadratojugal only contributes to the posterior margin. In *Montsecosuchus*, *Brillanceausuchus*, *Araripesuchus patagonicus* (Ortega et al., 2000), *Allodaposuchus precedens* (Delfino et al., 2008b), and eusuchians including *Wannchampsus* (Adams, 2014), *Acynodon iberoccitanus* (Martin, 2007), and *Shamosuchus* (Pol et al., 2009), the quadratojugal participates extensively in the dorsal and posterior margins of the lateral temporal fenestra.

- (S8) *Otic aperture between squamosal and quadrate posteriorly open, not closed by the quadrate and otoccipital (C157.0)*: This character state appears to be shared by *Alligatorium* and *Alligatorellus*, but cannot be assessed for *Atoposaurus* owing to the preservation of the skull. It is also shared with several other neosuchian taxa, including *Goniopholis simus* (Salisbury et al., 1999), *Pholidosaurus* (Salisbury, 2002), *Amphicotylus* (Mook, 1942), *Allodaposuchus precedens* (Delfino et al., 2008b), and *Shamosuchus* [Turner, 2015 (although this aperture appears to be closed in *Shamosuchus djadochtaensis*; Pol et al., 2009)]. In these taxa, the cranioquadrate passage lacks a lateral wall, forming a sulcus or canalis quadratosquamosoexoccipitalis (Salisbury et al., 1999). This feature is distinct from most mesoeucrocodylians, including *Susisuchus* and *Isisfordia*, as well as modern crocodylians, in which there is a sharp posterior rim and the passage is enclosed by the otoccipital and quadrate (Salisbury et al., 2006; Pol et al., 2009).
- (S9) *Homodont pseudocaniniform dentition (combination of C253.1, C254.1, C255.0, and C258.0)*: Although difficult to evaluate owing to the dorsal flattening of specimens, this type of dentition appears to be present for all specimens of *Alligatorellus* in which teeth are visible (Fig. 8), and in *Alligatorium meyeri* (Fig. 9A), and is synapomorphic amongst all putative atoposaurids (although see below). All species of *Theriosuchus* are clearly distinct from *Alligatorellus*, with their characteristic combinations of heterodont morphologies. The teeth of *Atoposaurus* are poorly known owing to preservation, although several damaged teeth preserved in the type specimen of *Atoposaurus oberndorferi* also appear to be pseudocaniniform. In *Alligatorium meyeri*, the tooth row is exposed in lateral view, but only one or two of these appear to actually be from the maxillary arcade, with the rest from the dentary, against which the maxilla is appressed. All of these exposed teeth appear to be pseudocaniniform in

morphology, and of a similar conical shape to *Alligatorellus*. Therefore, we tentatively regard this feature as being diagnostic for Atoposauridae, pending the further discovery and analysis of teeth in atoposaurids.

Below, we present revised diagnoses and discussions for all taxa included within our revised definition of Atoposauridae, and those previously regarded as putative atoposaurids. These are based on the character state distributions from the results of our parsimony-based phylogenetic analysis when *Pachycheilousuchus* and MB.R.3632 are excluded, and supplemented with details from original descriptions and personal observations where possible. Autapomorphies in the diagnoses are highlighted with an asterisk (S*).

DEFINITIVE ATOPOSAURID TAXA *ALLIGATORIUM* JOURDAN, 1862

Included species

Alligatorium meyeri (type species).

Previous diagnoses and comments

Alligatorium was erected by Jourdan (1862) for an incomplete skeleton from the lithographic limestones of Cerin, France, and described and figured by Lortet (1892). This genus has also been reported from the Upper Jurassic of Bavaria, Germany (von Zittel, 1890; Kuhn, 1961), and identified as *Alligatorium franconicum* and *Alligatorium paintenense* [all specimens of both lost or destroyed during World War II (Wellnhofer, 1971)], but we consider the latter species to be a junior synonym of the former (Tennant & Mannion, 2014), and regard '*Alligatorium*' *franconicum* to represent a non-atoposaurid taxon (see below). Vidal (1915) also described a specimen from the Early Cretaceous of Spain as *Alligatorium depereti*, later recombined as *Montsecosuchus depereti* (Buscalioni & Sanz, 1988, 1990a).

Revised diagnosis

As for the type and only species.

Distribution

Late Jurassic of southern France.

ALLIGATORIUM MEYERI JOURDAN, 1862 (TYPE SPECIES)

Type locality and horizon

Unknown bed, Kimmeridgian (Late Jurassic); Cerin, Ain, France.

Type specimen

MNHL 15646, partial skeleton and skull, with counterpart slab MNHL 15462.

Previous diagnoses and comments

Joffe (1967) considered *Alligatorium meyeri* to be an immature specimen based on a range of ontogenetically variable cranial characteristics. However, Clark (1986) and Benton & Clark (1988) considered *Alligatorium* to represent the most mature specimen of a lineage in which *Atoposaurus* and *Alligatorellus* represented younger growth stages. Tennant & Mannion (2014) were unable to confirm this based on the few specimens available for allometric analysis, but noted several morphological distinctions amongst the three genera. Our phylogenetic results are distinct from those of Clark (1986) and Benton & Clark (1988), as well as Buscalioni & Sanz (1990a) and Karl *et al.* (2006), which found a sister relationship between *Alligatorium* and *Theriosuchus*. This discrepancy is probably because of our increased sampling of paralligatorids, and our generally broader sampling of basal neosuchian taxa (*sensu* Benton & Clark, 1988). We recover *Alligatorium meyeri* at the base of Atoposauridae. However, it should be noted that our Bayesian analysis did not recover *Alligatorium meyeri* within a monophyletic Atoposauridae, and we were unable to resolve its position more precisely using this analytical approach.

Revised diagnosis and discussion

- (S1) *Paired and unfused nasals (C65.0)*: The presence of 'paired' nasal bones has been widely used in diagnoses of atoposaurids, and noted in other mesoeucrocodylians, including the notosuchian *Simosuchus* (Buckley *et al.*, 2000) and the neosuchian *Paluxysuchus* (Adams, 2013). However, it is not entirely clear what this means, as the nasal bones are always paired. Therefore, we consider this character to refer to whether or not the paired nasals are fused, and as such constitute a 'single' element, or are unfused. In *Alligatorium meyeri*, the nasals are fused along the midline, similar to *Wannchampsus*, *T. guimarotae*, *T. grandinaris*, and *T. pusillus*. In *Alligatorellus*, the nasals are only weakly fused or contact one another along the midline, comparable to goniopholidids, *Montsecosuchus*, and *Shamosuchus* (Pol *et al.*, 2009).
- (S2) *Lateral edges of the nasals subparallel to one another (C67.0)*: This morphology occurs anterior to the nasal contact with the periorbital elements, and is similar to *Montsecosuchus*, *Brillianceausuchus*, *Allodaposuchus precedens* (Delfino *et al.*, 2008b), and possibly

Araripesuchus patagonicus (Ortega *et al.*, 2000). *Alligatorellus* is distinct amongst atoposaurids in that the edges are oblique to one another and converge anteriorly (Tennant & Mannion, 2014), similar to *Bernissartia* (Buscalioni, Buffetaut & Sanz, 1984; Norell & Clark, 1990). They are laterally flared posteriorly in *T. pusillus*.

- (S3) *Jugal and lacrimal with confluent anterior margins (C78.0)*: The jugal and lacrimal have confluent anterior contacts, instead of a discrete convexity in which a notch develops and is filled by the maxilla. This morphology is also seen in '*T.*' *sympiestodon* (Martin *et al.*, 2010, 2014a), as well as *Protosuchus* (Colbert & Mook, 1951), *Amphicotylus* (Mook, 1942), and *Pholidosaurus* (Salisbury, 2002).
- (S4) *Frontal with single longitudinal ridge along midline suture (C100.1)*: The presence of a midline ridge on the frontal suture has often been considered diagnostic for *Theriosuchus* (e.g. Schwarz & Salisbury, 2005; Salisbury & Naish, 2011), being present on all specimens attributed to *Theriosuchus* in which the interorbital region is preserved. However, this ridge is also present in *Shamosuchus djadochtaensis* (Pol *et al.*, 2009) and *Wannchampsus* (Adams, 2014). It is likely that the presence of this character is related to ontogeny because in *T. guimarotae* this frontal ridge is only developed in more mature individuals (Schwarz & Salisbury, 2005). *Alligatorellus* and *Atoposaurus* do not show any evidence of this ridge, despite appearing to have completely fused frontals.
- (S5) *Anterior portion of frontal mediolaterally constricted, with convergent lateral margins (C109.1)*: We tentatively consider this feature to be diagnostic for *Alligatorium meyeri*, although it might also be present in '*Alligatorium*' *franconicum* (Wellnhofer, 1971), *T. guimarotae* (Schwarz & Salisbury, 2005), and *Amphicotylus* (Mook, 1942). This morphology is distinct from notosuchians, in which the frontal is slightly mediolaterally constricted, but remains broad between the prefrontals (Gomani, 1997; Buckley *et al.*, 2000), the goniopholidid *Calsoyasuchus* in which the frontal–nasal suture forms a 'valley' on the dorsal surface (Tykoski *et al.*, 2002), the neosuchian *Khoratosuchus* with a nonconstricted and bifurcated frontal anterior process (Lauprasert *et al.*, 2009), and eusuchians such as *Aegisuchus* in which the frontals are constant in width anterior to the orbits (Holliday & Gardner, 2012).
- (S6) *Supratemporal rims developed along entire medial margin (C119.2)*: *Alligatorium meyeri* possesses well-developed supratemporal rims

along the entire medial border of each external fenestra, similar to *Wannchampsus* and *T. pusillus*, *T. guimarotae*, *T. ibericus*, and *T. sympietodon*. This morphology is distinct from that in *Alligatorellus beaumonti* and *Brillanceausuchus*, in which this ridge is only developed posteriorly, and from that in *Alligatorellus bavaricus* and *Montsecosuchus* in which the medial edges are flat (Tennant & Mannion, 2014). *Pachycheilosuchus*, coelognathosuchians, and *Shamosuchus* (Pol et al., 2009) do not appear to possess supratemporal rims.

- (S7) *Dorsal margin groove for dorsal ear lid with a medial curvature (C137.1)*: This character state appears to be unique for *Alligatorium meyeri* within atoposaurids, but is also present in more advanced neosuchians, including *T. ibericus*, *Wannchampsus*, and *Brillanceausuchus*. In other atoposaurids, this margin, comprising the lateral edge of the postorbital and squamosal, is straight, similar to *T. guimarotae* (Schwarz & Salisbury, 2005) and *T. pusillus*.
- (S8) *External mandibular fenestra present (C207.1) and oval-shaped with anteroposteriorly orientated long axis (C210.0)*: The presence of an external mandibular fenestra is also shared with *T. guimarotae* (Schwarz & Salisbury, 2005) amongst those taxa included in our analysis as putative atoposaurids, but also represents the plesiomorphic crocodyliform condition, being present in goniopholidids (e.g. Halliday et al., 2015), *Protosuchus* (Colbert & Mook, 1951), as well as in notosuchians such as *Baurusuchus* (Nascimento & Zaher, 2011) and *Labidiosuchus* (Kellner et al., 2011), in which the opening is enlarged. This fenestra is lost in some advanced neosuchians, including paralligatorids (Montefeltro et al., 2013), but is present in most eusuchians and Crocodylia (Brochu, 2004; Salisbury et al., 2006; Pol et al., 2009), although in some cases it is strongly reduced (Brochu et al., 2012).
- (S9*) *Individual dorsal and caudal osteoderms with unsculpted edges (C304.1), square-shaped (C308.3), and lacking a dorsal keel anteriorly (C311.0) and posteriorly (C312.0)*: The individual osteoderms preserved in *Alligatorium meyeri* have unsculpted edges on all but the nuchal-most elements, a feature that cannot be a preservation artefact as the cranial table remains sculpted, and the centre of each osteoderm remains relatively lightly sculpted. Although this feature might be present in *'Alligatorium' franconicum* based on the figures provided in Wellnhöfer (1971), we cannot assess this first-hand. Furthermore, *Hoplosuchus* (Gilmore, 1926) also possesses unsculpted

osteoderms, although it is likely that this species represents a protosuchian-grade taxon (*sensu* Wu, Sues & Dong, 1997). Therefore, we consider this feature to be autapomorphic for *Alligatorium meyeri*, pending future discoveries of *'Alligatorium' franconicum*. The dorsal osteoderms of *Alligatorium meyeri* are also square-shaped in dorsal view, a feature shared with *T. pusillus*, *Pachycheilosuchus* (Rogers, 2003), and some of the osteoderms of *Protosuchus* (Colbert & Mook, 1951). The overall morphology of the osteoderm shield closely resembles that of the neosuchian *Araripesuchus patagonicus* (Ortega et al., 2000). In addition, the osteoderms of *Alligatorium meyeri* lack any presence of a dorsal keel, a feature shared with a range of neosuchian taxa, but that is distinct from *Alligatorellus*, in which the presence and morphology of this keel varies longitudinally axially (Tennant & Mannion, 2014).

UNNAMED CLADE: (ATOPOSAURUS + ALLIGATORELLUS)

Alligatorellus is united with *Atoposaurus* within all of our analyses (Figs 4–7). This is based on a range of character states, including: (1) a slit-like (i.e. medio-laterally narrow and anteroposteriorly elongated) external supratemporal fenestra (not visible in *Atoposaurus oberndorferi* owing to preservation) (C17.2); (2) smooth lateral surface of anterior jugal process near maxillary contact, not stippled or striated (C51; note that we did not code this as a separate character state owing to potential duplication, as in *Atoposaurus*, the entire external surface of the skull is smooth and unsculpted); (3) straight ventral edge of maxilla in lateral view (C52.0), similar to protosuchians (not sinusoidal or convex as in other neosuchians); (4) minimum mediolateral width between supratemporal fenestrae more than one-third of total width of cranial table (C126.1), acquired in parallel with *Montsecosuchus*, *Brillanceausuchus*, *T. pusillus*, and *T. sympietodon*; and (5) postorbital bar between orbit and supratemporal fenestra very narrow (with respect to lateral edge of postorbital lateral to supratemporal fenestra) and unsculpted, with superficial furrow on dorsal surface of postorbital connecting anterior edge of supratemporal fenestra to the posterior edge of and orbital (C128.2).

ATOPOSAURUS VON MEYER, 1850

Included species

Atoposaurus jourdani (type species, named first in von Meyer, 1850) and *Atoposaurus oberndorferi*.

Distribution

Late Jurassic of southern France and south-east Germany.

Previous diagnoses and comments

Both species of *Atoposaurus* were named by von Meyer (1850), with *Atoposaurus jourdani* receiving a full description by von Meyer (1851). Wellnhofer (1971) was the first to present a diagnosis for *Atoposaurus* based on the specimens from France and Germany, noting the lack of dermal armour, a feature that could be related to either ontogeny or taphonomy (Schwarz & Salisbury, 2005). Subsequently, *Atoposaurus* and its constituent species have largely been considered to be *nomina dubia*, and often regarded as juvenile representatives of *Alligatorellus* and/or *Alligatorium* (e.g. Clark, 1986; Buscalioni & Sanz, 1988). Clark (1986) considered *Alligatorellus*, *Alligatorium*, and *Atoposaurus* to be the same taxon represented by different growth stages. If this were the case, then *Atoposaurus* von Meyer, 1850; would retain priority, and *Alligatorium* Jourdan, 1862, along with *Alligatorellus* Gervais, 1871, would be synonymized with *Atoposaurus*. Almost all subsequent phylogenetic analyses have included just *Alligatorium* based on this conclusion, without consideration of the other taxa. The present analysis is the first to consider both potential species of *Atoposaurus* as independent OTUs, and finds them to be sister taxa in all cases (Figs 4–7), thus supporting their generic assignment.

Despite noting the same features in *Alligatorellus*, Wellnhofer (1971; see also Steel, 1973) stated that the presence of large orbits, a closed internal supratemporal fenestra, and divided external nares were all features defining *Atoposaurus*. The presence of an inwardly displaced postorbital bar (Steel, 1973) is not clear owing to the preservation of available specimens of *Atoposaurus oberndorferi*, but does appear to be a feature of *Atoposaurus jourdani*. Four of the five synapomorphies that we identify for *Atoposaurus* (S1–3, S5) are contentious as they could be indicative of a juvenile phase of growth (e.g. Joffe, 1967), but equally probably they could represent the retention of juvenile characteristics through paedomorphism related to the relatively small body size of *Atoposaurus*. Unfortunately, based on currently available specimens, it is impossible to distinguish between these two hypotheses (Tennant & Mannion, 2014).

Revised diagnosis and discussion

(S1) *Dorsal cranial bones comprising the skull roof unsculpted (C1.0)*: This lack of dermal sculpting, combined with their overall diminutive size, indicates that *Atoposaurus* specimens might be

represented by juveniles. However, it cannot be definitively confirmed that *Atoposaurus* is a juvenile representative of other contemporaneous atoposaurids based on allometric growth patterns alone (Tennant & Mannion, 2014), and it is likely that *Atoposaurus*, *Alligatorellus*, and *Alligatorium* represent three distinct genera, as our results indicate (Figs 4–7).

- (S2) *External surface of snout unsculpted (C3.0)*: We consider this to be a distinct feature from S1, as in *Alligatorellus* there is a different pattern of sculpting between the cranial table and the rostrum. *Atoposaurus* is similar to *Alligatorellus* in this respect, completely lacking any evidence of cranial ornamentation, although this cannot be assessed properly in *Atoposaurus oberndorferi* owing to the mode of preservation of the holotype specimen. As with S1, this character is likely to be highly influenced by either ontogeny or paedomorphism (Joffe, 1967).
- (S3) *Skull anteroposterior length to orbit length ratio <3.0 (C27.0)*: This feature is unique to *Atoposaurus*, and represents the characteristic proportionally large orbits and short snout of this taxon, noted by Joffe (1967) to be indicative of a juvenile status. Other atoposaurids have a ratio of between 3.0 and 4.0. *Karatausuchus* has a ratio of 3.36, slightly higher than *Alligatorellus bavaricus* (3.12), which approaches the state boundary for *Atoposaurus*, but it is likely that *Karatausuchus* represents a juvenile specimen of a (probably non-atoposaurid) crocodyliform (Storrs & Efimov, 2000; see below).
- (S4) *50 or more caudal vertebrae (C276.1)*: Complete axial columns are rarely preserved in specimens previously assigned to Atoposauridae, and the proportional numbers of cervical, dorsal, sacral, and caudal vertebrae remain poorly known, especially for *Theriosuchus*. Both species of *Alligatorellus* preserve complete and articulated caudal vertebral series, and have 40 vertebrae each. *Montsecosuchus* appears to only have 21 caudal vertebrae, and *Pachycheilosuchus* has just 18 (Rogers, 2003). *Protosuchus richardsoni* has 39 caudal vertebrae, and *Karatausuchus* has 46 (Storrs & Efimov, 2000), approaching the number for *Atoposaurus*, but no other crocodyliform taxon has 50 vertebrae. The presence of 50 or more caudal vertebrae, in all specimens of *Atoposaurus* in which this feature can be measured, is not known in any other mesoeucrocodylian taxon, and cannot be explained by ontogeny (Tennant & Mannion, 2014); therefore, we regard it as a diagnostic feature for *Atoposaurus*, irrespective of the ontogenetic stage of the specimens, and

therefore consider *Atoposaurus* to be a valid taxon.

- (S5) *Osteoderms absent*: The lack of osteoderms is unlikely to be a taphonomic artefact (contra Schwarz-Wings *et al.*, 2011), and is either a feature associated with extreme dwarfism in *Atoposaurus*, or relates to their lack of development in juvenile individuals. The only other putative atoposaurid that is similar in this respect is *Karatausuchus*, which Storrs & Efimov (2000) described as having reduced dermal ossicles.

ATOPOSAURUS JOURDANI VON MEYER, 1850
(TYPE SPECIES)

Type locality and horizon

Unknown bed, Kimmeridgian (Late Jurassic); Cerin, Ain, France.

Type specimen

MHNL 15679, articulated partial skeleton comprising dorsally flattened skeleton and skull, missing the posterior-most caudal vertebrae, with distal hindlimbs and distal left forearm preserved as impressions.

Referred specimen

MHNL 15680 (same locality as type specimen), posterior half of articulated skeleton, including trunk vertebrae and forearms.

Previous diagnoses and comments

von Meyer (1851) named *Atoposaurus jourdani*, and described this taxon in a subsequent paper (von Meyer, 1851). We find that a unique combination of metric characters, almost exclusively regarding the relative proportions of the forelimb and hindlimb elements, can be used to distinguish this taxon from *Atoposaurus oberndorferi*, along with a single autapomorphy.

Revised diagnosis and discussion

- (S1) *Skull mediolateral width to orbit width ratio of 1.80 (C28.0)*: This represents the lowest ratio for all atoposaurids, demonstrating that the orbits comprise almost the entire mediolateral width of the skull, separated by the narrow frontals. This is similar to *Alligatorellus bavaricus*, which also has enlarged orbits, but slightly mediolaterally wider frontals between the orbits (Tennant & Mannion, 2014).
- (S2*) *Six cervical vertebrae (C266.0)*: This character state is unique amongst all putative atoposaurids, with all others possessing seven

cervical vertebrae. We were unable to determine this character state for any specimens assigned to *Theriosuchus* owing to their preservation and/or incompleteness. This cervical count is distinct from *Protosuchus richardsoni* (nine) and *Hoplosuchus* (11), as well as *Karatausuchus* (eight; Storrs & Efimov, 2000) (Table 2).

- (S3) *Forelimb length to hindlimb length ratio of 0.63 (C285.0)*: This character state is similar to *Protosuchus richardsoni* (0.65) and *Montsecosuchus* (0.63). *Atoposaurus jourdani* is distinct in this respect from other atoposaurids, including *Alligatorellus beaumonti*, which has a ratio of 0.81, and *Atoposaurus oberndorferi*, which has a ratio of 0.78. *Alligatorellus bavaricus* has an intermediate ratio of 0.76 (Table 3).
- (S4) *Humerus length to femur length ratio of 0.67*: This feature is similar to *Protosuchus richardsoni* (0.66) and *Montsecosuchus* (0.70). *Alligatorellus beaumonti* is similar, with a ratio of 0.75, but *Alligatorellus bavaricus* is quite distinct, with a ratio of 0.89, similar to *Atoposaurus oberndorferi* (0.89). *Karatausuchus* also has similar limb proportions, with a ratio of 0.73. *Theriosuchus pusillus* falls within the range for atoposaurids, with a ratio of 0.76, but *T. guimarotae* is distinct with a ratio of 0.98, approaching that for *Pachycheilosuchus* (1.09) and *Brillianceausuchus* (1.11) (Table 3).
- (S5) *Radius to tibia length of 0.61 (C286.0)*: This character state is similar to *Protosuchus richardsoni* (0.63) and *Montsecosuchus* (0.64), along with *Pachycheilosuchus* (0.64). *Theriosuchus pusillus* has a proportionally long radius to tibia ratio (0.55), with this value only being exceeded by *Karatausuchus* (0.47). Based on Wellnhofer (1971), '*Alligatorium*' *franconicum* has the most extreme value, with a ratio of 0.89, reflecting a proportionally long radius. This value is similar to *Brillianceausuchus* (0.88). *Atoposaurus oberndorferi* and *Alligatorium meyeri* each have a ratio of 0.74, similar to *Shamosuchus* (0.72) and *Hoplosuchus* (0.76) (Table 3).
- (S6) *Metatarsals longitudinally grooved (C302.0)*: This feature also characterizes *Alligatorellus beaumonti* and *Montsecosuchus* (Tennant & Mannion, 2014), in contrast to the smooth and flat metatarsals that characterize most other mesoeucrocodylians. However, we are cautious in our interpretation of this feature, as there remains the possibility that it could represent post-mortem crushing of the delicate long bones in the tarsus.

ATOPOSAURUS OBERNDORFERI VON MEYER, 1850*Type locality and horizon*

Solnhofen Formation, early Tithonian (Late Jurassic, *Hybonoticer as hybonotum* ammonoid zone); Kelheim, Eichstätt, Bavaria, Germany.

Type specimen

TM 3956, near-complete skeleton, missing only the dorsal part of the skull and posterior portion of the tail.

Referred specimen

BSPG 1901 I 12, a counterpart specimen of a different individual comprising the impression of the complete skull and skeleton in lateral view.

Previous diagnoses and comments

Wellnhofer (1971) diagnosed *Atoposaurus oberndorferi* primarily on several size-based characteristics, but these are unlikely to represent diagnostic morphological characters. He also noted the presence of five premaxillary and eight maxillary teeth, but this could not be confirmed via observation of the type specimen because of the way in which it is preserved, and was not illustrated in the figure of the referred specimen in Wellnhofer (1971). Steel (1973) followed the diagnosis of Wellnhofer (1971), and also suggested that the inwardly displaced postorbital bar was diagnostic of *Atoposaurus oberndorferi*; however, this feature is now recognized as characterizing Atoposauridae (see above). Furthermore, because of the lateral compression of the type specimen, it was not possible to directly confirm the presence of this feature in *Atoposaurus oberndorferi*, and it is not figured by Wellnhofer (1971), and therefore cannot be supported. We present a revised diagnosis based on examination of the type specimen for *Atoposaurus oberndorferi*, and tentatively consider it to be a valid taxon based on three ambiguous autapomorphies.

Revised diagnosis and discussion

(S1) *Skull anteroposterior length to width ratio* ~2.00 (1.98) (C25.0): This feature is tentatively considered to be diagnostic for *Atoposaurus oberndorferi*, as the skull is highly incomplete and preserved only in ventrolateral aspect. This estimated skull length-to-width ratio is high, similar to *Eutretauranosuchus* (1.97), *Montsecosuchus* (1.80), which is represented by a mature specimen (Buscalioni & Sanz, 1990a), and *Theriosuchus guimarotae* (1.82) (Schwarz & Salisbury, 2005). *Atoposaurus jourdani* has a much lower ratio (1.28), more

similar to *Protosuchus* (1.31) and *Hoplosuchus* (1.35). The only taxa that have higher ratios are *Alligatorellus* (2.06–2.21), *Alligatorium meyeri* (2.26), '*Alligatorium*' *franconicum* (2.77), and *Koumpiodontosuchus* (2.04) (Table 3).

- (S2) *Skull anteroposterior length to orbit length ratio* <3.00 (2.86) (C27.0): As with (S1), we are cautious with our interpretation of this character state based on the way in which the observed type specimen of *Atoposaurus oberndorferi* is preserved, exposing the enlarged orbit only in ventral aspect. The only taxon with a lower ratio is *Atoposaurus jourdani* (2.33), with *Alligatorellus* and *Alligatorium* possessing ratio values between 3.0 and 4.0. *Protosuchus* has a ratio of 4.52 (Table 3), an intermediate value between atoposaurids and higher neosuchians.
- (S3) *Inwardly (dorsally) displaced splenial on the ventral mandibular surface* (C234.1): In all other taxa we analysed in which the ventral surface of the mandible was exposed, the anterior portion of the splenial is confluent ventrally with the posterior cavity that is formed from the two posteriorly divergent mandibular rami. In *Atoposaurus oberndorferi*, the splenial is slightly inset at its contact with the dentary, a feature shared only with *T. pusillus*. The ventral side of the skull and mandibular region is not preserved in *Atoposaurus jourdani*, and this character state might also be present in that taxon too. Therefore, we are cautious in our retention of *Atoposaurus oberndorferi* as a distinct, second species of *Atoposaurus*.

ALLIGATORELLUS GERVAIS, 1871*Included species*

Alligatorellus beaumonti (Gervais, 1871), *Alligatorellus bavaricus* (Wellnhofer, 1971; *sensu* Tennant & Mannion, 2014).

Distribution

Late Jurassic of southern France and south-east Germany.

Previous diagnoses and comments

Alligatorellus was diagnosed by Wellnhofer (1971) based on its overall size, the shape of its skull, and its relatively large orbits, features that are all more widespread amongst atoposaurids and other small-bodied neosuchians. Wellnhofer (1971) originally described two subspecies of *Alligatorellus beaumonti*,

based on relative sizes and differences and geographical distribution. Most recently, Tennant & Mannion (2014) documented a number of distinguishing characters between *Alligatorellus beaumonti beaumonti* from France and *Alligatorellus beaumonti bavaricus* from Germany, and reranked the latter to its own species, *Alligatorellus bavaricus*. Several of the diagnostic synapomorphies for *Alligatorellus*, presented below, might be related to ontogenetic factors, such as the heterogeneity of the cranial sculpting and the closed internal supratemporal fenestra (Joffe, 1967). However, these features could also be related to the proposed 'dwarfism' for atroposaurids, and there are other indicators that the available specimens of *Alligatorellus* represent a reasonably mature state of growth, such as neurocentral fusion and the degree of fusion of the cranial bones (Joffe, 1967; Tennant & Mannion, 2014).

Schwarz-Wings *et al.* (2011) referred a partial skeleton, MB.R.3632, from the early Tithonian of Franconia, Germany (*Gravesia gigas* ammonoid zone) to *Alligatorellus* sp., but Tennant & Mannion (2014) concluded that this specimen could only be referred to as Atroposauridae indet. In most of our analyses, this specimen is recovered as an indeterminate non-atroposaurid taxon (Figs 4, 7A). However, when we used implied weighting, this specimen groups with the other species of *Alligatorellus* within Atroposauridae (Fig. 6). Therefore, we tentatively regard its status as *Alligatorellus* sp. to be valid.

Revised diagnosis and discussion

- (S1) *Cranial table sculpting composed of homogeneous, subcircular shallow pits (C2.2)*: The cranial sculpting pattern for *Alligatorellus* is distinct from that of *Atoposaurus*, which has a smooth dorsal surface, and from *Alligatorium* and *Theriosuchus* in which the sculpting is much more prominent. It is similar to *Wannchampsus*, which is also lightly sculpted. The reduction or lack of sculpting has been noted in smaller specimens of the basal mesoeucrocodylian *Zosuchus* (Pol & Norell, 2004a,b), as well as the protosuchian *Gobiosuchus* (Osmólska, Hua & Buffetaut, 1997).
- (S2) *Rostrum unsculpted or relatively less than the cranial table (C3.1)*: Similar to (S1), the sculpting of the rostrum is relatively light compared with *Alligatorium meyeri*, *T. pusillus*, and *Wannchampsus*. Distinct from these taxa, however, is how the degree of sculpting appears to decrease anteriorly for *Alligatorellus*, with a more prominent pattern on the cranial table, and almost no sculpting on the dorsal surface of the rostrum. This morphology is similar to that seen in the

paratype of *Isisfordia*, which is represented by an adult specimen (Salisbury *et al.*, 2006), and *Pachycheilosuchus*, which is known from mature individuals (Rogers, 2003). In other taxa represented by mature specimens, such as *T. pusillus* and *Rugosuchus* (Wu, Cheng & Russell, 2001a), sculpting patterns are homogeneous across the entire dorsal surface of the skull. *Alligatorium meyeri* is unusual in that the degree of sculpting remains the same between the rostrum and cranial table, but anteriorly the subcircular pits become more elongated, a feature visible in the counterpart to its holotype specimen (MNHL 15462), and which helps to distinguish it from *Alligatorellus*.

- (S3) *Closed internal supratemporal fenestra (C16.1)*: This feature refers to the lack of opening of the internal supratemporal fenestra, as noted by Wellnhofer (1971). In all other specimens we observed, the internal supratemporal fenestra is completely open. Joffe (1967) described the opening as 'slit-like' for *T. pusillus*, and regarded it as indicative of an immature individual. However, our observations of the paratype specimen (NHMUK PV OR48330) did not confirm this, and the internal fenestrae appear to be fully open. Because of poor preservation, we were unable to determine whether the morphology of the internal supratemporal fenestra was open or closed in any specimen of *Atoposaurus*.
- (S4) *Frontal maximal mediolateral width between the orbits narrower than maximal width of nasals (C97.1)*: This character state relates to the proportionally large size of the orbits, which occupy the majority of the mediolateral width of the dorsal surface of the skull, with a proportionally narrow interorbital region composed of the fused frontals. Although this feature is shared by many other neosuchians, including *Theriosuchus* and *Wannchampsus*, the frontals are distinctly narrower in *Alligatorellus*. In protosuchians, such as *Protosuchus* and *Hoplosuchus*, the mediolateral width of the frontal is broader than the nasal, because in these taxa the orbit is more laterally facing, and therefore does not occupy as much of the mediolateral width of the skull in dorsal view.
- (S5) *Broad frontal anterior process with parallel lateral margins, not constricted (C109.0)*: This feature is distinct from the morphology described in (S4), and relates exclusively to the development of the frontals anteriorly to the anterior margin of the orbits, excluding the morphology of any frontal anterior process

where present. The broad anterior edge of the frontal with parallel lateral edges in *Alligatorellus* is similar to paralligatorids, *T. pusillus*, and *Montsecosuchus*, but contrasts with *T. guimarotae* in which the mediolaterally constricted anterior portions of the frontals distinctly underlap the nasals (Schwarz & Salisbury, 2005).

- (S6) *Flat and unsculpted anterior supratemporal margins (C119.0)*: In *Alligatorellus bavaricus*, the supratemporal rims are flat and unsculpted along their entire medial edge, similar to protosuchians, *Pachycheilosuchus*, coelognathosuchians, *Montsecosuchus*, and *Koumpiodontosuchus*. However, in *Alligatorellus beaumonti*, there is a slight posterior development of the supratemporal margins, similar to *Brillianceausuchus* (specimen UP BBR 203). This is distinct from *Alligatorium meyeri*, *Wannchampsus*, and all species referred to *Theriosuchus*, in which the supratemporal rims are consistently well developed along their entire medial margin.
- (S7*) *Anterior process of squamosal extends to the posterior orbital margin (C144.0)*: This character state appears to be diagnostic for *Alligatorellus*, although we are cautious in this assignment, as the postorbital region is poorly preserved, and the exact morphology of the postorbital with respect to the other posterior periorbital elements is difficult to assess. However, in the holotypes of *Alligatorellus beaumonti* and *Alligatorellus bavaricus*, there is no notable suture on the dorsal surface of the skull table, lateral to the supratemporal fenestra, which would represent the suture between the posterior process of the postorbital and the anterior process of the squamosal. We therefore infer that the anterior process of the squamosal reached the posterior orbital margin.
- (S8) *Posterodorsal margin of parietals and squamosals completely covers posterodorsal occipital region, excluding the supraoccipital from the dorsal surface of the skull (C197.1)*: This feature was proposed by Tennant & Mannion (2014) to be autapomorphic for *Alligatorellus*, but also appears to be present in a range of neosuchian taxa (e.g. *Acynodon adriaticus*; Delfino *et al.*, 2008b) in which the supraoccipital is excluded from the posterodorsal surface of the skull roof. We therefore consider it to only be locally diagnostic for *Alligatorellus*. In other mesoeucrocodylians, such as *Mahajangasuchus* (Turner & Buckley, 2008),

the supraoccipital is broadly visible in the midline portion of the posterodorsal region of the skull, contacting the parietals.

- (S9) *Smooth mandibular external surface, lacking sculpting (C201.0)*: This feature is difficult to observe in *Alligatorellus bavaricus* owing to the dorsal flattening of the holotype specimen, although what is visible indicates that the mandible, much like the anterior portion of the skull, lacks any sculpting pattern, unlike the dorsal surface of the cranial table. This is distinct from *Theriosuchus* and *Wannchampsus*, in which the sculpting pattern on the external surface of the dentaries and posterior mandibular elements is similar to that of the dorsal surface of the skull.
- (S10) *Proximal end of the radiale 'hatchet-shaped' (C290.1)*: This feature also characterizes MB.R.3632, and was used to refer this specimen to *Alligatorellus* (Schwarz-Wings *et al.*, 2011). However, this morphology is also shared by *Wannchampsus* (Adams, 2014), but is not known in *Theriosuchus* specimens, owing to lack of preservation of the radiales. In other atoposaurids, the proximal end of the radiale is more expanded equidimensionally, lacking the asymmetry observed in *Alligatorellus*.
- (S11) *Proportionally short metatarsal I relative to metatarsals II–IV (C303.1)*: In other atoposaurids, metatarsals I–IV are almost equidimensional, possibly reflecting different locomotor adaptations in *Alligatorellus*.
- (S12*) *Dorsal surface of dorsal osteoderms completely sculpted (C304.0), with parallel and straight anterior and posterior margins (C308.1), and a longitudinal ridge along entire lateral margin (C311.1 and C312.1)*: The utility of osteoderms in atoposaurid systematics, particularly regarding *Alligatorellus*, was discussed by Tennant & Mannion (2014). These authors noted that the mediolateral position and anteroposterior extent of the dorsal keel, and its serial variation along the axial column, are diagnostic for *Alligatorellus*, as well as for other crocodyliforms (e.g. teleosauroids, eusuchians) that preserve a dorsal series of paravertebral osteoderms.
- (S13) *Caudal osteoderms with smooth, nonserrated edges (C327.1)*: This morphology is similar to the osteoderms preserved for *T. guimarotae* and *T. pusillus*, but distinct from *Brillianceausuchus* and *Montsecosuchus* in which the margins of the caudal osteoderms are serrated. Serrated edges might also be present in caudal osteoderms of MB.R.3632,

based on at least three caudal osteoderms disassociated from the main osteoderm shield preserved on the specimen slab. However, we cannot discount the possibility that these elements are accessory dorsal osteoderms, as found in *Montsecosuchus* and in the proximal caudal series of *Alligatorellus beaumonti*.

ALLIGATORELLUS BEAUMONTI Gervais, 1871
(TYPE SPECIES)
ALLIGATORELLUS BEAUMONTI BEAUMONTI
Wellnhofer, 1971

Type locality and horizon

Unknown bed, Kimmeridgian (Late Jurassic); Cerin, Ain, France.

Type specimen

MNHL 15639, part and counterpart slabs comprising a near-complete and articulated skeleton, missing the distal-most caudal vertebrae (preserved as impressions) and part of the left forelimb. Parts of the skull roof and a large portion of the right maxilla, along with several axial fragments, are embedded into the counterpart slab.

Referred specimen

MNHL 15638, part slab comprising a near-complete and articulated skull and skeleton, missing just the distal-most caudal vertebrae, the right forelimb, and the distal left forelimb, all of which are preserved as impressions. The skull is exposed in ventrolateral aspect.

Previous diagnoses and comments

Alligatorellus beaumonti was originally named by Gervais (1871) for two specimens from the Late Jurassic of Cerin, eastern France. Subsequently, Wellnhofer (1971) diagnosed these specimens as a distinct subspecies, *Alligatorellus beaumonti beaumonti*. This was based largely on size differences between these and coeval specimens from Eichstätt, south-east Germany, for which Wellnhofer (1971) erected the subspecies *Alligatorellus beaumonti bavaricus* (see below). Together these specimens have largely been regarded as representing a single taxon, *Alligatorellus beaumonti*, by subsequent workers (e.g. Buscalioni & Sanz, 1988; Schwarz-Wings *et al.*, 2011). However, Tennant & Mannion (2014) redescribed the German remains, and observed a number of morphological differences with the French material. They provided a revised diagnosis for *Alligatorellus beaumonti*, and re-ranked the German material as *Alligatorellus bavaricus*.

Wellnhofer (1971) noted that as in *Theriosuchus*, the external nares in *Alligatorellus beaumonti* are

divided by an anterior projection of the nasals, a feature that also appears to be shared by *Alligatorium meyeri* and possibly *Alligatorellus bavaricus*, although the anterior-most portion of the snout in the holotype of the latter is damaged. *Alligatorellus beaumonti* is similar to *Alligatorium meyeri* in the presence of an unsculpted posterolateral 'lobe' of the squamosal, differing from *Alligatorellus bavaricus* in which the posterolateral corner of the squamosal instead displays orthogonal posterior and lateral edges. Buscalioni & Sanz (1988) suggested that another distinguishing feature between *Alligatorellus beaumonti* and *Alligatorium meyeri* is the contribution of the frontal to the supratemporal fenestra in the former; however, this feature is clearly also present in *Alligatorium meyeri*, and therefore cannot be used to distinguish the two taxa. The presence of a biserial osteoderm shield comprising singular sculpted osteoderms is not diagnostic for *Alligatorellus* (contra Wellnhofer, 1971), as it also characterizes both *T. pusillus* and *Alligatorium meyeri*. Tennant & Mannion (2014) proposed that the frontal width between the orbits being mediolaterally narrower than the nasals is an autapomorphy of *Alligatorellus beaumonti*; however, this condition is not considered to be diagnostic here, as it is also known in a wide range of neosuchian taxa, and the width of the paired nasals in *Alligatorellus bavaricus* might have been underestimated. *Alligatorellus beaumonti* also has the reversed condition to *Alligatorellus bavaricus*, in that the anterior extension of the frontal exceeds the anterior margin of the orbits, similar to almost all other neosuchian taxa.

Revised diagnosis and discussion

- (S1*) *Frontal with unsculpted anterior and posterior portions, and sculpted medial surface:* We elected not to code this as a distinct character state from that of S3 in our matrix in order to avoid duplication of character states. Nonetheless, Tennant & Mannion (2014) identified this heterogeneity in sculpting pattern as distinct from other atoposaurids and *Theriosuchus*, and considered it to be autapomorphic of *Alligatorellus beaumonti*.
- (S2) *Surface of rostrum notably less sculpted than cranial table (C4.1):* See S2 for *Alligatorellus* for discussion of this character state.
- (S3) *Relatively large lateral temporal fenestra, approximately 30% of the size of the orbit (C20.1):* A lateral temporal fenestra of this size with respect to the orbit represents the intermediate condition in our analyses. This relatively large size is unique amongst atoposaurids, but is also shared with *T. pusillus*, *Koumpiodontosuchus* (Sweetman

et al., 2015), and protosuchians, as well as the advanced neosuchians *Shamosuchus* (Pol *et al.*, 2009), *Isisfordia* (Salisbury *et al.*, 2006), and *Brillanceausuchus*. In other taxa, such as *Allodaposuchus precedens*, the lateral temporal fenestra approaches the size of the orbit (Buscalioni *et al.*, 2001).

- (S4) *Smooth contact between maxilla and jugal (C51.2)*: As noted above, the pattern of sculpting on the anterior portion of the dorsal surface of the skull is diagnostic for the different species of *Alligatorellus*. In *Alligatorellus bavaricus*, the entire dorsal surface is lightly sculpted, but *Alligatorellus beaumonti* has a smooth contact between the maxilla and jugal, similar to *Atoposaurus* and *Hoplosuchus*, although in both of these taxa the entire external surface of the skull is not ornamented. This is distinct from *T. guimarotae* and *T. pusillus*, which both have a contact in which the external surface is sculpted to the same degree as the rest of the cranial table, and from *Brillanceausuchus*, '*T.* ibericus', '*T.* sympiestodon', and *Montsecosuchus*, in which the contact is heavily striated.
- (S5*) *Medial longitudinal depression on posterior portion of nasal and anterior portion of frontal (C74.1)*: This is diagnostic of *Alligatorellus beaumonti* as a local autapomorphy, but is also present in the goniopholidid *Amphicotylus* (Mook, 1942). This condition differs from that in *Theriosuchus* and a range of paralligatorids, including *Brillanceausuchus*, in which a distinct midline longitudinal crest develops.
- (S6*) *Posteromedial border of supratemporal fenestra forms a low sagittal rim (C119.1)*: This feature is considered to be locally autapomorphic, as it is also present in *Brillanceausuchus*. *Alligatorellus bavaricus* and *Atoposaurus* have no supratemporal rim development, and the rims are strongly developed along the whole medial edge of the external supratemporal fenestra in *Alligatorium meyeri*, *T. pusillus*, and *Wannchampsus* (Adams, 2014).
- (S7*) *Smooth and unsculpted region on anterior portion of squamosal nearing orbit and posterolateral process of squamosal (C148.1)*: This feature appears to be locally diagnostic, but is also shared by *Khoratosuchus* (Lauprasert *et al.*, 2009). For all other OTUs for which this feature could be scored, the pattern of sculpting did not change between the main body of the squamosal and the immediate postorbital region.

- (S8*) *Ratio of forelimb to hindlimb length high (0.8) (C180.2)*: This feature is diagnostic for *Alligatorellus beaumonti* amongst all OTUs for which this character could be scored. *Atoposaurus oberndorferi* and *Alligatorellus bavaricus* both have similar ratios, 0.78 and 0.76, respectively, but *Atoposaurus jourdani* is distinct, with a ratio of 0.63 (Table 3). However, this character state could not be scored for *Theriosuchus*, or the majority of our outgroup taxa, because of the relative rarity with which these specimens preserve associated and complete limb material. Therefore, although these unusual ratios are diagnostic amongst atoposaurids, we cannot determine whether they are unique or only local autapomorphies.
- (S9) *Ratio of tibia to femur length low (0.9) (C300.0)*: The relative dimensions of the tibia and femur are a feature that is closely shared with MB.R.3632 (0.91), *Hoplosuchus* (0.92), *Alligatorium meyeri* (0.93), and *Atoposaurus jourdani* (0.94). This ratio far exceeds that for '*Alligatorium*' *franconicum* (0.64), and is distinct from *Alligatorellus bavaricus* (0.96) (Table 3). This feature was also noted by Tennant & Mannion (2014), but those authors used a ratio of femur to tibia length.
- (S10*) *Nuchal osteoderms reduced, <50% of the size of the dorsal osteoderms (C307.1)*: This feature is distinct from the condition in *Alligatorellus bavaricus*, *Alligatorium meyeri*, *Montsecosuchus*, and *Protosuchus*, in which the preserved nuchal osteoderms retain the same size and morphology as the dorsal series, or only decrease slightly.
- (S11*) *Dorsal keel in dorsal osteoderms shifts laterally in more posterior dorsal osteoderms (C317.1)*: The position of the dorsal keel on the dorsal osteoderm series is distinct from that in *Alligatorellus bavaricus*, in which the morphology is more consistent along the axial column (Tennant & Mannion, 2014). This feature is not present in any other of the OTUs that we sampled, and therefore we consider it to be diagnostic for *Alligatorellus beaumonti*.
- (S12*) *Lateral ridge on sacral osteoderms forms an incipient posterior projection*: The posterior development of the lateral keel (as noted in S9) into an incipient lateral projection amongst the more sacrally positioned osteoderms is diagnostic for *Alligatorellus beaumonti*. In *Alligatorellus bavaricus*, the morphology of the keel does not change anteroposteriorly (Tennant & Mannion, 2014),

and *Theriosuchus*, *Alligatorium meyeri*, and higher neosuchians do not seem to possess this keel at all. '*Alligatorium*' *franconicum* and *Hoplosuchus* are convergently similar, in that the lateral keel appears to form an anterolateral process, distinct from the 'peg and socket' articulation described for goniopholidids and *T. guimarotae* (Schwarz & Salisbury, 2005). We did not incorporate this as a character to avoid duplication and over-weighting of the observation that the morphology of the dorsal keel changes axially in *Alligatorellus beaumonti* (S11).

- (S13*) *Secondary osteoderms present in caudal series (C328.0)*: This feature does not appear to be present in any other atoposaurid that preserves caudal osteoderms.

Additional comments

In the holotype specimen of *Alligatorellus beaumonti*, the posterior-most maxillary teeth have a more labiolingually compressed, apically pointed morphology than the remaining teeth, similar to the 'lanceolate' morphology exhibited by several species of *Theriosuchus* (Schwarz & Salisbury, 2005; Lauprasert *et al.*, 2011) and *Brillianceausuchus*, as well as the bernissartiid *Koumpiodontosuchus* (Sweetman *et al.*, 2015). This is different to the homodont dentition typically reported for *Alligatorellus*, which is usually described as possessing simple pseudocaniniform teeth that are smooth and lack ridges or carinae (e.g. Buscalioni & Sanz, 1990a,b; Thies *et al.*, 1997). However, we do not assign this as a local autapomorphy of *Alligatorellus beaumonti* as it is only visible for one or two teeth in a specimen that shows strong evidence of dorsal compression. Its validity therefore requires further investigation pending the discovery of more specimens of *Alligatorellus*. Although this more lanceolate morphology was also figured for the posterior teeth of *Alligatorellus bavaricus* by Wellnhofer (1971), we have been unable to personally validate this on the figured specimen, and it is not visible on the holotype. Therefore, we urge caution in interpreting *Alligatorellus* as possessing lanceolate posterior teeth that are homologous to those found in *Theriosuchus*. Re-running our phylogenetic analysis [excluding '*Alligatorellus*' sp. (MB.R.3632) and *Pachycheilosuchus* as before] with *Alligatorellus* scored as possessing lanceolate posterior teeth, we achieve a single MPT with a length of 793 steps with an unchanged topology. However, the presence of a lanceolate dentition instead becomes the basal condition in the clade containing atoposaurids and higher neosuchians, secondarily lost in *Alligatorium meyeri*, *Brillianceausuchus*, '*T.*' *ibericus*, '*T.*' *sympiestodon*, and the clade containing *Koumpiodontosuchus* and coelognathosuchians.

ALLIGATORELLUS BAVARICUS WELLNHOFER, 1971
(RE-RANKED BY TENNANT & MANNION, 2014)
ALLIGATORELLUS BEAUMONTI BAVARICUS
WELLNHOFER, 1971

Type locality and horizon

Solnhofen Formation, early Tithonian (Late Jurassic, *Hybonoticerias hybonotum* zone); Eichstätt, south-east Germany.

Type specimen

BSPG 1937 I 26, a near-complete skeleton including the skull, lacking only the left forelimb, compressed onto a slab of lithographic limestone. Note that Tennant & Mannion (2014) incorrectly stated that the specimen number was LMU 1937 I 26.

Referred specimen

A specimen held in the private collection of E. Schöpfungel was described and referred to *Alligatorellus bavaricus* by Wellnhofer (1971), from the Wintershof Quarry (Solnhofen Formation, Eichstätt, southeast Germany).

Revised diagnosis and discussion

- (S1) *Concave profile of dorsal surface of snout in lateral view (C8.0)*: This feature represents a reversion back to the plesiomorphic state known for *Protosuchus* (Colbert & Mook, 1951) and *Hoplosuchus* (Gilmore, 1926), with other atoposaurids and neosuchians usually presenting a straight profile in lateral aspect (with exceptions such as the longirostrine goniopholidid *Amphicotylus*; Mook, 1942).
- (S2) *Small, slit-shaped antorbital fenestra, enclosed by nasals (C13.0 and C14.1)*: *Alligatorellus bavaricus* appears to possess a small, slit-like antorbital fenestra, similar to the notosuchians *Gondwanasuchus* (Marinho *et al.*, 2013) and *Malawisuchus* (Gomani, 1997). In other taxa with an antorbital fenestra, including *T. guimarotae* (Schwarz & Salisbury, 2005), *T. pusillus*, and '*T.*' *ibericus*, it is proportionally larger and rounded. *Alligatorellus beaumonti* does not appear to possess an antorbital fenestra, although part of the snout is embedded in the counterpart slab, with a small opening observable near the posterior margin of the nasals, which could be a diminutive fenestra. The presence of an antorbital fenestra is documented in basal crocodyliforms, including the protosuchians *Hoplosuchus* (Gilmore, 1926) and *Protosuchus haughtoni* (Gow, 2000), *Zosuchus* (Pol & Norell, 2004a), and thalattosuchians (Leari

et al., 2012), but becomes closed in shartegosuchids, including *Fruitachamps* (Clark, 2011). *Pachycheilosuchus* might have also possessed an antorbital fenestra (Rogers, 2003).

- (S3*) *Extremely narrow and short skull, with a low skull width to orbit width ratio (< 2.0) (C28.0)*: This character state is the lowest value for all atoposaurids, and much lower than all other OTUs in which this character was measurable. For other atoposaurids, this ratio is between 2.15 (*Alligatorellus beaumonti*) and 2.69 (*Atoposaurus jourdani*), and the only other taxon that comes close to this range is *Wannchampsus* (2.77). *Brillianceausuchus*, *Montsecosuchus*, and *Theriosuchus* species all have ratios between 3.0 and 3.5, with the ratio being considerably greater in longirostrine taxa and protosuchians (Table 3). It is likely that this character state is influenced by ontogeny (Joffe, 1967), but the broad distribution of ratios amongst the sampled OTUs, which possess a range of body sizes and ontogenetic states, means that ontogeny is unlikely to entirely control this feature.
- (S4) *Skull anteroposterior length to supratemporal fenestra length ratio ~ 7.2 (7.18) (C29.2)*: The proportional length of the external supratemporal fenestra is similar to *Wannchampsus kirpachi* (7.53), but distinct from *Alligatorium meyeri* (6.43) and *Alligatorellus beaumonti* (6.23), which have proportionally larger external supratemporal fenestrae. Consequently, we consider the proportionally short anteroposterior length of the supratemporal fenestra to skull length to be diagnostic for *Alligatorellus bavaricus*, because in *Montsecosuchus* this ratio is considerably higher (8.9) (Table 3), with a much smaller supratemporal fenestra.
- (S5*) *Posterior surface of nasals longitudinally crenulated (C69.0)*: The longitudinal crenulations on the dorsal surface of the nasals are not known in any other crocodyliform, in which the nasals are dorsally flat and sculpted like the rest of the cranial dorsal surface.
- (S6*) *Smooth anterior region of parietal dorsal surface with a transverse frontal–parietal ridge, and shallow emargination at the posterior parietal–squamosal contact (C117.1) that develops into a thin dorsal groove connected to the supratemporal fenestra (C147.1)*: The morphology of the parietal is diagnostic, with a small anterior concavity at

the posterodorsal suture contact between the parietal and squamosal, leading to a shallow sulcus along this contact into the posterior margin of the supratemporal fenestra, and a smooth anterior dorsal surface. This is distinct from the condition observed in *Theriosuchus* in which this contact is deep and expands mediolaterally towards the supratemporal fenestra border, and from *Alligatorellus beaumonti* and *Alligatorium meyeri* in which the grooved contact is bordered by raised crests. The presence of a transverse ridge at the parietal–frontal suture distinguishes *Alligatorellus bavaricus* from all other species, in which this suture is flat.

- (S7) *Squamosal posterolateral lobe absent (C139.1)*: The squamosal posterolateral lobe is completely absent in *Alligatorellus bavaricus*, a feature considered to be diagnostic amongst all atoposaurids.
- (S8*) *Distinct ridge on proximodorsal edge of scapula (C280.1)*: The scapula of *Alligatorellus bavaricus* can be distinguished from *Alligatorellus beaumonti* and other atoposaurids based on the presence of a distinct ridge on the proximodorsal surface. In all other specimens we analysed, the proximodorsal edge of the scapula is flat in lateral view, and confluent with the scapular shaft.
- (S9) *Extremely low radius proximodistal length to humerus length ratio (0.69) (C288.1)*: The radius to humerus ratio is extremely low, distinct from other atoposaurids in which the value is closer to 1.0. This low ratio is identical to that for '*Alligatorium*' *franconicum* and *Karatausuchus* (Storrs & Efimov, 2000), but higher than in *Pachycheilosuchus* (0.58).
- (S10*) *Low radius proximodistal length to tibia length ratio (0.64) (C289.1)*: This value is almost identical to that for *Montsecosuchus*, *Pachycheilosuchus*, *Atoposaurus jourdani* (0.61), and *Protosuchus richardsoni* (0.63), but much higher than that for *Karatausuchus* (0.47) and *T. pusillus* (0.55). Other taxa have proportionally long radii, including *Alligatorium meyeri* (0.74), *Alligatorellus beaumonti* (0.71), '*Alligatorium*' *franconicum* (0.89), and *Brillianceausuchus* (0.88).
- (S11*) *Dorsal osteoderms with longitudinal medial ridge, becoming more laterally placed anteriorly (C311.1 and C312.1)*: This feature pertains to the morphology of the dorsal osteoderm series, which are distinct from

those in *Alligatorellus beaumonti* (Tennant & Mannion, 2014), as well as MB.R.3632 (Schwarz-Wings *et al.*, 2011). In *Alligatorium meyeri* and *T. pusillus*, there is no evidence of a lateral keel.

PUTATIVE ATOPOSAURID TAXA

In this section, we provide comments on the systematic position of taxa that historically have been attributed to Atoposauridae, but are here recovered as non-atoposaurids. We provide emended diagnoses for *Montsecosuchus*, '*Alligatorium*' *franconicum*, *Theriosuchus*, '*T.*' *ibericus*, '*T.*' *sympiestodon*, and *Brillanceausuchus*, for which a non-atoposaurid position is novel to our study, and discuss the taxonomic affinities of taxa that have previously been recognized as non-atoposaurids (e.g. *Hoplosuchus*).

NEOSUCHIA BENTON & CLARK, 1988 *MONTSECOSUCHUS* BUSCALIONI & SANZ, 1988

Included species

Montsecosuchus depereti.

Revised diagnosis

As for the type and only species.

Distribution

Early Cretaceous of Spain.

Previous diagnoses and comments

Originally described as a species belonging to *Alligatorium* by Vidal (1915), the differences from *Alligatorium* were first noted by Buffetaut (1981), and subsequently formalized in the erection of the new genus by Buscalioni & Sanz (1988). *Montsecosuchus* is unusual in its relatively robust and shortened forelimbs with respect to its hindlimbs, including a large, transversely expanded distal humerus and proportionally small manus (Buscalioni & Sanz, 1990a). It was originally assigned to Atoposauridae based on its overall size, and is similar to other atoposaurids in the 'hatchet shaped' radiale morphology (Buscalioni & Sanz, 1988, 1990a), but distinct from *Atoposaurus* and *Alligatorellus* in the absence of a reduced fifth metatarsal (Buscalioni & Sanz, 1990a).

Buscalioni & Sanz (1988) found *Montsecosuchus* to be either the sister taxon to *Theriosuchus*, or to (*Alligatorium* + *Alligatorellus*), with this uncertainty reflecting the unusual morphology of *Montsecosuchus*. Many of the autapomorphies defined by Buscalioni & Sanz (1988) are metric, and therefore

might not be solely reliable in generic-level diagnoses within a group in which there is much uncertainty over ontogenetic allometry and potential dwarfism (Joffe, 1967; Schwarz-Wings *et al.*, 2011; Martin *et al.*, 2014a; Tennant & Mannion, 2014). The only recent formal phylogenetic analysis to include *Montsecosuchus* found it to be the sister taxon to *T. guimarotae*, to the exclusion of *T. pusillus* (Figueiredo *et al.*, 2011), although this analysis was not designed to assess the relationships between putative atoposaurids (see also Bronzati *et al.*, 2012). Our results mostly recover *Montsecosuchus* as a non-atoposaurid taxon, but also outside of Paralligatoridae, in an uncertain position along with *Pachycheilosuchus* (Figs 4B, 5A). Our analysis was not designed to constrain the phylogenetic position of non-atoposaurids, but to recover the composition and relative position of Atoposauridae, and we consider *Montsecosuchus* to be Neosuchia *incertae sedis*. However, in the results of the analysis using implied weights, *Montsecosuchus* nestles within Atoposauridae (Fig. 6). These inconclusive results warrant further comparison between *Montsecosuchus* and other neosuchians, to determine its affinities. Therefore, we await the inclusion of *Montsecosuchus* in analyses covering broader neosuchian relationships (e.g. Adams, 2014; Turner, 2015) to resolve its phylogenetic relationships.

Sanz, Ortega & Shibata (2014) identified a specimen as *Montsecosuchus* sp. from the late Barremian Huérgina Formation of Cuenca, Spain, but we have not observed this specimen directly so cannot comment on this further. Examination of this material, and further discoveries of additional material – particularly of the basicranial region – will be important in determining the relationships of this enigmatic taxon.

MONTSECOSUCHUS DEPERETI BUSCALIONI & SANZ, 1988

ALLIGATORIUM DEPERETI VIDAL, 1915

Type locality and horizon

Le Pedrera de Rubies Formation, late Berriasian–early Barremian (Early Cretaceous); Sierra del Montsec, Lérida Province, Spain.

Type specimen

MGB 512, near-complete skeleton and skull, and counterpart MGB 597.

Revised diagnosis and discussion

(S1) *Intertemporal mediolateral width greater than interorbital width (C19.1)*: The relatively high proportion of the interorbital relative to

intertemporal region is a feature shared with '*Alligatorium*' *franconicum*, *Alligatorellus beaumonti* (Wellnhofer, 1971; Tennant & Mannion, 2014), and *Pachycheilosuchus* (Rogers, 2003). In protosuchians, coelognathosuchians, paralligatorids, *Alligatorium meyeri*, and *T. pusillus*, the interorbital width exceeds the width of the intertemporal region. It is unlikely that variation in this feature is exclusively a result of relative growth differences through ontogeny in all of these species, as there are multiple additional lines of evidence that indicate that many specimens had reached skeletal maturity (e.g. neurocentral fusion).

- (S2*) *Intermandibular angle 61° (C24.3)*: *Montsecosuchus* has an extremely anteroposteriorly short and mediolaterally wide skull for its body size, as noted by Buscalioni & Sanz (1990a). The only other taxon to come close to this characteristically wide intermandibular angle is *Atoposaurus jourdani* (55°), in which this state could be a result of an allometric growth factor (Schwarz-Wings *et al.*, 2011; Tennant & Mannion, 2014). Other brevirostrine taxa, including *Wannchampsus*, *Brillanceausuchus*, *Shamosuchus*, and *T. pusillus*, have intermandibular angles in the range of 40–45°. Longirostrine taxa, including *Koumpiodontosuchus* and *Amphicotylus*, have a much lower intermandibular angle of 32–34° (Table 2).
- (S3) *Skull anteroposterior length to supratemporal fenestra length ratio 8.9 (C29.3)*: This dimension reflects the extremely small external supratemporal fenestra of *Montsecosuchus* despite its small skull size, and is similar to *Amphicotylus* (8.57) and *Koumpiodontosuchus* (8.0), as well as possibly *Karatausuchus* (8.41). *Brillanceausuchus* represents the opposite end of the spectrum, with a proportionally longer supratemporal fenestra (ratio of 5.36; Table 3). Atoposaurids, *T. guimarotae*, *T. pusillus*, and *Protosuchus richardsoni* fall within a range of around 6–7.5.
- (S4) *Longitudinal ridge on the jugal below lateral temporal fenestra (C87.1)*: The presence of a longitudinal ridge on the lateral surface of the jugal, just below the lateral temporal fenestra, is shared with *T. guimarotae* (Schwarz & Salisbury, 2005) and '*T. ibericus*'. In atoposaurids, the lateral margin of the jugal is smooth, although this cannot be observed in the holotypes of *Alligatorellus beaumonti* or *Atoposaurus jourdani* owing to the dorsal flattening of these specimens.
- (S5*) *Lateral border of the skull roof terminates immediately dorsal to the medial-most point of contact with the quadrate (C118.1)*: *Montsecosuchus* possesses a very mediolaterally narrow dorsal skull roof compared with the infratemporal region, similar to the eusuchians *Acynodon* (Delfino, Martin & Buffetaut, 2008a) and possibly *Hylaeochampsia* (Clark & Norell, 1992). The lateral extent of the skull roof with respect to the contact with the quadrate is a feature that we consider to be locally diagnostic for *Montsecosuchus*.
- (S6*) *Flat and ungrooved parietal–squamosal suture (147.0)*: The lack of a parietal–squamosal sutural groove is distinct for *Montsecosuchus* amongst all specimens that we scored, similar to *Hylaeochampsia* (Clark & Norell, 1992). In atoposaurids, there is a thin groove occupying the suture, flanked by slightly raised ridges, and in *Theriosuchus* the groove is deeper and expands anteriorly towards the posterior border of the supratemporal fenestra.
- (S7) *Supraoccipital exposed medially in posterodorsal surface of skull roof (C197.0)*: The dorsal exposure of the supraoccipital in the posterior margin of the skull roof is a feature shared with *T. pusillus*, *T. guimarotae* (Schwarz & Salisbury, 2005), *Wannchampsus* (Adams, 2014), and *Brillanceausuchus*. However, in the latter two taxa, the supraoccipital is restricted to a thin surface attached to the posterior-most portion of the parietal and squamosal, and is not as well exposed as it is in *Montsecosuchus*, *Theriosuchus*, and *Mahajangasuchus* (Turner & Buckley, 2008). In *Shamosuchus* (Pol *et al.*, 2009), protosuchians, goniopholidids, atoposaurids, and *Hylaeochampsia* (Clark & Norell, 1992), the supraoccipital is not exposed dorsally in the posterior margin of the skull roof.
- (S8) *Posteriorly domed occipital surface comprising the medial portion of the exoccipitals*: The posteriorly domed occipital region is autapomorphic for *Montsecosuchus* (the 'dolichocephalous' condition, *sensu* Buscalioni & Sanz, 1990a), whereas in other taxa this surface is flat and faces posteriorly or posteroventrally. However, we are cautious in our interpretation of this character state as autapomorphic, following Buscalioni & Sanz (1990a), as it is clear that this specimen has undergone a degree of dorsoventral flattening, and therefore a component of this character could pertain to the displacement of the exoccipitals.

- (S9*) *Posteriorly projecting and dorsally recurved retroarticular process (C242.3)*: This morphology is shared only with *Brillianceausuchus*, and we consider it to be a local autapomorphy for *Montsecosuchus*. The morphology of the retroarticular process appears to be highly phylogenetically informative, with taxa such as *Alligatorellus* having a posteriorly projecting but ventrally recurved form, similar to *Simosuchus* (Buckley *et al.*, 2000) and *Stolokrosuchus* (Serenó *et al.*, 2003), whereas in *T. pusillus* and *T. guimarotae* the process projects posteroventrally and is 'paddle-shaped' (Schwarz & Salisbury, 2005; Pol *et al.*, 2009), similar to *Rugosuchus* (Wu *et al.*, 2001a) and notosuchians (Gomani, 1997). More advanced neosuchians appear to have an extremely reduced, or completely absent, retroarticular process (e.g. *Wannchampsus* and *Shamosuchus*; Pol *et al.*, 2009), a condition similar to *Protosuchus* (Colbert & Mook, 1951) and the notosuchian *Yacarerani boliviensis* (Novas *et al.*, 2009).
- (S10*) *Preacetabular (anterior) process of the ilium absent (C291.2)*: The absence of the preacetabular process on the ilium is a feature that is shared with '*Alligatorium franconicum*' (Wellnhofer, 1971). This process is extremely reduced in *T. guimarotae* (Schwarz & Salisbury, 2005), *Pachycheilosuchus* (Rogers, 2003), and a specimen described as *Theriosuchus* sp. (IVPP V10613) by Wu *et al.* (1996), as well as the giant crocodyliform *Sarcosuchus imperator* (Serenó *et al.*, 2001), being 75% or less of the length of the postacetabular process. The reduction of the iliac anterior process is also the condition for notosuchians (Buckley & Brochu, 1999; Pol, 2005; Turner, 2006).
- (S11) *Three sacral vertebrae (C274.1)*: *Montsecosuchus* is unusual in that it appears to have three sacral vertebrae, a feature that seems to be shared exclusively with *Alligatorellus* (Buscalioni & Sanz, 1990a) within Neosuchia (Table 2), and could relate to reconfiguration of the pelvic girdle (also see S10) owing to mechanical requirements for adaptation to a more terrestrial mode of life. Other occurrences of a third sacral vertebra amongst crocodyliforms are documented in notosuchians (e.g. Pol, 2005; Riff & Kellner, 2001; 2011).
- (S12*) *Dorsal osteoderms not imbricated (C313.1) or sutured (C314.1), oval-shaped, and with medially placed anteroposterior keel on dorsal surface (C311.1 and C312.1)*: The osteoderms of *Montsecosuchus* are distinct from those assigned to *Theriosuchus* and atoposaurids, in that they appear not to contact each other, forming two evenly spaced rows. The shape and spacing are somewhat similar to some of the dorsal osteoderms observed in *Brillianceausuchus*. Cervical osteoderms are not preserved, and there is no evidence of an anterolateral process. In *Alligatorellus*, *Alligatorium*, *Pachycheilosuchus*, and *Theriosuchus*, the osteoderms are subrectangular to square shaped, and form a distinct dorsal shield. Similar to *Alligatorellus* is the presence of the anteroposterior dorsal keel (Tennant & Mannion, 2014), but this appears to have a uniform morphology anteroposteriorly along the axial column in *Montsecosuchus*.
- (S13*) *Accessory osteoderms present in dorsal series (C316.1)*: *Montsecosuchus* also possesses accessory osteoderms that do not contribute to the main dorsal dermal shield. The presence of accessory osteoderms is also known in a range of mesoeucrocodylians, including dyrosaurids (Schwarz-Wings, Frey & Martin, 2009a), the hylaeochampsid *Pietraroiasuchus ormezzanoi* (Buscalioni *et al.*, 2011), the advanced neosuchians *Susisuchus anatoceps* (Figueiredo *et al.*, 2011) and *Isisfordia* (Salisbury *et al.*, 2006), and the eusuchian *Acynodon adriaticus* (Delfino *et al.*, 2008a).
- (S14*) *Caudal osteoderms oval-shaped (C326.0) with serrated lateral edges (C327.0)*: The caudal osteoderms have an oval profile in dorsal view, a feature not known in any atoposaurid or *Theriosuchus*. The serration of the lateral edges of each caudal osteoderm is also diagnostic when combined with the overall morphology of the caudal series, but is a feature shared with *Brillianceausuchus* and *Pachycheilosuchus* (Rogers, 2003).

NEOSUCHIA BENTON & CLARK, 1988
THERIOSUCHUS OWEN, 1878A

Included species

Theriosuchus guimarotae (Schwarz & Salisbury, 2005), *T. grandinaris* (Lauprasert *et al.*, 2011), *T. pusillus* (Owen, 1878a, 1879). We exclude '*T. ibericus*' (Brinkmann, 1989) and '*T. sympiestodon*' (Martin *et al.*, 2010) from this genus (see below).

Distribution

Late Bajocian/Bathonian (Middle Jurassic) to Cenomanian (early Late Cretaceous) of western Europe; Bathonian (Middle Jurassic) of Morocco; Early Cretaceous (possibly latest Jurassic too) of Asia.

Note on taxonomy

Although generally attributed to Owen (1879), *T. pusillus* was actually first named by Owen (1878a) – see discussion of the type species below. In all of our analyses, we find *Theriosuchus* to be polyphyletic within Neosuchia. *Theriosuchus pusillus* and *T. guimarotae* are sister taxa, and form a clade with *T. grandinaris* (Lauprasert *et al.*, 2011) and *Theriosuchus* sp. (NMS G. 2014.52.1; Young *et al.*, 2016). The most surprising result is that *Theriosuchus* does not group with other atoposaurids, and is more closely related to more crownwardly placed neosuchians (i.e. paralligatorids). ‘*Theriosuchus*’ *ibericus* and ‘*T.*’ *sympiestodon* form a clade that is separated from the other species, and which occupies a position nested within paralligatorids. *Theriosuchus pusillus* was the first named species of this genus (Owen, 1878a,b, 1879), and therefore retains taxonomic priority for the genus name. Consequently, we erect a new genus name for ‘*T.*’ *ibericus* and ‘*T.*’ *sympiestodon* (see below), and our revised diagnosis presented below is exclusively for *Theriosuchus*, comprising *T. grandinaris*, *T. guimarotae*, and *T. pusillus* (as well as remains attributed to *Theriosuchus* sp.; e.g. Young *et al.*, 2016).

Previous diagnoses and comments

Theriosuchus was first identified by Owen (1878a,b, 1879), based on two specimens from the Purbeck beds of England. The genus was first referred to Atoposauridae by Joffe (1967), who noted numerous similarities between *T. pusillus* and atoposaurids from western Europe. Since then, its position has varied within Neosuchia, being positioned either as one of the basal-most taxa within Atoposauridae, or more recently in a much more advanced position as the sister taxon to Paralligatoridae, within Eusuchia (Turner, 2015; Turner & Pritchard, 2015). Jouve, Larochène Bouya & Amaghaz (2006) also noted the similarities between *Theriosuchus* and other ‘advanced’ neosuchians, including *Rugosuchus* and *Shamosuchus*, finding them to be closely related to a clade comprising bernissartiids, hylaeochampsids, and crocodylians. Although there are five named species of *Theriosuchus*, typically only *T. pusillus* (Owen, 1878a, 1879) has been included in phylogenetic analyses involving Neosuchia, sometimes with *Alligatorium meyeri* as a further representative of Atoposauridae. Exceptions to this comprise the analyses of Martin *et al.* (2010) and Turner (2015; see

also Turner & Pritchard, 2015), which also included *T. guimarotae* and ‘*T.*’ *sympiestodon*. Whereas the analysis of Martin *et al.* (2010) resulted in a monophyletic *Theriosuchus*, Turner & Pritchard (2015: fig. 7) recovered *Theriosuchus* as paraphyletic with respect to *Alligatorium meyeri*, when a series of alternative palatal character state scores for *Isisfordia duncani* (Salisbury *et al.*, 2006) (a possible non-eusuchian susisuchian; Turner, 2015) were applied. To our knowledge, neither ‘*T.*’ *ibericus* nor *T. grandinaris* have ever been included in a formal phylogenetic analysis. Therefore, the monophyly of *Theriosuchus* has never been fully examined, and nor have the character states that support this been tested.

Diagnoses of *Theriosuchus* have varied since the original description by Owen (1879). In his unpublished thesis, Clark (1986) provided a comprehensive redescription of *T. pusillus*, as well as an emended diagnosis. Brinkmann (1992) provided a diagnosis for *Theriosuchus*, but this was based only on ‘*T.*’ *ibericus* and *T. pusillus*. Schwarz & Salisbury (2005) included a diagnosis of *Theriosuchus* in their description and naming of *T. guimarotae*, which was repeated by Karl *et al.* (2006) in their description of a poorly known skull and partial skeleton from Germany, which they cautiously attributed to *T. pusillus*. However, Schwarz & Salisbury (2005) did not discuss ‘*T.*’ *ibericus* in detail (Brinkmann, 1989, 1992), and this was prior to the identification of *T. grandinaris* (Lauprasert *et al.*, 2011) and ‘*T.*’ *sympiestodon* (Martin *et al.*, 2010, 2014a). Salisbury & Naish (2011) presented the most comprehensive recent diagnosis of *Theriosuchus*, listing the following character states: (1) proportionately short and broad rostrum, with the maxillary rostrum forming between 40 and 45% of the total skull length; (2) proportionately small antorbital fenestra; (3) slit-like, horizontally orientated and rostrally pointed external nares, separated from each other by the rostral-most extent of the nasals; (4) shallow sulcus on the dorsal surface of the maxillary rostrum, immediately posterior to the junction between the maxilla, premaxilla, and nasal; (5) proportionally long jugal; (6) medial base of the postorbital process formed by the ectopterygoid; (7) median crest on the frontal and the parietal in later ontogenetic stages; (8) frontal and parietal partially unfused in early ontogenetic stages; (9) dorsal margin of the supratemporal fenestra smaller than the orbit throughout ontogeny; (10) lateral margin of the squamosal bevelled ventrally; (11) proportionally narrow quadrate with a concave mandibular articular surface; (12) secondary choanae bounded by the palatines rostrally and separated by a median septum of the pterygoids; (13) mandibular symphysis that does not extend posteriorly beyond a point level

with the sixth dentary tooth; (14) ilium with short preacetabular process and long postacetabular process; and (15) biserial dorsal shield comprising parasagittal osteoderms. However, it was not clear how all of these character states are distributed across the five named species of *Theriosuchus*. Furthermore, many of these characters can be demonstrated to be more broadly present in Atoposauridae, or characterize smaller subgroups within *Theriosuchus*. For example, feature 1 is consistently present in all small, brevirostrine crocodyliforms. The presence of an antorbital fenestra is variable (feature 2), with *T. guimarotae* clearly possessing a large fenestra, '*T. sympiestodon*' and '*T. ibericus*' possibly retaining one, and *T. pusillus* having a pinhole and dorsally placed antorbital fenestra. The presence of an antorbital fenestra is further documented for *Pachycheilosuchus* (Rogers, 2003), and possibly *Alligatorellus bavaricus* (Tennant & Mannion, 2014). The division of the external nares by an anterior projection of the nasals (feature 3) appears to be the condition for *Alligatorium meyeri* and '*Alligatorium*' *francicum*, as well as *Alligatorellus* (Tennant & Mannion, 2014) and *Wannchampsus* (Adams, 2014). Feature 4 might be diagnostic for *Theriosuchus*, as it was also documented by Schwarz & Salisbury (2005) for *T. guimarotae*, and by Martin *et al.* (2010) for '*T. sympiestodon*', with this sulcus in a position posterior to the maxilla–nasal–premaxilla triple junction; however, despite first-hand examination of the type specimens, we have been unable to locate this sulcus on *T. pusillus*, '*T. sympiestodon*', or '*T. ibericus*'. Therefore, this feature might be diagnostic only for *T. guimarotae*. We discuss these characters in more detail for each taxon below. These features have all been incorporated into the present analysis to test whether they are more broadly present in crocodyliforms, or can be used to diagnose *Theriosuchus* or a subset of species within *Theriosuchus*.

The dentition of Theriosuchus

Species previously assigned to *Theriosuchus* have four dentition-based morphotypes (Owen, 1879; Joffe, 1967; Brinkmann, 1992; Salisbury, 2002; Schwarz & Salisbury, 2005; Schwarz-Wings, Rees & Lindgren, 2009b; Lauprasert *et al.*, 2011; Salisbury & Naish, 2011), which are typically structured from an anteriorly to more posteriorly position in the following sequence: (1) slender and conical teeth with apicobasally aligned striations that are largely restricted to the lingual face of the crown, located in the premaxilla, and the rostral-most maxilla and dentary (pseudocaniniform morphotype); (2) lanceolate morphotype, moderately labiolingually compressed, with a radial distribution of the marginal

lingual striations and mesial and distal carinae, situated in the middle and posterior portions of the maxilla and dentary; (3) labiolingually compressed morphotype, in which teeth are broad and strongly labiolingually compressed, with both the lingual and labial surfaces covered with vertical, straight, and subparallel striations (although fan-shaped striations are present only on the lingual face; Thies *et al.*, 1997); and (4) a 'low-crowned' tooth morphotype that is characterized by the apical margins being orientated at <45° from the horizontal, forming a crown that is as mesiodistally broad (or broader) as it is apicobasally tall, and more posteriorly placed in the dental arcade.

In all of these morphotypes, there is variation within the profile shape, size, striation development and strength of carinae, degree of lingual curvature through asymmetrical compression, and shape of the transverse section (e.g. Thies *et al.*, 1997). *Theriosuchus guimarotae* possesses pseudocaniniform and lanceolate tooth morphotypes, all of which exhibit mesial and distal carinae (Schwarz & Salisbury, 2005). *Theriosuchus grandinaris* possesses a combination of pseudocaniniform, lanceolate-shaped, and labiolingually flattened teeth with faintly crenulated mesial and distal carinae (Lauprasert *et al.*, 2011). The strongly labiolingually compressed morphotype appears to be restricted to *T. pusillus* and '*T. ibericus*'. The low-crowned morphotype is only known in '*T. ibericus*', *T. pusillus*, and '*T. sympiestodon*' (Martin *et al.*, 2010).

This 'low-crowned' morphology is distinct from the 'low-crowned' tribodont dentition of *Bernissartia* and *Koumpiodontosuchus* (Buffetaut & Ford, 1979; Schwarz-Wings *et al.*, 2009b; Sweetman *et al.*, 2015), in which the teeth are multicusped. However, both morphologies probably had a similar function in crushing harder prey items (e.g. molluscs). This niche specialization fits in with the ecology and geographical distribution of bernissartiids and *Theriosuchus*, as these taxa represent crocodylomorphs of reduced body size constrained to island environments. In all four dental morphotypes, the apical edges range from smooth, to faintly crenulated or serrated, to possessing well-developed carinae. Ornamentation varies, but includes apicobasally orientated longitudinal ridges on the labial and lingual surfaces of the crown, sometimes more developed on the labial side, and with variation in the regularity of spacing between ridges. It is the presence of crenulations, formed from the faint ridges on the crown, that has been used to ascribe atoposaurids and *Theriosuchus* with their characteristic 'pseudozipodont' morphology (Prasad & De Lapparent De Broin, 2002). '*Theriosuchus*' *ibericus* is distinct in possessing more prominent serrations on the mesial and distal tooth

margins, approaching the fully ziphodont condition. The close packing of the maxillary and dentary alveoli in *Theriosuchus* is similar to a range of neosuchian taxa, including goniopholidids, *Bernissartia* (Buffetaut & Ford, 1979), *Wannchampsus* (Adams, 2014), and *Shamosuchus* (Pol *et al.*, 2009), but is distinct from *Pachycheilosuchus*, *Rugosuchus*, and crocodylians, in which the alveoli are consistently well separated by interalveolar septae (Wu *et al.*, 2001a; Rogers, 2003; Pol *et al.*, 2009).

This dental variation has led to several differing hypotheses as to the diet of *Theriosuchus*, including the consumption of small mammals (Owen, 1879) or insects (Buscalioni & Sanz, 1988), to herbivory (Brinkmann, 1992), ovivory (Kirkland *et al.*, 1994), or piscivory (Thies *et al.*, 1997), all based around a semi-aquatic or amphibious mode of life. There is sufficient evidence to accept all of these as valid hypotheses, suggesting that *Theriosuchus* was adept at adapting to take advantage of whichever trophic style fitted its ecological position. However, it is likely that, based on our results, that such a morphological or dietary plasticity evolved at least twice independently within advanced neosuchian lineages, or represents a highly adaptive continuum. Finally, it is worth noting that amongst definitive atoposaurids, *Alligatorium* and *Alligatorellus* both exclusively have smooth-surfaced teeth lacking ridges (Wellnhofer, 1971), and the teeth of *Atoposaurus* and *Montsecosuchus* are still unknown (Buscalioni & Sanz, 1988, 1990a; Thies *et al.*, 1997).

Young *et al.* (2016) identified some of the oldest known diagnosable remains of *Theriosuchus*, and provided a list of dentary synapomorphies that might diagnose *Theriosuchus*. This included the presence of a heterodont dentition, with a combination of pseudocanineiform, labiolingually compressed, and lanceolate (or 'leaf-shaped') tooth crown morphotypes (Schwarz & Salisbury, 2005; Lauprasert *et al.*, 2011), which have never previously been incorporated within a phylogenetic analysis that includes atoposaurids, despite their clear importance in diagnosing species of *Theriosuchus*. The more posteriorly placed teeth in *Theriosuchus* possess 'false denticles' (Prasad & De Lapparent De Broin, 2002), accompanied by a progressive reduction in alveolus size from the fourth to sixth dentary alveoli. Some of these dentary alveoli form a confluent chain, with the dental arcade occupying an anteroposterior sulcus. Young *et al.* (2016) also noted additional features that might be characteristic of less-inclusive subgroups within the *Theriosuchus* species complex, including: (1) a nonspatulate anterior dentary in lateral view (i.e. straight or slightly convex in dorsoventral profile); (2) a dual pair of foramina medial to the

dental arcade on the occlusal dental surface, the position of which may vary intraspecifically; (3) vertically festooned external alveolar margins; (4) raised internal alveolar margins; and (5) a symphyseal suture extending to the D5–D7 alveoli (D means dentary). We discuss the features that unite the clades (*T. pusillus* + *T. guimarotae*), and ('*T. ibericus* + '*T. sympiestodon*') below.

Revised diagnosis of Theriosuchus and discussion

- (S1) *Premaxilla–maxilla suture aligned posteromedially in dorsal view (C47.1)*: The posteromedial alignment of the premaxilla–maxilla suture was originally regarded as an autapomorphy of *T. grandinaris* (Lauprasert *et al.*, 2011), but it also characterizes *T. guimarotae* and *T. pusillus*, and we therefore consider it to be diagnostic for *Theriosuchus*. This feature cannot be assessed in '*T. sympiestodon*', but might be present in '*T. ibericus*' (PIFUB 102/21.43), although the posterior end of this premaxilla is broken, and we cannot be certain of the nature of the contact with the maxilla.
- (S2) *Absence of a maxillary occlusal pit for reception of an enlarged dentary tooth, anterior to maxillary dental arcade (C54.0)*: The absence of a maxillary occlusal pit is shared with *Pachycheilosuchus* (Rogers, 2003). There is an occlusal pit present in both '*T. sympiestodon*', for which a referred specimen (MCDRD 134) has an associated enlarged dentary tooth (Martin *et al.*, 2014a), and '*T. ibericus*', anterior to the hypertrophied fifth maxillary tooth. The goniopholidid *Amphicotylus* also appears to possess this occlusal pit, visible in lateral view (Mook, 1942).
- (S3) *Lacrimal tapers posteroventrally, not contacting jugal or only forming a point contact (C77.1)*: The morphology of the lacrimal is not known in '*T. ibericus*' or '*T. sympiestodon*', but the morphology exhibited by *Theriosuchus* is distinct from atoposaurids, *Wannchampsus* (Adams, 2014), *Brillanceausuchus*, and *Koumpiodontosuchus* (Sweetman *et al.*, 2015), in which the lacrimal extends posteroventrally and broadly contacts the jugal.
- (S4) *External surface of the dentary (C201.1) and splenial (C202.1) sculpted, including grooved or rugose patterning posteriorly*: The morphology of the dentary is poorly known amongst atoposaurids owing to poor preservation (Wellnhofer, 1971; Tennant & Mannion, 2014), but all species herein assigned to *Theriosuchus* exhibit strong ornamentation on the external surface of the dentaries, and sometimes on the splenial when preserved (Lauprasert *et al.*,

2011; Young *et al.*, 2016). This sculpting pattern is shared with *Shamosuchus* (Pol *et al.*, 2009) and *Hsisosuchus chowi* (Peng & Shu, 2005), but is distinct from *Montsecosuchus*, *Wannchampsus* (Adams, 2014), *Pachycheilosuchus* (Rogers, 2003), and *Brillanceausuchus* (Michard *et al.*, 1990), in which only the dentary is sculpted, and the external surface of the splenial is smooth and lacks ornamentation.

- (S5) *Presence of a combination of pseudocaniniform and lanceolate (C253.0), pseudozipodont maxillary teeth: Theriosuchus pusillus* also possesses two additional 'low-crowned' and labiolingually compressed tooth morphotypes. Labiolingually compressed teeth are absent in *T. guimarotae* (Schwarz & Salisbury, 2005), and this combination of dental morphologies is unique amongst other heterodont crocodyli-forms (e.g. bernissartiids, notosuchians). Low-crowned teeth are also absent in *T. guimarotae* and *T. grandinaris* (Schwarz & Salisbury, 2005; Lauprasert *et al.*, 2011). '*Theriosuchus ibericus* and '*T. sympiestodon* also possess an enlarged fifth maxillary tooth, typically with a corresponding notch on the dentary, whereas this tooth is not present in *T. grandinaris*, and remains only moderately enlarged in *T. guimarotae* and *T. pusillus*.

UNNAMED CLADE: (*THERIOSUCHUS PUSILLUS* +
THERIOSUCHUS GUIMAROTAE)

There is strong evidence for a sister-taxon relationship between *T. guimarotae* and *T. pusillus*, with this topology recovered in all of our trees, and possessing a Bremer support value of 4 and posterior node probability of 0.99. Synapomorphies uniting these two species include: (1) a posteriorly divided and dorsally facing external naris, similar to atoposaurids (Wellnhofer, 1971; Tennant & Mannion, 2014); (2) a proportionally small antorbital fenestra, less than half of the size of the orbit, similar to *Alligatorellus bavaricus* (Tennant & Mannion, 2014), *Pachycheilosuchus* (Rogers, 2003), and *Hoplosuchus* (Gilmore, 1926); (3) middle maxillary teeth implanted within single, confluent dental groove, similar to '*T. ibericus*, in which all maxillary teeth occupy a single groove; (4) frontal with bifurcated anterior process, penetrating the posterior border of the nasals; (5) lateral dentary surface with concavity for reception of enlarged maxillary tooth, a feature also present in '*T. ibericus*, '*T. sympiestodon*, and *Brillanceausuchus*; (6) transitional dentary tooth morphology posteriorly from the fifth alveolus; (7) distinct foramina on the

dentary occlusal surface lingual to the second and third dentary alveoli.

THERIOSUCHUS PUSILLUS OWEN, 1878A
(TYPE SPECIES)

BRACHYDECTES MINOR OWEN, 1879
OWENIASUCHUS MINOR WOODWARD, 1885

Type locality and horizon

Beccles' residuary marls (*sensu* Salisbury, 2002) Lulworth Beds, Purbeck Group, Berriasian (Early Cretaceous); Durlston Bay, Swanage, Dorset, England.

Lectotype

NHMUK PV OR48216, a near-complete partially articulated skeleton with skull.

Paratype

NHMUK PV OR48330, a near-complete articulated and three-dimensionally preserved skull.

Referred specimens

NHMUK PV OR48328 (holotype of '*Brachydetes minor*'), left mandibular ramus; NHMUK PV OR48244, an articulated lower jaw preserved in dorsal aspect and NHMUK PV OR48262, a well-preserved dentary and teeth, all from the same locality as the type series.

Previous diagnoses and comments

This species name was originally erected based upon seven paravertebral osteoderms figured by Owen (1878a), which are no longer within the NHMUK collections (Salisbury, 2002). These specimens were figured again in Owen (1879), but this time they were listed as belonging to an incertae sedis crocodyli-form. In the same paper, Owen (1879) also described and figured a near-complete skull (NHMUK PV OR48330) and a near-complete skeleton (NHMUK PV OR48216) as *T. pusillus* (Salisbury, 2002). Alongside this, Owen (1879) figured several additional craniomandibular elements as *T. pusillus*; however, until further analysis of this material, we do not consider it to be referable to *T. pusillus*. Clark (1986) regarded NHMUK PV OR48330 to be the holotype specimen of *T. pusillus*, but Salisbury (2002) designated NHMUK PV OR48216 and NHMUK PV OR48330 as the lectotype and paratype, respectively, which we follow here. Until a revision of the type species is conducted, including the referral of other putative specimens, our *T. pusillus* OTU is restricted to the lectotype and paratype, as well as NHMUK PV OR48244 and NHMUK PV OR48262, following Young *et al.* (2016). Salisbury (2002) followed Clark (1986) and Brinkmann (1992) in regarding '*Owenia-*

suchus ('*Brachydectes*') *minor*' (Owen, 1879; Woodward 1885) as a junior synonym of *T. pusillus* (see also Schwarz & Salisbury, 2005), an interpretation which we follow pending further analysis of the Purbeck crocodyliiform material.

Theriosuchus pusillus possesses an unusual combination of derived and plesiomorphic character states, the latter of which might be related to the retention of paedomorphic features associated with its small body size, although both of the specimens belonging to the type series are skeletally mature (Martin *et al.*, 2014a). This heterogeneity is emphasised by the equivocal phylogenetic positions recovered for this taxon (and Atoposauridae), possibly exacerbated by the representation of the '*Theriosuchus* complex' often as a single taxon (i.e. *T. pusillus*), and the lack of use of appropriately sampled character matrices to resolve its phylogenetic position. Features that might be driving the uncertainty in the phylogenetic position of *Theriosuchus* include:

1. The presence of a longitudinal ridge on the external surface of the angular, which is shared with the paralligatorids *Rugosuchus*, *Shamosuchus*, and *Wannchampsus* (Wu *et al.*, 2001a; Pol *et al.*, 2009) and, according to Turner (2015), is a feature uniting (*Theriosuchus* + Paralligatoridae). However, we were unable to confirm the presence of this feature on the type specimen of *T. pusillus*, or any other specimen assigned to *Theriosuchus*.
2. In *T. pusillus*, the splenial contributes significantly to the dorsal surface of the mandibular symphysis (Lauprasert *et al.*, 2011; Young *et al.*, 2016), similar to basal crocodylians and a range of basal mesoeucrocodylians (e.g. Buffetaut, 1981; Ortega, Buscalioni & Gasparini, 1996; Pol *et al.*, 2009). However, we have been unable to observe this feature in definitive atoposaurids, because of the manner in which they are preserved.
3. The presence of a raised supraorbital ridge in *T. pusillus* is similar to a range of neosuchians, including *Trematochampsia* (Buffetaut, 1976), *Bernissartia* (Buffetaut, 1975; Buffetaut & Ford, 1979), *Hylaeochampsia* (Clark & Norell, 1992), *Shamosuchus*, and several crocodylians (Pol *et al.*, 2009). This feature is absent in definitive atoposaurids, goniopholidids, dyrosaurids, and pholidosaurids, and secondarily lost amongst most crocodylians (Pol *et al.*, 2009).
4. A preorbital lacrimal–prefrontal sutural crest might be present in *T. pusillus*, a feature that Turner (2015) stated is common for *Theriosuchus*, and shared with more advanced neosuchians including *Shamosuchus*, *Rugosuchus*, *Wannchampsus*, and some goniopholidids. There does appear to be a slight longitudinal crest on the paratype specimen of *T. pusillus*, although we cannot rule out that this is a result of taphonomic distortion, as the skull shows evidence of dorsoventral compression.
5. The morphology of the retroarticular process in *T. pusillus*, as well as in *Alligatorellus* and *Alligatorium*, is similar to goniopholidids, *Shamosuchus*, and other advanced neosuchians (Pol *et al.*, 2009), in being reduced and 'paddle-shaped' (Pol *et al.*, 2009), and projects posteriorly or posteroventrally. This is distinct from crocodylians in which the dorsally facing retroarticular process is more anteroposteriorly elongated and subtriangular (Pol *et al.*, 2009).
6. The anterior ends of the palatine bar between the suborbital fenestrae are subparallel in *T. pusillus*, similar to some members of Eusuchia, dyrosaurids, and the pholidosaurid *Terminonaris robusta* (Wu, Russell & Cumbaa, 2001b), and not laterally flared as in other advanced neosuchians, such as *Shamosuchus* (Pol *et al.*, 2009) and *Wannchampsus* (Adams, 2014). Additionally, the expansion of the posterior ends of the palatines, just anterior to the choana and pterygoid contact, is similar to *Shamosuchus* (Pol *et al.*, 2009), *Batrachomimus pastosbonensis*, *Rugosuchus*, and *Paralligator gradilifrons* (Turner & Pritchard, 2015), but is distinct from *Wannchampsus* in which the posterior ends remain narrow and parallel (Adams, 2014).
7. *Theriosuchus pusillus* shares a single appendicular plesiomorphic feature with *Alligatorium meyeri* in that the coracoid is subequal in length to the scapula. This is distinct from paralligatorids and hylaeochampsids, in which the coracoid is proportionally smaller (Turner, 2015; note that the coracoid is about two-thirds the length of the scapula in *Pachycheilosuchus*, not subequal as stated by Turner, 2015).
8. Pol *et al.* (2009) stated that goniopholidids and *T. pusillus* share a well-developed anterolateral articular peg on the dorsal osteoderms (i.e. a 'peg and socket' articulation), a feature also noted for *T. guimarotae* (Schwarz & Salisbury, 2005) and *Theriosuchus* sp. from China (Wu *et al.*, 1996). However, this comparison was based on a figured osteoderm (now lost) in Owen (1878), and we agree with Joffe (1967) and Salisbury (2002) that this feature is not visible in any of the osteoderms preserved on the paratype specimen of *T. pusillus* (NHMUK PV OR 48216), or any other specimens definitively attributable to *T. pusillus*. Rare isolated and disassociated instances of osteoderms attributed to *Theriosuchus* (Wu *et al.*, 1996; Schwarz & Salisbury,

2005) with this articular morphology are more likely to be referable to a small goniopholidid (Salisbury & Frey, 2001). Goniopholidids are commonly found alongside specimens of *Theriosuchus*, and therefore the presence of this articular peg should not be used to unite *Theriosuchus* with goniopholidids until it can be shown that a specimen that definitively belongs to *Theriosuchus* possesses this morphology.

Revised diagnosis of Theriosuchus pusillus and discussion

- (S1) *Skull anteroposterior length to orbit length ratio between 3.5 and 4.0 [3.83 (NHMUK PV OR48330)] (C27.1)*: This feature illustrates the characteristically large orbits that *T. pusillus* possesses, and has often been used to support the referral of this taxon to Atoposauridae. This ratio is similar to *Wannchampsus* (3.72) and *Alligatorellus beaumonti* (3.86), but is higher than *Atoposaurus* (2.33–2.86), *Alligatorellus bavaricus* (3.12), *Alligatorium meyeri* (3.64), *Karatausuchus* (3.36) (Storrs & Efimov, 2000), and *Hoplosuchus* (3.10) (Gilmore, 1926). The relative sizes of the orbit and supratemporal fenestra do not appear to decrease through ontogeny in *Theriosuchus*, and the retention of this feature is therefore likely to be a paedomorphic state related to the generally small body size of *Theriosuchus* (Schwarz & Salisbury, 2005).
- (S2) *Abrupt mediolateral expansion of the nasals adjacent to the maxilla anterior to the lacrimals and prefrontals (C70.0)*: This feature is also present in *Koumpiodontosuchus* (Sweetman *et al.*, 2015) and *Brillanceausuchus*, but is distinct from the condition in *T. guimarotae*, in which the lateral margins of the nasals are parallel throughout their length (Schwarz & Salisbury, 2005). In atoposaurids, *Wannchampsus*, *Shamosuchus* (Pol *et al.*, 2009), *T. grandinaris*, protosuchians, and goniopholidids, the nasals gradually widen posteriorly.
- (S3) *Posterior tips of nasals perforated by an anterior, sagittal projection of the frontals (C73.1)*: This contact between the frontals and the nasals is similar to *Shamosuchus* (Pol *et al.*, 2009), *Brillanceausuchus*, and goniopholidids (e.g. Mook, 1942), contrasting with the transverse suture that characterizes *Alligatorellus* and other neosuchians (e.g. *Gilchristosuchus*; Wu & Brinkmann, 1993). Notosuchians are similar in possessing a transversely orientated suture, but this is distinct from the simple sutures seen in some

neosuchians because it displays a complex interdigitation between the frontals and nasals (e.g. Ortega *et al.*, 2000; Turner, 2006). Goniopholidids, including *Eutretauranosuchus* (Smith *et al.*, 2010) and *Amphicotylus* (Mook, 1942), possess an anterior projection of the frontals, which is sometimes anteriorly bifurcated. More advanced eusuchians, including *Acynodon iberoccitanus*, have a posteriorly convex frontal–nasal suture, although smaller individuals of this taxon have transversely orientated sutures (Martin, 2007).

- (S4) *Minimum intertemporal width more than one-third of total width of cranial table*: This feature describes a proportionally broad parietal–frontal region between the supratemporal fenestrae on the dorsal skull roof, and is a feature shared by a range of taxa, including atoposaurids (Wellnhofer, 1971; Tennant & Mannion, 2014), *Montsecosuchus* (Buscalioni & Sanz, 1990a), *T. sympiestodon* (estimated based on an incomplete skull table; Martin *et al.*, 2010, 2014a), and *Brillanceausuchus*. We did not create a new character to describe this feature, because of probable non-independence with C19, which describes the relative width of the interorbital and intertemporal regions.
- (S5*) *Palatines laterally diverge posteriorly, forming palatine bars around choanal groove (C176.1)*: The palatines of *T. pusillus* form the anterior and lateral borders of the choana, and laterally diverge posteriorly between the suborbital fenestrae, becoming thickened and rod-like lateral to the choana, where they overlap the anterior portion of the pterygoids that contributes to the lateral margins of the choana. *Wannchampsus* has a similar morphology, but possesses a deeper choanal groove, which is slightly more posteriorly placed (Adams, 2014). This is distinct from some notosuchians, in which the palatine rods are more laterally directed around the choanal groove (Godoy *et al.*, 2014), and from bernissartiids in which the bars are formed from the anterior extension of the pterygoids.
- (S6*) *Choana with anterior border mid-way anteroposteriorly between suborbital fenestrae (C181.0), with a V-shaped palatine–pterygoid contact defining anterior edge, and divided anteriorly by a pterygoidean choanal septum (C183.1)*: The choanal morphology of *T. pusillus* is distinct in that the anterior edge of the choanal groove is situated relatively anteriorly between the suborbital fenestrae, compared with more advanced neosuchians (e.g. bernissartiids and

paralligatorids). The choana in *T. pusillus* also receives an anterior and lateral contribution from the palatine, with a V-shaped contact similar to *Rugosuchus* (Wu *et al.*, 2001a), representing an intermediate morphology between basal neosuchians and eusuchians. The groove is divided by a choanal septum of the pterygoid, similar to *T. guimarotae* (Schwarz & Salisbury, 2005), *Araripesuchus* (Ortega *et al.*, 2000; Turner, 2006), *Hsisosuchus* (Peng & Shu, 2005), and paralligatorids such as *Batrachomimus* (Montefeltro *et al.*, 2013) and *Paralligator* (Turner, 2015).

- (S7) *Absence of external mandibular fenestra (C207.0):* *Theriosuchus pusillus* completely lacks an external mandibular fenestra, as is also the case in *Shamosuchus* (Pol *et al.*, 2009), *Wannchampsus* (Adams, 2014), *Goniopholis* (Salisbury *et al.*, 1999), and *Bernissartia* (Buffetaut & Ford, 1979; Norell & Clark, 1990). This is distinct from most eusuchians and crocodylians, in which the external mandibular fenestra is secondarily well developed (Salisbury *et al.*, 2006), or reduced to a slit-like opening (Brochu, 2004).
- (S8) *Dorsolateral edge of dentary presenting two concave 'waves' (dorsal expansions) (C232.1):* The dorsolateral edge of the dentary in *T. pusillus* is similar to *Wannchampsus* (Adams, 2014) and *Koumpiodontosuchus* (Sweetman *et al.*, 2015), as well as '*T. ibericus*' and '*T. sympiestodon*'. In *Alligatorium meyeri* and *T. guimarotae*, the dentary is straight, closer to the condition in *Shamosuchus* (Pol *et al.*, 2009) and *Brillanceausuchus*.
- (S9*) *Splénial dorsally inset into symphysis in ventral view (C234.1):* Where the splénial of *T. pusillus* enters into the symphysis, it is dorsally inset with respect to the ventral surface of the mandible, and slopes posterodorsally. This is a feature otherwise only observed in *Atoposaurus oberndorferi* and therefore we consider it to be locally autapomorphic. In other taxa in which the ventral surface of the mandible can be observed, the contact between the splénial and dentary portion of the symphysis is ventrally confluent.
- (S10*) *Heterodont dentition, possessing a combination of anteriorly positioned pseudocanineiform teeth, intermediately positioned labiolingually compressed 'lanceolate' teeth (C253.0), and posteriorly placed 'low-crowned' teeth (C254.0):* This unique combination of the three dental

morphotypes in *T. pusillus* is diagnostic amongst all known species of *Theriosuchus* and all other known heterodont crocodylomorphs. The low-crowned morphotype is not known in either *T. guimarotae* or *T. grandinaris* (Schwarz & Salisbury, 2005; Lauprasert *et al.*, 2011).

- (S11) *Biconvex first caudal vertebra (C278.1):* This is an unusual feature of the axial bracing system in crocodylomorphs (Salisbury & Frey, 2001), and related to the development of procoely throughout the axial series in neosuchians, which has a complicated and unresolved evolutionary history (Salisbury & Frey, 2001). The presence of a biconvex first caudal vertebra is also shared with *Pachycheilosuchus* (Rogers, 2003) and *Bernissartia*, as well as possibly *Brillanceausuchus* (Michard *et al.*, 1990), and characterizes all eusuchians (Salisbury *et al.*, 2006; Blanco *et al.*, 2014), including marine forms (Brochu, 2004).
- (S12*) *Posterior surface of tibial shaft curved, leaving a void between the tibia and fibula (C299.1):* The tibia and fibula of *T. pusillus* are unusual in that they are not confluent, as in other crocodylomorph taxa. Similar to *Montsecosuchus* (Buscalioni & Sanz, 1990a), the tibial shaft is curved, which leaves a void between the tibia and fibula, the mechanical implications of which are unclear.
- (S13) *Square-shaped dorsal osteoderms (in dorsoventral view) (C308.3):* The square-shaped osteoderms of *T. pusillus* form a well-developed biserial shield, and retain a similar outline shape to *Pachycheilosuchus* (Rogers, 2003) and *Alligatorium meyeri* (Wellnhofer, 1971). This is distinct from the oval-shaped dorsal osteoderms of *Montsecosuchus*, and those of *Alligatorellus*, in which they are subrectangular.

THERIOSUCHUS GUIMAROTAE SCHWARZ & SALISBURY, 2005

Type locality and horizon

Alcobaca Formation (lower 'Fundsichten' and upper 'Ruafolge' lignite coal layer), Kimmeridgian, (Late Jurassic); Guimarota Coal Mine, Guimarota, Portugal.

Type specimen

IPFUB Gui Croc 7308, partial skull and mandible, with partial isolated surangular, sacral vertebra II, and two partial osteoderms.

Referred specimens (from Schwarz & Salisbury, 2005)

A range of disarticulated cranial and postcranial material under the accession numbers 'IPFUB Gui Croc' (see Schwarz & Salisbury, 2005; for a complete list of individual specimens and ID numbers). All referred specimens are from the same locality as the holotype specimen. The majority are disarticulated, and were collected from at least two different horizons – the upper and lower lignite coal layers (Schwarz & Salisbury, 2005).

Previous diagnoses and comments

Schwarz & Salisbury (2005) documented a range of diagnostic cranial and axial characteristics for *T. guimarotae*, and included a detailed comparative discussion of this taxon and other specimens assigned to *Theriosuchus*. However, a number of these features are more widespread amongst neosuchians. For example, Schwarz & Salisbury (2005) noted that the squamosal of *T. guimarotae* is bevelled ventrally, and possesses a notch anteriorly on the lateral surface, both features that these authors regarded as autapomorphic. However, these features are also visible in *T. pusillus* (NHMUK PV OR48216) and *Brillanceausuchus*. Additionally, Schwarz & Salisbury (2005) considered the morphology of the posterolateral corner of the squamosal to be diagnostic, in that it forms a rounded 'lobe', which projects posteriorly and is similarly sculpted to the rest of the cranial table. Although distinct from *T. pusillus* and '*T. ibericus*', which both possess an unsculpted lobe, this overall morphology is similar to *Rugosuchus* (Wu *et al.*, 2001a), *Alligatorium meyeri*, and *Alligatorellus beaumonti*. Furthermore, an unsculpted posterolateral lobe is present in *Shamosuchus* (Pol *et al.*, 2009; Turner, 2015), *Sunosuchus* (Wu *et al.*, 1996), and *Goniopholis* (Ortega *et al.*, 2000), but might be an ontogenetic feature that occurs in younger individuals. Clark (1986) considered this feature to be synapomorphic for Atoposauridae, but we consider the presence of this lobe to be a synapomorphy that unites *Theriosuchus* and Paralligatoridae (Turner, 2015), and a feature that was acquired independently in some atoposaurids.

Revised diagnosis and discussion

(S1) *Subrectangular-shaped external supratemporal fenestra, in dorsal view (C17.0)*: The shape of the supratemporal fenestra (Schwarz & Salisbury, 2005) is distinct from that of other species of *Theriosuchus* and advanced neosuchians, which have a circular or subcircular outline. The subrectangular morphology in *T. guimarotae* is similar to that of pholidosaurids, such as *Pholidosaurus*

(Salisbury, 2002), *Sarcosuchus* (Serenio *et al.*, 2001), and *Chalawan thailandicus* (Martin *et al.*, 2014b) and dyrosaurids (e.g. Jouve, Bouya & Amaghazaz, 2005a; Jouve *et al.*, 2005b), as well as *Protosuchus richardsoni* (Colbert & Mook, 1951).

(S2) *Proportionally large lateral temporal fenestra, with an area >50% the area of the orbit (C20.2)*: The lateral temporal fenestra is relatively larger than that of *T. pusillus*, *Isisfordia* (Salisbury *et al.*, 2006), and notosuchians (Buckley *et al.*, 2000; Novas *et al.*, 2009). Goniopholidids, *Rugosuchus* (Wu *et al.*, 2001a), *Wannchampsus* (Adams, 2014), and the eusuchians *Allodaposuchus precedens* (Buscalioni *et al.*, 2001) and *Iharkutosuchus makadii* (Ösi, Clark & Weishampel, 2007; Ösi, 2008), are similar to *T. guimarotae* in the large proportional size of the lateral temporal fenestra to the orbit. In dyrosaurids, the fenestra becomes approximately the same size as the supratemporal fenestra, and proportionally larger than the orbit (Jouve *et al.*, 2005a,b).

(S3) *Notch on the posterolateral surface of the premaxilla within the dorsal margin of the external nares (C39.1)*: Similar to the goniopholidid *Amphicotylus* (Mook, 1942), *T. guimarotae* possesses a shallow fossa, or notch, on the dorsolateral surface of the premaxilla, immediately adjacent to the external nares (Schwarz & Salisbury, 2005), and we consider this feature to be a local autapomorphy for this taxon.

(S4) *Nasal-lacrimar contact absent on dorsal surface (C71.1)*: The lacrimal does not contact the nasal (Schwarz & Salisbury, 2005), instead being medially restricted and only contacting the prefrontal. This contact is also absent in *Protosuchus richardsoni* (Colbert & Mook, 1951), *Shamosuchus* (Pol *et al.*, 2009), *Hylaeochampsia* (Clark & Norell, 1992), and *Iharkutosuchus* (Turner, 2015), but is present in the notosuchian *Araripesuchus gomesii* (Turner, 2006) and atoposaurids (Wellnhofer, 1971), and represents a series of reconfigurations of the periorbital elements with respect to the remainder of the rostrum in advanced neosuchians.

(S5) *Jugal with posteriorly directed (C83.0), anteriorly placed (C84.0), and ventromedially displaced (C85.1) postorbital process (C83.0)*: The jugal postorbital process is slightly anteriorly placed, instead of being medially placed, as in other species of *Theriosuchus*, which have equally long anterior and posterior

processes of the jugal. This process also has a dorsally directed base similar to *Montsecosuchus* and *Brillanceausuchus*, instead of the posterodorsal orientation that characterizes atoposaurids, *T. pusillus*, and '*T. ibericus*'.

- (S6) *Anterior process of frontal constricted between the prefrontals (C109.0)*: This feature excludes the sagittal projection of the frontals into the nasals anterior to the orbits, which some crocodyliforms possess, and refers to the convergence between the lateral margins of the anterior portion of the frontals. This feature is shared with *Alligatorium meyeri*, '*Alligatorium*' *franconicum*, and *Amphicotylus* (Mook, 1942). In other crocodyliforms, including *Alligatorellus* and other species of *Theriosuchus*, the lateral edges of the nasal are not mediolaterally constricted and remain subparallel.
- (S7*) *Ectopterygoid with well-developed anterior process, reaching the posterior-most two maxillary teeth (C170.0)*: The anterior process of the ectopterygoid is extremely well developed, reaching a point level with the anterior margin of the suborbital fenestra and the posterior-most maxillary teeth. In *T. pusillus*, goniopholidids, and paralligatorids, this process is short and poorly developed in ventral aspect.
- (S8) *Anterior margin of palatines anteriorly pointed (C173.1)*: The maxilla–palatine suture is posteroventrally directed towards the anterior margin of the suborbital fenestra along the midline, level with the sixth maxillary tooth (Schwarz & Salisbury, 2005). In *T. pusillus*, this contact is gently rounded anteriorly, similar to *Koumpiodontosuchus* (Sweetman *et al.*, 2015). However, this region of the palate is not preserved in many of the specimens included in our analysis – especially atoposaurids – and therefore we consider this to be a tentative autapomorphy at present.
- (S9) *Parallel posterolateral margins of interfenestral bar between suborbital fenestrae (C175.1)*: The interfenestral bar of *T. guimarotae* is formed entirely from the paired and fused palatines, and the lateral margins of the posterior portion nearing the paired choanae run parallel to one another. This is distinct from *Brillanceausuchus*, in which the lateral margins converge posteriorly, and *T. pusillus*, *Wannchampsus*, and *Shamosuchus*, in which the lateral margins flare posterolaterally.
- (S10*) *Pterygoids excluded from the posterior margin of suborbital fenestra by ectopterygoid–*

palatine contact (C180.1): The exclusion of the pterygoid ventral lamina from the posterior margin of the suborbital fenestra is unique in *T. guimarotae*. In all other specimens analysed, for which the presence or absence of this feature can be assessed (including *T. pusillus*, '*T. sympiestodon*', protosuchians, goniopholidids, and paralligatorids), the pterygoids contribute to the posterior margin of the suborbital fenestra.

- (S11*) *Completely septated choanal groove (C183.2)*: The choanae of *T. guimarotae* are completely septated, formed anteriorly by the palatines and posteriorly by the pterygoids, similar to the goniopholidids *Amphicotylus* (Mook, 1942) and *Eutretauranosuchus* (Smith *et al.*, 2010). This morphology is distinct from in *T. pusillus*, in which the choanal groove is partially septated, and '*T. sympiestodon*' (Martin *et al.*, 2010, 2014a,b) and other paralligatorids, in which the groove is open and undivided.
- (S12) *Basisphenoid ventrally exposed anteriorly to the basioccipital (C188.0), and ventral surface continuous with surrounding cranial elements (C190.0)*: The conformation of the basisphenoid to the remainder of the occipital plane is distinct from that in *T. pusillus* and other advanced neosuchians in which the main body of the basisphenoid is separated by a sulcus and posteroventral step.
- (S13) *Mandibular symphysis of moderate posterior length, posteriorly reaching the fifth–sixth dentary tooth position (C204.1)*: The relative length of the symphysis to the dental arcade is highly variable within species currently and previously assigned to *Theriosuchus*, being short up to the fifth alveolus in '*T. ibericus*' (also shared with *Brillanceausuchus*), terminating medial to the fifth and sixth alveolus in *T. guimarotae*, medial to the sixth in '*T. sympiestodon*', and medial to the seventh alveolus in *T. pusillus*, *T. grandinaris*, and *Theriosuchus* sp. (NMS G. 2014.52.1; Young *et al.*, 2016).
- (S14*) *External mandibular fenestra present (C207.1)*: *Theriosuchus guimarotae* possesses the plesiomorphic condition in the retention of a triangular-shaped external mandibular fenestra, as also occurs in *Alligatorium meyeri*, *Protosuchus richardsoni* (Colbert & Mook, 1951), and *Eutretauranosuchus* (Smith *et al.*, 2010). This morphology is not known in any atoposaurid specimen, although the posterior portions of the dentaries of

Alligatorellus, *Atoposaurus*, *Montsecosuchus*, and *T. grandinaris* are partially obscured or unknown.

THERIOSUCHUS GRANDINARIS LAUPRASERT ET AL., 2011

Type locality and horizon

Sao Khua Formation, Khorat Group, early Aptian (Early Cretaceous); Phu Phok, Kok Prasit Sub-district, Phu Phan District, Sakon Nakhon Province, north-western Thailand.

Type specimen

PRC-2, fused anterior rostrum and mandible (note that the specimen ID is stated as 'PPC' in Lauprasert *et al.*, 2011, but the institutional abbreviation is given as PRC).

Previous diagnoses and comments

Lauprasert *et al.* (2011) assigned *T. grandinaris* to *Theriosuchus* (and therefore to Atoposauridae) based on the possession of a brevirostrine skull with the maxilla transversely flattened, symmetrical, and pointed at the apex, which is a feature common in numerous small neosuchian crocodyliforms. The premaxilla–maxilla suture of *T. grandinaris* is aligned posteromedially in dorsal view, deemed to be diagnostic by Lauprasert *et al.* (2011), but this feature is also present in *T. guimarotae* (Schwarz & Salisbury, 2005) and *T. pusillus*, and is more likely to characterize the genus *Theriosuchus* (see above). It is not entirely clear what is meant by the 'weak notch' present at the premaxilla–maxilla suture (Lauprasert *et al.*, 2011), although a notch is present ventrally in this suture in *T. pusillus* and possibly *T. guimarotae* (Schwarz & Salisbury, 2005), which is for the enlarged dentary tooth. This feature is distinct from '*T. ibericus*' and '*T. sympiestodon*', in which there is a distinct occlusal pit within the dental arcade to accommodate the enlarged dental tooth. The relatively long mandibular symphysis, terminating posteriorly medial to the D7 alveolus, is a feature shared with *T. pusillus*, but not unique within *Theriosuchus* (contra Lauprasert *et al.*, 2010; see also Young *et al.*, 2016). The presence of an anteriorly tapering and slender prefrontal was also stated as diagnostic for *T. grandinaris* by Lauprasert *et al.* (2011), but this morphology is present in both *T. pusillus* and *T. guimarotae*, as well as *Alligatorellus* and paralligatorids.

Revised diagnosis and discussion

(S1) *Fully divided external nares (C10.0)*: The presence of paired external nares (i.e. divided

by either the premaxilla or an anterior extension of the nasals) might be synapomorphic for Atoposauridae (see above), but is clearly present in *T. grandinaris* too.

(S2) *Premaxilla–maxilla suture ventrally confluent (C42.0), with ventral diastema at the contact suture*: Lauprasert *et al.* (2011) stated that there is a diastema at the premaxilla–maxilla suture, not a lateral concavity as in *T. pusillus* and *T. guimarotae*, which might be diagnostic for this species.

(S3) *Nasals gradually widen adjacent to the maxilla (C70.1)*: The gradual widening of the nasal bones posteriorly is distinct from the condition in *T. pusillus*, in which the lateral margins expand rapidly adjacent to the maxilla and anterior to the periorbital elements, and *T. guimarotae* in which the nasals are consistently narrow (Schwarz & Salisbury, 2005). This gradual widening of the nasals is reminiscent of longirostrine neosuchians, such as *Rugosuchus* (Wu *et al.*, 2001a).

(S4*) *Unique combination of pseudocaniniform, lanceolate-shaped (C253.0), and labiolingually flattened (C354.0) teeth with faintly crenulated mesial and distal carinae (C245.0)*: The heterodont dentition of species attributed to *Theriosuchus* has long been recognized as diagnostic. Heterodonty is not exclusive to *Theriosuchus*, also being known in bernissartiids, notosuchians, and a range of other neosuchian taxa (Ösi, 2014). However, variation in dentition differentiates the species of *Theriosuchus* from one another (see above).

Additional comment

Theriosuchus grandinaris shares many similarities with a fragmentary specimen described as *Theriosuchus* sp. (NMS G. 2014.52.1) from the Isle of Skye, known solely from the anterior portion of a right dentary (Young *et al.*, 2016). The two are recovered as sister taxa in our analyses, and shared features include: (1) a straight lateral margin of the dentary in dorsolateral view; and (2) a parallel dentary symphysis to the dental arcade. Although this might indicate that *Theriosuchus* sp. is referable to *T. grandinaris*, they are widely separated from one another spatiotemporally, and other features allow us to distinguish the two taxa (Young *et al.*, 2016).

THERIOSUCHUS SP.

European occurrences

Additional material referred to *Theriosuchus* has been described from a host of other continental Euro-

pean localities, but is typically fragmentary or isolated in nature, and therefore difficult to assign to a particular species. The majority of these have been assigned to *Theriosuchus* based on its highly diagnostic tooth morphotypes, as discussed above. These teeth are usually small, no more than 2–3 mm in either dimension. The bases of the crowns are always mesiodistally constricted, and there are varying degrees of labiolingual compression, which can be asymmetrical, leading to a convex labial face and a flat lingual face. A lanceolate tooth morphology is also diagnostic for *Theriosuchus* (Schwarz & Salisbury, 2005; see above). These occurrences include, in stratigraphical order from oldest to youngest:

1. *Theriosuchus* sp. is known from a dentary from the late Bajocian–Bathonian of the Isle of Skye, UK (Young *et al.*, 2016). This specimen (NMS G. 2014.52.1), although based on highly fragmentary material, appears to have several unique dental characteristics that distinguish it from *T. grandinaris* and other species of *Theriosuchus*, including: (1) posterolaterally orientated crenulations on the posterior end of the dental arcade; (2) a longitudinally crenulated occlusal surface; and (3) the symphysis not contributing to the splenial (Young *et al.*, 2016). Although additional crocodyliform material is in preparation from the Isle of Skye that might be referable to this taxon (S. Brusatte, pers. comm., 2015), the currently available material appears to possess a unique combination of character states amongst *Theriosuchus* species. Despite this, Young *et al.* (2016) did not refer it to a new species because of the fragmentary nature of the remains, a taxonomic decision that we follow here.
2. Isolated tooth crowns from the late Bathonian Forest Marble microvertebrate horizon of the UK were referred to Atoposauridae, but described as ‘*Theriosuchus*’-like (Evans & Milner, 1994). Based on the information provided in Evans & Milner (1994: fig. 18.6e, p. 315), at least one of these teeth possesses a pseudozipodont morphology, and characteristic labiolingually compressed and lanceolate morphology. We therefore tentatively regard these specimens as cf. *Theriosuchus* sp.
3. Fifty-nine variably worn or abraded teeth, from the Oker and Uppen sections of the Kimmeridgian of north-west Germany, assigned to cf. *Theriosuchus* sp. by Thies *et al.* (1997). These teeth possess the characteristic lanceolate morphology of *T. pusillus* and *T. guimarotae*, and we therefore consider them to represent *Theriosuchus* sp.
4. Another specimen (DFMMh 200, the anterior part of a crushed skeleton) from the Kimmeridgian of northern Germany was tentatively referred to *T. pusillus* by Karl *et al.* (2006), although it is probably of a different ontogenetic age to the type material. This specimen has a posterior maxillary dental arcade situated within a confluent dental groove, similar to the feature that we identify as synapomorphic for (*T. pusillus* + *T. guimarotae*) (see above). The teeth of DFMMh 200 are morphologically similar to *T. pusillus* (Karl *et al.*, 2006), owing to the presence of faint carinae, a slightly labiolingually compressed and lanceolate morphology, an enlarged fourth maxillary tooth, and caniniform third and fourth dentary teeth. However, the external nares are almost completely divided by an anterior projection of the nasals, a feature that we consider to be diagnostic of Atoposauridae, to the exclusion of *Theriosuchus*. Despite this latter feature, we tentatively refer DFMMh 200 to *Theriosuchus* cf. *pusillus*, pending a more detailed description of this potentially important specimen. Additional material referable to *Theriosuchus* sp. comes from the same region as DFMMh 200, including DFMMh 605 (a partial and damaged skull, probably of a hatchling); DFMMh 325 (four ventral osteoderms, two ribs, and a fragment of a dorsal vertebra; DFMMh 236 (numerous dorsal osteoderms); DFMMh 279 (single femur); and DFMMh 507 (a solitary tooth) (Karl *et al.*, 2006). However, the dorsal osteoderms possess an anterior process, a feature that we do not consider to be present in *Theriosuchus*, and therefore at least some of the osteoderms comprising DFMMh 236 are more likely to belong to a goniopholidid. The femur and axial material cannot be definitively attributed to *Theriosuchus* based on our revised understanding of this genus, and we consider it to belong to an indeterminate mesoeucrocodylian. We tentatively consider the partial skull and the single tooth to be referable to cf. *Theriosuchus* sp., owing to the dental similarities they possess.
5. Isolated teeth from two localities in the Tithonian of north-eastern France were referred to cf. *Theriosuchus* sp. (Cuny *et al.*, 1991). One of the figured teeth (PMC MO2.15) appears to possess a lanceolate and pseudozipodont morphology. We therefore designate the specimen as *Theriosuchus* sp.
6. Isolated teeth (MO-CHA-30, 31, 32) from the Tithonian of western France were referred to *Theriosuchus* cf. *pusillus* (Vullo *et al.*, 2014). These teeth possess a lanceolate morphology, as

well as carinae that are 'festooned' on the apical margins of each tooth, giving a pseudozipodont appearance. This morphology is characteristic of *T. pusillus*, and therefore we agree with Vullo *et al.* (2014) in their reference to *Theriosuchus* cf. *pusillus*, pending the discovery of more complete material.

7. *Theriosuchus* sp. was described based on teeth from the Berriasian of south-west France (Pouech, Mazin & Billon-Bruyat, 2006; Pouech *et al.*, 2014). A single anterior tooth is figured in lingual view by Pouech *et al.* (2006) (CHEM03.506), and possesses faint apicobasal striations, a mesiodistally compressed crown base, and a pointed apex, giving it a lanceolate morphology. This is characteristic of *Theriosuchus*, and therefore we retain the status of these specimens as *Theriosuchus* sp., noting that these are of the same age as *T. pusillus* from the UK (Owen, 1878a, 1879; Salisbury, 2002).
8. Schwarz-Wings *et al.* (2009b) referred 284 teeth to *Theriosuchus* sp. from the Berriasian of southern Scandinavia (Skyttegard Member, Rabekke Formation of Bornholm, Denmark, and Annero Formation, Vitaback Clays, of Skane, Sweden). These teeth possess the labiolingually compressed and lanceolate morphologies characteristic of *T. pusillus* and *T. guimarotae* (Schwarz & Salisbury, 2005), and also the broader 'low-crowned' morphotype. This third morphotype is also known in '*T. ibericus*', and therefore we consider these teeth as a whole to represent cf. *Theriosuchus* sp., but recognize that more than one heterodont species, including one closely related to *T. pusillus*, might be present.
9. Hornung (2013) described, but did not figure, a partial left mandible (GZG.BA.0139) from the Bückeberg Formation (Berriasian–Valanginian) of northern Germany (Old comital quarry, Harl Hill, approximately 1.7 km south-east of Bückeburg). It was assigned to *Theriosuchus* sp. based on the presence of a ridge on the ventrolateral surface of the angular, a posteriorly directed retroarticular process, and the absence of the external mandibular fenestra. The absence of the latter feature suggests that it is not referable to *T. guimarotae* (see above). This specimen is about three times the size of the holotype of *T. pusillus*, and might therefore represent one of the largest known individuals of *Theriosuchus*. Hornung (2013) also noted a distinct knob-like lateral swelling on the anterior end of the lateral shelf of the angular. Combined with its relatively large size, GZG.BA.0139 might therefore represent a novel species of *Theriosuchus*, but we refer it to cf. *Theriosuchus* sp., pending examination of this material. Several osteoderms were also briefly mentioned by Hornung (2013) from an unspecified locality near Sehnde (Lower Saxony) as resembling *Theriosuchus*, including one (GZG.STR.50293) that was identified as closely reminiscent of *T. pusillus*. Hornung (2013) also noted that complete 'atoposaurid' skeletons are preserved in the Cherves-de-Cognac region in south-western France (Berriasian), and remain undescribed.
10. *Theriosuchus* sp. has been identified from multiple localities in the Early Cretaceous (early Berriasian to early Barremian) Teruel region of eastern Spain (Ruiz-Omeñaca *et al.*, 2004). However, these occurrences were only documented as part of faunal lists, and no further details are given, although a brief description without figures is provided for this material by Canudo *et al.* (2010). Therefore, we consider these occurrences to represent aff. *Theriosuchus* sp., pending examination of the identified material.
11. *Theriosuchus*-like teeth have been described from the Cenomanian of south-western France, and assigned to Atoposauridae (Vullo & Néraudeau, 2008). Based on the figured specimen, these teeth possess a pseudozipodont morphology, formed by the apical extension of the lingual carinae. Although the only tooth figure has a worn apex, it is clear that these teeth possess a lanceolate morphology, with evidence of labiolingual compression. We therefore assign these specimens to *Theriosuchus* sp., pending further examination.
12. Two teeth from the Maastrichtian of north-eastern Iberia have been referred to an indeterminate atoposaurid (Marmi *et al.*, 2016). These teeth have a lanceolate morphology, are labiolingually compressed, and apically blunt. Faint apicobasally orientated ridges are present and more prominent on the lingual surface, where they develop into pseudozipodont crenulations. Based on this combination of characteristics, we tentatively regard these teeth as representing cf. *Theriosuchus* sp., but based on their age it is more likely that they represent a crocodyliiform more closely related to '*T. sympiestodon*' (Martin *et al.*, 2014a,b).

Non-European occurrences

Outside of Europe, reports of *Theriosuchus* are less frequent, but provide further evidence that this genus was a common component of Cretaceous Asian semi-aquatic ecosystems. These occurrences comprise:

1. Haddoumi *et al.* (2016) documented numerous small teeth from the Bathonian of eastern Morocco, and ascribed them to cf. *Theriosuchus* sp. based on their lanceolate crown morphology and

pseudoziphodont carinae. As a consequence of our revision of Atoposauridae and *Theriosuchus*, we refer these teeth to *Theriosuchus* sp. These specimens currently represent the only confirmed occurrences of *Theriosuchus* from Gondwana.

2. Lauprasert *et al.* (2011) assigned a partial left dentary (PRCMR CCC-1) and a single tooth (PRCMR 283) to cf. *Theriosuchus* sp. from the Phu Kradung Formation (latest Jurassic to Early Cretaceous) of the Nong Bua Lum Phu Province in Thailand. This belongs to a heterodont crocodyliform with a combination of pseudocaniniform and lanceolate teeth that display the presence of festooned crenulations, formed by anastomosing and irregular ridges on the crown (the characteristic pseudoziphodont apical morphology). Furthermore, the presence of interalveolar septae and dental teeth occupying a single groove (Lauprasert *et al.*, 2011) can be used to assign this specimen to *Theriosuchus* (Young *et al.*, 2016).
3. A single tooth was ascribed (PRCMR 218) to cf. *Theriosuchus* sp. from the Early Cretaceous of Thailand (Cuny *et al.*, 2010). This tooth has a similar morphology to other teeth assigned to *Theriosuchus* from Thailand (see above), and therefore the assignment to *Theriosuchus* sp. is supported. It might be that these teeth represent isolated occurrences of *T. grandinaris* based on their near-identical morphologies.
4. Mo *et al.* (2016) described a tooth as cf. *Theriosuchus* from the Aptian of southern China. This tooth is similar to the Asian occurrences of *Theriosuchus*, and therefore we agree with Mo *et al.* (2016), retaining its status as cf. *Theriosuchus* sp.

NEOSUCHIA BENTON & CLARK, 1988
'ALLIGATORIUM' FRANCONICUM AMMON, 1906
ALLIGATORIUM PAINTENENSE KUHN, 1961

Type locality and horizon

Unknown bed, late Kimmeridgian (Late Jurassic); Painten, 10 km north of Kelheim, south-east Germany.

Type specimen

BSPG specimen (number unknown): destroyed or lost; articulated hindlimb and pelvic girdle.

Referred specimen

BSPG specimen (number unknown): destroyed or lost; type of *Alligatorium paintenense*, a skull and near-complete skeleton missing most of the tail and the right hindlimb.

Previous diagnoses and comments

Ammon (1906) originally named *Alligatorium franconicum* based on an articulated right hindlimb from the Late Jurassic of Painten, Bavaria. Subsequently, Broili (1931) tentatively referred a partial skeleton from the same locality to this species. Kuhn (1961) referred this latter skeleton to a new species, *Alligatorium paintenense*, without detailed discussion, an interpretation followed by Kuhn (1966). Wellnhofer (1971) provided emended diagnoses for both species and considered them to be valid, along with *Montsecosuchus* ('*Alligatorium*') *depereti* (Vidal, 1915) and *Alligatorium meyeri* (Gervais, 1871). Most recently, Tennant & Mannion (2014) concluded that the differences in limb proportions were not enough to distinguish '*Alligatorium paintenense*' from '*Alligatorium franconicum*', and synonymized the former with the latter, an interpretation that we follow here.

Buffetaut (1981) described a small brevirostrine skull from the Late Jurassic of Brauvilliers, Meuse, France, and assigned it to *Alligatorium* cf. *paitenense*. This assignment was based on the significantly longer and pointed rostrum compared with other atoposaurids, the posteriorly placed orbits, a mediolaterally narrow interorbital region, and the dense external surface sculpting. Buffetaut (1981) also noted some differences, including the overall larger size and moderate development of the posterolateral squamosal 'lobe', as noted for *Alligatorium meyeri*, *Alligatorellus beaumonti*, and *T. pusillus*. Unfortunately, we have been unable to examine this specimen first-hand and, based on the figures in Buffetaut (1981), we cannot determine its relationship to the now lost German specimens of '*Alligatorium franconicum*' (Wellnhofer, 1971).

Wellnhofer (1971) noted that the skull of '*Alligatorium franconicum*' was strongly sculpted and more longirostrine than the typically brevirostrine atoposaurids, and that the external nares were fully open and not divided by a septum, the presence of which is a feature that we consider to be diagnostic for atoposaurids, but also possessed by *T. pusillus* (Owen, 1879). Additionally, '*Alligatorium franconicum*' possesses biserial paravertebral rows of sculpted dorsal osteoderms, similar to atoposaurids and *T. pusillus*, but with a central keel that diminishes anteriorly.

Most of our analyses found '*Alligatorium franconicum*' to be united within a clade comprising *Pholidosaurus* (Salisbury, 2002), *Eutretauranosuchus* (Smith *et al.*, 2010), *Amphicotylus* (Mook, 1942), and *Koumpiodontosuchus* (Sweetman *et al.*, 2015), representing Bernissartiidae, Goniopholididae, and Pholidosauridae. However, resolving the position of these groups within Neosuchia is not the focus of our study, although it is noteworthy that we found them to be more closely related to paralligatorids than ato-

posaurids. The characters uniting '*Alligatorium*' *franconicum* with these non-atoposaurid taxa include: (1) an intermandibular angle of $<40^\circ$ (36°); (2) a total anteroposterior skull length to snout length (measured from the anterior margin of the orbit to the anterior edge of the premaxilla in dorsal view) ratio of <2.0 (1.81); (3) a skull anteroposterior length to orbit length ratio of >5.0 (5.27), a feature also shared with *Brillianceausuchus* and *Shamosuchus* (Pol *et al.*, 2009); (4) a nasal that only participates posteriorly in the margin of the external nares, a feature that appears to only be shared with *Amphicotylus* (Mook, 1942), and distinct from atoposaurids and *Theriosuchus* in which the nasal participates posteriorly and medially, often projecting anteriorly into and dividing the external nares; and (5) asymmetrical dorsal osteoderms in dorsal aspect (excluding any anterolateral peg articulation), a feature more widespread across Neosuchia, including *Alligatorellus* (Tennant & Mannion, 2014), *Pachycheilosuchus* (Rogers, 2003), and *Wannchampsus* (Adams, 2014).

Buscalioni (1986) also found '*Alligatorium*' *franconicum* to be closely related to goniopholidids, bernissartiids, and paralligatorids, based on a combination of factors including longer rostral length, undivided external nares, proportionally broad supratemporal fenestra, and transversely broad osteoderms. However, Buscalioni & Sanz (1988) considered it to be a *nomen dubium*, owing to the fact that the specimen is lost, and because the single autapomorphy proposed by Wellnhofer (1971; a reduced anterior process of the ilium) is present in *Montsecosuchus* and atoposaurids, and more broadly within Neosuchia. We regard '*Alligatorium*' *franconicum* as a potentially diagnostic non-atoposaurid taxon, but refrain from erecting a new genus name because all specimens are lost/destroyed and our proposed autapomorphies are tentative pending the discovery of additional material. Future discoveries referable to '*Alligatorium*' *franconicum* should shed light on the taxonomy of specimens attributed to *Alligatorium* and the evolution of the biserial osteoderm shield in Neosuchia, as well as the early development of a longirostrine cranial morphology in non-thalattosuchian Jurassic taxa.

Revised diagnosis and discussion

(S1) *Minimum mediolateral width between supratemporal fenestrae broader than minimum mediolateral width between orbits* (C19.0): This feature describes the relatively high intertemporal mediolateral width compared with the interorbital region, a feature that '*Alligatorium*' *franconicum* shares not only with some atoposaurids, but also *Montsecosuchus* (Buscalioni & Sanz, 1990a) and *Pachycheilosuchus* (Rogers, 2003).

(S2) *Skull length to width ratio >2.5* (2.77) (C25.2): The skull length to width ratio reported here is diagnostic only in the sense that we have not sampled many fully longirostrine taxa, with the exception of *Pholidosaurus* (Salisbury, 2002), with which it also shares this character state. *Koumpiodontosuchus* (Sweetman *et al.*, 2015) and the two goniopholidid taxa are semi-longirostrine, but not to the extent of pholidosaurids and fully marine crocodyliforms. As such, '*Alligatorium*' *franconicum* might represent a transitional form towards a more aquatic lifestyle, but this requires much more detailed investigation pending the discovery of new remains.

(S3) *Presence of a lateral keel on posterior part of dorsal osteoderms* (C312.1): This character state is shared with *Alligatorellus*, but the morphology of the osteoderms of '*Alligatorium*' *franconicum* appears to be distinct, with a central longitudinal keel, and a lateral sulcus with an anterolateral projection, similar to the 'peg and socket' morphology described for *T. guimarotae* (Schwarz & Salisbury, 2005) and goniopholidids (Salisbury & Frey, 2001). This overall geometry appears to be different from the dorsal osteoderm shield for any known atoposaurid (Tennant & Mannion, 2014), and from any goniopholidid, and identifies '*Alligatorium*' *franconicum* as a distinct neosuchian taxon.

NEOSUCHIA BENTON & CLARK, 1988
PARALLIGATORIDAE KONZHUKOVA, 1954
(*SENSU* TURNER, 2015)
SABRESUCHUS GEN. NOV.

([HTTP://ZOOBANK.ORG/NOMENCLATURALACTS/35B479C6-7620-428A-92A7-F613B43FEC24](http://zoobank.org/NOMENCLATURALACTS/35B479C6-7620-428A-92A7-F613B43FEC24))

Etymology

'Sabre' in reference to the enlarged and curved fifth maxillary tooth, and 'suchus' from the Ancient Greek, *soukhos*, for crocodile.

Included species

Sabresuchus ibericus (type species) and *Sabresuchus sympiestodon*.

Distribution

Cretaceous of Europe.

Comments

'*Theriosuchus*' *sympiestodon* shares a number of features with '*T.*' *ibericus*, and these two taxa form a sister-taxon relationship in all of our analyses, distantly related to other species definitively ascribed to *Theriosuchus*. These taxa have never been directly

compared or included together in a phylogenetic analysis, and based on this novel finding here we erect the name *Sabresuchus* gen. nov. to include them both. The name refers to the hypertrophied fifth maxillary tooth, which is at least four times the size of adjacent teeth in both species, and is the most striking feature of this genus.

Our phylogenetic analyses place *Sa. sympiestodon* and *Sa. ibericus* within Paralligatoridae. The Bremer support uniting these two species is 3–4 (Fig. 5), with a posterior node probability of nearly 1 (Fig. 7), providing strong support for their sister-taxon relationship. *Sabresuchus* is the sister taxon to *Wannchampsus* (Adams, 2014), often cited alongside *T. pusillus* as an important transitional form on the lineage leading to Eusuchia (Langston, 1974). A number of dental features characterize this relationship with *Wannchampsus*, including the maxillary teeth with denticulate carinae on the mesiodistal margins, and ridged ornamentation on the enamel surface in middle to posterior teeth. However, the instability of this relationship with *Wannchampsus* is highlighted by the fact that if *Pachycheilosuchus* (Rogers, 2003) is retained in phylogenetic analyses *a priori*, then *Brillanceausuchus* and *Shamosuchus* instead form a polytomy with *Wannchampsus*, with *Sabresuchus* as the sister taxon to that clade (Fig. 5A). However, our analyses were not designed to resolve paralligatorid relationships and, irrespective of this lack of consensus, we still find a sister-taxon relationship between *Sa. ibericus* and *Sa. sympiestodon* that is nestled within this paralligatorid assemblage, in a more crownward position than *Theriosuchus*. This relationship between *Sabresuchus* and other paralligatorids is further supported by a number of unequivocal synapomorphies, including: (1) a striated external surface of the posterior portion of the maxilla (C51.0); (2) an anteroposterior ridge occupying the entire length of the frontal dorsal surface (restricted to the median portion of this surface in *Sa. sympiestodon*) (C101.3); and (3) the presence of an obliquely orientated ridge on the dorsal surface of the squamosal (C145.0).

Diagnosis and discussion

(S1) *Ventral edge of the groove for the upper ear lid positioned directly ventral to dorsal edge (C136.1)*: This morphology is distinct from *T. guimarotae* (Schwarz & Salisbury, 2005) and *T. pusillus*, in which the ventral edge of the ear lid is laterally displaced with respect to the dorsal edge. However, it is similar to a range of neosuchians, including *Brillanceausuchus*, *Wannchampsus*, and *Koumpiodontosuchus* (Sweetman *et al.*, 2015), *Alligatorellus*, *Pholidosaurus* (Salisbury, 2002), *Eutretauranosuchus* (Smith *et al.*, 2010), *Mahajangasuchus* (Turner

& Buckley, 2008), and *Shamosuchus* (Pol *et al.*, 2009; Turner, 2015), as well as *Protosuchus richardsoni* (Colbert & Mook, 1951).

- (S2) *Squamosal posterolateral process ('lobe') offset from the dorsally flat skull table (C140.1)*: The depression of the squamosal posterolateral lobe and its confluence with the paroccipital process is similar to the condition seen in the paralligatorids *Brillanceausuchus* and *Shamosuchus* (Turner, 2015) and the eusuchian *Allodaposuchus precedens* (Buscalioni *et al.*, 2001), as well as the crocodyliform *Zosuchus* (Pol & Norell, 2004a) (see Discussion).
- (S3) *Squamosal with an oblique ridge on the dorsal surface (C145.0), posterior to the posterior margin of the supratemporal fenestra (C146.0)*: This morphology of the dorsal surface of the squamosal is distinct from *Brillanceausuchus*, *Shamosuchus*, and *Wannchampsus*, in which the ridge is positioned laterally to the external supratemporal fenestra. In protosuchians, coelognathosuchians, atoposaurids, bernissartiids, *Montsecosuchus*, 'Alligatorium' *franicum*, and *Theriosuchus pusillus*, there does not appear to be any ridge. *Theriosuchus guimarotae* is distinct from *Sabresuchus* in possessing a rounded and longitudinally orientated crest that occupies the whole of the anteroposterior length of the flat dorsal surface, separating it from the bevelled lateral portion (Schwarz & Salisbury, 2005).
- (S4) *Lateral surface of dentary with concavity for reception of enlarged maxillary tooth (C212.1)*: The presence of this lateral concavity is similar to *Brillanceausuchus*, *T. pusillus*, and *T. guimarotae*, which all possess either an individual enlarged maxillary tooth, or a wave of enlarged teeth. To accommodate this, the lateral surface of the dentary becomes invaginated, with the maxillary teeth occluding laterally to this surface. In protosuchians, and all other neosuchians that we observed, the lateral surface of the dentary is smooth and confluent with the rest of the external surface of the dentary at the position where the anterior maxillary teeth occlude.
- (S5) *At least some medially positioned confluent maxillary teeth, implanted in a dental groove (C217.1 and C217.2)*: In both species of *Sabresuchus*, at least some of the maxillary teeth are implanted in a confluent dental groove, instead of individual alveoli. This is shared by *T. guimarotae* (Schwarz & Salisbury, 2005), *Eutretauranosuchus* (Smith *et al.*, 2010), and *Koumpiodontosuchus* (Sweetman *et al.*, 2015), as well as by some notosuchians, in which an 'alveolar trough' develops (Gomani, 1997;

Buckley *et al.*, 2000; O'Connor *et al.*, 2010). This feature is distinct from the condition in thalattosuchians (Gasparini *et al.*, 2006), goniopholidids (Tykoski *et al.*, 2002), and eusuchians (Buscalioni *et al.*, 2001; Salisbury *et al.*, 2006; Ōsi *et al.*, 2007), in which individual teeth are differentially spaced, and occupy isolated alveoli, separated by interalveolar septae.

- (S6) *Maxillary teeth with low-crowned and strongly labiolingually compressed morphotype (C254.0)*: The presence of a 'low-crowned' dental morphology has been observed and used as a defining feature for some *Theriosuchus* species, without ever giving a precise definition of what this characterizes. We consider this morphology to describe a dental crown that is mesiodistally broader than it is apicobasally tall, and with apical margins orientated at <45° from the horizontal. This dental morphotype is diagnostic for *Sabresuchus*, but also shared with *T. pusillus*.
- (S7) *Maxillary tooth 5 hypertrophied, at least 4.0 times the size of adjacent maxillary teeth (C258.1)*: In all other specimens we observed (including *T. pusillus* and atoposaurids), the maxillary teeth were subequal in size or developed one or two enlarged 'waves' (e.g. goniopholidids). In protosuchians, maxillary teeth 1–3 are proportionally and variably the largest (Wu *et al.*, 1997; Gow, 2000; Pol *et al.*, 2004), and in notosuchians there is a progressive reduction in size posteriorly from the enlarged second maxillary tooth (Ortega *et al.*, 2000; Pol & Apesteguía, 2005; Zaher *et al.*, 2006; Campos *et al.*, 2011). In *Sabresuchus*, the fifth maxillary tooth is larger than the fourth, which is in turn larger than the third tooth.

SABRESUCHUS IBERICUS COMB. NOV.
THERIOSUCHUS IBERICUS BRINKMANN, 1989

Type locality and horizon

Lowest horizon of an abandoned lignite mine, La Huérguina Formation (Uña), Upper Barremian (Early Cretaceous); south-west of the eastern edge of Uña, Serranía de Cuenca, eastern Spain.

Type specimen

MfN MB.R IPFUB 102/21.2, partial right maxilla with *in situ* teeth.

Referred material (specimens housed at the MfN MB.R, unless stated)

IPFUB 102/11.2 (incomplete left maxilla); IPFUB 102/11.3 (incomplete right maxilla); IPFUB 102/11.5 (frontal); IPFUB 102/11.6 (incomplete mandible);

IPFUB 102/11.7 (cranial fragments); IPFUB 102/12.1 (incomplete left dentary); IPFUB 102/12.2 (incomplete right dentary); IPFUB 102/21.1 (left maxilla fragment with a tooth); IPFUB 102/21.3 (incomplete frontals); IPFUB 102/21.4 (parietal); IPFUB 102/21.5 (incomplete left jugal); IPFUB 102/21.6 (incomplete right jugal); IPFUB 102/21.7 (incomplete right squamosal); IPFUB 102/21.8 (left quadrate fragment with incomplete left squamosal and left quadratojugal); IPFUB 102/21.9 (right quadrate fragment); IPFUB 102/21.10 (near-incomplete pterygoid and basisphenoid); IPFUB 102/21.18 (basioccipital fragment); IPFUB 102/21.11 (incomplete left dentary); IPFUB 102/21.12 (left splenial fragment); IPFUB 102/21.13 (left angular fragment); IPFUB 102/21.14 (left fractured surangular); IPFUB 102/21.15 (incomplete right angular with right surangular fragment and right coronoid); IPFUB 102/21.16 (incomplete left articular); IPFUB 102/21.17 (right articular); IPFUB 102/21.19 (24 teeth, representing three different morphotypes); IPFUB 102/21.43 (right premaxilla); IPFUB 102/21.44 (caudal vertebra); IPFUB 102/21.45 (anterior caudal vertebrae and various other cranial bones); IPFUB 102/22.1 (two teeth and roots, one incomplete tooth crown); IPFUB 102/22.2 (two teeth and roots, one fragmentary tooth crown); IPFUB 102/22.3 (angular fragment); IPFUB 102/22.4 (incomplete left dentary); IPFUB 102/22.5 (one caudal and two dorsal vertebrae); IPFUB 102/22.6 (proximal left femur fragment). This material is likely to all be from the same individual, and Brinkmann (1989, 1992) regarded all of the referred material as belonging to the holotype individual, a view that we follow here.

Tentatively referred material

BUE4-NT2#25 (teeth) (La Huérguina Limestone Formation, late Barremian (Early Cretaceous); El Inglés Quarry, Serranía de Cuenca, eastern Spain); provisionally housed in the Unidad de Paleontología, Universidad Autónoma de Madrid, and will be eventually stored in the Museo de Ciencias de Castilla-La Mancha in Cuenca, Spain, at which point permanent catalogue numbers will be assigned (Buscalioni *et al.*, 2008).

Previous diagnoses and comments [3]

Both Brinkmann (1989, 1992) referred to *T. ibericus* as a new species, and therefore Brinkmann (1989) has taxonomic priority. The original specific designation was based on a range of features, including variation in tooth morphology and the width of the internal choanae, as well as the presence of procoelous caudal vertebrae. However, Schwarz & Salisbury (2005) and Martin *et al.* (2010) regarded this species to be of questionable validity, and it remains poorly understood. Here, we demonstrate that

'*T. ibericus* is a valid taxon, with the new combination *Sa. ibericus*.

In spite of the differences we have recovered here, and the novel phylogenetic position for *Sa. ibericus*, this taxon retains some morphological similarities to *T. pusillus*, observations that resulted in its original generic assignment to *Theriosuchus*. Similar to *T. pusillus*, *Sa. ibericus* possesses a longitudinal median ridge on the parietal and frontal, and a deep groove between the squamosal and parietal on the dorsal surface of the skull table (Brinkmann, 1992). However, these features have since been found to be more widespread within crownward neosuchians, including Paralligatoridae (Turner, 2015; Turner & Pritchard, 2015), and cannot be used to unambiguously unite *Sa. ibericus* with *Theriosuchus*.

Sabresuchus ibericus retains several of the diagnostic dental morphotypes of *Theriosuchus*, possessing labiolingually compressed pseudocaniniform, and low-crowned teeth, but these teeth are fully ziphodont (i.e. with denticulate carinae) in *Sa. ibericus*. There is a third morphotype figured in Brinkmann (1989), in which the labial surface of one of the teeth from the middle of the tooth rows is punctured by a series of small pits, which might prove to be an additional dental morphotype. The bases of the middle to posterior tooth crowns are mesiodistally constricted and, despite an overall labiolingual compression, contain a thickened central core to each tooth. The pseudocaniniform teeth of *Sa. ibericus* show evidence of apicobasal striations on the labial sides of the teeth, which terminate 40% of the way towards the tip of the crown (Brinkmann, 1989).

Teeth that might be referable to *Sa. ibericus* (BUE4-NT2#25) have also been reported from a second locality in the Barremian of eastern Spain (Buscalioni *et al.*, 2008). We tentatively follow this referral, pending their further study.

Diagnosis and discussion

(S1) *Palatal surface of maxilla sculpted throughout by ridged ornamentation (C57.2)*: The palatal surface of *Sa. ibericus* (IPFUB 102/21.2) is sculpted with longitudinal ridges, a feature otherwise found only in *Amphicotylus* (Mook, 1942). This is distinct from the condition seen in notosuchians (e.g. Pol & Powell, 2011) and other advanced neosuchians (e.g. Salisbury *et al.*, 2006; Ösi *et al.*, 2007; Adams, 2013), as well as *Theriosuchus* and *Sa. sympiestodon* (Martin *et al.*, 2014a), in which the maxillary palatal surface is flat and smooth. The posterior palatal surface of the maxilla is slightly crenulated in the mesoeucrocodylian *Mahajangasuchus* (Turner & Buckley, 2008), but this is not the same as the marked sculpting seen in *Sa. ibericus*.

(S2*) *Dorsal surface of the parietal depressed relative to the squamosal (C115.2)*: This depression might be partially explained by mediolateral compression of this element. However, for taphonomic processes to fully explain this dorsal concavity, it would be expected for this degree of compression to be visible on other specimens from the type locality, which is not the case. In other mesoeucrocodylians, including *Sa. sympiestodon* (Martin *et al.*, 2014a), the posterior portion of the dorsal surface of the skull table is horizontal and flat (e.g. Sereno *et al.*, 2003; Ösi *et al.*, 2007; Adams, 2013).

(S3) *Proportionally short mandibular symphysis, extending posteriorly medial to the fifth dentary alveolus (C205.0)*: The posterior extension of the symphysis in *Sa. ibericus* is proportionally shorter than in *Theriosuchus* (see also Young *et al.*, 2016) and notosuchians (e.g. Pol & Apesteguía, 2005), terminating medial to the D5 alveolus. This condition is only found in other brevirostrine taxa, such as *Brillanceausuchus*, *Pachycheilosuchus* (Rogers, 2003), and possibly *Iharkutosuchus* (Ösi *et al.*, 2007). In *Sa. sympiestodon*, the symphysis extends posteriorly to the sixth dentary alveolus (based on specimen MCDRD 134; Martin *et al.*, 2014a).

(S4*) *All dentary teeth occupy single, continuous, longitudinal groove (C217.2)*: In *Theriosuchus*, at least some of the dentary alveoli are independent from one another, with each tooth occupying a single alveolus and separated by interalveolar septae of varying thickness. However, *Sa. ibericus* is unique in that all of its dentary teeth appear to occupy a single continuous alveolar groove, along a mediolaterally narrow dentary occlusal surface. This feature is considered to be locally autapomorphic for *Sa. ibericus*, as it has also been documented in basal notosuchians (Pol & Apesteguía, 2005), the hylaeochampsid *Iharkutosuchus* (Ösi *et al.*, 2007), and the posterior dentary teeth of *Isisfordia* (Salisbury *et al.*, 2006).

(S5) *Occlusal dentary surface strongly mediolaterally compressed and devoid of nutrient foramina (C220.0)*: *Sabresuchus ibericus* does not appear to possess any distinctive foramina on the dorsal surface of the dentary, lingual to the mediolaterally compressed dental arcade (Young *et al.*, 2016). By contrast, *Theriosuchus*, *Sa. sympiestodon* (Martin *et al.*, 2014a), and notosuchians (e.g. *Araripesuchus*) have a mediolaterally broad dentary occlusal surface, pierced by at least one foramen (Pol & Apesteguía, 2005; Young *et al.*, 2016). The overall morphology of the dentary of *Sa. ibericus*

is similar to that of *Pachycheilosuchus*, but the latter has a medially curved anterior end, giving a 'scimitar-shaped' profile in dorsal aspect.

- (S6) *Grooved ornamentation (rugose patterning) present posteriorly on the external surface of the dentary (C227.1)*: The presence of a grooved ornamentation on the external surface of the dentary is similar to the condition observed in *Theriosuchus*, as well as *Pachycheilosuchus* (Rogers, 2003), *Brillanceausuchus*, and notosuchians (Ortega *et al.*, 2000; Pol & Apesteguía, 2005), but distinguishes *Sa. ibericus* from *Sa. sympiestodon* (Martin *et al.*, 2014a). In basal crocodyliforms, sculpture patterns consist exclusively of evenly spaced subcircular pits (e.g. Pol *et al.*, 2004)
- (S7*) *Hypertrophied fifth maxillary tooth with fully caniniform morphology (C257.1), directed posteroventrally with respect to rest of maxillary tooth row (C259.0)*: The enlarged maxillary tooth is at least four times the total size of the adjacent teeth, possesses growth rings of varying coloration, and is posteroventrally recurved. In *Sa. sympiestodon*, an enlarged tooth is also present at this position, but is directed ventrally, and not as proportionally enlarged with respect to the adjacent maxillary teeth. This level of heterodonty is not seen in *Theriosuchus*.
- (S8) *Tooth crowns with denticulate carinae (fully ziphodont condition) (C245.1)*: Ziphodonty is known in a range of mesoeucrocodylians, including notosuchians (Pol & Powell, 2011). The difference between the heterodont morphologies of the maxillary tooth crowns of *T. pusillus* and *Sa. ibericus* is that whereas the former have slightly crenulated enamel surfaces leading to 'false' ziphodonty (pseudoziphodonty; Prasad & De Lapparent De Broin, 2002), the latter have 'true' serrations on the apical surfaces of the teeth, giving a fully ziphodont morphology. The 'false' ziphodont condition forms via the apical prolongation of the enamel ridges on the labial and lingual enamel surfaces (Prasad & De Lapparent De Broin, 2002), rather than through the development of an incisive and serrated texture.

SABRESUCHUS SYMPIESTODON COMB. NOV.
THERIOSUCHUS SYMPIESTODON MARTIN *ET AL.*,
 2010

Type locality and horizon

Densus-Ciula Formation (upper part of unnamed middle member), Maastrichtian (Late Cretaceous);

Oltoane Hill, Tustea, Hateg Basin, western Southern Carpathians, Romania.

Type specimen

FGGUB R.1782, a right maxilla with *in situ* teeth.

Paratype

FGGUB R.1781, skull roof that might belong to the holotype individual.

Referred material

MCDRD 134, anterior portion of a right dentary from the Sânpetru Formation (Maastrichtian) at Cioaca Târnovului, Sânpetru, Romania; MCDRD 793, a maxilla with teeth from the Sânpetru Formation (Maastrichtian) at La Cărare, Sânpetru, Romania; LPB (FGGUB) R.1945, a fragmentary maxilla from the Densus-Ciula Formation (Maastrichtian), Valioara-Fântânele, in the Hateg Basin, Romania.

Previous diagnoses and comments

Martin *et al.* (2010) assigned a series of fragmentary mesoeucrocodylian remains to *Theriosuchus*, erecting the new species *T. sympiestodon*. Additional material was subsequently referred to this taxon from nearby localities of approximately the same age (Martin *et al.*, 2014a). A dentary (MCDRD 134) of a different provenance was referred to '*T.* *sympiestodon*' based upon the similarity of its tooth morphology to that of *T. pusillus*. However, this specimen is poorly preserved and does not share any clear features to unite it with the type specimen of '*T.* *sympiestodon*', although we have followed its referral here. The original referral of '*T.* *sympiestodon*' to *Theriosuchus* was based on: (1) the presence of a transversely (or ventrolaterally) directed groove on the anterolateral side of the maxilla; (2) a longitudinal crest on the frontal; and (3) the presence of low-crowned, labiolingually compressed, pseudoziphodont posterior maxillary teeth. However, the presence of this maxillary groove could not be confirmed via personal examination of the type specimen, nor was it observed in *Sa. ibericus* or *T. pusillus*. Schwarz & Salisbury (2005) noted its presence for *T. guimarotae* and possibly *Sa. ibericus*, and Turner (2015) reported its presence on the paratype specimen of *T. pusillus*. On NHMUK PV OR48330, the left maxilla does exhibit a longitudinal mark, but this is parallel to the nasal-maxilla suture, almost orthogonal to that figured for '*T.* *sympiestodon*' (Martin *et al.*, 2010, 2014a), and does not appear to occur on any of the other specimens referred to *Theriosuchus* in the NHMUK collections. A referred specimen of *Sa. sympiestodon* (MCDRD 793) has a depression of some description in this area (Martin *et al.*, 2014a), at an oblique orientation to that of the holotype specimen, although

we have not been able to examine this specimen first-hand, and so we cannot comment on whether it is a groove, bite mark, post-mortem artefact, or a pathology. Therefore, the presence and orientation of any potential maxillary groove, and indeed its functional significance, remain uncertain, especially given that almost all specimens assigned to *Theriosuchus* have undergone taphonomic distortion or damage. We do not consider it to be diagnostic for '*T.* *sympiestodon*', or the genus *Theriosuchus*, although it might be autapomorphic for *T. guimarotae* (Schwarz & Salisbury, 2005). Martin *et al.* (2010) concluded that '*T.* *sympiestodon* lies outside of Eusuchia because of the anterior contribution of the palatine to the 'internal nares' (which we assume to mean choana, owing to the progressive posterior migration of this feature from the anterior rostrum in Crocodyliformes), a feature that is not actually visible in the holotype specimen. The entire basioccipital region around the choana is poorly preserved, and it is difficult to assess whether the choana was fully pterygoidean or bound anteriorly by the posterior palatines. However, it does seem to be situated close to the posterior margin of the suborbital fenestra, similar to paralligatorids and *T. pusillus*. Here, we demonstrate that '*T.* *sympiestodon* is a valid taxon, with the new combination *Sa. sympiestodon*.

Revised diagnosis and discussion

- (S1*) *Longitudinal ridge on dorsal surface of frontal restricted to median portion (C101.1)*: The presence of a midline frontal crest is likely to be related to ontogeny and the fusion of the frontals, as small individuals of *T. guimarotae* lack this crest (Schwarz & Salisbury, 2005). *Alligatorium meyeri* also possesses this feature, as well as a range of non-atoposaurid neosuchians, including *Wannchampsus* (Adams, 2014), *Shamosuchus* (Pol *et al.*, 2009), and *Isisfordia* (Salisbury *et al.*, 2006). However, the position of the ridge and its continuation on the parietal appear to be phylogenetically informative; in *Sa. sympiestodon*, this ridge is restricted to the middle portion of the frontal, whereas in *T. guimarotae* and *T. pusillus* it is restricted to the posterior portion (Schwarz & Salisbury, 2005). In *Sa. ibericus*, *Wannchampsus*, and *Shamosuchus* (Pol *et al.*, 2009), this ridge occupies the entire length of the frontal, and therefore it is likely that this heterogeneity in anteroposterior extent is taxonomically informative.
- (S2) *Dentary internal alveolar margins not raised, but flat and confluent with remainder of dentary occlusal surface (C22.1)*: The lack of raised internal alveolar rims in

Sa. sympiestodon distinguishes it from *Theriosuchus* and *Sa. ibericus*, which have raised rims at least in the anterior alveoli (Young *et al.*, 2016). Eusuchians (e.g. Salisbury *et al.*, 2006), thalattosuchians, and tethysuchians also lack raised alveolar rims (Young *et al.*, 2014), whereas they appear to be raised in notosuchians (e.g. Campos *et al.*, 2011). This feature is not observable in atoposaurids because of the nature of their preservation.

- (S3*) *Diastema present on dentary between D7 and D8 alveoli (C225.0)*: *Sabresuchus sympiestodon* possesses a diastema between the D7 and D8 alveoli, in contrast with *Theriosuchus*, as well as *Pachycheilosuchus* and *Wannchampsus*. We therefore consider this feature to be locally diagnostic for *Sa. sympiestodon*. However, as a result of the lack of anatomical overlap between this dentary and the type material of *Sa. sympiestodon*, we are cautious in our recognition of this feature as diagnostic for the species.
- (S4*) *Maxillary teeth lacking striae on the labial and lingual surfaces (C250.0), with hypertrophied (C258.0) and ventrally directed fifth maxillary tooth (C259.1)*: Martin *et al.* (2010) distinguished '*T.* *sympiestodon* from other species of *Theriosuchus* based on the presence of a single, enlarged maxillary caniniform tooth, and the anterior maxillary teeth lacking striae on the labial and lingual faces, a conclusion with which we agree. *Sabresuchus ibericus* also possesses this enlarged maxillary tooth, although in the one available specimen this tooth is strongly posteriorly recurved, and not directed ventrally as in *Sa. sympiestodon*. In *Shamosuchus*, the fifth maxillary tooth is also the largest, whereas in *T. pusillus* and *Allodaposuchus* the fourth tooth is the largest (Delfino *et al.*, 2008a), but in none of these cases does the proportional size difference come close to that for either *Sa. sympiestodon* or *Sa. ibericus*. Therefore, we consider this combination of maxillary dental character states to be diagnostic for *Sa. sympiestodon*.

BRILLANCEAUSUCHUS BABOURIENSIS

MICHARD *ET AL.*, 1990

Type locality and horizon

Unnamed bed, ?Barremian (Early Cretaceous), Babouri-Figuil Basin, north Cameroon.

Type specimen

UP BBR 201, skull and partial skeleton.

Previous diagnoses and comments

Despite noting numerous similarities with atoposaurids, Michard *et al.* (1990) assigned *Brillanceausuchus* to its own family, Brillanceausuchidae, within Neosuchia. However, a monogeneric family has no systematic purpose, and Brillanceausuchidae has not been used by subsequent workers. Pending the recovery of closely related taxa that do not already form a named clade, we recommend disuse of Brillanceausuchidae. *Brillanceausuchus* has remained a neglected taxon in phylogenetic and comparative analyses, despite its apparent important morphology in possessing a number of 'primitive' character states (e.g. possession of a partially septated external nares and presence of a biserial osteoderm shield) alongside more 'transitional' morphologies between advanced neosuchians and eusuchians (e.g. reduced ventral exposure of the basisphenoid and procoelous presacral vertebrae) (Michard *et al.*, 1990). It was regarded as an atoposaurid by Salisbury & Frey (2001) and Salisbury *et al.* (2006), and as an 'advanced neosuchian' by Turner (2015), without additional comment. To our knowledge, the only phylogenetic analysis to include *Brillanceausuchus* was conducted by Ōsi *et al.* (2007: 174), who commented that its inclusion 'gave much less resolution inside Eusuchia due to its incompleteness' and did not report the results.

Discussion

Brillanceausuchus possesses procoelous cervical and dorsal vertebrae (Michard *et al.*, 1990), as well as fully pterygoidean choanae that are situated posteriorly to the posterior edge of the suborbital fenestrae, as in eusuchians (Buscalioni *et al.*, 2001; Pol *et al.*, 2009). Many authors have considered the presence of this combination of vertebral and palatal morphologies to imply that the eusuchian condition has evolved in parallel in several different neosuchian lineages, based on the underlying assumption that *Brillanceausuchus* is an atoposaurid, and therefore more basally positioned within Neosuchia (e.g. Brochu, 1999; Buscalioni *et al.*, 2001; Salisbury *et al.*, 2006). However, our preliminary results indicate that *Brillanceausuchus* belongs to Paralligatoridae (Figs 4B, 5, 6, 7), a clade most recently placed within Eusuchia (Turner, 2015). Therefore, the eusuchian condition might not be as homoplasious as previously regarded. Additional material assigned to *Brillanceausuchus* is currently being prepared, and comprises numerous skeletons (including skulls) preserved in three dimensions (J. Martin, pers. comm., 2015). We await the full description of this material before a comprehensive taxonomic assessment of *Brillanceausuchus* can be made, and preliminarily assign it to Paralligatoridae.

Preliminary emended diagnosis

(S1) proportionally long supratemporal fenestra, with anteroposterior length exceeding that of the orbit, and a skull length to supratemporal fenestra length ratio of <6.0 (5.36) (C29.0), and a skull width to supratemporal fenestra width ratio of 7.0 (C30.3); (S2) sinusoidal lateral nasal borders oblique to one another (C66.3), with abrupt widening adjacent to maxilla (C70.1); (S3) base of jugal postorbital process directed dorsally (C83.1); (S4) flat frontal dorsal surface (no longitudinal crest or periorbital rims) (C100.0); (S5) parietal–postorbital suture visible on the dorsal surface of the skull roof (C112.1) and within the supratemporal fenestra (C113.1); (S6) concavity at posterodorsal edge of squamosal–parietal contact (C117.1); (S7) lateral margins of squamosal and postorbital medially concave in dorsal view (C134.2), and dorsal surface of squamosal bevelled ventrally (C138.1), becoming unsculpted anteriorly (C148.1); (S8) squamosal posterolateral process elongate, distally tapered (C143.0) and depressed from skull table (C140.1); (S9) basisphenoid ventral surface mediolaterally narrower than basioccipital (C191.0), and basioccipital with large, well-developed bilateral tuberosities (C192.1); (S10) ventrolateral surface of anterior portion of dentary strongly mediolaterally compressed and flat (C215.0), with grooved ornamentation on external surface (C227.1); (S11) retroarticular process projects posteriorly and dorsally recurved (C242.3); (S12) posterior dentary teeth occlude medial to opposing maxillary teeth (C263.0); (S13) rounded and ovate dorsal osteoderm shape (C308.0).

PACHYCHEILOUSUCHUS TRINQUEI, ROGERS 2003

Pachycheilosuchus trinquei is known from a near-complete, disarticulated skeleton and partial skull from the Albian (Early Cretaceous) Glen Rose Formation of Erath County, Texas, USA. Initially described as a possible atoposaurid (Rogers, 2003), a position at the base of Atoposauridae was subsequently demonstrated in the analyses of Turner & Buckley (2008) and Pol *et al.* (2009). However, more recent analyses have placed *Pachycheilosuchus* outside of Atoposauridae, either within the basal eusuchian clade Hylaeochampsidae [Buscalioni *et al.*, 2011 (although note that this study used *Theriosuchus* as an outgroup, and included no definite atoposaurids); Turner & Pritchard, 2015], or just outside the eusuchian radiation (Adams, 2013; Narváez *et al.*, 2015). Rogers (2003) based his assignment to Atoposauridae primarily on the presence of a jugal with equally broad anterior and posterior processes, and the possession of procoelous presacral vertebrae. However, this jugal morphology is known in other neosuchians, including *Paluxy-*

suchus, as well as thalattosuchians (Adams, 2013). The presence of procoelous vertebrae could be more broadly distributed amongst non-neosuchian eusuchians than previously recognized, and full procoely is not definitively known amongst any atoposaurid species (see also Salisbury & Frey, 2001). Hylaeochampsid affinities are supported by the reinterpretation of a defining character state for Atoposauridae, pertaining to whether the bar between the orbit and supratemporal fenestra is narrow, with sculpting restricted to the anterior surface (Clark, 1994). Buscalioni *et al.* (2011) regarded this feature to be associated more broadly with 'dwarfism' (as initially proposed for *Pachycheilosuchus*) or immature specimens, and not a synapomorphy of Atoposauridae. *Pachycheilosuchus* is additionally unusual in the retention of an antorbital fenestra, to which the maxilla contributes (Rogers, 2003), which is similar to *T. guimarotae* (Schwarz & Salisbury, 2005) and *Alligatorellus bavaricus* (Tennant & Mannion, 2014).

The present study was not designed to resolve the phylogenetic placement of *Pachycheilosuchus*, except whether or not to include it within Atoposauridae. We support its exclusion from Atoposauridae, but cannot provide further comment on its placement within Hylaeochampsidae (Buscalioni *et al.*, 2011). It is unusual in that we recover *Pachycheilosuchus* in a more stemward position than Atoposauridae. We anticipate that inclusion of a broader range of atoposaurid specimens, *Theriosuchus* species, hylaeochampsids (including *Pietraroiasuchus ormezzanoii*; Buscalioni *et al.*, 2011), and additional paralligatorids within a larger Neosuchia-focussed data matrix, will help to resolve the position of *Pachycheilosuchus* and its clearly important role in the ascent of advanced neosuchians and Eusuchia.

WANNCHAMPSUS KIRPACHI ADAMS, 2014

The 'Glen Rose Form' has been commonly referred to in neosuchian systematics since it was first briefly mentioned and figured by Langston (1974). Comprising a skull and lower jaw from the Early Cretaceous (late Aptian) Antlers Formation of Montague County, Texas, USA, it was described as resembling the extant dwarfed crocodile *Osteolaemus tetraspis*, and Langston (1974) also noted similarities to *T. pusillus*. Subsequently, Adams (2014) erected *Wannchampsus kirpachi* for two skulls and postcranial material from the late Aptian (Early Cretaceous) Twin Mountains Formation of Comanche County (Texas, USA), and assigned the 'Glen Rose Form' to this taxon. Adams (2014) noted that the skull of *Wannchampsus* was similar to that of *T. pusillus*, sharing features such as medial supraorbital rims, and therefore prompting its inclusion in the present analysis and discussion here.

However, *Wannchampsus* is distinct from *T. pusillus* in: (1) the possession of an enlarged third maxillary tooth (instead present at the fourth position in *T. pusillus*); (2) the absence of an antorbital fenestra; (3) choanae with an anterior margin close to the posterior edge of the suborbital fenestra (whereas it is more anteriorly placed in *T. pusillus*); and (4) the definitive presence of procoelous dorsal and caudal vertebrae. We recovered *Wannchampsus* in a position close to *Shamosuchus* [Pol *et al.*, 2009; see also Adams (2014) and Turner (2015)], forming a paralligatorid clade with *Sabresuchus* and *Brillanceausuchus*.

KARATAUSUCHUS SHAROVI EFIMOV, 1976

Karatausuchus sharovi is known only from a single skeleton of a juvenile individual from the Late Jurassic (Oxfordian–Kimmeridgian) Karabastau Formation in southern Kazakhstan. It was considered to be an atoposaurid by Efimov (1976, 1988), but more closely related to paralligatorids by Efimov (1996). Storrs & Efimov (2000) argued that it was a relatively basal crocodyliform owing to the possession of amphiplatyan vertebral centra, and designated it as a questionable atoposaurid. It is generally similar to atoposaurids in being small, at only 160 mm in total anteroposterior body length, but possesses reduced dermal osteoderms, suggestive of a juvenile phase of growth. Intriguingly, Storrs & Efimov (2000) observed over 90 small, labiolingually compressed teeth within the jaws, a feature unique amongst crocodyliforms. It also possesses 46 caudal vertebrae, approaching the condition known for *Atoposaurus*. However, it has eight cervical vertebrae, placing it intermediate to *Protosuchus* (nine cervical vertebrae) and the majority of other atoposaurids (seven cervical vertebrae, with the exception of *Atoposaurus jordanii*, which appears to have six). *Karatausuchus* is similar to atoposaurids in that its skull length to orbit length ratio is relatively low, between 3.0 and 4.0 (3.37), but the other diagnostic features presented in this study for Atoposauridae cannot be assessed in the single known specimen. Therefore, we agree with Buscalioni & Sanz (1988) that *Karatausuchus sharovi* is currently too poorly known to be assigned to any family, including Atoposauridae, and regard it as an indeterminate crocodyliform. However, we still tentatively regard it as a valid taxon, owing to the high number of cervical and caudal vertebrae, and the possession of an anomalously high number of teeth.

HOPLOSUCHUS KAYI GILMORE, 1926

Gilmore (1926) originally recognized this taxon, based on a near-complete and articulated skeleton from the Late Jurassic Morrison Formation at Dino-

saur National Monument (Utah, USA), as a pseudosuchian archosaur. Subsequently, several authors assigned *Hoplosuchus kayi* to Atoposauridae (Romer, 1956; Kuhn, 1960; Steel, 1973), based on its overall size, and the possession of relatively large, posteriorly placed, and anterolaterally facing orbits. However, Buffetaut (1982) and Osmólska *et al.* (1997) regarded *Hoplosuchus* as more similar to protosuchians, but noted that its phylogenetic affinities remained uncertain. In their phylogenetic assessment of Atoposauridae, Buscalioni & Sanz (1988) concluded that *Hoplosuchus* is a 'protosuchian-grade' crocodyliform.

Our examination of this taxon could not confirm any definitive atoposaurid affinities. *Hoplosuchus* retains features present in basal crocodyliforms, including a small and circular antorbital fenestra, and a triangular lateral temporal fenestra that is nearly as large as the orbit. Potential autapomorphies for *Hoplosuchus* include: (1) a steeply posteriorly inclined quadrate; (2) the pterygoid bearing a descending process that is extensively conjoined in the mid-line anterior to the basisphenoid; and (3) a lower jaw lacking the external mandibular fenestra (Steel, 1973). *Hoplosuchus* has slender limbs, the dorsal armour is composed of paired oblong plates, and the caudal region is completely enclosed by dermal ossifications. A full revision of protosuchian crocodyliforms is currently underway (A. Buscalioni, pers. comm., 2014), and we await this before drawing any conclusions about the affinities of *Hoplosuchus*. Nonetheless, we exclude *Hoplosuchus* from Atoposauridae.

SHANTUNGOSUCHUS CHUHSIENENSIS YOUNG, 1961

Young (1961) initially identified this taxon, based on a near-complete skeleton and skull from the Early Cretaceous Mengyin Formation of Shandong Province, China, as an atoposaurid. This referral was subsequently supported by Steel (1973), who provided an emended diagnosis in his discussion of Atoposauridae. This included: (1) a triangular-shaped skull; (2) closely set teeth deeply implanted in independent alveoli; (3) seven cervical and 18 dorsal vertebrae; (4) short cervical vertebral centra; (5) relatively long dorsal vertebral centra; (6) a slightly shorter ulna than humerus; (7) the tibia significantly exceeding the femur in length; and (8) the forelimbs being proportionally long. However, Buffetaut (1981) and Buscalioni & Sanz (1988) both excluded *Shantungosuchus* from Atoposauridae. Wu *et al.* (1994) regarded much of the original interpretation of Young (1961) as incorrect, and revised *Shantungosuchus*, finding it to be more closely related to protosuchians than to atoposaurids. We concur with these authors and exclude *Shantungosuchus chuhsienensis* from Atoposauridae, supporting a basal position

within Crocodyliformes. However, we note that atoposaurids do share numerous metric features with protosuchians, reflecting their small body size and paedomorphic retention of basal morphologies.

INDETERMINATE REMAINS PREVIOUSLY ATTRIBUTED TO ATOPOSAURIDAE

Alongside these named taxa, numerous additional remains (primarily teeth) have been referred to Atoposauridae. These referrals have generally been based on the dental morphotypes that have been regarded as characteristic of *Theriosuchus* and, in stratigraphical order, comprise:

1. Teeth comparable to those of *Theriosuchus* were described from two localities from the early Bathonian of southern France (Kriwet *et al.*, 1997). Their referral to Atoposauridae was based on the presence of different morphotypes, and the teeth were thought to represent two distinct species. The first of these 'species' includes several dozen teeth (Larnagol, IPFUB Lar-Cr 1-20, and Gardies, IPFUB Gar-Cr 1-20). Amongst this set of teeth, Kriwet *et al.* (1997) identified four gradational morphotypes, based on their inferred positions in the dental arcade. However, their referral to Atoposauridae is based mainly upon them being heterodont, a feature that is not exclusive to either Atoposauridae or *Theriosuchus*. The second 'species' (Larnagol, IPFUB Lar-Cr 21-40) differs in possessing more prominent ridges on the crown surfaces (Kriwet *et al.*, 1997). These were referred to Atoposauridae by Kriwet *et al.* (1997) based on their inferred heterodonty; however, it cannot be determined whether or not all of these morphotypes belong to the same heterodont taxon, or two or more homodont or heterodont taxa. As atoposaurids are now considered to have a homodont (pseudocaniniform) dental morphology, these teeth cannot be referred to this group. They probably represent at least one (and probably more) small-bodied heterodont taxon, and therefore we consider them to be only referable to Mesoeucrocodylia indet. at present.
2. Small crocodyliform teeth were noted from the Bathonian 'stipite' layers of the Grand Causses (France) by Knoll *et al.* (2013) and Knoll & López-Antoñanzas (2014), and referred to an indeterminate atoposaurid. No further details were given, and therefore we regard these as representing indeterminate crocodyliforms pending further description of this material.
3. 1391 specimens comprising teeth, osteoderms, and a jaw fragment with teeth, as well as undescribed cranial and postcranial specimens, from

the Bathonian of Madagascar were referred to Atoposauridae (Flynn *et al.*, 2006). Based on the description and figures provided, these teeth appear to be pseudocaniniform in morphology, with well-developed mesial and distal carinae and a ridged enamel surface. Although they vary in shape and size (up to 10 mm in apicobasal length), none can be defined as pseudozipodont, zipodont, lanceolate, labiolingually compressed, or low-crowned. Based on the brief description, we cannot conclude that these teeth belonged to an atoposaurid, and therefore regard them as Mesoeucrocodylia indet., pending further description. Further examination of this material, along with remains identified as *Theriosuchus* sp. by Hadoumi *et al.*, [2016 (see above)], will be important in examining evidence for the presence of atoposaurids and *Theriosuchus* in the Middle Jurassic of Gondwana.

4. Thies & Broschinski (2001) described teeth from the Kimmeridgian of northern Germany as '*Theriosuchus*-like', but identified them as belonging to a small-bodied mesosuchian. Karl *et al.* (2006) provisionally referred these teeth to Mesoeucrocodylia indet., stating that their morphology is not known for any other crocodylomorph. We follow this decision of Karl *et al.* (2006), pending the direct comparison of this material with *Theriosuchus* and other small-bodied crocodyliforms.
5. A fragmentary set of specimens (IVPP V10613) from the Early Cretaceous of Inner Mongolia, including cranial and mandibular elements, were assigned to cf. *Theriosuchus* sp. (Wu *et al.*, 1996). However, the material might not be referable to a single individual or even taxon, as it was collected from across an extensive outcrop. The figured osteoderm (Wu *et al.*, 1996) is almost identical in overall morphology to *Alligatorellus* sp. (MB.R.3632; Schwarz-Wings *et al.*, 2011), including the position and extent of the lateral keel, and the near-absence of the anterior process of the ilium is similar to that of *Montsecosuchus*. The dorsal vertebrae possess the 'semi-procoelous' condition, similar to *Pachycheilosuchus*. The cranioquadrate canal is closed, and therefore IVPP V10613 can be excluded from Atoposauridae. The external mandibular fenestra is absent, similar to paralligatorids and *T. pusillus*. Additionally, the parietals bear a longitudinal median ridge on the dorsal surface, which Wu *et al.* (1996) used to link IVPP V10613 with *Theriosuchus*, although this feature is herein shown to be more widespread throughout Neosuchia. Wu *et al.* (1996) assigned IVPP V10613 to *Theriosuchus* based on the broad intertemporal region, raised supratemporal rims, and elevated medial orbital margin, but these features are found in numerous other taxa. Based on this combination of unusual characteristics, we think it likely that IVPP V10613 comprises more than one taxon, including at least one non-atoposaurid, non-*Theriosuchus* taxon, and one *Theriosuchus*-like taxon. We therefore regard IVPP V10613 as representing Neosuchia indet. pending further study of this material.
6. A skull fragment (NHMUK PV OR176) was assigned to *Theriosuchus* sp. from the Berriasian–Barremian of the Isle of Wight, UK (Buffetaut, 1983; Salisbury & Naish, 2011). Buffetaut (1983) assigned the posterior portion of a skull to *Theriosuchus* sp. based on comparison with the lectotype specimen of *T. pusillus* (NHMUK PV OR48216). It has a median longitudinal ridge on the parietal, similar to all specimens assigned to *Theriosuchus*, but also to *Alligatorium meyeri* and paralligatorids. The otoccipitals also meet dorsal to the foramen magnum, separating it from the supraoccipitals, a feature shared with *T. pusillus*, *T. guimarae*, and paralligatorids. The contact between the parietal and the squamosal on the dorsal surface, posterior to the external supratemporal fenestra, is also weakly developed, not forming the deep groove that characterizes *T. pusillus*. Therefore, we cannot determine whether this specimen represents *Theriosuchus* or another advanced neosuchian, and thus we consider this specimen to represent Neosuchia indet., pending its comparison to a broader set of neosuchians. In addition, Buffetaut (1983) assigned some procoelous vertebrae (the type of '*Heterosuchus valdensis*') from the Early Cretaceous of the UK to *Theriosuchus*. The presence of procoely indicates that it is not referable to *Theriosuchus* (see below), and it is instead regarded as an indeterminate neosuchian.
7. Indeterminate remains (primarily teeth) attributed to atoposaurids, usually referred to *Theriosuchus* based on heterodont tooth morphotypes, have been identified from numerous sites in the Aptian–Albian (late Early Cretaceous) of North America (e.g. Pomes, 1990; Winkler *et al.*, 1990; Cifelli *et al.*, 1999; Eaton *et al.*, 1999; Fiorillo, 1999; Garrison *et al.*, 2007; Oreska, Carrano & Dzikiewicz, 2013). However, because of our removal of *Theriosuchus* from Atoposauridae, it is more likely that these 'atoposaurid' remains represent other small-bodied taxa. We tentatively consider these remains to represent Mesoeucrocodylia indet., pending further study.

8. *Theriosuchus*-like teeth (MTM V 2010.243.1) were described from the Santonian of western Hungary (Iharkút), but conservatively referred to Mesoeucrocodylia indet (Ösi *et al.*, 2012). These teeth are lanceolate in crown morphology, and possess pseudozipodont carinae. Martin *et al.* (2014a) briefly mentioned the presence of two additional undescribed maxillae from the same locality, which together with the teeth might be referable to *Theriosuchus*. As we have recombined the Maastrichtian occurrences of '*Theriosuchus*' into a new taxon, *Sa. sympiestodon*, it is best that these teeth be regarded as Neosuchia indet., pending further analysis of this material and the possibly associated maxillae.
9. A *Theriosuchus*-like tooth was described from the Campanian–Maastrichtian of Portugal by Galton (1996). This tooth is distinct from *Theriosuchus*, possessing a fully zipodont morphology, and was suggested to instead belong to *Bernissartia* (Lauprasert *et al.*, 2011). However, here we consider it to belong to an indeterminate neosuchian based on the more widespread distribution of zipodont dentition.
10. The stratigraphically youngest material assigned to Atoposauridae comes from the middle Eocene Kaninah Formation of Yemen (Stevens *et al.*, 2013). This fragmentary material was tentatively designated as an atoposaurid, based on the presence of a zipodont tooth crown, a procoelous caudal vertebral centrum, a biserial osteoderm shield (although see below), and polygonal gastral osteoderms. However, none of these characteristics is unambiguously diagnostic under our revised definition of Atoposauridae, and this material probably comprises a small, advanced eusuchian, based on the presence of procoelous caudal vertebrae. The presence of a biserial osteoderm shield is usually considered diagnostic for Atoposauridae; however, our analyses demonstrate that this feature is more widespread amongst small-bodied neosuchians. Furthermore, the material from Yemen is too fragmentary to confidently infer that the osteoderm shield was biserial. Therefore, we regard this material as an indeterminate eusuchian pending the discovery of more complete and better preserved specimens.

DISCUSSION

PHYLOGENETIC RELATIONSHIPS AND SYSTEMATIC IMPLICATIONS

In all of our analyses, Atoposauridae is recovered in a basal position within Neosuchia, supporting several

recent analyses (e.g. Figueiredo *et al.*, 2011; Adams, 2014). Atoposauridae is a much more restricted clade than previously recognized, comprising *Atoposaurus* (*Atoposaurus jourdani* and *Atoposaurus oberndorferi*), *Alligatorellus* (*Alligatorellus bavaricus* and *Alligatorellus beaumonti*), and *Alligatorium meyeri*, and excluding *Theriosuchus*, *Montsecosuchus*, *Brillanceausuchus*, and '*Alligatorium*' *franconicum* (as well as taxa previously demonstrated to lie outside Atoposauridae, e.g. *Hoplosuchus*).

The majority of previous phylogenetic analyses focused on crocodyliforms or basal neosuchians generally only incorporated *Theriosuchus* (usually *T. pusillus*) and *Alligatorium meyeri*, with other atoposaurid taxa rarely included (e.g. Pol *et al.*, 2009; Adams, 2014). It is likely that this taxonomic under-sampling is at least partly responsible for the conflicting systematic positions previously recovered for Atoposauridae (Fig. 2). *Alligatorium meyeri* does not display any clear derived eusuchian features, whereas *Theriosuchus* has an unusual combination of derived, plesiomorphic, and 'transitional' character states. This is the most likely explanation for the results recovered here, in which specimens traditionally assigned to Atoposauridae are 'split', representing clusters of basal neosuchians (i.e. 'true' atoposaurids), advanced non-paralligatorid neosuchians (i.e. *Theriosuchus*), and paralligatorids (i.e. *Sabresuchus*; see below). Our results further demonstrate that *Theriosuchus* had become a taxonomic 'waste-basket', to which discoveries of teeth representing small-bodied heterodont crocodyliforms were consistently attributed. It is likely that some of these teeth (and other fragmentary remains) from the Northern Hemisphere instead represent a much more taxonomically diverse group of neosuchians, including paralligatorids.

EVOLUTIONARY HISTORY OF ATOPOSAURIDAE, THERIOSUCHUS, AND SABRESUCHUS

As a result of our systematic revision, Atoposauridae is now restricted to the Late Jurassic of western Europe. Specimens previously assigned to Atoposauridae from the Middle Jurassic of Europe and Gondwana cannot be assigned to this clade, and most likely represent taxa closely related to *Theriosuchus*, or other small-bodied mesoeucrocodylian forms. This more restricted view demonstrates that atoposaurids were highly specialized, with a small body size, semi-aquatic lifestyle, and unusual limb proportions. They also possessed a biserial dorsal osteoderm shield, and their dentition was homodont. Atoposauridae appear to have gone extinct at the Jurassic/Cretaceous (J/K) boundary (Fig. 10), as part of an overall drop in biodiversity in both marine and terrestrial crocodyli-form groups (Mannion *et al.*, 2015), an event that

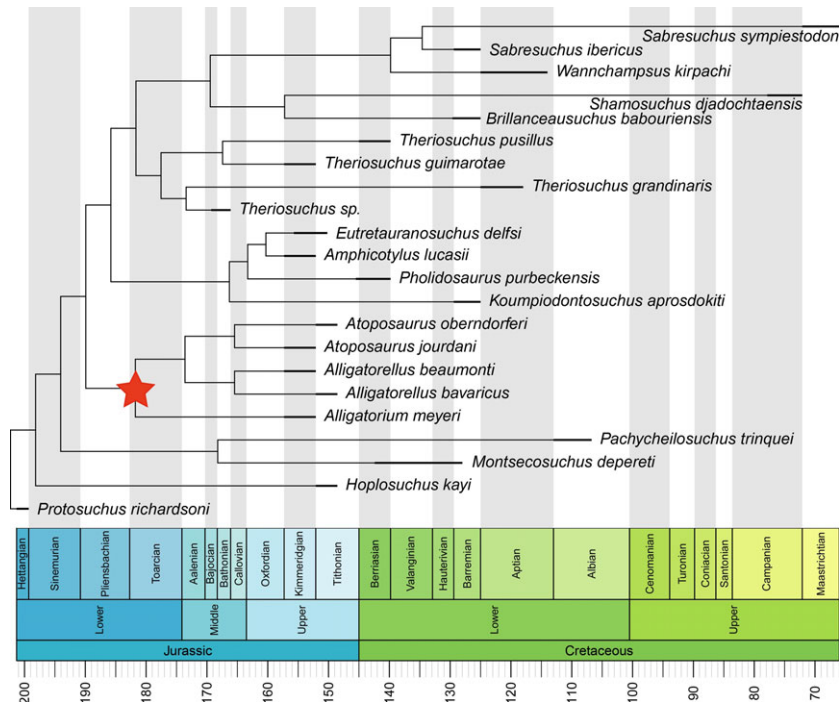


Figure 10. Time-scaled phylogeny showing the relationships of Atoposauridae to the other taxa analysed in the present study (based on the topology provided in Fig. 5A). Atoposauridae is marked with a red star. Created using the strap package (Bell & Lloyd, 2015), using the geoscalePhylo() function and an 'equal' time-scaling method.

was related to a major regression and the closing off of shallow marine basins in Europe across the J/K boundary (Hallam, 1986; Miller *et al.*, 2005; Smith & McGowan, 2007; Tennant, Mannion & Upchurch, 2016; Tennant *et al.*, in press).

The implications for our removal of *Theriosuchus* from Atoposauridae, and restriction of this genus to include just *T. guimarotae*, *T. grandinaris*, and *T. pusillus*, are complicated by the numerous referrals of teeth and poorly preserved fossils to *Theriosuchus* from across Laurasia (as well as less common referrals from Africa and North America). Therefore, although *Theriosuchus* appears to have been highly successful, spanning the Middle Jurassic–early Late Cretaceous, it was more temporally restricted than previously regarded, and did not persist into the latest Cretaceous (contra Martin *et al.*, 2010, 2014a). Based on our current understanding, *Theriosuchus* was present in the Middle Jurassic to early Late Cretaceous of Europe, the Middle Jurassic of North Africa, and the Early Cretaceous of Asia. The unequivocal presence of *Theriosuchus* in the Cretaceous of Asia supports the hypothesis of intermittent connections between western Europe and Asia through part of the Early Cretaceous (Baraboshkin, Alekseev & Kopaevich, 2003; Lauprasert *et al.*, 2011). Despite our taxonomic revisions, *Theriosuchus* remains one of the most temporally long-lived archosaurian lineages of all time, which could be attributed to its small body size and flexible morphology and ecology, or indicate that further splitting is required (pending the discovery of additional, well-preserved and complete specimens). Our results have recognized two separate and distinct clusters within *Theriosuchus*, possibly based on our more comprehensive sampling of definitive and putative atoposaurids, resulting in the formal erection of a new genus, *Sabresuchus*. Given the temporal distance between the two species of *Sabresuchus*, we would not be surprised if new material of either species (especially the fragmentary *Sa. sympiestodon*) led to the recognition of two distinct genera.

THE TRANSITION TO EUSUCHIA

Background

In this section, we follow the phylogenetic definition of Eusuchia provided by Brochu (1999): the last common ancestor of *Hylaeochampsia vectiana* and *Crocodylia* and all of its descendants. Along with *Wannchampsus* (including the 'Glen Rose Form'), *Theriosuchus* (and by association, atoposaurids) has been considered to be an important taxon in understanding the transition to Eusuchia, because of the relatively advanced development of their secondary palates (e.g. Joffe, 1967; Brochu, 1999; Buscalioni

et al., 2001; Pol *et al.*, 2009). A close relationship between *Theriosuchus* and Eusuchia is based on a number of features that are evident primarily in the type species *T. pusillus*, including: (1) an undivided external nares; (2) subdermal postorbital bars; (3) a lack of contribution from the frontals to the supratemporal fenestra; (4) relatively small internal supratemporal fenestrae; (5) development of the squamosal posterolateral process; (6) fully pterygoidean choanae within the secondary palate; (7) an enclosed eustachian canal; (8) procoelous vertebrae; and (9) a biconvex first caudal vertebra (Joffe, 1967; Rogers, 2003; Pol *et al.*, 2009; Turner, 2015; Turner & Pritchard, 2015). *Theriosuchus* shares combinations of these features with a range of more advanced neosuchians, particularly those assigned to Paralligatoridae (Turner, 2015; Turner & Pritchard, 2015). In addition, *T. guimarotae* shares a posteriorly opened cranioquadrate canal with *Sa. sympiestodon*, comparable to the paralligatorid *Shamosuchus* (Turner, 2015). As is also the case in the paralligatorids *Sabresuchus*, *Shamosuchus*, and *Wannchampsus*, the parietal of *T. pusillus* has a longitudinal midline ridge along its dorsal surface. Unfortunately, no specimens of *Alligatorellus*, *Alligatorium*, or *Atoposaurus* are preserved in a manner that would allow us to assess features such as the morphology of the choanae or the nature of presacral vertebral articulations, and we must await future examination of these specimens using 3D scanning techniques. Below, we discuss the evolution of several 'key' anatomical features that have played a significant role in discussions of the transition from basal neosuchians to Eusuchia.

Development of the squamosal posterolateral process

Basal crocodyliforms and mesoeucrocodylians do not possess a posterolateral process (or 'lobe') on the squamosal (e.g. Pol & Norell, 2004a). Atoposaurids and other basal neosuchians, such as *Paluxysuchus*, have a posterolateral lobe that is in the same horizontal plane as the dorsal surface of the skull table, with this lobe sculpted in the latter taxon (Adams, 2013). In goniopholidids, the process is short, narrow, and typically unsculpted (e.g. Averianov, 2000), and in notosuchians it is proportionally longer and rhombohedral-shaped (Buckley *et al.*, 2000), distinct from atoposaurids, *Theriosuchus*, or eusuchians. *Theriosuchus pusillus* and *T. guimarotae* possess this posterolateral process, but it is ventrally deflected and unsculpted in these taxa, similar to that of *Rugosuchus* and *Shamosuchus* (although in the latter taxon the 'lobe' is sculpted as in the rest of the dorsal surface of the cranial table; Turner, 2015). In paralligatorids (e.g. *Sa. ibericus*; see also Turner, 2015) and eusuchians (e.g. *Allodaposuchus*; Bus-

calioni *et al.*, 2001) the posterolateral process is posteroventrally confluent with the paroccipital process, enclosing the otic aperture, and in most Brevirostres the posterior margin of the otic aperture is invaginated (Brochu, 1999). *Sabresuchus ibericus* is also similar to the peirosaurid *Pepehsuchus* (Campos *et al.*, 2011) and to *Rugosuchus* (Wu *et al.*, 2001a) in that the 'lobe' is separated by a step from the main body of the squamosal, and remains unsculpted compared with the skull roof. The ventral deflection of the posterolateral process from the plesiomorphic horizontally orientated state seems to have been an important stage in the acquisition of this eusuchian morphology. In dyrosaurids (Wu *et al.*, 2001b; Jouve *et al.*, 2005a,b) and gavialoids (Jouve *et al.*, 2008), this process is ventrally directed and blade-like, forming the anterior face of the paroccipital process, and possibly relates to the transition to an aquatic lifestyle.

Development of the choanae

In crocodyliforms, the paired choanae have migrated from an anterior position within the primary palate (as in protosuchians), posteriorly through the ventral interorbital bar in neosuchians, and are positioned posteriorly within the pterygoids in eusuchians (e.g. Pol *et al.*, 2009). This posterior positioning of the choanae, with respect to the suborbital fenestrae, coupled with the complete ventral enclosure by the pterygoids, has long been regarded as diagnostic for Eusuchia (Benton & Clark, 1988; Norell & Clark, 1990; Clark & Norell, 1992; Buscalioni *et al.*, 2001; Salisbury *et al.*, 2006; Pol *et al.*, 2009).

Basal neosuchians, such as the goniopholidids *Amphicotylus* (Mook, 1942) *Eutretauranosuchus* (Smith *et al.*, 2010; Fig. 11A), and *Sunosuchus* (Wu *et al.*, 1996), possess the plesiomorphic choanal condition, with the anterior portion of the choanae receiving a significant contribution from the palatines. In their reconstruction of *T. guimarotae*, Schwarz & Salisbury (2005: fig. 5B) placed the anterior border of the choanae in a more posterior position than that of *T. pusillus*, closer to the posterior border of the suborbital fenestra. However, based on the specimens figured, the anterior edge of the choanae and the pterygoid flanges appear to be broken (Schwarz & Salisbury, 2005: fig. 4I), and it seems more likely that the choanae extended anteriorly to a position similar to *T. pusillus* (see our reconstruction in Fig. 11B). *Theriosuchus pusillus* possesses an intermediate choanal morphology, with the anterior border of the choanae placed anteriorly with respect to the posterior border of the suborbital fenestra (Fig. 11C). The paired choanae in *T. guimarotae* appear to be mediolaterally narrower than those of *T. pusillus*, and seem to be fully bifurcated by a mid-

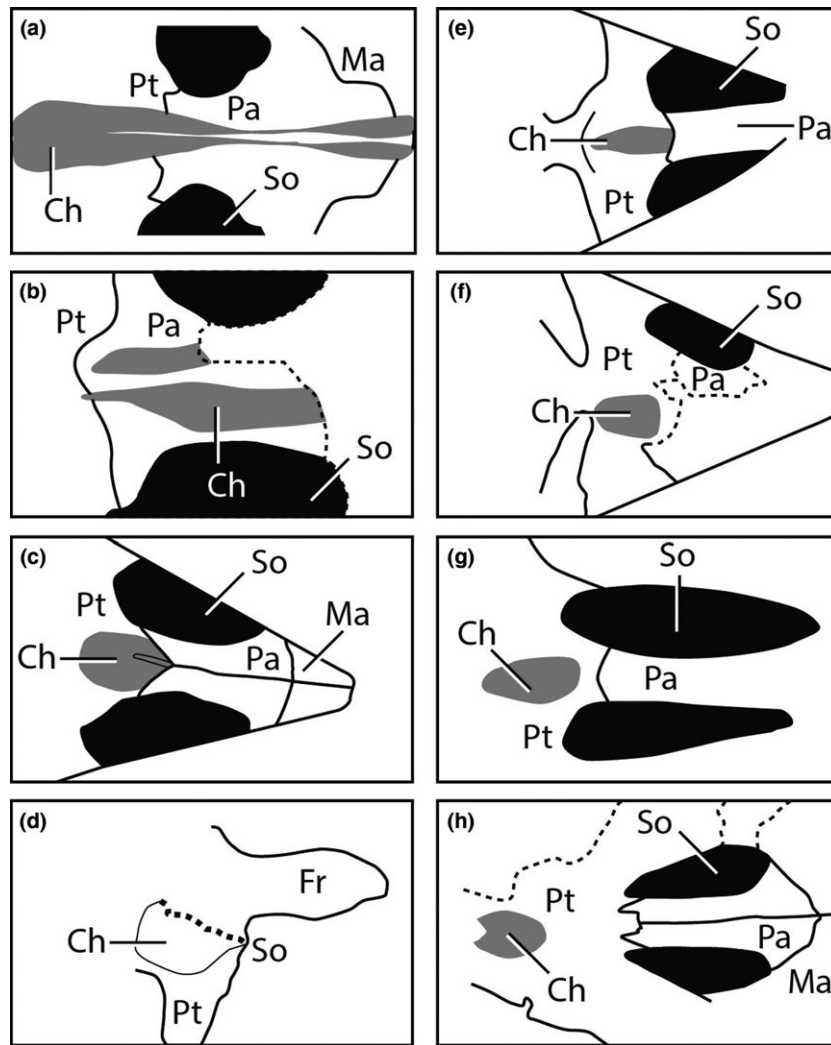


Figure 11. Relative positions of the choanae with respect to the main palatal bones in a range of neosuchian taxa. Citations are given where these reconstructions are based on in-text illustrations. (A) *Eutretauranosuchus delfsi* (Smith *et al.*, 2010); (B) *Theriosuchus guimarotae* (Schwarz & Salisbury, 2005); (C) *Theriosuchus pusillus*; (D) *Theriosuchus sympiestodon*; (E) *Wannchampsus kirpachi*; (F) *Shamosuchus djadochtaensis* (Pol *et al.*, 2009); (G) *Koumpiodontosuchus aprosdokiti* (Sweetman *et al.*, 2015); (H) *Hylaeochampsia vectiana* (Clark & Norell, 1992).

line pterygoidean septum, closer to the general morphology seen in goniopholidids (Mook, 1942; Wu *et al.*, 1996; Smith *et al.*, 2010) and notosuchians (Ortega *et al.*, 2000; Pol & Apesteguia, 2005). However, in *T. pusillus* only the anterior portion of the choanal groove appears to be septated. In *Sa. sympiestodon* (Martin *et al.*, 2010, 2014a; Fig. 11D) and other paralligatorids (e.g. *Rugosuchus*; Wu *et al.*, 2001a; Fig. 11E–G), the choanal groove is fully open and undivided, similar to *Hylaeochampsia* (Clark & Norell, 1992; Fig. 11H).

In both *T. guimarotae* and *T. pusillus*, the anterior edge of the choanae is formed by the posterior portion of the palatines, similar to *Rugosuchus* (Wu *et al.*, 2001a). However, in *T. guimarotae* the choa-

nae enter into the ventral lamina of the palatines (Schwarz & Salisbury, 2005), rather than just being bordered by it as in *T. pusillus*. In this respect, *T. pusillus* is similar to the advanced neosuchian *Khoratosuchus*, in which the palatines form only a point contact with the anterior margin of the fully open choanae (Lauprasert *et al.*, 2009). Furthermore, the palatines contribute to the lateral margins of the choanal opening in *T. pusillus*, forming a bar-like, overlapping contact with the pterygoids. This morphology in *T. pusillus* is distinct from more crownward taxa [e.g. *Brillanceausuchus*, *Gilchristosuchus* (Wu & Brinkmann, 1993), *Pietraroiasuchus* (Buscalioni *et al.*, 2001), *Shamosuchus* (Pol *et al.*, 2009), and *Wannchampsus* (Adams, 2014)], in which the

choanae are almost entirely enclosed by the pterygoids. The fact that this range of basal eusuchians (Turner, 2015; Turner & Pritchard, 2015) therefore appears to retain a palatine contribution to the anterior edge of the choana raises doubt over whether or not a fully pterygoidean choana is a synapomorphy for Eusuchia, rather than for a slightly more inclusive grouping. *Theriosuchus*, as the sister taxon to Paralligatoridae, exhibits a possible transitional morphology leading to the development of fully pterygoidean choanae. The sequence appears to involve the posterolateral widening of the choanal groove, coincident with migration to a point level with the posterior border of the suborbital fenestra, and reduction and eventual loss of the pterygoidean septum. This transition might have occurred in several lineages of advanced neosuchians (e.g. *Susisuchidae*, *Theriosuchus*), and it is possible that additional features of *Theriosuchus*, such as the relatively anterior positions of the mandibular tooth rows (distinct from eusuchians, dyrosaurids, and *Susisuchus*, in which the tooth rows extend posteriorly), are related to the formation of the eusuchian palatal morphology (Salisbury *et al.*, 2006).

Our understanding of the development of this morphology is potentially complicated by taxa such as *Isisfordia*, considered by Salisbury *et al.* (2006) to be a basal eusuchian, but placed outside of Eusuchia in many subsequent analyses (e.g. Turner & Pritchard, 2015). In this taxon, the choanae appear to have become fully enclosed by the pterygoids, with the anterior border located at the same level as the posterior edge of the suborbital fenestra (Salisbury *et al.*, 2006), which would indicate that the 'eusuchian' condition had evolved independently in at least one other lineage. However, Turner & Pritchard (2015) reassessed this morphology and re-interpreted *Isisfordia* as possessing a palatine-ptyergoid contact within the choanae, and therefore lacking completely pterygoidean choanae.

The neosuchian *Bernissartia* was also originally reported to have fully pterygoidean choanae based on its holotype (Buffetaut, 1975), but this specimen is poorly preserved, and Norell & Clark (1990) argued that it is unlikely that the choanae receive a pterygoidean contribution. However, the bernissartiid *Koumpiodontosuchus* does have a fully pterygoidean choana (Sweetman *et al.*, 2015: fig. 11G). Although the position of *Bernissartia* within Neosuchia is unstable [see Turner (2015) for both a eusuchian and non-eusuchian placement], the presence of fully pterygoidean choanae in its sister taxon *Koumpiodontosuchus* (Sweetman *et al.*, 2015) indicates that either: (1) it was secondarily lost in *Bernissartia*, or (2) that its presence in *Koumpiodontosuchus* represents an independent acquisition.

Regardless of whether the 'eusuchian' condition evolved more than once, it appears that the existing terminology does not describe the condition in basal eusuchians. As such, a more appropriately worded synapomorphy for Eusuchia could be the possession of posteriorly placed choanae, with an anterior margin medial to the posterior edge of the suborbital fenestra, often with a posterior contribution from the pterygoids and the complete loss of any sagittal pterygoidean septum.

Development of vertebral procoely

Norell & Clark (1990) identified the presence of procoelous presacral vertebrae to be diagnostic for Eusuchia. Based on a damaged anterior cervical vertebra referred to *T. pusillus* (NHMUK PV OR48723), Norell & Clark (1990) stated that *Theriosuchus* must have evolved procoely convergently (see also Clark & Norell, 1992), owing to the phylogenetic distance between *Theriosuchus* and Eusuchia. Both *Pachycheilosuchus* and *T. pusillus* have been described as possessing 'semi-procoelous' dorsal centra, in which there is a convex posterior condyle, with a central depression sometimes filled by a plug. This intermediate morphology between amphicoely and procoely has been hypothesized as an alternative 'route' to the fully procoelous condition (Rogers, 2003). The degree of procoely decreases posteriorly along the axial column in *Pachycheilosuchus*, with the posterior caudal vertebrae possessing thickened centrum margins, which might represent the development of an incipient articular condyle, inferred as the possible origin of caudal procoely (Rogers, 2003). Salisbury & Frey (2001) examined the paratype of *T. pusillus* using X-ray scanning, and found that all presacral vertebrae are gently amphicoelous (contra Norell & Clark, 1990), as is also the case for *T. guimarotae* (Schwarz & Salisbury, 2005). Despite this, Salisbury & Frey (2001) tentatively concluded that at least some of the cervical vertebrae of *T. pusillus* were procoelous, based on NHMUK PV OR48273, an interpretation followed in the scoring of this taxon in many data matrices (e.g. Turner, 2015). However, NHMUK PV OR48273 is embedded in a block comprising several fragments (including a poorly preserved mandibular ramus) that was not found in association with the type specimen, and it does not preserve diagnostic features that would allow it to be unequivocally assigned to *T. pusillus*. Furthermore, examination of this specimen could not confirm the presence of procoely, with the vertebra instead being amphicoelous, with thickened rims along the centrum articular surfaces. Therefore we reject the hypothesis that this specimen, and thus *T. pusillus*, possessed any procoelous vertebrae.

By contrast, the presacral vertebrae are procoelous in the paralligatorids *Wannchampsus* (Adams, 2014) and *Shamosuchus* (Pol *et al.*, 2009). *Pachycheilosuchus* appears to possess a vertebral morphology more similar to paralligatorids than *Theriosuchus*, and therefore more likely to be representative of a transitional morphology between the neosuchian and eusuchian conditions. *Isisfordia* and *Susisuchus* both possess weakly or ‘incipiently’ procoelous vertebrae (Salisbury *et al.*, 2006; Figueiredo *et al.*, 2011), which has been suggested to also represent a transitional morphology from the plesiomorphic amphicoelous condition (Turner & Pritchard, 2015).

Brinkmann (1989, 1992) described a series of fully procoelous caudal vertebrae, and others with a central depression (i.e. the ‘semi-procoelous’ condition), along with the material of *Sa. ibericus* and *Bernissartia* reported from the Uña locality. Although the direct association of the procoelous caudal vertebrae with either of these taxa cannot be confirmed (Salisbury & Frey, 2001), Brinkmann (1989) stated that this vertebral series was found alongside the skull elements referred to *Sa. ibericus*. Based on the size of these vertebrae and the purported presence of a form of procoely in *T. pusillus* (Clark, 1986; Salisbury & Frey, 2001), coupled with the absence of this condition in *Bernissartia* (although some specimens of *Bernissartia* might have procoelous caudal vertebrae; Norell & Clark, 1990), Rogers (2003) also deemed it more probable that the fully procoelous vertebrae belong to *Sa. ibericus* (Brinkmann, 1989). However, their argument relies on the congeneric status between *T. pusillus* and *Sa. ibericus*, which we do not support here. Goniopholidids, also known from the Uña region, can be excluded from ‘ownership’ of these vertebrae, because they have exclusively amphicoelous vertebrae (Brinkmann, 1989). *Unasuchus reginae*, also found at the Uña locality, is only known from fragmentary cranial and mandibular material, and its affinities are uncertain within Neosuchia (Brinkmann, 1992). The semiprocoelous vertebrae are from a larger individual than that of the type of *Sabresuchus*, and might be referable to *Unasuchus* or an additional taxon. We have incorporated this uncertainty over the vertebral morphology of *Sa. ibericus* into our data matrix, electing not to code this taxon for the presence of procoely or a biconvex first caudal vertebra (see below). Nonetheless, this taxon groups with paralligatorids (which all show a degree of procoely), and therefore is the most likely candidate taxon at Uña for the series of procoelous vertebrae. If this is correct, the entire vertebral column of *Sa. ibericus* would appear to show some form of procoely, and supports the findings of our study that *Sabresuchus* is closely related to eusuchians.

Pending the discovery of associated remains, we agree with Brinkmann (1989) and Salisbury & Frey (2001) that procoely, including semiprocoely, cannot currently be determined for *Sabresuchus*. Nevertheless, it seems likely that well-developed vertebral procoely only evolved once within the lineage leading to Eusuchia. However, the presence of weak procoely in the vertebrae of *Susisuchidae* (*Isisfordia* + *Susisuchus*; Turner & Pritchard, 2015) and semiprocoely in *Pachycheilosuchus* indicates that a number of neosuchian lineages developed some form of incipient procoely.

Biconvex first caudal vertebra

The first caudal vertebra of *Pachycheilosuchus* is biconvex (Rogers, 2003), a feature also proposed for *Brillianceausuchus* (Michard *et al.*, 1990), but not confirmed through direct observation of the holotype specimen. A biconvex first caudal vertebra has also been documented for *T. guimarotae* (Schwarz & Salisbury, 2005), *T. pusillus* (Salisbury & Frey, 2001), and probably *Sa. ibericus* (Brinkmann, 1989, 1992; Salisbury & Frey, 2001; although see above regarding association). Moreover, a biconvex first caudal vertebra is a feature of all eusuchians (Salisbury *et al.*, 2006), and its development is probably an important morphological aspect of the neosuchian–eusuchian transition. Whether we code a biconvex first caudal vertebra as present or absent for *Sa. ibericus* has no effect on the topology of our tree, irrespective of whether or not we exclude *Pachycheilosuchus a priori*. This indicates that if a biconvex first caudal vertebra is indeed present in *Brillianceausuchus*, along with *Pachycheilosuchus* (Rogers, 2003) and *Theriosuchus* (Salisbury & Frey, 2001; Schwarz & Salisbury, 2005), then it is likely to have been independently acquired at least twice. The acquisition of this biconvex first caudal vertebra in *Theriosuchus* and other taxa close to the eusuchian radiation might have been important in the initiation of procoely in advanced neosuchians, and the differential acquisition of a concave posterior centrum condyle in different regions of the axial column.

CONCLUSION

Atoposauridae is now considered to be a much more restrictive clade of basal neosuchians, comprising only *Atoposaurus jourdani*, *Atoposaurus oberndorferi*, *Alligatorellus beaumonti*, *Alligatorellus bavaricus*, and *Alligatorium meyeri*. Based on this more exclusive taxonomic grouping, atoposaurids were restricted to the Late Jurassic of western Europe, and went extinct at the J/K boundary. We exclude *Theriosuchus* from Atoposauridae, recovering this genus as polyphyletic. *Theriosuchus* is a more crownward neosuchian than

atoposaurids, and is here restricted to *T. pusillus* (the type species), *T. guimarotae* (Schwarz-Wings *et al.*, 2011), and *T. grandinaris* (Lauprasert *et al.*, 2011). In addition, a specimen described by Young *et al.* (2016) from the Middle Jurassic of the UK might represent a distinct species of *Theriosuchus*. *Theriosuchus* is known from the Middle Jurassic–early Late Cretaceous, with occurrences from Europe, Asia, and North Africa. '*Theriosuchus*' *ibericus* and '*T.*' *sympiestodon* are recombined under the new genus denomination, *Sabresuchus* gen. nov. Along with *Brillanceausuchus*, *Sabresuchus* is recovered as a paralligatorid.

'*Alligatorium*' *franconicum* is recovered outside of Atoposauridae, and is not referable to *Alligatorium*, but instead appears to be more closely related to longirostrine forms, such as bernissartiids and coelognathosuchians. As the only specimens referable to this taxon are lost or destroyed (Wellnhofer, 1971), we do not provide a new genus name, pending the discovery of new material. *Montsecosuchus* cannot be unequivocally confirmed to be an atoposaurid, and in the majority of our analyses we find it to cluster with *Pachycheilosuchus*.

Our revised placements of Atoposauridae and *Theriosuchus* have important implications for the transition from Neosuchia to Eusuchia. *Theriosuchus* exhibits one possible transitional route to the development of a pterygoidean-bound choana, involving the posterior migration and posterolateral widening of the choanal groove, with the reduction of the pterygoidean septum. No definitive atoposaurid possesses procoelous vertebral centra, and no specimen ascribed to *Theriosuchus* can be demonstrated to possess this feature. Therefore, current evidence suggests that full vertebral procoely only evolved once within the lineage leading to Eusuchia.

Future research on the systematic placement of Atoposauridae, *Theriosuchus*, and Paralligatoridae within Neosuchia will need to incorporate a wider set of taxa into phylogenetic analyses, such as the basal neosuchian *Stolokrosuchus lapparenti* (Larsson & Gado, 2000), hylaeochampsids [e.g. *Paluxysuchus newmani* (Adams, 2013), *Hylaeochampsia vectiana* (Clark & Norell, 1992), and *Pietraroiasuchus ormezzanoi* (Buscalioni *et al.*, 2011)], *Bernissartia fagesii*, and additional paralligatorids [e.g. *Batrachomimus pastosbonensis* (Montefeltro *et al.*, 2013) and *Rugosuchus nonganensis* (Wu *et al.*, 2001a)]. These additions should help to develop a clearer understanding of the Neosuchia–Eusuchia transition.

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Note

* Note that at the time of visit, the collections from the MNHL were housed at the Centre de Conservation in Lyon, but remained under the same accession numbers.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Appendix S1 Full character list for phylogenetic analysis.

Appendix S2 Character state codings for taxa used for phylogenetic analysis.

APPENDIX 1

CHARACTER LIST

Sources for characters are provided, and new characters indicated. Where characters have been modified, details are given at the end of the character statement. All characters have been reformatted to a standardized notation to be as explicit as possible about the morphology. New characters are indicated, although some of these are the product of splitting previously used characters, or modified from statements in previously published works. Additional references have been incorporated into the main reference list above.

The following 47 characters are ordered: 3, 7, 10, 13, 20, 23–30, 33, 37, 56, 58, 84, 89, 99, 100, 103, 115, 119, 128, 133, 150, 153, 175, 179, 183, 203, 204, 217, 246, 264–266, 272, 285, 288–291, 300, 305, 321.

Cranial characters

1. Dorsal cranial bones (skull roof, cranial table), external surface: smooth (0); ornamented (1) (Clark, 1994).
2. Dorsal cranial bones (skull roof, cranial table), external surface: slightly grooved (0); heavily ornamented with deep pits and/or grooves (1); with shallow pits (2) (Clark, 1994) (character state 2 added here; added 'or' to state 1).
3. Snout, external surface, sculpting: absent (0); present but to a lesser degree than cranial table (1); present, as prominent as on cranial table (2) (Gasparini *et al.*, 2006) (character state 1 added here; added 'as prominent as on cranial table' to character state 2) [ordered].
4. Rostrum, dorsal projection posterior to the external nares, relative to remainder of rostrum: absent, rostrum straight or low (0); rostrum upturned (1) (Andrade *et al.*, 2011) (added 'posterior to the external nares, relative to remainder of rostrum').
5. Skull, lateral expansion at orbits relative to rostrum: gradual (0); abrupt (1) (Clark, 1994) (added 'lateral' and 'relative to rostrum').
6. Snout, lateral contour, in dorsal view: straight (0); sinusoidal ('festooned') (1) (Ortega *et al.*, 2000).
7. Snout, overall proportions: narrow oreinrostral (tall and domed) (0); nearly tubular (1); platy-rostral (broad and flat) (2) (Clark, 1994; *sensu* Rayfield & Milner, 2008) [ordered].
8. Snout, profile of dorsal edge in lateral view (anterior to cranial table): concave (0); convex (1); approximately straight (2) (Sweetman *et al.*, 2015).
9. External nares, orientation: facing anterolaterally (0); facing dorsally (1); facing anterodorsally (2) (Clark, 1994) (character state 2 added here).
10. External nares: completely divided by a septum (0); partially divided posteriorly (1); confluent, no indication of a septum (2) (Clark, 1994) [ordered].
11. Orbit, orientation: facing anterolaterally (0); facing fully laterally (1) (Wilkinson, Young & Benton, 2008).
12. Orbit, anterolateral border: continuous margin (0); develops as a small groove into pre-orbital elements (1) (new character).
13. External antorbital fenestra: large, >0.5 times the size of the orbit (0) small, ≤0.5 times the size of the orbit (1); absent (2) (Andrade *et al.*, 2011) (changed to a multistate, adding character states 0 and 1 to replace character state 'present') [ordered].
14. Antorbital fenestra, shape: rounded or dorsoventrally high (0); dorsoventrally low and anteroposteriorly elongate, slit-like (1) (Gasparini *et al.*, 2006).
15. External supratemporal fenestra: present (0); absent (1) (Ortega *et al.*, 2006).
16. External supratemporal fenestra: perforated (0); imperforated (1) (new character, adapted from Joffe, 1967).
17. External supratemporal fenestra, shape: square to subrectangular (0); circular to subcircular (1); mediolaterally narrow and slit-like (2) (Andrade *et al.*, 2011) (deleted character state 'triangular, converging medially'; added character state 2).
18. External supratemporal fenestra, maximum anteroposterior length: equal to or shorter than orbits (0); longer than orbits (1) (Clark, 1994) (added 'maximum' to refine character).
19. Intertemporal mediolateral width (minimum between supratemporal fenestrae), relative to interorbital mediolateral width (minimum

- between orbits): intertemporal region broader (0); intertemporal region equal or narrower (1) (new character).
20. Lateral temporal fenestra in lateral view, size proportional to orbit in dorsal view: small to absent, no more than 20% of the area of the orbit (0); more than 20 to <50% of the area of the orbit (1); area is larger than 50% of the area of the orbit (2) (Andrade *et al.*, 2011) (character state 1 added here) [ordered].
 21. Lateral temporal fenestra, orientation: faces laterally (0); faces dorsolaterally (1) (Andrade *et al.*, 2011).
 22. Lateral temporal fenestra, shape: triangular (0); elliptical to subpolygonal (1) (Ortega *et al.*, 2000).
 23. Suborbital fenestra: small, <50% of orbital area (0); between 50% and the same size as the orbit (1); larger than the orbit (2) (Andrade *et al.*, 2011) (quantified state 1) [ordered].
 24. Intermandibular angle (degrees): lower than 40° (0); 40–45° (1); 46–50° (2); >50° (3) (new character) [ordered].
 25. Skull length : skull width, ratio: <2.0 (0); 2.0 to <2.5 (1); 2.5 or greater (2) (new character) [ordered].
 26. Skull length : snout length, ratio: <2.0 (0); 2.0 to <2.5 (1); 2.5 to <3.0 (2); 3.0 or greater (3) (new character) [ordered].
 27. Skull length : orbit length, ratio: <3.0 (0); 3.0 to <4.0 (1); 4.0 to <5.0 (2); 5.0 or greater (3) (new character) [ordered].
 28. Skull width : orbit width, ratio: <2.5 (0); 2.5 to <3.5 (1); 3.5 or greater (2) (new character) [ordered].
 29. Skull length : supratemporal fenestra length, ratio: <6.0 (0); 6.0 to <7.0 (1); 7.0 to <8.0 (2); 8.0 or greater (3) (new character) [ordered].
 30. Skull width : supratemporal fenestra width, ratio: <3.0 (0); 3.0 to <5.0 (1); 5.0 to <6.0 (2); 6.0 or greater (3) (new character) [ordered].
 31. Premaxilla, maximum mediolateral width of paired premaxillae relative to that of the rostrum at the level of alveoli 4 or 5: premaxillae equal or narrower (0); rostrum narrower (1) (Jouve, 2009).
 32. Premaxilla, anterior to nares: narrower than, or equal to, twice the anterior nasal mediolateral width (0); broader than twice the anterior nasal width (1) (Clark, 1994) (quantified).
 33. Premaxilla–maxilla, distance between the anterior tip of the snout and the anterior-most position of the premaxilla–maxilla suture in dorsal view, relative to the distance between the anterior-most position of the premaxilla–maxilla suture and the posterodorsal extremity of the premaxilla in dorsal view: distance between the tip of the snout and the anterior-most position of the premaxilla–maxilla suture larger (0); distances approximately equal (1); distance between the anterior-most position of the premaxilla–maxilla suture and the posterodorsal extremity of the premaxilla larger (2) (Jouve, 2004) [ordered].
 34. Premaxilla–maxilla suture, small foramen in lateral surface (not for large mandibular teeth): absent (0); present (1) (Pol, 1999).
 35. Premaxilla, projection of the internarial bar relative to the main body of premaxilla and narial opening: does not project anterior to the main body of the premaxilla (0); strongly projected anteriorly from narial opening, extending anterior to main body of maxilla (1) (Andrade *et al.*, 2011).
 36. Premaxilla, participation in internarial bar: forming at least the anterior half (0); with little participation (1) (Clark, 1994) (replaced ‘ventral’ with ‘anterior’ in character state 0).
 37. Premaxilla, ventral edge relative to maxilla: lower than ventral edge of maxilla, with dorsal contour of anterior part of dentary strongly concave to accommodate (0); at same height as ventral edge of maxilla (1); premaxilla ventral edge dorsal to maxilla (2) (Ortega *et al.*, 2000) (character state 2 added here) [ordered].
 38. Premaxilla, perinarial crests: absent (0); present as well-defined and distinct ridges, cornering the lateral to posterior borders of the naris (1) (Andrade *et al.*, 2011).
 39. Premaxilla, notch on lateral edge of external nares: absent (0); present on the dorsal half of the lateral edge of the external nares (1) (Pol, 1999).
 40. Premaxilla, perinarial fossa: absent (0); present (1) (Pol & Apesteguía, 2005).
 41. Premaxilla, postnarial fossa: absent (0); present (1) (Andrade *et al.*, 2011).
 42. Premaxilla–maxilla, suture: confluent ventrally (0); opened contact on ventral edge of rostrum (1) (Clark, 1994).
 43. Premaxilla–maxilla contact, orientation in dorsal view, whether or not posterodorsal process is present: anteromedially directed (0); posteromedially directed (1) (Schwarz & Salisbury, 2005) (added ‘whether or not posterodorsal process is present’).
 44. Premaxilla, posterodorsal process: absent (0); present, extending posteriorly and wedging between maxillae and nasals (1) (Pol, 1999).
 45. Premaxilla, orientation of anterior alveolar margin: vertical (0); out-turned (1) (Serenio *et al.*, 2001) (character state 1 modified from ‘inturned’).

46. Maxillae, posterior palatal branches anterior to palatines: do not meet (0); meet (1) (Clark, 1994).
47. Maxilla–premaxilla, suture in palatal view medial to alveolar region: sinusoidal, posteromedially directed on lateral half and anteromedially directed along medial region (0); posteromedially directed (1) (Pol, 1999) (character states ‘anteromedially directed’ and ‘premaxillae–maxillae suture U-shaped’ removed).
48. Maxilla–premaxilla, lateral fossa excavating alveolus of last premaxillary tooth: absent (0); present (1) (Larsson & Sues, 2007).
49. Maxilla, depression on posterolateral surface, laterally positioned: absent (0); present (1) (Wu *et al.*, 1997) (added ‘on posterolateral’).
50. Maxilla, depression on anterolateral surface, medially positioned: absent (0); present (1) (new character).
51. Maxilla, lateral surface of jugal process (posterior portion): heavily striated (0); ornamented, like rest of rostrum (1); smooth (2) (new character).
52. Maxilla, ventral edge in lateral view: straight or convex (0); sinusoidal (1) (Ortega *et al.*, 2000).
53. Maxilla and premaxilla, general shape of external surface: single plane facing laterally (0); with ventral region facing laterally and dorsal region facing dorsolaterally (1) (Pol, 1999).
54. Maxilla, presence of occlusal pit for reception of enlarged dentary tooth anterior to dental arcade (or M2, M stands for ‘maxillary alveolus’): present (0); absent (1) (new character, adapted from Martin *et al.*, 2014a,b).
55. Maxilla, evaginated alveolar edges: absent (0); present (1) (Gasparini *et al.*, 2006).
56. Maxilla, lateral surface, unsculpted region along alveolar margin: absent (0); present (1) (Wu & Sues, 1996).
57. Maxilla, sculpturing of palatal surface: absent, palatal surface smooth (0); present anteriorly, absent posteriorly (1); present throughout, palatal surface ornamented with ridges (2) (Ortega *et al.*, 2000) [ordered].
58. Maxilla, foramen on palatal surface, dorsomedial to enlarged fifth tooth: absent (0); present (1); develops elongate groove (2) (new character) [ordered].
59. Maxillary teeth, dental implantation, middle teeth: confluent, located in dental groove (0); in isolated alveoli (1) (new character).
60. Maxillary teeth, dental implantation, posterior teeth: confluent, located in dental groove (0); in isolated alveoli (1) (new character).
61. Maxilla, palatine process: absent (0); present, next to the anterior border of suborbital fenestrae (1) (Andrade & Bertini, 2008).
62. Maxilla–nasal, suture, orientation with respect to snout lateral margins: parallel (0); oblique (1) (new character).
63. Nasal, participation in dorsal margin of external nares: present (0); absent (1) (new character).
64. Nasal participation in margins of external nares: present posteriorly (0); present posteriorly and medially (1) (Clark, 1994).
65. Nasals: paired and unfused (0); partially or completely fused (1) (Gasparini *et al.*, 2006) (added ‘and unfused’ to character state 0).
66. Nasal, lateral border posterior to external nares: concave (0); straight (1); convex (2); sinusoidal (3) (character states 2 and 3 added) (Pol, 1999).
67. Nasal, lateral edges: subparallel (0); oblique to one another, converging anteriorly (1) (Pol, 1999).
68. Nasal, participation in antorbital fenestra: present (0); absent (1) (Ortega *et al.*, 2000).
69. Nasal, posterior portion of the dorsal surface: anteroposteriorly crenulated (0); smooth or sculpted as rest of rostrum (1) (new character).
70. Nasals, posterior mediolateral widening adjacent to the maxilla (anterior to contact with periorbital elements): abrupt (0); gradual (constant) (1); (new character, adapted from Laurasert *et al.*, 2011).
71. Nasal–lacrimal contact: present (0); absent (1) (Clark, 1994).
72. Nasal–lacrimal contact: along medial surface of lacrimal (0); lacrimal forms a point contact with nasal (1) (Clark, 1994) (changed character state 1 from ‘along medial and anterior surfaces of lacrimal’ to ‘forms a point contact with nasal’).
73. Nasal, posterior tips of nasals: converge along the sagittal plane (0); separated by anterior projection of frontals (1) (Ortega *et al.*, 2000).
74. Nasal, posterior portion and anterior portion of frontal, midline anteroposterior depression: absent (0); present (1) (Montefeltro, Larsson & Langer, 2011).
75. Lacrimal, total anteroposterior length relative to anteroposterior length of prefrontal: longer (0); shorter or equal to (1) (Brochu, 1999) (combined states 1 and 2).
76. Lacrimal, shape: anteroposteriorly longer than mediolaterally broad (0); as anteroposteriorly long as mediolaterally broad (1) (Sereno & Larsson, 2009).
77. Lacrimal, posterior extent and relationship with jugal: extending posteroventrally, widely contacting jugal (0); tapering posteroventrally, does not contact jugal or only point contact with jugal (1) (Zaher *et al.*, 2006).

78. Lacrimal and jugal, anterior margins: confluent, with no notch at the anterior contact (0); jugal edge convex, producing an anterior notch at contact (filled with maxilla) (1) (Larsson & Sues, 2007).
79. Jugal, anterior extension below orbit, in dorso-lateral view: does not extend beyond anterior margin of orbit (0); extends beyond anterior margin (1) (Pol, 1999).
80. Jugal, dorsoventral depth of orbital portion in relation to infratemporal portion: almost the same to less than twice the depth (0); orbital portion twice the depth of the infratemporal portion (1) (Clark, 1994) (added 'to less than twice the depth' to character state 0).
81. Jugal, foramen on the lateral surface near the anterior margin: absent (0); present (1) (Zaher *et al.*, 2006).
82. Jugal, anterior process length relative to infratemporal fenestrae anteroposterior length: 1.0 or less times the length (0); longer than 1.0 times the length (1) (Larsson & Sues, 2007) (changed character states 0 and 1 to define state boundary ratio).
83. Jugal, orientation of base of postorbital process: directed posterodorsally (0); directed dorsally (1) (Pol, 1999).
84. Jugal, location of postorbital process relative to main jugal body: anteriorly placed (0); in the middle (1); posteriorly positioned (2) (Pol, 1999) [ordered].
85. Jugal portion of postorbital bar, relative to lateral surface of jugal: flush with lateral surface of jugal (0); inset (1) (Ortega *et al.*, 2000).
86. Jugal, anterior fossa: bordered by ornamented ridge (0); continuous with lateral surface (1) (new character).
87. Jugal, anteroposterior ridge on lateral surface below infratemporal fenestrae: absent (0); present (1) (Pol & Norell, 2004b).
88. Jugal-ectopterygoid, suture ridge: absent (0); present (1) (Montefeltro *et al.*, 2011).
89. Preorbital elements, anterior palpebral bone: no notable depression or projection (0); marked depression, developing into an incipient lateral projection (1); marked depression forming a prominent lateral projection for the support of the anterior palpebral (2) (Serenio & Larsson, 2009) (character state 0 added here) [ordered].
90. Prefrontal, lateral development: reduced, no notable lateral projection (0); enlarged, extending laterally or posterolaterally over orbit (1) (Gasparini *et al.*, 2006) (changed to 'laterally or posterolaterally' in character state 1).
91. Prefrontal, anterior morphology: tapers anteriorly to a point (0); anteriorly broad (1) (new character).
92. Prefrontal-frontal sutures, form paired dorsal crests: absent (0); present (1) (Pol & Powell, 2011).
93. Prefrontal-lacrimal suture, crest: absent (0); present, situated anterior to orbit (1) (Andrade *et al.*, 2011) (changed 'dorsal' to 'anterior' in character state 1).
94. Prefrontal and lacrimal around orbits: forming flat rims (0); evaginated, forming elevated rims from the dorsal surface of the skull (1) (Gasparini *et al.*, 2006).
95. Prefrontal pillars (ventral process): not contacting palate (0); contacting palate (1) (Clark, 1994).
96. Frontals: unfused (0); fused (1) (Clark, 1994) (changed to indicate degree of fusion).
97. Frontal, mediolateral width of paired frontals between orbits: broader than nasals (0) equal or narrower than nasals (1) (Clark, 1994) (added 'equal or' to character state 1).
98. Frontals, mediolateral width between orbits: narrower than posterior end (posterior end flares laterally posterior to orbits) (0); equal width or broader than posterior end (1) (new character, adapted from Sweetman *et al.*, 2015).
99. Frontal, morphology of anterior-most border of anterior process: truncated (0); wedge-like (1); bifurcated (2) (character state 2 added here) (Andrade *et al.*, 2011) [ordered].
100. Frontals, dorsal surface: flat (0); with anteroposterior ridge along midline suture (1) (Clark, 1994) (added 'along midline suture' to character state 1) [ordered] [note: see Schwarz & Salisbury (2005) for discussion of how this character relates to ontogeny].
101. Frontal, dorsal anteroposterior ridge(s): restricted to the posterior portion (0); restricted to median portion (1); restricted to anterior portion (2); occupy entire length of frontal (3) (Montefeltro *et al.*, 2011) (character state 3 added).
102. Frontal, anterior extension of anterior margin: level with, or anterior to, the orbits (0); does not reach the anterior margin of the orbits (1) (Andrade *et al.*, 2011).
103. Frontal, participation in orbit border: forming great part of posterior, medial, and anterior (or anteromedial) regions (0); restricted to posterior and posteromedial region (1); restricted to medial margin (2) (Montefeltro *et al.*, 2013) (character state 'restricted to the posterior region' removed; character states 1 and 2 added here) [ordered].
104. Frontal, transverse ridge crossing anteromedial to the orbits: absent (0); present (1) (Pol *et al.*, 2009).

105. Frontal, participation in supratemporal fenestra: absent (0); present (1) (new character).
106. Frontal, participation in supratemporal fenestra: anteromedially (0), anteriorly only (1) (new character).
107. Frontal, anterior ramus with respect to the anterior tip of the prefrontal: does not extend past the anterior tip (0); extends beyond the anterior tip of the prefrontal (1) (Sereno *et al.*, 2001) (modified states from 'ending anteriorly' and 'ending posteriorly' to remove potential gap between states).
108. Frontal, lateral margin relative to the skull surface: flush (0); elevated, forming ridged orbital margins (1) (Brochu, 1999).
109. Frontal, anterior process constriction with respect to main body of frontal, excluding sagittal projection into nasals anterior to orbits: absent, lateral edges parallel to subparallel (0); present, anterior portion mediolaterally constricted, with convergent lateral margins (1) (Montefeltro *et al.*, 2013) (added 'with respect to main body of frontal, excluding sagittal projection into nasals anterior to orbits').
110. Postorbital, anterolateral process: absent or poorly developed (0); well-developed, long and distally acute (1) (Clark, 1994).
111. Postorbital-jugal contact, configuration: postorbital medial to jugal (0); postorbital dorsal to jugal (1) (Clark, 1994).
112. Parietal-postorbital suture: absent from the dorsal surface of the skull roof (0); present on the dorsal surface of the skull roof (1) (Clark, 1994) (character broken down into characters 107–109).
113. Parietal-postorbital suture: absent from the supratemporal fossa (0); present within the supratemporal fossa (1) (new character).
114. Parietal-postorbital suture within the supratemporal fossa: present within the ventral region (0); broadly present (1) (new character).
115. Parietal, dorsal surface: projects dorsally, relative to the skull roof (0); same level as squamosal (1); depressed relative to the squamosal (2) (Andrade *et al.*, 2011) (character state 2 added here) [ordered].
116. Parietal, posterior region dorsal surface: smooth (0); presenting a anteroposterior dorsal ridge (1); marked ventral deflection ('bevelled') in posterior portion (2); sculpted as with the rest of the skull table (3) (Montefeltro *et al.*, 2013) (added 'anteroposterior' to character state 1; added character states 2 and 3 here).
117. Parietal-squamosal emargination (anterior concavity at suture contact), posterior margin in dorsal view: absent (0); present (1) (Wilkinson *et al.*, 2008).
118. Supratemporal roof, dorsal surface: postorbital and squamosal with flat shelves extending laterally beyond quadrate contact (0); lateral edge terminating medial or immediately dorsal to medial-most point of contact with quadrate (1) (Clark, 1994) (character state 'complex' removed; character state 1 added).
119. Supratemporal fenestra, medial border: flat, sculpted region (or unsculpted if rest of cranial table unsculpted) (0); forming a low sagittal crest (rims) posteriorly (1); forming a low sagittal crest (rims) along full length (2) (Clark, 1994) (character state 1 added here) [ordered].
120. Supratemporal fenestra, dermal bone overhang: absent (0); present (1) (Norell, 1988).
121. Supratemporal fenestra, dermal bone overhang: present only medially and posteriorly (0); present about the entire edge (1) (Norell, 1988).
122. Supratemporal fenestra, shallow fossa at anteromedial corner: present (0); absent, corner smooth (1) (Brochu, 1999).
123. Supratemporal medial rims: continuous with orbital rims (0); separated from orbital rims by the postorbital bar (1) (new character).
124. Supratemporal medial rims, extend posteriorly to contact posterior skull margin: present (0); absent (1) (new character).
125. Supratemporal fenestra, relative contribution of frontal and parietal to medial margin: parietal with equal or greater contribution (0); frontal excluded from margin (1) (new character).
126. Supratemporal fenestrae, minimum width between fenestrae, with respect to maximum width of cranial table: one-third or less of total width (0); more than one-third of total width (1) (new character; adapted from Schwarz & Salisbury, 2005).
127. Orbitotemporal channel, size of the dorsal aperture: area of foramen $\leq 30\%$ of that of the internal supratemporal fenestra (0); larger than 30% of the internal supratemporal fenestrae area (1) (Montefeltro *et al.*, 2013).
128. Postorbital bar between orbit and supratemporal fossa, shape: broad and solid, as broad as dorsal surface of the cranial table lateral to the supratemporal fenestra (0); much narrower (1); much narrower and connected to orbit via a thin, superficial furrow in postorbital (2) (Clark, 1994) (replaced 'with broadly sculpted dorsal surface if sculpture present' with size-related quantifier in character state 0; removed 'sculpting restricted to anterior surface' from character state 1; added character state 2) [ordered].
129. Postorbital bar between orbit and supratemporal fenestra, external texture: sculpted (0); unsculpted (1) (Clark, 1994).

130. Postorbital bar, lateral surface formed by: postorbital and jugal (0); only by postorbital (1) (Gasparini *et al.*, 2006).
131. Postorbital bar, shape: transversely flattened (0); transversely broad, with elliptical cross-section (1); slender and cylindrical (2) (Clark, 1994).
132. Postorbital bar, shape of dorsal end nearing skull table: continuous with dorsal part of postorbital (0); dorsal part of postorbital bar constricted, distinct from the dorsal part of the postorbital (1) (Clark, 1994).
133. Cranial table (skull roof), width with respect to ventral portion of skull: as wide as ventral portion of skull (quadrates covered by squamosal) (0); narrower, but still covering more than half of the mediolateral region of quadrates (1); narrower, exposing more than half of mediolateral region of quadrate (2) (Wu *et al.*, 1997) (added 'more than half' to character states 1 and 2) [ordered].
134. Squamosal and postorbital, lateral margins, dorsal view excluding the squamosal posterolateral process: parallel (0); diverging posteriorly (1); medially concave (2); converging posteriorly (3) (Ortega *et al.*, 2000) (character state 2 added; added 'excluding the squamosal posterolateral process' to character state 0).
135. Squamosal, lateral surface, longitudinal groove for attachment of the upper ear lid: absent (0); present (1) (Clark & Sues, 2002).
136. Squamosal groove for upper ear lid: ventral edge is laterally displaced relative to dorsal edge (0); ventral edge is directly beneath dorsal edge (1) (Clark & Sues, 2002).
137. Squamosal, dorsal edge of groove for dorsal ear lid: parallel to ventral edge (0); dorsal margin with a medial curvature (1) (Montefeltro *et al.*, 2013).
138. Squamosal, dorsolateral edge: straight and parallel to skull roof (0); bevelled ventrally, with anterolateral notch (1) (new character, adapted from Schwarz & Salisbury, 2005).
139. Squamosal, posterolateral process: present (0); absent (1) (new character, adapted from Buscalioni & Sanz, 1990a).
140. Squamosal, posterolateral process: level with skull table (0); depressed from skull table (1) (Serenio & Larsson, 2009).
141. Squamosal, posterolateral process projection: ventrally directed, confluent with ventral rim of groove for the earflap (0); posteriorly directed and parallel to skull roof (1) (Ortega *et al.*, 2000) (removed character state 2).
142. Squamosal, posterolateral process, ornamentation: absent (0); present (1) (Larsson & Sues, 2007).
143. Squamosal, posterolateral process, distal end: tapered and pointed (0); broad and rounded (1) (Larsson & Sues, 2007).
144. Squamosal, anterior process extending anteriorly to the orbital margin, overlapping the postorbital, in lateral view: absent (0); present (1) (Turner & Buckley, 2008).
145. Squamosal, obliquely orientated ridge on dorsal surface: present (0); absent (1) (new character).
146. Squamosal, oblique ridge on dorsal surface, position with respect to the supratemporal fenestra: posterior to supratemporal fenestra (0); posterolateral or lateral to supratemporal fenestra (1) (new character).
147. Squamosal–parietal suture: flat, not elevated from the skull table (0); forms a well-developed anteroposterior groove (often bounded by elevated ridges) (1) (new character, adapted from Buffetaut, 1983).
148. Squamosal, anterior portion nearing orbital edge: sculpted or unsculpted, consistent with the rest of the skull table (0); sculpting pattern changes (1) (new character).
149. Quadratojugal, ornamentation at base (dorsolateral surface): absent (0); present (1) (Pol, 1999).
150. Quadratojugal, length of anterior process relative to the lower temporal bar: absent or less than one-third of lower temporal bar (0); one-third to one half the length of the lower temporal bar (1); long, greater than half of the lower temporal bar (2) (Larsson & Sues, 2007) (changed character states to close gap between 'short' and 'half' of length of lower temporal bar) [ordered].
151. Quadratojugal, shape of posterolateral end and relationship with quadrate: acute or rounded, tightly overlapping quadrate (0); sinusoidal ventral edge, and wide and rounded posterior edge slightly overhanging lateral surface of quadrate (1) (Pol & Norell, 2004a).
152. Quadratojugal, contribution to the lateral temporal fenestra, in dorsal view: extensive contact with the ventral and posterior margins (0); contributes to the posterior and dorsal margins (1); only contributes to the posterior margin (2) (new character).
153. Quadratojugal–postorbital contact, in lateral view: not in contact (0); small, point contact (1); broad contact between the quadratojugal and the posterior portion of the postorbital descending flange (2) (Clark, 1994) (added character state 0 here) [ordered].
154. Infratemporal fenestra, posterior margin, dorsal view: straight (0); with an anterior projection, forming an acute angle (1) (Ortega *et al.*,

- 2000) (added 'forming an acute angle' to character state 1).
155. Quadrate, posterior edge: broad medial to tympanum, gently concave (0); narrow dorsal to otoccipital contact, strongly concave (1) (Clark, 1994).
 156. Quadrate, dorsal surface fenestration: absent (0); present (1) (Clark, 1994).
 157. Otic aperture (not including additional quadrate fenestrae): open posteriorly (0); closed posteriorly by quadrate and otoccipital (1) (Clark, 1994).
 158. Quadrate, distal body: anterior margin oriented at a right angle in relation to quadratojugal (0); anterior margin gently slopes relative to quadratojugal (1) (Montefeltro *et al.*, 2011).
 159. Quadrate, pterygoid ramus: with flat ventral edge (0); with deep groove on ventral surface (1); rod-like (2) (Clark, 1994) (character state 2 added here).
 160. Quadrate, anterodorsal ramus in ventral view: developed, forming more than or equal to 50% of the lateral edge of the internal supratemporal fenestra (0); restricted, forming <50% of the lateral edge of the supratemporal fenestra (1) (Montefeltro *et al.*, 2011).
 161. Quadrate, ventral surface: smooth, with simple muscle scars (0); with multiple developed ridges (1) (Ösi *et al.*, 2007).
 162. Quadrate, condyles: with poorly developed intercondylar groove (0); medial condyle expands ventrally, being separated from the lateral condyle by a deep intercondylar groove (1) (Ortega *et al.*, 2000).
 163. Quadrate, development of distal body ventral to otoccipital–quadrate contact: distinct, developing posteroventrally to contact (0); indistinct, not surpassing contact (1) (Wu *et al.*, 1997) (added 'developing posteroventrally to contact' to character state 0, and 'not surpassing contact' to character state 1).
 164. Quadrate, dorsoventral height of the proximal region: $\leq 50\%$ of the skull roof total width (0); more than 50% of the skull roof total width (1) (Montefeltro *et al.*, 2013) (added 'or equal to' to character state 0).
 165. Cranioquadrate canal: opened laterally (0); closed laterally (1) (Clark, 1994).
 166. Ectopterygoid–maxilla, contact: present (0); absent (1) (new character).
 167. Ectopterygoid, contribution to postorbital bar: absent (0); present (1) (Sereno & Larsson, 2009).
 168. Ectopterygoid, main axis orientation: mediolaterally or slightly anterolaterally (0); anteroposteriorly, subparallel to anteroposterior axis of skull (1) (Pol *et al.*, 2004) (changed laterally to mediolaterally in character state 0, and anteriorly to 'anteroposteriorly' in character state 1).
 169. Ectopterygoid, extent of medial projection on the ventral surface of pterygoid flanges: barely extended (0); widely extended, covering approximately the lateral half of the ventral surface of the pterygoid flanges (1) (Zaher *et al.*, 2006).
 170. Ectopterygoid, anterior process: developed (0); reduced or absent (1) (Pol, 1999).
 171. Ectopterygoid, posterior process: developed (0); reduced or absent (1) (Pol, 1999).
 172. Palatines, palatal processes: do not meet on palate below narial passage (0); meet ventral to narial passage, forming part of secondary palate (1) (Clark, 1994).
 173. Palatine–maxilla, suture when fused at midline: palatine anteriorly rounded (0); palatine anteriorly pointed (1); suture transverse to midline axis (2) (Brochu, 1999) (character state 'palatine invaginated' removed).
 174. Interfenestral bar, anterior half between suborbital fenestrae, lateral margins: parallel to subparallel (0); flared anteriorly (1) (Pol *et al.*, 2009) (added 'lateral margins').
 175. Interfenestral bar, posterior half between suborbital fenestrae, lateral margins: flared posteriorly (0); parallel to subparallel (1); converge posteriorly (2) (Pol *et al.*, 2009) (added 'lateral margins'; character state 2 added here) [ordered].
 176. Palatines, anteroposterior axis: run parasagittally (0); diverge laterally, becoming rod-like and forming palatine bars posteriorly (1) (Martinelli, 2003).
 177. Palatine–pterygoid, contact on palate: run parasagittally (0); palatines firmly sutured to pterygoids (1) (Pol & Norell, 2004a).
 178. Pterygoids, contact with one another on palate: not in contact anterior to basisphenoid on the palate (0); pterygoids in contact (1) (Wu *et al.*, 1997).
 179. Pterygoid, role of primary palate in forming choanal opening: forms posterior half of choanal opening (0); forms posterior, lateral, and part of anterior margin of choana (1); completely encloses choana (2) (Clark, 1994) [ordered].
 180. Pterygoid, participation in the suborbital fenestra, ventral view: forms margin of suborbital fenestra (0); excluded from suborbital fenestra by ectopterygoid–palatine contact (1) (Turner & Sertich, 2010).
 181. Choanae, anterior edge, location: situated between suborbital fenestrae (or anteriorly) (0); near posterior edge of suborbital fenestrae (1) (Clark, 1994).

182. Choanal opening, conformation in palate: continuous with pterygoid ventral surface except for anterior and anterolateral borders (0); opens into palate through deep choanal groove (1) (Clark, 1994).
 183. Choanal groove: undivided (0); partially septated (1); completely septated (2) (Clark, 1994) [ordered].
 184. Pterygoid, quadrate process: well developed, extending posterolaterally beyond anterior margin of basioccipital (0); poorly developed, only present as an incipient projection (1) (Pol, 1999) (added 'extending posterolaterally beyond anterior margin of basioccipital' to character state 0, and 'only present as an incipient projection' to character state 1).
 185. Pterygoid, quadrate ramus, in ventral view: narrow and bar-like (0); broad and laminar (1) (Wu *et al.*, 1997) (added 'bar-like' to character state 0, and 'laminar' to character state 1).
 186. Pterygoid, palatal surface: smooth (0); sculpted (1) (Clark, 1994).
 187. Pterygoid flanges: mediolaterally expanded, laterally surpassing the quadrate medial condyle (0); relatively short, and do not reach laterally to the level of the quadrate medial condyle (1) (Ösi *et al.*, 2007).
 188. Basisphenoid, ventral exposure on braincase: exposed on ventral surface of braincase (0); virtually excluded from ventral surface by pterygoid and basioccipital (1) (Clark, 1994).
 189. Basisphenoid, lateral exposure on braincase: absent (0); present (1) (Pol, 1999).
 190. Basisphenoid: ventral surface continuous with surrounding bones (0); body ventrally developed and separated from the remaining elements by a posteroventral step formed by a sulcus separating it from the main occipital plane, forming a postchoanal pterygoid-basisphenoid tuberosity (1) (Montefeltro *et al.*, 2011).
 191. Basisphenoid, ventral surface, mediolateral size relative to basioccipital: shorter than basioccipital (0); equal or longer than basioccipital (1) (Clark, 1994) (added 'mediolateral').
 192. Basioccipital: without well-developed bilateral tuberosities (0); with large, pendulous tubera (1) (Clark, 1994).
 193. Basioccipital, midline crest on basioccipital plate below occipital condyle: absent (0); present (1) (Turner & Sertich, 2010).
 194. Basioccipital and ventral part of otoccipital, orientation (when skull held horizontally): posteriorly (0); posteroventrally (1) (Gomani, 1997).
 195. Otoccipital, ventrolateral contact with quadrate: very narrow, otoccipital only abuts quadrate (0); broad, ventrolateral margin of otoccipital extensively contacts ventromedial portion of quadrate (1) (Clark, 1994) (added 'otoccipital only abuts quadrate' to character state 0, and 'ventrolateral margin of otoccipital extensively contacts ventromedial portion of quadrate' to character state 1).
 196. Supraoccipital, posterodorsal exposure in skull roof: absent (0); present (1) (Ortega *et al.*, 2000).
 197. Supraoccipital, posterodorsal exposure: exposed in midline portion of posterior region of skull table (0); restricted to a thin surface attached to posterior-most portion of parietal and squamosal (1) (Montefeltro *et al.*, 2011).
 198. Supraoccipital, relationship with foramen magnum: forms dorsal edge (0); otoccipitals meet dorsally, separating the foramen magnum from the supraoccipital (1) (Clark, 1994).
 199. Cranial nerves IX–XI, passage through braincase: all pass through common large foramen vagi in otoccipital (0); cranial nerve IX passes medial to nerves X and XI in separate passage (1) (Clark, 1994).
 200. Mastoid antrum, location: does not extend into supraoccipital (0); extends through transverse canal in supraoccipital to connect middle ear regions (1) (Clark, 1994).
- Mandibular characters*
201. Mandible, outer surface sculpture, lateral surface: absent (0); present (1) (Montefeltro *et al.*, 2011).
 202. Mandible, outer surface sculpture, ventral surface: present on dentary (0); present on dentary and splenial (1) (Montefeltro *et al.*, 2011).
 203. Mandibular symphysis, anteroposterior length relative to mediolateral width: short, length and width subequal or shorter than wide (0); proportionally long, longer than wide (1); extremely long, length at least five times its width (2) (Andrade *et al.*, 2011) [ordered].
 204. Mandibular symphysis, posterior extension, terminating medial to the dentary alveoli: short, up to the D5 (0); to the D5–D6 (1); to the D7 or greater in length (new character) [ordered]. D: dentary alveolus.
 205. Mandibular symphysis, lateral view: shallow and tapering dorsoventrally anteriorly (0); deep and tapering dorsoventrally anteriorly (1); shallow and anterior margin convex (2) (Wu & Sues, 1996) (character state 'deep and anteriorly convex' removed).
 206. Mandibular symphysis, shape, in ventral view: tapering mediolaterally anteriorly, forming an

- angle (0); U-shaped, smoothly curving anteriorly (1); lateral edges anteroposteriorly orientated with convex anterolateral corner and extensive, transversely orientated anterior edge (2) (Pol, 1999).
207. External mandibular fenestra: absent (0); present (1) (Clark, 1994).
208. External mandibular fenestra, size: present as a diminutive passage, <50% of the total size of the lateral temporal fenestra (0); present as an evident fenestra, 50% or greater than the total size of the lateral temporal fenestra (1) (Clark, 1994) (quantified both character states).
209. External mandibular fenestra, orientation of main axis: horizontal to subhorizontal (0); inclined, directed anteroventrally–posterodorsally (Andrade *et al.*, 2011) (added ‘to subhorizontal’ to character state 0).
210. External mandibular fenestra, shape: subcircular to elliptical (0); triangular (1) (Andrade *et al.*, 2011) (character states ‘highly elliptic, anteroposterior axis much longer than dorsoventral axis, three times or more, but both ends rounded’, ‘slit-like, proportionally very long and both ends acute’, and ‘teardrop-like’ removed.)
211. Jaw joint, location of dorsal edge: level with or dorsolateral to occipital condyle (0); ventrolateral occipital condyle (1) (Wu & Sues, 1996).
212. Dentary, lateral surface adjacent to seventh alveolus: smooth (0); with lateral concavity for reception of enlarged maxillary tooth (1) (Buckley & Brochu, 1999).
213. Dentary, lateral surface below alveolar margin, at middle to posterior region of tooth row: vertically orientated, continuous with rest of lateral surface of the dentaries (0); flat surface exposed dorsolaterally, divided by ridge from the rest of the lateral surface of the dentary (1); flat, unsculpted surface confluent with rest of the lateral surface (2) (Pol & Apesteguía, 2005) (character state 2 added here).
214. Dentary, relative to external mandibular fenestra: extends posteriorly beneath mandibular fenestra, posteriorly exceeding anterior margin (0); does not extend beneath fenestra, either terminating anteriorly to fenestra or only forming a point contact (1) (Clark, 1994).
215. Dentary, mediolateral compression and ventrolateral surface anterior to mandibular fenestra (or of anterior portion posterior to symphysis if fenestra is absent): compressed and flat (0); uncompressed and convex (1) (Ortega *et al.*, 1996) (added ‘mediolateral’).
216. Dentary, sculpted below the tooth row: lacking sculpting (0); present (1) (Pol, 1999).
217. Dentary alveoli: all independent of one another (0); some confluent (1); all confluent, within continuous alveolar groove (2) (new character) [ordered].
218. Dental alveoli, transitional shape morphology from circular to subcircular or oval: absent (0); present (1) (new character).
219. Dentary alveoli, transitional shape morphology: posteriorly from D4 (0); posteriorly from D5 (1) (new character).
220. Dentary, distinct foramina on occlusal surface, lingual to dental arcade: absent (0); present (1) (new character).
221. Dentary, distinct foramina on occlusal surface, lingual to dental arcade: at D2–D3 (0); at D4 or positioned more posteriorly (1) (new character).
222. Dentary, external alveolar margins, dorsal edge: vertically festooned, forming raised rims about each alveolus (0); flat (1) (new character).
223. Dentary, internal alveolar margins: forming raised rims (0); flat and confluent with dentary occlusal surface (1) (new character).
224. Dentary, anterior portion, lateral margin shape in dorsoventral view: straight (0); distinctly spatulate, with abrupt lateral expansion (1); laterally convex (2) (new character).
225. Dentary, diastema (gap) between D7 and D8: present (0); absent (1) (new character).
226. Dentary, pitted ornamentation of external surface: absent (0); present (1) (new character).
227. Dentary, grooved ornamentation of external surface: absent (0); present (1) (new character).
228. Dentary, interalveolar septae within anterior dental arcade (D4–D8): present (0); absent (1) (new character).
229. Dentary, symphysis and dentary arcade lateral to symphysis, in dorsoventral view: parallel (0); oblique (1) (new character).
230. Dentary, occlusal surface: smooth (0); anteroposteriorly crenulated (1) (new character).
231. Dentary, obliquely inclined crenulations posterodorsal to D8–D9: present (0); absent (1) (new character).
232. Dentary, dorsolateral edge: slightly concave or straight and subparallel to anteroposterior axis of skull (0); sinusoidal, with two concave waves (1) (Ortega *et al.*, 1996) (character state ‘with single dorsal expansion and concave posteriorly’ removed).
233. Splenial, involvement in symphysis, in ventral view: not involved (0); involved (1) (Clark, 1994).
234. Splenial, contact with dentary, in ventral view: confluent (0); dorsally inset (1) (new character).
235. Splenial, posterior to symphysis: approximately constant mediolateral thickness throughout element (0); more robust posterodorsally (1)

- (Ortega *et al.*, 1996) (changed character state 'thin' to 'approximately constant mediolateral thickness throughout element'; changed character state 1 to 'more robust posterodorsally').
236. Angular and posterior surangular, strong pitted pattern: absent (0); present (1); lateral surface with rugose pattern instead of pits (2) (Andrade *et al.*, 2011) (character state 2 added here).
 237. Surangular, dorsal edge in lateral view: mostly straight (0); arched dorsally, excluding articular projection (1) (Clark, 1994).
 238. Surangular, anteroposterior ridge along the dorsolateral surface: absent (0); present (1) (Pol & Norell, 2004b).
 239. Surangular, extension toward posterior end of retroarticular process: along entire length (0); pinched off anterior to posterior tip (Norell, 1988).
 240. Articular, posterior ridge on glenoid fossa: posterior margin well developed, evidently high (0); posterior margin poorly delimited, crest absent (1) (Pol & Apesteguía, 2005).
 241. Articular, medial process articulating with otoccipital and basisphenoid: absent (0); present (1) (Clark, 1994).
 242. Retroarticular process: absent or extremely reduced (0); posteroventrally projecting and paddle-shaped (1); pointed, projects posteriorly and ventrally recurved (2); projects posteriorly and dorsally recurved (3) (Clark, 1994) (character states 'with an extensive rounded, wide, and flat (or slightly concave) surface projected posteroventrally and facing dorsomedially' and 'posteriorly elongated, triangular, and facing dorsally' removed; character states 2 and 3 added).
- Dental characters*
243. Premaxillary teeth, number: five or more (0); four or fewer (1) (Wu & Sues, 1996) (character states 'six', 'three', and 'two' removed, and replaced with 'or more' and 'or fewer' in remaining character states).
 244. Posterior premaxillary teeth, apicobasal length: <1.5 times the size of the anterior teeth (0); 1.5 times or greater than anterior teeth (1) (Clark, 1994) (quantified and set character state boundary).
 245. Maxillary teeth, mesiodistal margin carinae: absent or with smooth and crenulated carinae (0); with denticulate carinae (ziphodont condition) (1) (Ortega *et al.*, 1996) (character state 'with tubercular heterogenic denticles' removed).
 246. Maxillary tooth rows, middle to posterior elements: crowns not mesiodistally compressed, subcircular in cross-section (0); crowns slightly compressed mesiodistally (mesiodistal to labiolingual diameter ratio more than 0.5 at mid-height) (1); crowns highly compressed mesiodistally (mesiodistal to labiolingual diameter ratio ≤ 0.5 at mid-height) (2) (Pol, 1999) [ordered].
 247. Maxillary tooth rows, mesiodistal compression of middle to posterior elements: absent, or symmetrical compression (0); asymmetrical compression, occurring only along the distal margin giving teeth a teardrop shape (1) (Andrade & Bertini, 2008) (added 'or symmetrical compression' to character state 0).
 248. Maxillary teeth, middle to posterior elements, ridged ornamentation on enamel surface: absent (0); present (1) (Andrade *et al.*, 2011).
 249. Maxillary teeth, enamel surface: smooth or slightly crenulated (0); with ridges at base of crown (often extending apically) (1) (Turner & Sertich, 2010).
 250. Maxillary teeth, striations on labial and lingual faces: present (0); absent (1) (new character, adapted from Martin *et al.*, 2014a,b).
 251. Cheek teeth, base (i.e. immediately apical to root), with respect to remainder of tooth crown: not constricted (0); constricted (1) (new character, adapted from Martin *et al.*, 2014a,b).
 252. Maxillary teeth, width of root with respect to crown: narrower (0); wider in anterior teeth and equal in posterior teeth (1) (Ortega *et al.*, 2000) (changed character state 1 to 'wider in anterior teeth and equal in posterior teeth'; removed 'or equal' from character state 0).
 253. Maxillary teeth, posterior teeth, mediolaterally compressed lanceolate-shaped morphotype (sometimes called 'leaf-shaped'), visible in labial or lingual view, with wide crown tapering apically to a sharp point (note that the point can often be abraded): present (0); absent (1) (new character, adapted from Schwarz & Salisbury, 2005).
 254. Maxillary teeth, low-crowned and strongly labiolingually compressed morphotypes, forming a crown that is mesiodistally broader than it is apicobasally tall: present, apical margins orientated at $<45^\circ$ from horizontal (0); absent (1) (new character, adapted from Schwarz & Salisbury, 2005).
 255. Tooth, present at premaxilla-maxilla contact with transitional size-based morphology: absent (0); present (1) (Turner & Sertich, 2010) (added 'size-based').
 256. Maxillary teeth, size variation waves: absent, no tooth size variation (0); one wave of enlarged teeth (1); enlarged maxillary teeth occur in two waves (festooned) (2) (Clark, 1994).

257. Enlarged maxillary teeth (at least 1.5 times the apicobasal size of remaining teeth): present at M2 and/or M3 (0); present at M4 and/or M5 (1) (Martin *et al.*, 2014a,b). M: maxillary alveolus.
258. Maxillary tooth 5, apicobasal size relative to adjacent maxillary teeth: subequal, or <4.0 times the size of adjacent teeth (0); hypertrophied, at least 4.0 times the size of adjacent teeth (1) (new character).
259. Maxillary tooth 5, hypertrophied: directed posteroventrally (0); directed ventrally (1) (new character).
260. Maxillary teeth 6 and 7: continuous with tooth row (0); dorsally inset (1) (new character).
261. Maxillary teeth, bulbous tooth morphotype (tribodont): present (0); absent (1) (Sweetman *et al.*, 2015).
262. Dentary teeth, anterior teeth (opposite premaxilla–maxilla contact) apicobasal length, relative to rest of dentary teeth: no more than twice the length (0); more than twice the length (1) (Clark, 1994).
263. Dentary teeth, posterior teeth: occlude medial to opposing maxillary teeth (0); occlude lateral to, or interlock with, opposing maxillary teeth (1) (new character, adapted from Sweetman *et al.*, 2015).
271. Dorsal vertebrae: amphicoelous or amphiplatyan (0); procoelous (1) (Clark, 1994) (replaced ‘trunk’ with ‘dorsal’).
272. Dorsal vertebrae, number: 14 or fewer (0); 15–16 (1); 17 or more (2) (new character) [ordered].
273. Posterior dorsal vertebrae, transverse process shape: dorsoventrally low and laminar (0); dorsoventrally high (1) (Buscalioni & Sanz, 1988).
274. Sacral vertebrae, number: two (0); three or more (1) (Buscalioni & Sanz, 1988).
275. Sacral vertebrae, orientation of transverse processes: project laterally (horizontally) (0); deflected markedly ventrally (1) (Gasparini *et al.*, 2006).
276. Caudal vertebrae, number: fewer than 50 (0); 50 or more (1) (new character).
277. Caudal vertebrae: amphicoelous or amphiplatyan (0); procoelous (1) (new character, adapted from Salisbury & Frey, 2005).
278. Caudal vertebrae, first: same morphology as rest of caudal series (0); biconvex (1) (new character, adapted from Salisbury & Frey, 2001).
279. Caudal vertebrae, anteroposterior ridge/lamina separating centrum and neural arch: present (0); absent (1) (new character; note that this could be an ontogenetic feature).

Axial characters

264. Vertebrae, centra shape along axial column: cylindrical throughout (0); grade continuously from cylindrical to elongated spool-shaped (1); spool-shaped throughout (2) (Buscalioni & Sanz, 1988) (character state 1 added) [ordered].
265. Cervical vertebrae: amphicoelous or amphiplatyan (0); procoelous, and posterior centrum face (condyle) with a central depression (‘semi-procoely’) (1); fully procoelous (2) (Clark, 1994) (character state 1 added) [ordered].
266. Cervical vertebrae, number: six or fewer (0); seven (1); eight or more (2) (new character) [ordered].
267. Atlas, intercentrum size: mediolaterally wider than anteroposteriorly long (0); subequal diameters or anteroposteriorly longer (Clark, 1994).
268. Cervical vertebrae, neural spine: absent, or extremely reduced (0); present, distinct from centrum body (1) (new character).
269. Cervical vertebrae, neural spines: rod-like and elongate (0); short and transversely flattened (1) (new character).
270. Cervical and dorsal vertebrae, hypapophyses or anterior keels: absent (0); present (1) (Bus-

Appendicular characters

280. Scapula, proximodorsal edge in lateral view: flat and confluent with scapular shaft (0); forms a distinct crest (1) (new character).
281. Coracoid, medial process: elongate posteromedial process (0); distally expanded ventromedial process (1) (Wu & Sues, 1996).
282. Coracoid, distal expansion: equal to or larger than the proximal expansion (0); less expanded than the proximal region (1) (Pol *et al.*, 2012).
283. Humerus, circular depression on the posterior surface of the proximal end, for the insertion of the M. scapulohumeralis caudalis: absent (0); present (1) (Pol *et al.*, 2012).
284. Humerus, lateral and medial surfaces of distal end: flat and anteroposteriorly broad, similar in anteroposterior length to the transverse width of the distal end of the humerus (0); convex and reduced in comparison with the transverse width of the distal humerus (1) (Pol *et al.*, 2012).
285. Forelimb : hindlimb length, ratio: <0.7 (0); 0.7 to <0.8 (1); 0.8 or greater (2) (new character) [ordered].
286. Humerus : femur length, ratio: <0.75 (0); 0.75 to <1.0 (1); 1.0 or greater (2) (new character) [ordered].

287. Ulna, morphology of olecranon process: narrow and subangular (0); wide and rounded (1) (Brochu, 1999).
 288. Radius : humerus length, ratio: <0.6 (0); 0.6 to <0.75 (1); 0.75 or greater (2) (new character) [ordered].
 289. Radius : tibia length, ratio: <0.6 (0); 0.6 to <0.7 (1); 0.7 or greater (2) (new character) [ordered].
 290. Radiale, proximal end, shape: expanded symmetrically, similar to distal end (0); more expanded laterally than medially ('hatchet shaped') (1) (Buscalioni & Sanz, 1988).
 291. Ilium, anterior (preacetabular) process, length relative to posterior (postacetabular) process: >75% of the length of the posterior process (0); 75% or less of the length of the posterior process (1); completely absent (2) (Clark, 1994) (changed 'similar in length' to '>75% of the length of the posterior process' in character state 0; changed 'one-quarter' to '75%' in character state 1) [ordered].
 292. Ilium, development of the posterior (postacetabular) process: well-developed as a distinct process that extends anteroposteriorly for 60% or more of the acetabular length (0); extremely reduced or absent, extending anteroposteriorly <60% of the acetabular length (1) (Pol *et al.*, 2012) (character state 1 changed to '<60%' to remove gap between 50 and 60%).
 293. Ilium, posterior end of the postacetabular process: tapering posteriorly to an acute tip (0); subrectangular with a vertically orientated posterior margin (1) (Pol *et al.*, 2012) (removed 'with its dorsoventral height being at least 60% of the height at the origin of the postacetabular process' from character state 1).
 294. Pubis, shape: rod-like without expanded distal end (0); with anterodorsally–posteroventrally expanded distal end (1) (Clark, 1994) (added 'anterodorsally–posteroventrally' to character state 1).
 295. Pubis, anterior process: absent (0); present (1) (Clark, 1994).
 296. Femur, proximal development of greater trochanter: prominent, ridge-like lateral border that separates the lateral surface of the proximal femur from a flat posterior surface reaching down to the level of the fourth trochanter (0); proximodistally short trochanteric surface lacking a distinct ridge, terminating well above the fourth trochanter (1) (Pol *et al.*, 2012).
 297. Femur, femoral head: mediolaterally flattened (0); hemispherical (1) (new character).
 298. Tibia, distal projection of articular surfaces: medial region of distal articular surface extends further distally than the lateral region, forming a strongly oblique distal margin of the tibia (0); medial and lateral regions subequally extended, with distal margin subhorizontally orientated (1) (Pol *et al.*, 2012).
 299. Tibia, posterior surface of shaft: flattened and confluent with fibula (0); twists posteriorly, leaving a void between the tibia and fibula (1) (new character).
 300. Tibia : femur length, ratio: <0.9 (0); 0.9 to <1.0 (1); 1.0 or greater (2) (new character) [ordered].
 301. Astragalus, anterior margin of the tibial facet: forming a well-defined ridge that reaches medially the ball-shaped region for the articulation of metatarsals I–II and closes the proximomedial corner of the anterior hollow of the astragalus (0); forming a low ridge that is medially separated by a notch from the ball-shaped region for the articulation of the metatarsals I–II, failing to close the proximomedial corner of the anterior hollow (1) (Pol *et al.*, 2012).
 302. Distal tarsals, digits 2–4, dorsal surface: longitudinally grooved (0); smooth and flat (1) (new character).
 303. Metatarsals I–IV: equidimensional (0); metatarsal I shorter than metatarsals II–IV (1) (new character).
- Osteoderm characters*
304. Osteoderms, dorsal surface: entirely sculpted (0); partially or completely unsculpted (1) (new character).
 305. Presacral armour: cervical and dorsal trunk shields undifferentiated, morphology grading continuously (0); cervical shields clearly differentiated from dorsal trunk shields by size and general morphology (regardless of contact between nuchal and trunk series) (1); anterior-most cervical osteoderms developed into distinct shield (2) (Andrade *et al.*, 2011) (character state 2 added) [ordered].
 306. Nuchal osteoderms: consistent morphology along series (0); vary substantially in size in a random fashion (1); systematically increase in size posteriorly (2) (new character).
 307. Nuchal osteoderms, with size variation: nuchals no less than half of the size of dorsal osteoderms (0); some smaller than one half of the size of the dorsal osteoderms (1) (new character).
 308. Dorsal osteoderms, shape: rounded or ovate (0); subrectangular (mediolaterally wider than anteroposteriorly long) (1); subtriangular (2); square (3) (Clark, 1994) (character state 2 added).
 309. Dorsal osteoderms, articular anterior process: absent (0); present (1) (Clark, 1994).
 310. Dorsal osteoderms, articular anterior process: as discrete convexity on anterior margin (0);

- well-developed process located anterolaterally ('peg and socket' articulation) (1) (Clark, 1994).
311. Dorsal osteoderms, anteroposterior keel on anterior part of dorsal surface: absent (0); present (1) (new character).
 312. Dorsal osteoderms, anteroposterior keel on posterior part of dorsal surface: absent (0); present (1) (new character).
 313. Dorsal and cervical osteoderms: some or all imbricated (0); not in contact (1) (new character).
 314. Dorsal osteoderms, sutured anterior and posterior contacts: present (0); absent (1) (new character).
 315. Dorsal primary osteoderms (*sensu* Frey, 1988), rows: two parallel rows (0); four rows or more (1) (Clark, 1994).
 316. Dorsal osteoderms, accessory osteoderms (*sensu* Frey, 1988; i.e. osteoderms not forming part of the dorsal shield): absent (0); present (1) (Turner & Sertich, 2010).
 317. Dorsal osteoderms, dorsal keel: same morphology in anterior-most dorsal osteoderms as remainder of dorsal series (0); keel shifts laterally in more posterior dorsal osteoderms (1) (new character).
 318. Dorsal osteoderms, anterior edge of dorsal surface (i.e. articular surface, if present): sculpted, undifferentiated from main osteoderm body (0); unsculpted (1) (new character).
 319. Dorsal osteoderms, outline in dorsal aspect (excluding peg articulation): symmetrical about anteroposterior axis (0); asymmetrical (1) (new character).
 320. Dorsal osteoderms, mediolateral contacts: contact but not sutured (0); sutured (1) (new character).
 321. Dorsal osteoderms, ventral to dorsal vertebrae beneath trunk: absent (0); present (1) (Clark, 1994).
 322. Caudal osteoderms: absent (0) present on dorsal surface only (1); completely surrounding tail (2) (Clark, 1994) [ordered].
 323. Caudal osteoderms: ovate (0); subcircular (1); subrectangular (2) (new character).
 324. Caudal osteoderms, bearing anteroposterior ridge: present (0); absent (1) (new character).
 325. Caudal osteoderms, anteroposterior ridge: present medially (0); forms a distinct lateral step in posterior-most elements (1) (new character).
 326. Caudal osteoderms, geometry: continuous from short to elongate oval (0); continuous from subrectangular (rounded corners) to suboval (1); isometric (equal geometry along series) (2) (new character).
 327. Caudal osteoderms, medial and lateral edges: serrated (0); smooth (1) (new character).
 328. Caudal osteoderms, secondary osteoderms: present (0); absent (1) (new character).
 329. Caudal osteoderms, anteroposterior ridges: same morphology along series (0); becoming more pronounced posteriorly, coincident with a decrease in osteoderm size (1) (new character).