Revision of the Late Jurassic crocodyliform *Alligatorellus*, and evidence for allopatric speciation driving high diversity in western European atoposaurids

Comment [S1]: atoposaurids are indeed crocodylomorphs but are part of a less inclusive clade Crocodyliformes Hay, 1930. Tthey should therefore be referred to as crocodyliforms

Atoposaurid crocodyliforms represent an important faunal component of Late Jurassic to Early Cretaceous Laurasian semi-aquatic to terrestrial ecosystems, with numerous spatiotemporally contemporaneous atoposaurids known from western Europe. In particular, the Late Jurassic of France and Germany records evidence for high diversity and possible sympatric atoposaurid species belonging to *Alligatorellus*, *Alligatorium* and *Atoposaurus*. However, atoposaurid taxonomy has received little attention, and many species are in need of revision. As such, this potentially high European diversity within a narrow spatiotemporal range might be a taxonomic artefact. Here we provide a taxonomic and anatomical revision of the Late Jurassic atoposaurid *Alligatorellus*. Initially described as *A. beaumonti* from the Kimmeridgian of Cerin, eastern France, additional material from the Tithonian of Solnhofen, south-eastern Germany, was subsequently referred to this species, with the two occurrences differentiated as *A. beaumonti beaumonti* and *A. beaumonti bavaricus*, respectively. We provide a revised diagnosis for the genus *Alligatorellus*, and note a number of anatomical differences between the French and German specimens, including osteoderm morphology and the configuration and pattern of sculpting of cranial elements. Consequently, we restrict the name *Alligatorellus beaumonti* to include only the French remains, and raise the rank of the German material to a distinct species, erecting the name *Alligatorellus bavaricus* sp. nov. A new diagnosis is provided for both species, and we suggest that a recently referred specimen from a coeval German locality cannot be conclusively referred to *Alligatorellus*. Although it has previously been suggested that *Alligatorellus*, *Alligatorium* and *Atoposaurus* might represent a single growth series of one species, we find no conclusive evidence to support this proposal, and provide a number of morphological differences to distinguish these taxa that appear to be independent of ontogeny. Consequently, we interpret high

atoposaurid diversity in the Late Jurassic island archipelago of western Europe as a genuine biological signal, with closely related species of *Alligatorellus*, *Alligatorium* and *Atoposaurus* in both French and German basins providing evidence for allopatric speciation, potentially driven by fluctuating sea levels. It is possible that the small body size of atoposaurids resulted from island dwarfing during this interval, but testing of this idea will have to await the discovery of more basal forms from non-island settings.

Comment [S2]: Pure speculation, without foundation, that should not be included. Furthermore, elsewhere small atoposaurids co-occur with other diminutive taxa e.g bernissartids and with large taxa e.g. goniopholids

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Introduction

Atoposaurids comprise a clade of small-bodied, terrestrial and semi-aquatic crocodyliforms (Owen, 1879; Joffe, 1967; Buscalioni and Sanz, 1990a; Thies *et al*., 1997; Lauprasert *et al*., 2011). Historically, they were considered to be the sister group to Eusuchia (Joffe, 1967; Buffetaut, 1982), but are now recovered in all recent phylogenetic analyses as the basal-most members of Neosuchia Benton and Clark, 1988 which includes crown group crocodylians (see also: Buscalioni and Sanz 1990b; Salisbury *et al*., 2006; Brochu *et al*., 2009; Pol and Gasparini, 2009; Adams, 2013; Sertich and O'Connor, 2014). Atoposaurids were an important component of a range of Late Jurassic to Early Cretaceous western European ecosystems (Fig. 1), with less common occurrences extending their known stratigraphic range from the Middle Jurassic (168.3 Ma) to the end-Cretaceous (66 Ma) (Fig. 2) (Owen, 1879; Buscalioni and Sanz, 1984, 1987a; Salisbury, 2002; Martin *et al*., 2010; Salisbury and Naish, 2011). There is tentative evidence to suggest that atoposaurids might have persisted beyond the Cretaceous/Paleogene boundary, based on fragmentary material from the Middle Eocene of the Republic of Yemen (Stevens *et al*., 2013). The earliest known atoposaurid specimens are *Theriosuchus*-like teeth from the early (Kriwet *et al*., 1997) and middle (Knoll *et al*., 2013) Bathonian (late Middle Jurassic) of southern France and the Bathonian of the UK (Evans and Milner, 1994), with *Theriosuchus sympiestodon* from the Maastrichtian of Romania the last known occurrence (Martin *et al.,* 2010; 2014). Other putative and fragmentary occurrences potentially extend the distribution of Atoposauridae into the Late Jurassic – Early Cretaceous of Asia (Young 1961; Efimov, 1976; Wu *et al*., 1994, 1996, 1997; Storrs and Efimov, 2000; Cuny *et al*., 2010; Wings *et al*., 2010) and North America (Gilmore, 1926; Cifelli *et al*., 1999; Eaton *et al*., 1999; Fiorillo, 1999; Rogers, 2003), and a late Early Cretaceous occurrence, *Brillanceausuchus babouriensis*, from Cameroon, might represent evidence for the presence of the clade in Gondwana (Michard *et al*., 1990).

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Comment [S4]: Say here how the clade is diagnosed and particularly how Atoposauridae differs from Bernissartidae, crocodyliforms of similar size and superficially similar morphology (see Sweetman et al. in press, Acta Pal. Pol.

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The first atoposaurid specimens were described by Meyer (1850, 1851) from the Late Jurassic of France and Germany, with Gervais (1871) subsequently erecting the family Atoposauridae (initially written as 'Atoposauridés'). Both *Atoposaurus jourdani* and *Atoposaurus oberndorferi* were named by Meyer (1850), and the former was described by Meyer (1851); however, *A. oberndorferi* remained a *nomen nudum* until its formal description by Wellnhofer (1971). Numerous additional genera and species of atoposaurids have since been described, but the taxonomy of the group as a whole has received little systematic attention since Wellnhofer (1971), and no comprehensive analysis of their phylogenetic relationships has been undertaken other than genus-level investigations by Buscalioni and Sanz (1988, 1990a, b) and Karl *et al*. (2006). The monophyly of several multispecific genera has, therefore, never been tested, and a number of putative taxa extending the geographical and temporal range of Atoposauridae have never been incorporated into a comprehensive species-level phylogenetic analysis (e.g., *Theriosuchus grandinaris*,

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Lauprasert *et al.*, 2011; *Theriosuchus sympiestodon*, Martin *et al.*, 2010, *Karatausuchus sharovi*, Efimov, 1976).

Despite this history and the range of recent discoveries, there is currently little species-level taxonomic clarity or consensus on atoposaurid inter-relationships (Owen, 1878, 1879; Wellnhofer, 1971; Buffetaut, 1982; Clark, 1986; Buscalioni and Sanz, 1988; Brinkmann, 1989, 1992; Wu *et al.*, 1996; Schwarz and Salisbury, 2005). Steel (1973) considered Atoposauridae to comprise *Alligatorellus*, *Alligatorium*, *Atoposaurus*, *Hoplosuchus*, *Shantungosuchus*, and *Theriosuchus*. More recently, Lauprasert *et al*. (2011) recognised only four valid genera*, Alligatorellus, Alligatorium, Montsecosuchus* (see below), and *Theriosuchus*, with the latter genus comprising four species: *T. grandinaris, T. guimarotae*, *T. ibericus* and *T. pusillus*. Martin *et al*. (2010) augmented this species list with their description of *T. sympiestodon* from the Maastrichtian of Romania. Schwarz-Wings *et al*. (2011) followed this taxonomic scheme, but also regarded *Atoposaurus* as a valid genus, comprising the two aforementioned species *A. jourdani* and *A. oberndorferi*. There are three currently recognised species of *Alligatorium*: *A. meyeri* from France (Vidal, 1915); and *A. franconicum* (Ammon, 1906) and *A. paintenense* (Kuhn, 1961; originally described by Broili [1931] as a possible occurrence of *A. franconicum*) from Germany. However, specimens of the latter two were lost or destroyed during World War II. The Early Cretaceous Spanish species originaly placed in *Alligatorium, A. depereti,* has since been assigned to a new genus, *Montsecosuchus* (Vidal, 1915; Peybernes and Oertli, 1972; Buscalioni and Sanz, 1988, 1990a).

Gervais (1871) originally erected the species name *Alligatorellus beaumonti* for two specimens from the Late Jurassic of Cerin, in eastern France. Wellnhofer (1971) later assigned these specimens to the subspecies *A. beaumonti beaumonti*, in recognition of differences between coeval specimens from Eichstatt, southeast Germany, for which he erected the subspecies *A. beaumonti bavaricus*. Both the French and German specimens have been regarded as *Alligatorellus beaumonti* by subsequent workers (e.g., Buscalioni and Sanz, 1988; Schwarz-Wings *et al.*, 2011). As a result of these factors, the species-level composition of the atoposaurids *Alligatorellus*, *Alligatorium*, *Atoposaurus*, and *Montsecosuchus*, remains poorly understood in the context of current understanding of crocodyliform systematics. This in part reflects a paucity of specimens, but also the flattened mode of preservation of the specimens concerned which often obscures much of their morphology (Meyer, 1850, 1851; Gervais, 1871; Wellnhofer, 1971; Buscalioni and Sanz, 1990a). This taphonomic signature results from their exclusive occurrence in lithographic limestones. Furthermore, *Theriosuchus* appears to have become a 'waste-basket taxon' for recently discovered small, basal neosuchian specimens from Asia and Europe, and seems to have had different environmental preferences. Unlke *Alligatorellus, Alligatorium, Atoposaurus,* and *Montsecosuchus which occur in lagoonal settings*, *Theriosuchus* occurs in a range of transitional brackish onshore or near-shore environments (Schwarz and Salisbury, 2005; Lauprasert *et al.*, 2011). Part of this ambiguity in atoposaurid systematics might stem from an absence of comprehensive species level diagnoses, which clouds the inter-relationships of the group.

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Given such potentially high European atoposaurid diversity within a narrow geographic and temporal range, and a lack of taxonomic consensus, a full revision of atoposaurid systematics is overdue. Presented here is a re-assessment of specimens of *Alligatorellus* from the Late Jurassic of France and Germany in the first of a series of papers in which we will revise the taxonomy, systematics and phylogenetic relationships of Atoposauridae. We refer the German occurrence to a new species of *Alligatorellus*, providing an comprehensive re-description, and make detailed comparisons with the French type species. We also consider the taxonomic affinities of an additional German specimen described as *Alligatorellus* sp. (Schwarz-Wings *et al.*, 2011), and examine the osteoderm morphology of *Alligatorellus*, investigating its utility in atoposaurid systematics. Finally, we examine the taxonomy and validity of the contemporaneous, multispecific taxa *Alligatorium* and *Atoposaurus*, and discuss the diverse atoposaurid faunal composition of the Late Jurassic of western Europe.

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Institutional Abbreviations

LMU, Ludwig-Maximilians Universitat, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; MfN, Museum für Naturkunde, Berlin, Germany; MNHN, Muséum National d'Histoire Naturelle, Centre de Conservacion, Lyon, France; NHMUK, Natural History Museum, London, UK; TMH, Teylers Museum, Haarlem, The Netherlands.

Anatomical Abbreviations

Comment [S12]: If journal style permits I would place these here and amend figure captions accordingly

Systematic Palaeontology

Crocodylomorpha Walker 1970

Crocodyliformes Hay 1930

Mesoeucrocodylia Whetstone and Whybrow 1983

Neosuchia Benton and Clark 1988

Atoposauridae Gervais 1871

Alligatorellus Gervais 1871

Comment [S13]: Hay, O.P. 1930. *Second Bibliography and Catalogue of the Fossil Vertebrata of North America*. xiv + 1074 pp. Carnegie Institute, Washington DC.

Comment [S14]: Whetstone, K.N. and Whybrow, P.J. 1983. A "cursorial" crocodilian from the Triassic of Lesotho (Basutoland), southern Africa. *Occasional Papers of the Museum of Natural History, University of Kansas* 106: 1–37.

Note on taxonomy**:** Gervais (1871) did not designate a holotype specimen in his original description of *Alligatorellus beaumonti*. Wellnhofer (1971) elected MNHN 15639 as the holotype of *A. beaumonti beaumonti*. As this is one of the two specimens described by Gervais (1871), we follow Wellnhofer (1971) in considering MNHN 15639 to be the holotype for the genus and type species, *Alligatorellus beaumonti*.

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Wellnhofer (1971, p. 144) provided the following diagnosis of *Alligatorellus* (translation adapted from Schwarz-Wings *et al.* 2011): (1) a large-sized atoposaurid (420–550mm) with an acute-triangular skull and large orbits; (2) the supratemporal fossae are not internally fenestrated, and are connected to the orbit by a superficial furrow; (3) the nasal aperture is divided; (4) the tail is longer than half of the precaudal body length; (5) presence of a biserial osteoderm shield from the nuchal to the caudal region; (6) single osteoderms are sculpted; (7) presence of a lateral keel on the nuchal and dorsal osteoderms, whereas the caudal osteoderms bear a more medial keel; (8) ventral armour possesses two rows of scutes in the tail region; (9) the ventral scutes are oval and medially keeled.

Comments: In light of more recent atoposaurid discoveries and an improved understanding of their anatomy, much of Wellnhofer's (1971) diagnosis requires revision. The first putative autapomorphy (1) is a feature that also describes the sizes of *Alligatorium meyeri, A. franconicum*, *Montsecosuchus depereti*, and *Theriosuchus pusillus,* and may in fact be an over-estimation of their size. The lack of internal fenestration (2) of the supratemporal fenestra is not seen in other atoposaurids, with the exception of *Theriosuchus pusillus* (Owen, 1879), and is thus retained as a local autapomorphy. The division of the nasal aperture (3) is not visible in LMU 1937 I 26 as a result of crushing of the anterior-most portion of the snout, but is present in MNHN 15639. Regardless, this appears to be a feature shared by other atoposaurids including *Theriosuchus pusillus* (NHMUK 48330) and *Theriosuchus grandinaris* (Lauprasert *et al.*, 2011). The relative length of the tail (4) is a feature seen in other atoposaurids including *Atoposaurus* and *Theriosuchus pusillus* and appears to be widespread among Atoposauridae as are characters (5) and (6). Indeed, osteoderm sculpting and a biserial osteodermal shield are present in *Alligatorium, Montsecosuchus,* and *Theriosuchus*. The presence, prominence, and position of a dorsal keel on the biserial osteoderms might be diagnostic at the generic level (7), although there are differences between the German and French specimens, as discussed below. The presence of a dual row of ventral osteoderms in the caudal region is also questionable (8), especially with respect to their morphology (9) – they are rarely and poorly preserved in the ventral region in both French and German specimens. It is probable that post-mortem flattening has re-arranged the paravertebral dorsal osteoderms, which, when viewed laterally, might easily be misinterpreted as belonging to a ventral series. Finally, it should be noted that in the referred specimen of *A. beaumonti* (MNHN 15638), the osteoderms are much less apparent, with just a single row overlying the anterior caudal vertebrae, and possibly a single row concealed underneath the dorsal vertebrae.

Revised diagnosis: Among currently recognised atposaurids *Alligatorellus* can be diagnosed based on the following unique combination of characters and autapomorphies (highlighted with an asterisk): (1*) a skull length to width ratio of 1.5 or above; (2) rostrum unsculpted or substantially less so than cranial table; (3) absence of hypertrophied maxillary tooth 5; (4) absence of raised orbital or supratemporal rims; (5) unperforated supratemporal fenestra; (6*) anterior process of squamosal extends to the orbital margin; (7) dorsal surface of dorsal osteoderms completely sculpted, with parallel and straight anterior and posterior margins ; (8*) dorsal osteoderms with longitudinal ridge along entire lateral margin; (9) caudal osteoderms with smooth, non-serrated edges; (10*) nuchal and sacral osteoderms notably smaller than dorsal and caudal series; (11*) humerus to femur ratio of 0.62-0.66.

A. beaumonti Gervais 1871

Comment [S16]: This section needs careful revision. I have made some suggestions below.

Comment [S17]: I have not read and do not have access to Wellnhoffer's paper but I do not think that his diagnosis is based on what he considered to be autapomorphies. There are many other examples of taxa diagnosed without any recognized autapomorphies, but which differ from other members of the clade to which they belong in a unique combination of primitive and derived characters. Nevertheless I agree that the 1971 diagnosis is unsatisfactory

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Comment [S18]: This doesn't make sense to me

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Comment [S19]: Division of the nasal aperture may well be a character shared by all atoposaurids but is not unique to Atoposauridae being seen in a number of other crocodddyliforms

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Comment [S21]: Within Crocodyliformes this is not an autapomorphy

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Comment [S22]: Not evident from the reconstruction provided in Fig. 2

Comment [S23]: You should provide a differential diagnosis here stating how *Alligatorellus* resembled and differs from other atoposaurid taxa

A. beaumonti beaumonti Wellnhofer 1971

Holotype: MNHN 15639, part and counterpart slabs preserving a near-complete, articulated skull and skeleton, missing the distal forelimb elements and part of the left hindlimb (Fig. 2).

Referred specimen: MNHN 15638, part and counterpart slabs (?) preserving a near-complete articulated skeleton, missing the distal-most caudal vertebrae and part of the left forelimb (Fig. 3).

Type localities and horizons: Cerin, Ain, eastern France; Kimmeridgian (Late Jurassic).

Preservation of holotype: The specimen is dorsolaterally flattened and on the part the dorsal surface of the skull is embedded in matrix comprising a grey lithographic limestone. This obscures both the lateral and ventral surfaces, and much of the mandible. Thirteen maxillary teeth are preserved. The complete, articulated axial skeleton is preserved, with the exception of the three posterior-most caudal vertebrae, and is overlain by a continuous sheath of parasagittal, biserial osteoderms. At least eleven ribs are preserved *in situ* on the left hand side. A partial right scapula is the only preserved element of the pectoral girdle. The right forelimb is missing the proximal humerus and manus, and the left forelimb is disarticulated, lacking the manus. Some fragmentary pelvic elements remain, including both ilia. The left hindlimb is articulated but damaged, missing part of the femoral midshaft, the proximal tibia and fibula, and distal tarsals. The right hindlimb is articulated but missing both the proximal femur and the distal phalanx on digit I. The counterpart preserves two osteoderms and fragments of skull material embedded within the impressions. There is some dendritic mineral growth propagating from the skeleton, possibly composed of goethite.

Preservation of referred specimen: The entire skeleton is laterally flattened on a brick-red and grey slab of lithographic limestone . The skull is ventrolaterally flattened, exposing only the ventral and sinistral sides of the mandible, and the ventrolateral portion of the skull, and nine teeth. The right forelimb is preserved only as an impression, as are the posterior-most caudal vertebrae. Otherwise, the entire axial skeleton is preserved, together with three ribs (and several rib impressions), and the left pectoral and pelvic girdles. Both hindlimbs are complete. A single row of osteoderms is preserved along the nuchal-dorsal series. The cervical vertebrae are recurved slightly posteriorly, and the posteroventrally deflected limbs give the impression of hanging loosely from the trunk.

Additional comments: Wellnhofer (1971) provided a detailed description of both specimens of *Alligatorellus beaumonti*. Here, we provide only a revised diagnosis as the basis for its taxonomic discrimination from the Bavarian specimens of *Alligatorellus*. Using linear morphometrics, Wellnhofer (1971) regarded the Cerin and Bavarian specimens to be of similar, adult ages, and largely based his justification for recognising two distinct taxa on the relatively smaller size of the Cerin specimens (which are approximately 50 mm shorter in total length). However, size and geographical distribution are not the only

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Comment [S26]: Really? Not normally dendritic. I would have thought it more likely to be another Iron /Manganese mineral

Comment [S27]: And there is no counterpart??

Comment [S28]: In the dentary, maxilla, premaxilla or a combination?

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Comment [S30]: Obviously they don't literally 'hang' attributes demarcating the two as distinct taxa, as outlined below.

Revised diagnosis: *Alligatorellus beaumonti* can be diagnosed based on the following unique combination of characters and autapomorphies (highlighted with an asterisk): (1) smooth contact between maxilla and jugal; (2) equal contribution of frontal and parietal to supratemporal fenestra; (3*) frontal with unsculpted posterior and anterior portions; (4) surface of rostrum notably less sculpted than cranial table; (5) relatively large lateral temporal fenestra, approximately 30% the size of the orbit; (6*) medial longitudinal depression on posterior portion of nasal and anterior portion of frontal; (7*) frontal width between orbits narrower than nasals; (8) smooth and unsculpted region on anterior portion of squamosal nearing orbit and posterolateral process of squamosal; (9) sub-rectangular anterior palpebral; (10*) vertebral centra shape grades continuously posteriorly from cylindrical to elongate-spool; (11) secondary osteoderms in caudal series present; (12*) lateral ridge on sacral osteoderms forms an incipient posterior projection; (13*) ratio of femur to tibia extremely high (1.24).

Comment [S31]: Here and below in respect of *A. bavaricus* an additional figure with skull diagrams is required

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Alligatorellus bavaricus n. sp.
Alligatorellus beaumonti bavaricus Wellnhofer 1971

Note on taxonomy: Wellnhofer (1971) regarded LMU 1937 I 26 as the holotype of *A. beaumonti bavaricus*, and we elect this specimen as the holotype of *A. bavaricus* sp. nov. The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/". The LSID for this publication is: zoobank.org:pub:B7CC4367-4203-4AED-8C30-2D7E4E71665D. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS.

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Holotype specimen: LMU 1937 I 26 (Fig. 4).

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Referred specimen: Wellnhofer (1971) also described a second specimen of *A. bavaricus*, held in the private collection of E. Schöpfel. Based on the images and description provided by Wellnhofer (1971), we follow this. However in view of the fact that the specimen remains in private hands and is not accessioned in a registered collection such referral is informal and is used only to draw attention to the existence of a second specimen.

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Type locality and horizon: Solnhofen beds near Eichstatt, southeast Germany; early Tithonian (Late Jurassic).

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Preservation: The specimen is a semi-three-dimensional body fossil preserved obliquely on a slab of Solnhofen 'Plattenkalk', and is fully articulated with its head dorsally recurved. The as preserved spinal column is rod-like with a slight ventral flex, and the limbs are splayed out beneath the trunk. Trunk elements (posterior cervical and dorsal vertebrae, ribs, and osteoderms) are mostly damaged and crushed beyond recognition in an agglomeration, where there is a noticeable trace of soft tissue residue. Poor skeletal preservation means that the anterior-most vertebrae (atlas, axis, and anterior cervical vertebrae) are indistinguishable from one another. Only the eleven anterior-most dorsal paravertebral osteoderms are substantially preserved with a minor and variable degree of caudal imbrication. The next four osteoderms in the series are missing (anteriorly adjacent to the sacrum) but twenty five paired osteoderms are preserved along the tail. Poorly preserved ventral osteoderms are part of the agglomeration around the torso, and are present along the sacrum and tail. The ventral osteoderms terminate posteriorly at the same position as the dorsal series.

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Etymology of species name: bavaricus, based on the area of the type locality, and also the sub-species name provided by Wellnhofer (1971).

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Additional comments: The majority of the features Wellnhofer (1971) proposed as autapomorphies of *A. bavaricus* characterise atoposaurids in general, or are more widespread within Atoposauridae. For example, an 'acute-triangular skull with large orbit' is a general feature seen in all atoposaurids, and the 'biserial osteoderm shield from the nuchal to caudal region' is found in both *Theriosuchus* (Owen, 1879) and *Alligatorium* (Wellnhofer, 1971).

Comment [S34]: As above, did he?

Comment [S35]: And bernissartids

Diagnosis: Alligatorellus bavaricus sp. nov. can be diagnosed based on the following unique combination of characters and autapomorphies (highlighted with an asterisk): (1*) extremely narrow and short skull (ratio of skull width to orbit length is 1.29); (2*) posterior surface of nares longitudinally crenulated; (3) small, slit-shaped antorbital fenestra, with nasal participation in border; (4) anterior ramus of frontal extends beyond anterior tip of the prefrontal; (5*) prominent transverse ridge defining frontal-parietal suture, medial to supratemporal fenestrae; (6*) complex interdigitating contact between dentary and surangular; (7) smooth posterior region of parietal dorsal surface; (8*) dorsal osteoderms with longitudinal medial ridge, becoming more laterally placed anteriorly; (9) isometric caudal osteoderm morphology; (10*) distinct ridge on proximodorsal edge of scapula; (11*) an extremely low humerus to ulna ratio of 1.06; (12*) an extremely low femur to tibia ratio of 1.0; (13*) an extremely high tibia to ulna ratio of 1.72; (14) metatarsals I-IV equidimensional.

Comment [S36]: See above concerning an additional figure

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Description and comparisons of *Alligatorellus bavaricus* n. sp.

The following description is solely of the type specimen LMU 1937 I 26 but, based on the images presented in Wellnhofer (1971), the referred specimen does not appear to differ in any notable way. Bones of the skull of the type are fully fused and vertebrae display complete neurocentral fusion, implying that this specimen of *Alligatorellus* had reached a mature stage of growth (Joffe, 1967).

Skull: Observations of the skull are restricted to the dorsal and right-lateral surfaces. These external surfaces display a moderate degree of sculpting, although to a lesser extent than that of *Theriosuchus* (Owen, 1879; Brinkmann, 1992; Wu *et al*., 1996; Schwarz and Salisbury, 2005) and *Alligatorium* (Wellnhofer, 1971). The skull has an acute-triangular morphology (platyrostral) in dorsal view, typical of atoposaurids, with concave lateral margins along the relatively short snout. The intramandibular angle (defined as the angle between the lateral extremities of the cranial table and the distal snout tip, in dorsal aspect) is slightly greater (37°) than that of *Theriosuchus* (30-32°). Several teeth are preserved *in situ*, and are peg-like (pseudocaniniform), pointed and possess apicobasally and mesiodistally oriented, parallel striations. None of the teeth appear to be serrated, and in general aspect they are indistinguishable from teeth observed in the Cerin specimens of *Alligatorellus beaumonti*. *A. bavaricus* may possess one more maxillary tooth than the French species, although this is difficult to assess with confidence due to the mode of preservation. The dentition of *Theriosuchus* (Owen, 1879; Joffe, 1967; Brinkmann, 1992; Martin *et al*., 2010)is substantially differeeent being heterodont, suggesting a different feeding modes and/or diet. No palatal elements are visible, and aspects of the anatomy of the premaxilla, maxilla, nasals, and external nares are difficult to discern due to dorsal flattening into the matrix and mandible, and because of the absence of the distal snout tip. The occipital region of the skull is also obscured by matrix and crushed, granular bone fragments, which probably represent the anterior-most elements of the axial skeleton.

There is a ventrolateral notch between the premaxilla and maxilla but, unlike *Theriosuchus ibericus* (Brinkmann, 1992) and *Theriosuchus sympiestodon* (Martin *et al*., 2010), this is not occupied by an enlarged tooth. The paired nasals contribute to the external nares via a sagittal anterior projection, as in *Alligatorellus beaumonti*, *Alligatorium meyeri*, and *Theriosuchus pusillus*. Wellnhofer (1971) regarded this feature as diagnostic of *Alligatorellus*, but it may in fact be a synapomorphy of all atoposaurids. A small, slit-like antorbital fenestra is present, a feature that is absent in *A. beaumonti* and other atoposaurids for which the dorsal skull is preserved, but broadly present within *Theriosuchus*, so we consider it to be locally diagnostic. The dorsal surface of the nasals is sculpted by faint longitudinal crenulations, a feature unique within Atoposauridae, but also present in the goniopholidid *Eutretauranosuchus delfsi* (Smith *et al*., 2010; Pritchard *et al*., 2013). As such, this feature is considered a local autapomorphy of *A. bavaricus*. Posterior to the external nares, the lateral margins of the nasals are straight, contrasting with the concave margins observed in *A. beaumonti*. The dorsolaterally facing orbits are large with respect to the cranium, occupying

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Comment [S41]: Is it or isn't it? If it is present in some species but not in others say in which species it is seen and which it is not about one third of the total cranial length and the majority of the skull width. This is comparable to *Atoposaurus oberndorferi* but distinct from *A. beaumonti*, in which the orbits occupy one quarter of the skull length. The relatively large size of the orbits might represent retention of a paedomorphic characteristic (Joffe, 1973). A large amount of secondary calcite growth is present within the orbit, obscuring much of the internal cranial morphology. The right lateral temporal fenestra is deep and arcuate in cross-sectional morphology, but largely obscured as a result of the crushing of the skull. It is separated from the orbit by a mediolaterally-oriented postorbital bar, which descends steeply into the posterolateral internal margin of the orbit. The lateral temporal fenestra is similar in size to the dorsally located supratemporal fenestra, and is approximately a quarter of the size of the external opening of the orbit.

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The frontals are mediolaterally concave, to a slightly greater degree than the parietals, and become extremely thin at the orbital margin, lacking the elevated orbital rims seen in *Theriosuchus* (Owen, 1879). Compared to the nasals, they are relatively wide with respect to the frontals in *A. beaumonti*. The anterior frontal ramus extends slightly beyond the anterior tip of the prefrontal, a feature which we consider to be a local autapomorphy because of its absence in other atoposaurids, but that is present in some other non-eusuchian neosuchians, including *Eutretauranosuchus delfsi* (Pritchard *et al.*, 2013) and *Pholidosaurus purbeckensis* (Salisbury, 2002; Montefeltro *et al.*, 2013). The anterior contacts between the frontals, prefrontals and lacrimals are largely obscured, as is the overall morphology of these pre-orbital elements. However, the majority of the anterior margin of the orbits comprises a deep and thick wedge of bone that descends as a vertical sheet into the orbit, forming a distinctive anterodorsal brow. The maxilla contributes extensively to the ventral margin of the orbit, with the contact between the maxilla and the lacrimal becoming indiscernible more anteriorly due to the mode of preservation. The jugal occupies half of the ventral margin of the orbit, posterior to the maxilla. Palpebrals were either absent or are not preserved, but appear to be present in the anterior orbit of *Alligatorellus beaumonti*.

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The dorsal surface of the skull is mildly sculpted posterior to the orbits by anisotropic and heterogeneously spaced pits that are similar to *Alligatorellus beaumonti*, but are less prominent than those seen in *Theriosuchus* and *Alligatorium*. In contrast, this surface is smooth and unsculpted in *Atoposaurus* (Wellnhofer, 1971; JPT, pers. obv.). It is plausible that the heterogeneous degree of cranial sculpting seen in atoposaurids including *Alligatorellus* and *Montsecosuchus* is useful in distinguishing specimens at the species level. Between the supratemporal fenestrae is a prominent mediolateral ridge defining the suture between the frontal and parietal, a feature we consider diagnostic of *A. bavaricus*. The anterior parietal is not sculpted where it contacts the frontals, unlike *A. beaumonti* where the whole cranial table (excluding the frontals) is homogeneously sculpted. The squamosal is also homogeneously sculpted, with a dorsally convex dorsal surface and orthogonal lateral and posterior margins, differing from *Theriosuchus pusillus* which has a smooth posterolateral process (Owen, 1879; JPT, pers. obv.). The cranial table is mostly flat, in contrast to the slightly domed structure that characterises *Montsecosuchus* (Buscalioni and Sanz, 1990a), and possibly *Atoposaurus*. The anterolateral portion of the squamosal is sharply pointed and curves

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posteromedially around the supratemporal fenestra. Here, it is initially gently arcuate then straight as it contacts the parasagittally-directed and straight medial edge. This gives the squamosal an overall distorted rhombohedral shape in dorsal aspect. The majority of the dorsomedial margin of the squamosal contributes to the supratemporal fenestra, with the lateral portion obscuring most of the ventrally-placed quadrate and quadratojugal. The posterolateral process of the squamosal is greatly reduced compared to other atoposaurids, in which it generally tapers to a point, and is therefore considered to be a local autapomorphy of *A. bavaricus*, being similarly present in other basal neosuchians such as *Amphicotylus lucasii* (Mook, 1942). In *Alligatorellus beaumonti*, there is no development of the posterolateral process, the posterior edge instead being slightly anterolaterally directed. Between the supratemporal fenestrae, the paired, rectangular parietals are as mediolaterally wide as the frontals between the orbits. The parietals contribute to the posteromedial margin of the supratemporal fenestra, but the relationship with the postorbitals is difficult to see due to post-mortem damage. However the postorbital bar is present and weakly developed, possessing a superficial furrow connecting the orbit and the supratemporal fenestra. The frontal only contributes to the supratemporal fenestra at its anteromedial edge. Here, the frontal and parietal form a lateral wedge, which thins laterally into the postorbital bar. The posterior portion of the dorsal surface of the parietal is smooth, a feature otherwise only found in *Atoposaurus*, although in that taxon the skull is entirely unsculpted (Wellnhofer, 1971; JPT, pers. obv.); as such, we consider this heterogeneous pattern of cranial sculpting to be autapomorphic for *A. bavaricus*. The lateral and ventral surfaces of the skull are largely obscured by the displaced and crushed mandible, and the preserved orientation of the skeleton.

The mandible is not visible ventral and anterior to the orbit, and is largely obscured posteriorly. It has been slightly dorsally displaced into the ventrolateral portion of the right-lateral face of the skull. The mandible broadens posteriorly both mediolaterally and dorsoventrally, developing a lateral shelf as it flares out beneath the lateral temporal fenestra, possibly at the position at which the mandibular fenestra would have been situated. The ventral margin of the mandible curves medially and thins mediolaterally substantially at its posterior extremity, where it forms an acute and recurved process, the posterior margin of which is gently concave and slightly set back from the posterior edge of the cranial table. The contact between the surangular and dentary appears to be complex, as opposed to smooth and arcuate as in other atoposaurids, and we tentatively consider this to be a local autapomorphy for *A. bavaricus*, given that the mandible has undergone post-mortem taphonomic distortion.

Axial skeleton: One of the most striking features of atoposaurids is that the tail length is greater than the length of the torso, and comprises approximately one-half of the total length of the skeleton. In *Alligatorellus bavaricus* there are seven cervical (including the axis and atlas) and fifteen dorsal vertebrae (note that Wellnhofer (1971) observed only seventeen presacral vertebrae, using osteoderm count as a proxy). These vertebrae are mostly indistinguishable from one another, but their presence is estimated based on their associated dorsal paravertebral osteoderms which, along with the poor preservation of the trunk region, largely obscure the morphology of the vertebral column. As noted by Wellnhofer (1971), three sacral vertebrae seem to be present, but their preservation means that this cannot be determined with any certainty, with all elements crushed beyond distinction. If correctly determined, sacral count might be a distinguishing feature between *A. bavaricus* and *A. beaumonti*, with the latter only having two sacral vertebrae, but variation in sacral count is difficult to discern in atoposaurids due to poor preservation. There are around forty caudal vertebrae, although the precise number is difficult to determine, with the distal-most two or three absent, as indicated by impressions. Much of the caudal vertebral series is variably covered in martix and fixing glue, obscuring much of the morphological detail and intervertebral articulations. In the central caudal series, a melange composed of dorsal and ventral paravertebral osteoderms obscures much of the anatomical detail. Only the first four caudal vertebrae can be used to observe any of the anatomy from a right-lateral perspective. It is unknown whether the vertebrae were procoelous, as in *Theriosuchus* and eusuchians (e.g., Pol *et al*., 2009), or amphicoelous.

The dorsal osteoderms occur in a biserial row from the anterior-most cervical vertebrae to about the mid-point of the caudal series, a feature that characterises all unambiguous atoposaurids, with the exception of *Atoposaurus*, and that is also absent in the putative atoposaurid *Karatausuchus* (Efimov, 1976; Storrs and Efimov, 2000). The osteoderms of *A*. *bavaricus* are imbricated along their entire length, and there is no ‘peg and socket’ articulation as described in two scutes assigned to *Theriosuchus pusillus* (Owen, 1879; Schwarz-Wings *et al*., 2011) and in *Theriosuchus guimarotae* (Schwarz and Salisbury, 2005). The osteoderms of *A. bavaricus* are rounded, and the lateral edges are predominantly convex, with one or two being marginally concave. There is a central longitudinal ridge on the dorsal surface of osteoderms of *A. bavaricus*, similar to some of the caudal osteoderms in *Theriosuchus*, but contrasting with *Alligatorium meyeri* and other atoposaurids. The degree of sculpting on the osteoderm dorsal surfaces increases posteriorly, as does the prominence of the longitudinal keel which shifts to a slightly medial position from an initially more central position, unlike *Alligatorellus beaumonti* in which it is consistently laterally placed as a distinct shelf. The osteoderm lateral and medial edges are smooth and either straight or convex, and the straight anterior and posterior margins are parallel. The morphology of the ventral osteoderm series is very similar, where visible, but with more prominent longitudinal ridges in the more posterior elements. There is no visible morphological heterogeneity in the nuchal and sacral osteoderms, contrasting with *Alligatorellus beaumonti* in which this feature is highly distinctive. It is unknown whether the ventral series are paired or not in *A*. *bavaricus*, as the ventral portion of the skeleton is mostly unobservable.

Other minor axial elements are partially visible beside the osteoderms. Two thoracic ribs are preserved embedded within the trunk melange. They are gently arcuate in their overall morphology, and not *in situ*. There are several other rib elements more anterior to these and just ventral to the anterior-most osteoderms, but they are largely obscured by the overlying martix and axial elements. Three posteroventrally directed chevrons are *in situ* with their proximal caudal vertebrae, positioned just posterior to the only visible three-dimensionally preserved vertebrae.

Pectoral girdle: Only the right scapula is preserved, and is fragmented at both ends, including both

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the glenoid fossa and coracoidal contact. It is bow shaped, with a distinct dorsoventral contraction and mediolateral thickening into a compressed cylindroid at mid-length. The dorsal surface becomes thin and sharp anteriorly, culminating in a broad and deep, basin-like medial depression, contrasting with *Montsecosuchus depereti* in which the entire element is flat (Buscalioni and Sanz, 1990a). The proximodorsal edge overhangs this depression, a feature not observed in other atoposaurids, and is considered to be a diagnostic feature of *A. bavaricus*. Posteriorly, the scapula flares out in a similar fashion to the anterior blade, but the distal portion is mostly absent so the complete morphology is unknown. A posteroventral process projects out from the posterior blade, twisting from the ventral surface into a short, thickened rod.

Forelimbs: The right forelimb is nearly complete with an articulated humerus, radius and ulna, but with a crushed manus. The proximal third of the humerus is also crushed, with the external cortices of the exposed shaft removed, revealing the internal bone. The humerus expands slightly proximally, and the shaft is straight and broader mediolaterally than anteroposteriorly. The morphology of the deltopectoral crest cannot be determined. The radial condyle is broad and directed anteriorly. The distal articular surface of the humerus is strongly rugose, and oriented at 40° to the long axis of the shaft, with the lateral margin forming a gently downwardly-depressed shape. The shaft is relatively straight, similar to more advanced neosuchians such as *Shamosuchus* (Pol *et al*., 2009). The anterior intercondylar groove is not visible, but the supracondylar fossa forms a deep posterior furrow, terminating a short distance up the shaft, and is bound medially by the relatively weaker ulnar condyle, the morphology of which is mostly obscured. The external surfaces of the condylar heads are smooth. The humerus is slightly shorter than that of *A. beaumonti*, but the radius is proportionally longer. The stylopod to zeugopod ratio in both limbs is proportionally lower than in all other atoposaurids, a feature that we consider diagnostic of *A. bavaricus.*

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The radius is slightly longer than the more robust ulna, the two resting against each other without twisting sharply; as such the respective proximal and distal articular surfaces have long axes in the same orientation. The radius is gently longitudinally arcuate in its proximal third, conforming to the gentle curvature of the distal ulnar shaft. The radial head is mediolaterally expanded, and is about two-thirds the size of the ulnar head it rests against. The ulnar head is damaged, and the radial head and the associated humeral condyle actually appear quite mismatched in size suggesting a large volume of cartilage or muscle attachment at this joint, also emphasised by the heavily rugose articular surface. The lateral part of the radial shaft thins to about 70% of its width and becomes ridge-like at around two-thirds of its length. The ulnar shaft is equidimensional through its entire length, and finishes with a triangular-shaped distal articular surface. The carpus cannot be fully observed.

Little of the left forelimb is preserved: the distal humerus is crushed with the proximal ulna and entire radius missing, left only as impressions. However, aspects of the morphology of the carpus can be observed. The radiale is long and slender, with expanded proximal and distal ends, much like *A. beaumonti* in which the elements are well-preserved in the holotype. The ulnare is slightly shorter, with a stronger mediolateral compression of the shaft, and overall more gracile morphology. In *A. beaumonti*, the ulnare has a proximal groove on the lateral surface, terminating at 80% of the length of the element, but whether this is present in *A. bavaricus* cannot be determined. However, the ulnare in *A. bavaricus* is not 'hatchet shaped' as in *A. beaumonti* or the specimen assigned to *Alligatorellus* sp. by Schwarz-Wings *et al*. (2011). Furthermore, the radiale in *A. beaumonti* is larger than the ulnare, distinguishing the two species of *Alligatorellus*. All additional carpal elements in *A. bavaricus* are distorted to the point where their morphology cannot be meaningfully observed. The entire manus is bent backwards, indicated by its impression and in a similar manner to the pedal orientations. All of the elements are highly distorted and crushed, with only moderate lateral compression indicated by the slight crushing of the more gracile elements.

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Pelvic girdle: Only fragments of the pelvic girdle are preserved. The ilium forms an elongated S-shape in dorsal view, and is thickened anteriorly. Much of the morphology is obscured by the orientation of the specimen on the rock slab, but the postacetabular process appears to be fenestrated at its tip (although this might be a post-mortem artefact), greatly thickened, and leads into a deep and broad acetabulum. An element just below this on the slab is one of the pubes. Much of the morphology is again obscured by the orientation in which it is embedded in the matrix. The proximal head is expanded into a broad wedge-shape and twists slightly to become oblique to the stouter distal end which is more circular in cross section. The proximal portion of the shaft is transversely flattened and sub-elliptical in cross-section, and has a strongly rugose surface, partially obscured by an overlying displaced rib. There is a fan-shaped structure situated anterior to the ilium, which we interpret as a fragment of the anteriorly displaced ischium. The distal end is thin and gently convex, with a slightly crenulated distal extremity. Gentle striations from the distal end are directed towards the transversely thickened shaft, which increases in breadth more proximally on the dorsal margin and has a more slender ventral margin. The proximal end is hidden underneath the skeleton so that the remaining morphology cannot be observed.

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Hindlimbs: Overall, the hindlimbs are about 1.4 times the length of the forelimbs. The right hindlimb is mostly complete with a laterally flattened tarsus and pes. The femur is missing from the left hindlimb (although it is possibly hidden underneath the skeleton), and the tibia and fibula are both crushed. The left pes is well-preserved, with partially crushed tarsal and pedal elements. The femur is the most robust limb bone of the skeleton, and is morphologically similar to the ulna, being gently sigmoidal down the length of the shaft. The femoral head is moderately expanded and equidimensional to the distal end of the femur. The femoral head grades smoothly into the posteriorly placed fourth trochanter, which is weakly developed, ridge-like, and distally thickened, terminating at one-sixth of the length from the proximal end. Adjacent to this, on the lateral surface, there is an accompanying groove for attachment of the femoral-pelvic musculature. The distal end of the right femur is damaged and fractured and the distal condylar morphology cannot therefore be determined.

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The left tibia and fibula are mostly concealed within the slab and underneath other bones, and only the straight shafts are exposed. The lateral surfaces of both elements from the right hindlimb are fully exposed, and demonstrate that they are equal in length to the femur. Both ends of the tibial shaft are anteroposteriorly compressed, with the distal end slightly more so. The proximal portion of the tibia is slightly posteriorly deflected, but to a lesser degree than in *Alligatorellus beaumonti*. The tibial shaft becomes slightly anteroposteriorly expanded at mid-length. Distally, the lateral margin of the tibia thins anteroposteriorly, culminating in a sharp ridge at the distal end, and resulting in a triangular cross-section. The proximal half of the fibula is gently twisted to accommodate the mid-tibial expansion and articulate with the posterior face of the proximal head of the tibia. As a result of the fully articulated nature of the tibia and fibula, the morphology of the proximal and distal articular surfaces is obscured. Furthermore, the distal end of the fibula is damaged. In lateral view, the fibula is much more slender than the tibia, and has a more circular cross section than the elliptical to triangular tibia. The astragalus is not visible in either hindlimb. The calcaneum is present, but is obscured by matrix and glue.

On the right hindlimb, metatarsals I-III and part of metatarsal IV are preserved, as well as a poorly preserved, vestigial fifth metatarsal that is less than one-third the length of the other four metatarsals. Their long axes are parallel to one another, with the proximal and distal ends resting against each other. The nature of the distal articulations is obscured. The left pes is preserved in an oblique view, and provides a better perspective of the metatarsal morphology, although metatarsal V is not visible. The tarsal phalangeal formula, as stated by Wellnhofer (1971), is 2, 3, 4, 4, (1). The metatarsals are long, gracile, and transversely expanded at their proximal ends with an overall similar morphology. Their distal ends have been slightly anteroposteriorly compressed, and the straight shafts all have an elliptical cross-section. On the left pes, the proximal tip of metatarsal I is obscured beneath metatarsals II-IV, but where visible the metatarsal is anteroposteriorly compressed, and twists anteromedially towards its distal end where it thickens and broadens into a sub-oval cross section. The distal articular surface of metatarsal I is only partially visible; this rugose surface curves medially to occupy the distal-most edge of the medial surface. Metatarsal II is slightly longer than metatarsal I, with a mediolaterally compressed proximal end, and a ventral surface that forms a thin ridge. Metatarsal II gradually thickens distally, and the shaft twists in a similar manner to metatarsal I, but instead the ventromedial edge becomes more prominent as a ridge, bounding the medial edge of a small distal depression on the ventral surface. The distal end of metatarsal II is convex, and the articular surface is obscured. Most of metatarsal III except for the shaft is obscured, with the shaft appearing to be as long as metatarsal II but thickened to a lesser degree distally. Metatarsal III is slightly more gracile than the others. The sharpness of the proximoventral ridge is also less apparent in metatarsal III. Metatarsal IV is mostly obscured but has a straighter, less twisted shaft that is more continuously oval in cross-sectional morphology than the others.

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Additional material previously referred to *Alligatorellus*

Atoposauridae indet.

(‘*Alligatorellus* sp.’ Schwarz-Wings *et al*., 2011)

Specimen: MfN MB. R. 4317.1-12, a partial disarticulated skeleton.

Locality and horizon: Kelheim, Bavaria, Germany; early Tithonian (lithographic limestones).

Preservation: Disarticulated axial and appendicular elements adjacent to a single row of paravertebral osteoderms. Some limb elements have been prepared out of the matrix.

Comments: An additional specimen from Bavaria was recently assigned to *Alligatorellus* sp. by Schwarz-Wings *et al*. (2011). This is a substantially larger individual than the four known specimens comprising *A. beaumonti* and *A. bavaricus*, and is represented by a disarticulated, partial postcranial skeleton. With the revised diagnosis presented above for *Alligatorellus*, the only comparable diagnostic material is the osteoderms which differ in morphology to those of *A. beaumonti* and *A. bavaricus* . In MfN MB. R. 4317.1-12,: (1) dorsal osteoderms are square-shaped, rather than rectangular, with a possible anterior articular process (similar to the ‘peg and socket’ morphology seen in some specimens of *Theriosuchus* and goniopholidids); (2) dorsal osteoderms are distinctly asymmetrical about their long-axis; (3) ventral osteoderms bear a series of nutrient foramina, as well as an anteroposteriorly oriented ridge along their anterior portions (although note that this aspect of the osteoderms is not visible in any additional specimen of *Alligatorellus*); and (4) caudal osteoderms are often laterally serrated, grading from a narrow to elongated elliptical shape. Several of these features regarding osteoderm morphology may be diagnostic within Atoposauridae. An additional difference is the more laterally than medially expanded proximal end of radiale, with a proximodistally oriented crest extending along the anterior surface of the shaft. This together with the outlined differences in osteoderm morphology indicate that MfN MB. R. 4317.1-12 may represent a distinct atoposaurid taxon, or another species of basal neosuchian outside of Atoposauridae.

Based on the revised diagnosis for *Alligatorellus* presented in this study and the notable differences in preserved osteoderm morphology, it is questionable whether the specimen described by Schwarz-Wings *et al*. (2011) can be assigned to *Alligatorellus*. Its initial assignment to this genus was based on several lines of evidence, including the longitudinally elliptical shape of the caudal osteoderms, a feature otherwise only seen in the distal-most caudal osteoderms of *Alligatorellus beaumonti*, although they are more rectangular in the French taxon. However, the morphology of the osteoderms of MB. R. 4317.1-12 is similar to the dorsal osteoderms of *Montsecosuchus depereti*, including the presence of a continuous, medially-positioned keel along the external surface (Buscalioni and Sanz, 1990a; JPT, pers. obv), but *Montsecosuchus* does not preserve any osteoderms of similar size or morphology to the imbricated series preserved in MB. R. 4317.1-12. The imbrication of these dorsal osteoderms cannot be used to assign MB. R. 4317.1-12 to *Alligatorellus*, as this is a feature also present in *Theriosuchus pusillus* and *Alligatorium*, as well as the putative atoposaurid *Brillanceausuchus*, and is therefore perhaps a feature characteristic of Atoposauridae.

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The higher degree of sculpting of the osteoderms was regarded as ontogenetic variation by Schwarz-Wings *et al*. (2011), but all other specimens of *Alligatorellus* also appear to represent mature individuaals. Therefore, the greater degree of sculpting observed in the osteoderms of MfN MB. R. 4317.1-12 may represent a taxonomic difference. The position of the dorsal keel on these osteoderms, and the lack of symmetry in their outlines in dorsal aspect also represent differences between those of MfN MB. R. 4317.1-12 and those observed in other specimens assigned to *Alligatorellus*. Additionally, the limb ratios presented in table 2 of Schwarz-Wings *et al*. (2011) imply that this specimen is allometrically quite distinct from *Alligatorellus*, and perhaps more closely related to *Alligatorium*. For now, we consider MB. R. 4317.1-12 to be an indeterminate atoposaurid pending a comprehensive species-level phylogenetic analysis of Atoposauridae (in preparation)in which it is included.

Discussion

Osteoderm morphology in atoposaurid systematics

The morphology of the parasagittally-arranged postcranial osteoderms of atoposaurids has not previously been regarded as an important characteristic in atoposaurid taxonomy, generally due to their relatively rare preservation *in situ* (e.g., Buscalioni and Sanz 1990a; Michard *et al*., 1990; Wu *et al*., 1996). The exception to this is a study of western European specimens by Schwarz-Wings *et al*. (2011). However, as noted here for specimens referred to *Alligatorellus*, subtle differences in osteoderm morphologies, particularly the extent, position, and continuity of the longitudinal keels on the dorsal surfaces, can prove to be diagnostic at species level.

The pattern of ornamentation on the osteoderms of atoposaurid taxa, as with other osteoderm-bearing crocodylomorphs (Vickaryous and Hall, 2008), is similar to that seen in dermatocranial ornamentation, particularly with respect to the dorsal surface of the skull table. Exceptions to this are *Atoposaurus* and the possible atoposaurid *Karatausuchus*, in which there is no evidence of cranial sculpting, and for which there are no preserved osteoderms (Wellnhofer, 1971). Furthermore, the general distribution of osteoderms in *Alligatorellus* is similar to that observed in basal crocodylomorphs such as sphenosuchians and protosuchians, which have biserial rows of imbricated, rectangular dorsal osteoderms that might have served in a more functional support role than that proposed for atoposaurids (Clark and Sues 2002; Pol *et al*., 2004).There remains the possibility that osteoderm morphology varies intraspecifically, with multiple morphotypes represented within a population, as is the case in some other archosaurs (e.g., ankylosaurs [Burns, 2008]). However, sample sizes are currently too small to ascertain if this might be the case for atoposaurids. Nevertheless, unequivocal intrageneric differences in osteoderm morphology are observed in *Alligatorium* and *Theriosuchus* (e.g., Owen, 1879; Wellnhofer, 1971; Wu *et al*., 1996), prompting consideration of its utility for systematic placement of *Alligatorellus.*

Establishing the positional homology of osteoderms is important for evaluating taxonomic status in many tetrapod groups, including crocodylians (Ross and Meyer, 1983), aetosaurians (Parker, 2007; Parker

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and Martz, 2010), and chronosuchians (Buchwitz *et al*., 2012). This is difficult in the case of less complete or disarticulated specimens, such as that described by Schwarz-Wings *et al*. (2011) comprising articulated and disarticulated elements which they consider to represent a single individuaal with heterogeneous osteoderm morphology and which was assigned by them to *Alligatorellus* sp. In *Alligatorellus*, both the positional homology and differences in morphology in the discrete axial regions are diagnostic at species level. There are four regions; cervical (or nuchal), dorsal, sacral, and caudal. These regions typically comprise continuous rows of anteroposteriorly arranged (paramedian or paravertebral) osteoderms. On the basis of osteoderm morphology and arrangement *Alligatorellus* differs from *Theriosuchus pusillus* and advanced eusuchians such as *Leidyosuchus* which have the ventral body encased within an articulating (but not overlapping or imbricating) shield of parasagittal rows of singular osteoderms (Owen, 1879; Brochu, 1997). It also differs from from *Alligatorium* in which osteoderms bear no dorsal keel, and from *Montsecosuchus* which has two to three rows of non-imbricating, and longitudinally oval dorsal osteoderms. Below, we discuss the three distinct morphotype series found in specimens ascribed to *Alligatorellus*.

A. bavaricus morphotype

The dorsal keel in osteoderms of *A. bavaricus* is in a more medial position nuchally, gradually migrating laterally along the dorsal series before becoming medially placed in the sacral and caudal series (Fig. 5A). Throughout this gradation, individual osteoderms are similarly robust, but adopt an increasingly more sub-rectangular to elliptical morphology posteriorly. Whereas they imbricate in the dorsal series, this change in shape leads to them abutting one another longitudinally, with no overlap. The longitudinal keel always occupies the entire length of the dorsal surface, and becomes more prominent posteriorly. There may have been a caudal ventral series of secondary osteoderms, but these are few in number and do not extend beyond the anterior half of the tail. This is similar to the condition in *Montsecosuchus depereti* (Buscalioni and Sanz, 1990a), but contrasts with *Theriosuchus*, in which they extend to the end of the caudal series. In contrast to *A. beaumonti*, the dorsal keel observed in sacral and anterior caudal osteoderms of *A. bavaricus* never develops an incipient posterior projection. It is likely that the 'accessory osteoderms' of *Alligatorellus bavaricus* described by Wellnhofer (1971) are the result of incomplete osteoderm development. The evidence for this is that they appear to be mostly comprised of the longitudinal keel, which forms as part of the earliest phase of osteoderm development (Vickaryous and Hall, 2008).

A. beaumonti morphotype

The biserially arranged osteoderms of *A. beaumonti* form a continuous dorsal shield, similar to *Theriosuchus pusillus* and other atoposaurids (Fig. 3). Their longitudinally imbricating arrangement is comparable to that of extant alligatoroid species like *Caiman crocodilus* and *Alligator mississippiensis* (Burns *et al*., 2013), but with fewer paramedian dorsal series. The extent of the caudal ventral series is much greater than in *A.*

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bavaricus, forming a complete dermal coating. The distal-most osteoderms are small, seemingly under-developed, sculpted elements. In the caudal series, the longitudinal ridges are pronounced, longitudinally extensive, and medially placed, similar to *A. bavaricus*. The more sacrally placed caudal elements have less pronounced keels, unlike *A. bavaricu*. They also become smaller and more ovate, with the ridges gradually almost disappearing and only occupying the posterior portion of each element, while sculpting remains the same. This skewing of the keels is most pronounced in the dorsal and sacral osteoderms, where they form rounded protrusions on the dorsal side and become laterally displaced on the ventral series. This unusual shift is particularly evident in the dorsal series where the lateral keel becomes prominent, more anteroposteriorly extensive and forms a distinct step from the main body of each osteoderm (Fig. 5B). The ventral and dorsal morphology is quite similar, with the ventral keels almost seeming to diverge ventrally with each accompanying rib. The sacral and anteriormost caudal osteoderms develop an incipient lateral projection, almost appearing to diverge into two individual elements medial to this. The ventral series either terminates around the position of the third dorsal rib or is not preserved anteriorly from this point. The dorsal series adopts a heterogeneous range of morphologies, with some elements reducing to around one-sixth the size of the other osteoderms more nuchally, and with all losing the presence of the keel. This contrasts with *Alligatorium meyeri* and *Theriosuchus pusillus*, where they are morphologically continuous.

MfN MB. R. 4317.1-12 ('*Alligatorellus* sp.') morphotype

The deeper sculpting present in this specimen was ascribed to ontogenetic variation by Schwarz-Wings *et al*. (2011), based on its larger size compared to other specimens of *Alligatorellus* (Fig. 5C). Maturity of the type specimens of both species of *Alligatorellus* is discussed above as are differenced in osteoderm morphology suggesting that this specimen represents a taxon distinct from *Alligatorellus*. These differences include the more medial position of the keel in '*Alligatorellus* sp.', and the lateral deflection of the body of the osteoderms adjacent to this. The keel is also not as longitudinally continuous in MfN MB. R. 4317.1-12 as it is in *A. beaumonti* and *A. bavaricus*. Additionally, the lateral edge is serrated, and there are unsculpted areas on the dorsal surface. Moreover, they are less robust overall than the other specimens of *Alligatorellus* in spite of their greater size, and overall appear similar to the osteoderm ascribed to *Theriosuchus* sp. by Wu *et al*. (1996). Future histological analyses may prove useful in increasing our understanding of the taxonomic utility of atoposaurid osteoderms (e.g., Witzmann, 2009; Burns *et al*., 2013).

The taxonomic validity of Atoposaurus* and *Alligatorium

Alligatorellus beaumonti coexisted with *Atoposaurus jourdani* and *Alligatorium meyeri* in eastern France, while *Alligatorellus bavaricus* coexisted with *Atoposaurus oberndorferi*, and possibly *Alligatorium paintenense* and *Alligatorium franconicum* in southeastern Germany (Wellnhofer, 1971; Figs. 1, 2). This high diversity of atoposaurids in the Late Jurassic of Germany and France, combined with potential juvenile

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features in *Atoposaurus*, has led some to suggest that '*Atoposaurus*' might in fact represent a juvenile of one of the other sympatric atoposaurid species (Buscalioni and Sanz, 1988). Furthermore, Benton and Clark (1988) have also suggested that that *Atoposaurus, Alligatorellus* and *Alligatorium* might represent a single growth series.

Atoposaurus is unique among all unequivocal atoposaurids in lacking osteoderms, Schwarz-Wings *et al*. (2011) suggested that this might merely be a taphonomic artefact; however preservational selectivity of this sort seems unlikely given that there is no clear reason why similarly ossified parts of the skeleton would undergo differential preservation. However, diminutive size, the absence of any cranial sculpting and calcified palpebrals, might do suggest juvenile status. Furthermore, *Atoposaurus* looks superficially similar to the alligatoroid *Diplocynodon* from Messel (Eocene; Delfino and Sánchez-Villagra, 2010), in terms of the relatively long caudal vertebral series, large orbits, lack of ossification of the dermal armour, and proportionally short skull. As such, *Atoposaurus* superficially takes on the appearance of more advanced eusuchians, while retaining paedomorphic characteristics (e.g., the proportionally large orbits). In crocodylians, the initiation of osteoderm ossification is usually substantially delayed relative to skeletal ossification (Vickaryous and Hall, 2008), so it is difficult to infer a more accurate ontogenetic age for *Atoposaurus* specimens based on a lack of osteoderms. However, there are additional morphological aspects that demonstrate that *Atoposaurus* might not be a juvenile.

Similar to most other atoposaurids, *Atoposaurus* has a relatively short, low, acute, triangular skull. However, as with some theropod dinosaurs, the extant crocodylian *Osteolaemus*, and perhaps even the alligatoroid *Alligator*, shortening of the rostral region may be a paedomorphic feature, with the morphology similar to juveniles and sub-adult specimens of *Melanosuchus* (the black caiman) (Foth, 2013). A platyrostral skull is also known in basal eusuchians such as *Iharkatosuchus maxakii* (Osi *et al*., 2007), and is distinct from the majority of contemporaneous crocodylomorphs, including goniopholidids and thalattosuchians. Heterochrony in crocodylomorphs may be directly related to body size or diet, as atoposaurid species and *Osteolaemus* are relatively small forms and occupy distinctive ecologies. However, patterns of heterochrony, particularly relating to paedomorphosis, in 'dwarfed' specimens are currently poorly understood in crocodylomorphs, but could be responsible, at least in part, for the lack of osteoderm ossification in *Atoposaurus*.

The degree of suturing between the vertebral centrum and neural arch provides ontogenetic information (Mook, 1933; Brochu, 1996). Closure of cervical sutures is a consistent indicator of morphological maturity, and is known in more basal crocodylomorphs (e.g. thalattosuchians; Delfino and Dal Sasso, 2006) and advanced eusuchians (Brochu, 1996). In *Atoposaurus jourdani*, the neural arches are fused to the centra (MNHN 15680; JPT, pers. obv.), which implies that these specimens are not juveniles, and despite their size represent a more mature growth stage. We therefore suggest that *Atoposaurus* represents an extreme case of dwarfism. Furthermore, it is interesting to note that other putative atoposaurids of diminutive size, such as the 160 mm long *Karatausuchus* (Efimov, 1976) also lack

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osteoderms, suggesting that osteoderm development might be positively correlated with body size in atoposaurids.

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Alligatorium is currently composed of three species: *A. meyeri* from Cerin, France (Vidal, 1915), and *A. franconicum* (Ammon, 1906) and *A. paintenense* (Kuhn, 1961) from Painten, central Bavaria, Germany. However, based on the figures and descriptions provided by Wellnhofer (1971), *A. franconicum* (based on an articulated hindlimb and pelvic girdle) cannot be distinguished from *A. paintenense* (a near-complete, articulated skeleton), aside from slight differences in femur-to-tibia length proportions. Given that both specimens are from the same locality, we tentatively conclude that they do not represent distinct species, and regard *A. paintenense* (Kuhn, 1961) as synonymous with *A. franconicum* (Ammon, 1906), pending the relocation of the type material and/or discovery of new material. The type specimen of *A. paintenense* is clearly distinct from *A. meyeri* and both species of *Alligatorellus*, based on its more longirostrine snout, and dorsal osteoderms which each possess a longitudinal keel and an anterolateral hook (Wellnhofer, 1971). *A. meyeri* can be distinguished from *Alligatorellus* based on the absence of a longitudinal keel on all osteoderms in the latter taxon, as well as disparity in the cranial sculpting between the two taxa.

The French specimens of *Alligatorellus* and *Atoposaurus* both are proportionally smaller with respect to their total length to skull length (ratios of 5.4-5.59) compared to their generic German equivalents (6.73-6.78), and members of both genera are smaller still than *Alligatorium* (6.88-7.15). However, the skull length to orbit length ratio is 2.5 in *Atoposaurus jourdani* and 4.0 in *A. beaumonti*, with both *A. bavaricus* and *A. oberndorferi* having a ratio of approximately 3.2. *Alligatorellus* has a relatively longer skull to width ratio than *Atoposaurus* (*A. beaumonti* = 1.8; *A. bavaricus* = 1.5; *Atoposaurus jourdani* = 1.38). A further difference between the two genera is the larger humerus to femur ratio in *Alligatorellus*. If *Atoposaurus* was indeed a juvenile of *Alligatorellus*, then we would expect the same scaling relationships between the geographically different taxa. As such, we find no convincing evidence to ssuggest that *Atoposaurus* is a juvenile of a contemporaneous atoposaurid. This taxonomic reappraisal suggests that there were three sympatric atoposaurid taxa – *Alligatorellus*, *Alligatorium*, and *Atoposaurus* – in both Late Jurassic French and German basins.

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European Atoposaurid Diversity

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The Late Jurassic–Early Cretaceous of Europe records high atoposaurid diversity, comprising the multispecific genera *Alligatorellus*, *Alligatorium*, *Atoposaurus* and *Theriosuchus*, as well as *Montsecosuchus depereti* (Gervais, 1871; Owen, 1879; Wellnhofer, 1971; Buscalioni and Sanz, 1990a; Brinkmann, 1992; Schwarz and Salisbury, 2005). Currently valid European species of *Theriosuchus* include: *T. guimarotae* from the Kimmeridgian of Portugal (Schwarz and Salisbury, 2005); *T. pusillus* from the Berriasian of England (Owen, 1879; Salisbury, 2002); *T. ibericus* from the Barremian of Spain (Brinkmann, 1989, 1992); and *T. sympiestodon* from the Maastrichtian of Romania (Martin *et al.*, 2010; 2014). However, support for the monophyly of these species of *Theriosuchus* has yet to be adequately evaluated. Such evaluation is

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particularly required in view of the temporal distribution of the genus as currently understood spanning some 90 million years, and a putative Asian occurrence (*T. grandinaris*; Lauprasert *et al*., 2011).

Late Jurassic outcrops of the Eichstatt-Solnhofen region of Bavaria, south-eastern Germany, have now yielded *Alligatorellus bavaricus*, as well as up to three additional atoposaurid species: *Atoposaurus oberndorferi, Alligatorium franconicum* (including *Alligatorium paintenense*; see above), and the atoposaurid described by Schwarz-Wings *et al*. (2011) as *Alligatorellus* sp. The Late Jurassic limestones of Cerin, eastern France, have yielded *Alligatorellus beaumonti*, *Alligatorium meyeri*, and *Atoposaurus jourdani* (Wellnhofer, 1971). From Montsec in Spain, only the late Berriasian–early Valanginian *Montsecosuchus* (‘*Alligatorium*’) *depereti* is known (Vidal, 1915; Peybernes and Oertli, 1972; Buscalioni and Sanz, 1990a). Along with these, there is a host of European material ascribed to *Theriosuchus* sp. from: the Kimmeridgian of northwest Germany (Thies *et al*., 1997; Karl *et al*., 2006); the Berriasian of Scandinavia (Schwarz-Wings *et al*., 2009); the Berriasian of Charente, France (Pouech, 2006); the Berriasian–Valanginian of northern Germany (Hornung, 2013); the Valanginian–Barremian of England (Buffetaut, 1983); and the Hauterivian–Barremian of Iberia (Buscalioni and Sanz, 1984, 1987b; Ruiz-Omenaca *et al*., 2004; Buscalioni *et al*., 2008; Canudo *et al*., 2010). Indeterminate atoposaurid remains from the Cenomanian of France (Vullo and Néraudeau, 2008), and mid-Coniacian Kaiparowits Formation of Utah, US (Eaton *et al*., 1999), as well as *Theriosuchus*-like teeth from the Santonian of Hungary (Osi *et al*., 2012) and the Upper Campanian-Maastrichtian of Portugal (Galton, 1996), bridge the temporal gap between these Late Jurassic–Early Cretaceous atoposaurid remains and *Theriosuchus sympiestodon* from the latest Cretaceous of Romania (Martin *et al*., 2010, 2014). They also hint at a high cryptic diversity of mid-Late Cretaceous atoposaurids, as well as their presence in North America. Additionally, tracks from the Kimmeridgian of Asturias, Spain (Avanzini *et al*., 2010) might be attributable to atoposaurids, extending their Late Jurassic geographic range.

It is possible that the high diversity of Late Jurassic to Early Cretaceous European atoposaurids is related to the island archipelago that existed during this time (Fig. 6), with epicontinental seas and fluctuating sea levels (Ziegler, 1988; Schwarz and Salisbury, 2005; Miller *et al*., 2005). The separation of areas (e.g., basins in present day Cerin and Bavaria) might have led to allopatric speciation, evidenced by closely related species found in each region (i.e., *Alligatorellus beaumonti, Alligatorium meyeri* and *Atoposaurus jourdani* in Cerin, and *Alligatorellus bavaricus*, *Alligatorium franconicum* and *Atoposaurus oberndorferi* in Bavaria). The small body size of atoposaurids in general might also be explained by these environmental conditions, with insular dwarfism driven by the reduction in range size, as also proposed for the contemporaneous Late Jurassic German sauropod *Europasaurus* (Sander *et al*., 2006; Marpmann *et al*., in press). This reasoning is also supported by the persistence of atoposaurids into the Maastrichtian as part of an assemblage of insular island dwarfs in a range of environments and localities including the Haţeg Basin of Romania (Benton *et al*., 2010; Csiki and Benton, 2010; Martin *et al*., 2010; 2014). Dwarf crocodiles are also known from the Quaternary of the Aldabara Atoll (western Indian Ocean), with *Aldabrachampsus dilophus* (Brochu, 2006) indicating that island dwarfism in crocodylomorphs might not be an uncommon

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Comment [S65]: I do not agree for reasons set out in a comment on the title and abstract and expanded upon in the review feature. Multiple contemporaneous dwarf species within a similar geographic region is analogous to that of the extant African dwarf crocodile, *Osteolaemus*, which is divided into a Congo Basin form (*O. osborni*), a West African form (*O. tetraspis*), and possibly a third distinct lineage within West Africa (Eaton *et al*., 2009; Shirley *et al*., 2013), as well as other extant crocodylians (e.g., Cedeno-Vásquez *et al*., 2008; Marioni *et al*., 2008; Milá-García *et al*., 2011; Villamarín *et al*., 2011; Velo-Antón *et al*., 2014). This modern day sympatry supports the idea that atoposaurids could similarly have had multiple co-existing lineages, such as that seen in the French and German basins, and additional, indeterminate material from other European localities might represent further, cryptic diversity of atoposaurid crocodyliformss. Recognition of additional fossil species might be made even more difficult in that modern dwarf crocodiles are morphologically conservative, with cryptic species only recognised through molecular sequencing analyses (Eaton *et al*., 2009).

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Currently, testing of these hypotheses is limited as a result of the small number of localities preserving atoposaurids. To support the hypothesis of insular dwarfism, basal members of Atoposauridae should be expected to be much larger than these Late Jurassic European forms; however, we will only be able to demonstrate this with the discovery of well preserved, stratigraphically older forms, from non-island archipelago settings.

Conclusions

We have presented a new description of a Late Jurassic German atoposaurid specimen previously referred to *Alligatorellus beaumonti*, otherwise known only from coeval deposits in France. We recognise it as a distinct species of *Alligatorellus*, based on numerous features across the skeleton, and erect the new species *Alligatorellus bavaricus*. Emended diagnoses are provided for the genus, as well as the French and German species. Comparisons with contemporaneous atoposaurids support the validity of *Atoposaurus* and *Alligatorium*, alongside *Alligatorellus*, with a species of each genus present in Late Jurassic basins in both France and Germany, providing evidence for sea level-driven allopatric speciation.

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We are grateful to Oliver Rauhut (LMU), Didier Berthet (MNHN), Lorna Steel (NHMUK), Herman Voogd (TMH) and Daniela Schwarz-Wings (MfN) for providing access to specimens in their care. Comments from Trevor Valle, Joseph Hancock and [reviewers] greatly improved an earlier draft of this manuscript.

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