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Isolated tooth reveals hidden spinosaurid dinosaur diversity in the British Wealden Supergroup (Lower Cretaceous)

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Isolated spinosaurid teeth are relatively well represented in the Lower Cretaceous Wealden Supergroup of southern England, UK. Until recently it was assumed that these teeth were referable to *Baryonyx*, the type species (*B. walkeri*) and specimen of which is from the Barremian Upper Weald Clay Formation of Surrey. British spinosaurid teeth are known from formations that span much of the c. 25 Ma depositional history of the Wealden Supergroup, and recent works suggest that British spinosaurids were more taxonomically diverse than previously thought. On the basis of both arguments, it is appropriate to doubt the hypothesis that isolated teeth from outside the Upper Weald Clay Formation are referable to *Baryonyx*. Here, we use phylogenetic, discriminant and cluster analyses to test whether an isolated spinosaurid tooth (HASMG G369a, consisting of a crown and part of the root) from a non-Weald Clay Formation unit can be referred to *Baryonyx*. HASMG G369a was recovered from an uncertain Lower Cretaceous locality in East Sussex but is probably from a Valanginian exposure of the Hastings Group and among the oldest spinosaurid material known from the UK. Spinosaurid affinities are both quantitatively and qualitatively supported, and HASMG G369a does not associate with *Baryonyx* in any analysis. This supports recent reinterpretations of the diversity of spinosaurid in the Early Cretaceous of Britain, which appears to have been populated by multiple spinosaurid lineages in a manner comparable to coeval Iberian deposits. This work also reviews the British and global records of early spinosaurids (known mainly from dental specimens), and revisits evidence for post-Cenomanian spinosaurid persistence.

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Abstract

Isolated spinosaurid teeth are relatively well represented in the Lower Cretaceous Wealden Supergroup of southern England, UK. Until recently it was assumed that these teeth were referable to *Baryonyx*, the type species (*B. walkeri*) and specimen of which is from the Barremian Upper Weald Clay Formation of Surrey. British spinosaurid teeth are known from formations that span much of the c. 25 Ma depositional history of the Wealden Supergroup, and recent works suggest that British spinosaurids were more taxonomically diverse than previously thought. On the basis of both arguments, it is appropriate to doubt the hypothesis that isolated teeth from outside the Upper Weald Clay Formation are referable to *Baryonyx*. Here, we use phylogenetic, discriminant and cluster analyses to test whether an isolated spinosaurid tooth (HASMG G369a, consisting of a crown and part of the root) from a non-Weald Clay Formation unit can be referred to *Baryonyx*. HASMG G369a was recovered from an uncertain Lower Cretaceous locality in East Sussex but is probably from a Valanginian exposure of the Hastings Group and among the oldest spinosaurid material known from the UK. Spinosaurid affinities are both quantitatively and qualitatively supported, and HASMG G369a does not associate with *Baryonyx* in any analysis. This supports recent reinterpretations of the diversity of spinosaurid in the Early Cretaceous of Britain, which appears to have been populated by multiple spinosaurid lineages in a manner comparable to coeval Iberian deposits. This work also reviews the British and global records of early spinosaurids (known mainly from dental specimens), and revisits evidence for post-Cenomanian spinosaurid persistence.

Introduction

Spinosaurids are an unusual clade of large-bodied tetanuran theropods exclusive to the Cretaceous and perhaps best known for the multiple lines of evidence indicating specialisation for a semi-aquatic ecology and the associated controversy over their lifestyle (Amiot et al. 2010a; Bertin 2010; Charig & Milner 1997; Fabbri et al. 2022; Hassler et al. 2018; Holtz 1998; Hone & Holtz Jr 2021; Ibrahim et al. 2020a; Sereno et al. 2022; Taquet 1984). Spinosaurids are widely distributed and important specimens come from England, South America, northern Africa, the Iberian Peninsula and Southeast Asia, and the clade is generally considered to consist of the sister-clades Baryonychinae (anchored on *Baryonyx walkeri* from southern England) and Spinosaurinae (anchored on *Spinosaurus aegyptiacus*, first described from Egypt though since reported from other north African countries)(Allain et al. 2012; Arden et al. 2019; Benson 2010; Bertin 2010; Carrano et al. 2012; Charig & Milner 1997; Holtz et al. 2004; Ibrahim et al. 2020a; Ibrahim et al. 2014; Mateus & Estraviz-López 2022; Rauhut & Pol 2019; Sereno et al. 1998; Sereno et al. 2022; Stromer 1915; Sues et al. 2002). However, several recent analyses suggest that support for this dichotomy may not be as robust as usually supposed (Barker et al. 2021; Evers et al. 2015; Sales & Schultz 2017).

The fossiliferous Early Cretaceous (late Berriasian–early Aptian) Wealden Supergroup of southern England is a significant location for the clade, notably following the 1983 discovery of the *Baryonyx walkeri* holotype (Charig & Milner 1986; Charig & Milner 1997). The discovery of *B. walkeri*, represented by a partial skeleton, was integral to the reinterpretation of Spinosauridae (Naish & Martill 2007), and resulted in the realisation that isolated teeth known from throughout the succession – traditionally regarded as crocodilian – also pertain to spinosaurids (Buffetaut 2007; Buffetaut 2010; Fowler 2007). Indeed, among the first dinosaur remains to be scientifically illustrated and described are spinosaurid teeth from the English Wealden Supergroup, discovered in or around 1820 and given the binomial name "*Suchosaurus cultridens*" (Buffetaut 2010; Owen 1840–1845). These were misinterpreted as crocodilian for nearly two centuries (one of the longest cases of taxonomic misidentification), and were not correctly identified as spinosaurid until more recently (Buffetaut 2007; Buffetaut 2010). "*Suchosaurus cultridens*" is currently considered a *nomen dubium*, being best interpreted as an indeterminate spinosaurid (Mateus et al. 2011; Salisbury & Naish 2011). More recent finds from the Wealden Supergroup succession on the Isle of Wight include the incomplete skeletons of the baryonychine taxa *Ceratosuchops inferodios* and *Riparovenator milnerae* from the Wessex Formation (Barker et al. 2021), and the as-yet-unnamed "White Rock" spinosaurid (a possible spinosaurine) from the overlying Vectis Formation (Barker et al. 2022).

Spinosaurid skeletal material is rare (Hone et al. 2010), but tooth crowns attributed to the group are regularly discovered; numerous isolated specimens have been reported from England (Charig & Milner 1997; Fowler 2007; Martill & Hutt 1996; Turmine-Juhel et al. 2019), Spain (Alonso & Canudo 2016; Isasmendi et al. 2020; Ruiz-Omeñaca et al. 2005), China (Buffetaut et al. 2008; Shu'an et al. 2022), Malaysia (Sone et al. 2015), Japan (Hasegawa et al. 2003; Katsuhiro & Yoshikazu 2017), Thailand (Buffetaut & Ingavat 1986; Buffetaut et al. 2019; Wongko et al. 2019), Algeria (Benyoucef et al. 2015; Benyoucef et al. 2022), Cameroon

(Congleton 1990), Morocco (Richter et al. 2013), Libya (Le Loeuff et al. 2010), Niger (Sereno et al. 1998), Tunisia (Benton et al. 2000; Bouaziz et al. 1988) and Brazil (Medeiros 2006; Sales et al. 2017) (see also Bertin (2010) for further references and notes). Putative spinosaurid dental material may also extend the temporal span of the clade, though reported teeth from the Jurassic of France (Vullo et al. 2014), Tanzania (Buffetaut 2012) and Niger (Serrano-Martínez et al. 2015; Serrano-Martínez et al. 2016), as well as the Late Cretaceous of China (Hone et al. 2010) and Patagonia (Salgado et al. 2009), likely belong to other archosaur clades (Hendrickx et al. 2019; Soto et al. 2020).

Spinosaurid teeth are specialised and distinctive relative to those of other theropods, and possess a list of autapomorphies (Hendrickx & Mateus 2014; Hendrickx et al. 2019). These allow them to be differentiated from the teeth of crocodylomorphs and plesiosaurs, two groups with which they have occasionally been confused (Bertin 2010; Buffetaut 2010; Hone et al. 2010; Sánchez-Hernández et al. 2007; Sanguino 2020; Soto et al. 2020). Key spinosaurid tooth characters, which are likely adaptions towards piscivory, include conidont (cone-shaped) morphology, fluted enamel surfaces, and veined enamel surface texture (Charig & Milner 1997; Hendrickx et al. 2019; McCurry et al. 2019). Spinosaurid teeth are not homogenous: those conventionally attributed to baryonychines possess minutely denticulated carinae, while those conventionally attributed to spinosaurines are unserrated and weakly recurved (Barker et al. 2021; Carrano et al. 2012; Hendrickx et al. 2019). Spinosaurid teeth have been important with respect to discussions on the palaeobiology of the clade: they not only provide data on diet, ecology and lifestyle (Amiot et al. 2009; Amiot et al. 2010a; Amiot et al. 2010b; Buffetaut et al. 2004; Hassler et al. 2018; Hone & Holtz Jr 2021) but also physiology (Heckeberg & Rauhut 2020) and – most importantly for the present study – species-level diversity and palaeoenvironmental and stratigraphic distribution (Alonso & Canudo 2016; Beevor et al. 2021; Fanti et al. 2014; Ruiz-Omeñaca et al. 2005; Sales et al. 2016).

Those spinosaurid teeth discovered throughout Wealden Supergroup strata were initially assumed to be referable to *Baryonyx* (albeit not necessarily to *B. walkeri*) on the basis of general similarity. Charig & Milner (1997) referred isolated crowns from the Wessex, Upper Weald Clay and “Ashdown Sands” formations to cf. *Baryonyx*. Isolated teeth of the NHMUK collections, some previously referred to “*Megalosaurus*” and “*Suchosaurus*”, were also referred to *Baryonyx* by Milner (2003). Buffetaut (2010) agreed that many of the “*Suchosaurus*” crowns from the Wealden Supergroup could be attributed to *Baryonyx*. More recently, Turmine-Juhel et al. (2019) referred incomplete crowns from the Wadhurst Clay Formation to *Baryonyx* sp. Attributing these various Wealden teeth to *Baryonyx* (or cf. *Baryonyx*) was a reasonable proposal in view of knowledge of Wealden spinosaurid diversity at the time but recent finds demonstrate higher diversity across the supergroup (Barker et al. 2021; Barker et al. 2022). In addition, it should be noted that these fossils come from strata spanning a time frame (~25 million years) not considered typical for the duration of a genus-level dinosaur taxon (Naish 2011). However, these teeth differ in several ways from the dentition of the *Baryonyx walkeri* holotype and we consider it plausible that they represent additional taxa (Buffetaut 2010; Naish 2011; Naish & Martill 2007).

A collection of archosaur teeth (HASMG G369) accessioned at Hastings Museum and Art Gallery (East Sussex, UK) includes one specimen (HASMG G369a) bearing the conidont appearance and minute denticles typical of baryonychine spinosaurids. An associated note indicates that these teeth were discovered close to the village of Netherfield in West Sussex (Fig. 1), and from the Purbeck Group, a succession that underlies the Wealden Supergroup and spans the Jurassic-Cretaceous boundary (Tithonian–Berriasian; see below). A Purbeck origin for HASMG G369a would be important, as theropods are the rarest terrestrial vertebrate fossils from the Purbeck Group (Barrett et al. 2010; Benson & Barrett 2009; Milner 2002) and Purbeck spinosaurid remains have not previously been reported.

Isolated theropod teeth are common in the Mesozoic fossil record (Hendrickx et al. 2019; Smith et al. 2005) but their identification to lower taxonomic levels has been fraught with issues, among which are rampant homoplasy and a scarcity of sufficiently detailed anatomical accounts (Hendrickx et al. 2015a; Hendrickx et al. 2020b). Obviously, theropods possess a wide variety of dental morphologies (Hendrickx & Mateus 2014; Hendrickx et al. 2015b; Hendrickx et al. 2019), and various characters have the potential to allow the identification of isolated specimens to their respective clades (Hendrickx et al. 2020b). Recent works advocate for the combined use of cladistic, discriminant and cluster methods in order to provide robust support and minimise the misleading impact of homoplasy (Hendrickx & Mateus 2014; Hendrickx et al. 2020b). Here, we aim to identify HASMG G369a via the application of these methods, and to test the aforementioned assumption that British spinosaurid material should be considered referable to *Baryonyx* by default. The specimen's provenance is also discussed, and the fossil record of early spinosaurids is reviewed.

Geological context and provenance of HASMG G369a

The collection of teeth labelled as HASMG G369 consists of 10 specimens, and is associated with a note, which states:

"*If no specific locality is mentioned, these specimens are from Netherfield (Purbeck)*"

No specific locality is mentioned for any of the specimens, and it is unclear when or by whom this note was written. Importantly, the note is inconsistent with the accession record for HASMG G369, which details a "*collection of local Wealden Fossils*" gifted by the Reverend Pierre Tielhard de Chardin (1881–1955); the provenance and contents of this "collection" are unknown. Tielhard is known to have collected from the Ashdown and Wadhurst Clay formations around Hastings, and donated many specimens (including some vertebrate remains) to Hastings Museum (Brooks 2008). Thus, within the Weald sub-basin, HASMG G369a was either found from the Purbeck Group near Netherfield or the overlying Wealden Supergroup strata surrounding Hastings (Fig. 1A).

Three fault-bounded inliers result in surface exposures of the Purbeck Group within the Weald sub-basin, located north and northwest of Battle in East Sussex, and are surrounded by the overlying Hastings Group (most of which comprise of deposits of the Ashdown Formation)

(Howitt 1964; Milner 1922; Radley & Allen 2012a). These are the oldest exposed rocks in the region, with the inliers located north of Brightling, between Hollingrove and Netherfield, and near Archer Wood (Lake & Shepard-Thorn 1987); the foremost pair have been respectively referred to as the Rounden Wood/Brightling-Heathfield and Limekiln Wood/Mountfield inliers (Howitt 1964; White 1928). The Purbeck Group in the area was previously quarried and mined, with data also provided from boreholes, however, surface exposures are poor and are mainly visible following valley denudation; those exposed in stream valleys have often been disturbed by valley-bulging, landslips and slope cambers (Lake & Shepard-Thorn 1987; Topley 1875). Nevertheless, exposures of the Purbeck Group in the region are represented by both of its constituent Lulworth and Durlston Formations (Fig. 1B), which are principally Berriasian in age (Cope 2007; Hopson et al. 2008; Howitt 1964; Lake & Shepard-Thorn 1987). As mentioned above, Purbeck theropods are very rare, and documented specimens from Sussex outcrops include material referred to "*Megalosaurus* sp." (Benton & Spencer 1995; Topley 1875; White 1928).

The Hastings Group, itself the basal unit of the Wealden Supergroup within the Weald sub-basin (Batten 2011), dominates the area surrounding Hasting and is comprised of the older (late Berriasian–early Valanginian) Ashdown Formation, followed by the Wadhurst Clay Formation (Valanginian) and Tunbridge Wells Formation (late Valanginian; Fig. 1B), several of which are well exposed along coastal sections (Hopson et al. 2008; Lake & Shepard-Thorn 1987; Radley & Allen 2012a). Only a small outcrop of the overlying Weald Clay Group is known near Cooden (Lake & Shepard-Thorn 1987). Vertebrate fossils from the coastal exposures around Hastings in particular have been collected for over a century (Benton & Spencer 1995). Documented theropod finds from the Hastings area include an allosauroid tibia (HASMG G378) (Naish 2003) and material referred to "*Megalosaurus dunkeri*" (e.g. NHMUK PV R19154) and "*M. oweni*" (Benton & Spencer 1995; White 1928). Allosauroid and spinosaurid teeth are also known from the Wadhurst Clay around Bexhill (Charig & Milner 1997; Turmine-Juhel et al. 2019), as are the remains of a tiny maniraptoran (Naish & Sweetman 2011). The enigmatic theropod *Altispinax* (NHMUK PV R1828) is also known from the Hastings Group of Battle (Maisch 2016; Naish 2011; von Huene 1923), located between Netherfield and Hastings.

We were unable to clarify the conflicting accession information surrounding HASMG G369a or ascertain its provenance. Given the rarity of Purbeck Group theropods, limited exposure of the succession around Netherfield, and accession history, we consider it highly unlikely this tooth originates from the Purbeck Group. Further, in the overlying Hastings Group, vertebrate fossils (bar fish detritus) are also extremely rare in the Ashdown Formation around Hastings and the exposures of the Weald Clay Formation are highly limited (Lake & Shepard-Thorn 1987). Taken together, the upper units of the Hastings Group succession are thus the more likely candidates regarding HASMG G369a's provenance, and we thus provisionally consider the specimen to be Valanginian in age.

Materials & Methods

Orientation and terminology

Dental nomenclature and protocols for crown and denticle morphometry follow the recommendations of Hendrickx et al. (2015b) and references therein.

Measurements

The specimen was examined via a DinoLite (AM4113TL) digital microscope. Measurements were taken using a 150mm digital calliper (accuracy 0.01mm), as well as the measurement tools in DinoXcope (v2.0.4) software. A full list of measurements is provided in the supplementary information.

As HASMG G369a is missing its apex, several ordinary least-squares regression analyses were conducted where the specimen's crown height (CH) was compared against crown base length (CBL) and crown base width (CBW) for other spinosaurid teeth. Measurements were collected from the dataset of Hendrickx et al. (2020b). Variables were log-transformed to fit a normal distribution and the analyses were conducted using the *Bivariate regression* function (*Model>Linear*) in Past4 (v.4.11) (Hammer et al. 2001). Of the different spinosaurid samples analysed (see supplementary information), logCBW from *Baryonyx walkeri* lateral teeth provided the most favourable regression coefficient (r^2=0.86), the slope and intercept of which was then used to estimate crown height in HASMG G369a. Other measurements or descriptions derived from CH (e.g. mid-crown length and width, number of denticles at mid-crown etc.) were based on the estimation detailed above.

Crown angle (CA) was estimated using the *Angle* tool in FIJI (Schindelin et al. 2012) via the creation of a vertex delimited by the CBL and a line trending through the midpoint of the preserved apex as the specimen was observed in lateral view. The landmarks used to delineate CBL follows (Hendrickx et al. 2015b). Hendrickx et al. (2015b) described a method to calculate CA using the law of cosines and several morphometric landmarks, but photographs and FIJI has also been employed for isolated theropod crowns (Hendrickx et al. 2020b).

Cladistic analysis

We examined the phylogenetic affinities of HASMG G369a by including it in an updated version of Hendrickx & Mateus (2014) data matrix designed to test the affinities of non-avian theropod teeth (Hendrickx et al. 2020b). This updated matrix was used to assess the affinities of an isolated theropod tooth associated with the *Aerosteon riocoloradensis* holotype: the latter operational taxonomic unit (OTU) was replaced by HASMG G369a, and the final matrix was composed of 146 characters (Ch.) scored across 106 theropod OTUs (the "whole dentition" dataset). The mesial and lateral dentitions of spinosaurids are difficult to distinguish (Hendrickx et al. 2015b). However, as early spinosaurids possessed supernumerary lateral teeth (e.g.

Baryonyx NHMUK PV R9951), it is more likely that HASMG G369a originated from the more distal maxillary or dentary dentition. HASMG G369a was thus scored as a lateral tooth.

We performed the cladistic analysis in TNT 1.5 (Goloboff & Catalano 2016) following the methods outlined in Young et al. (2019) and Hendrickx et al. (2020b), based on a backbone tree topology and the positive constraint command (*force* +), setting HASMG G369a as a floating terminal. The references used to create the tree can be found in Hendrickx et al. (2020b). A pair of additional cladistic analyses was also performed using the whole dentition dataset without constraints, and a reduced matrix consisting only of crown-based characters (see Young et al. 2019; Hendrickx et al. 2020b: 11). The latter included 91 characters (Ch. 38–122 and 141–146) scored for 101 OTUs, with all edentulous taxa removed.

The tree searching strategy involved a combination of algorithms: Wagner trees, TBR branch swapping, sectorial searches, Ratchet (perturbation phase stopped after 20 substitutions) and Tree Fusing (5 rounds) were used until 100 hits of the same minimum tree length were reached. The recovered trees were subsequently subjected to an additional round of TBR branch swapping. In the unconstrained analyses, wildcard OTUs were identified using the iterPCR function (Goloboff & Szumik 2015; Pol & Escapa 2009), and Bremer support values were calculated as a measure of nodal support in the resulting reduced consensus.

Hendrickx & Mateus (2014) use hypodigms for their spinosaurid OTUs, given the type specimens for several do not preserve dental elements (e.g. *Suchomimus*) or have been lost entirely (e.g. *Spinosaurus*). We note that their *Baryonyx* OTU includes the *B. walkeri* holotype NHMUK PV R9951 and the Iberian specimen ML 1190, and that the latter was recently considered the type specimen of a distinct taxon, *Iberospinus natarioi* (Mateus & Estraviz-López 2022). Mateus & Estraviz-López (2022) combined the dental character matrix of Hendrickx et al. (2020a) – itself a version of the matrix used in the present work – with the modified pan-skeletal matrix of Arden et al. (2019) in their phylogenetic analysis of ML 1190. The latter specimen was coded for 36 observable dental characters, however it would appear that Mateus & Estraviz-López (2022) did not realise that the *Baryonyx* OTU employed in their analysis is a hypodigm and already contained ML 1190 Hendrickx & Mateus (2014:supplementary information). Nevertheless, the spinosaurid OTUs used in our analysis of the Hendrickx et al. (2020b) matrix were not modified given the fact that the dental material of *I. natarioi* is limited, positionally overlaps with that of *B. walkeri*, and possesses the same (observable) character scores as the *Baryonyx* OTU.

Elsewhere, the OTU of *Irritator* also includes the type specimen of *Angaturama*, following previous authors who consider the latter congeneric with the former (and may represent the same specimen) (Buffetaut & Ouaja 2002; Charig & Milner 1997; Dal Sasso et al. 2005; Sereno et al. 1998; Sues et al. 2002). Specimens used for the cf. *Suchomimus* and cf. *Spinosaurus* hypodigm OTUs can be found in Hendrickx & Mateus (2014: Table 1) Regarding character scores, those of Ch. 82 (concerning the basalmost position of the mesial serration in lateral teeth) were scored by a process of elimination: although the basalmost mesial serration is not preserved in HASMG G369a, it likely possessed state 1 given the preserved extent of the mesial denticles and the probable inapplicability of states 0 and 2. Meanwhile, Ch. 90 (denticle number in lateral teeth respectively) were extrapolated from the observable data due to the incomplete nature of the carinae and preservation of denticles.

Discriminant function analyses

Pan-theropodan datasets

To classify and predict its optimal classifications inside "family-level" groupings based on quantitative data, HASMG G369a was included in a large published dataset of theropod teeth (Hendrickx et al. 2020b) and subjected to a discriminant function analysis (DFA) in Past4, where it was treated as an unknown taxon and classified at genus or clade levels. Pertinent to this work, the British spinosaurids previously included in this dataset were the type specimens of *Baryonyx walkeri* (NHMUK PV R9951) and "*Suchosaurus cultridens*" (NHMUK PV R36536). As above, HASMG G369a replaced the tooth associated with the *Aerosteon* holotype examined in Hendrickx et al. (2020b). The discriminant function analysis was performed following the protocol detailed by Young et al. (2019) and implemented in Hendrickx et al. (2020b), where all variables were log-transformed to normalize the quantitative variables, and a log (x+1) correction was applied to LAF and LIF to account for the absence of flutes on the crown, and an arbitrary value of 100 denticles per five mm was used for unserrated carinae (see Young et al. (2019) regarding justification of the latter modification).

The final dataset included 1335 teeth belonging to 89 taxa (84 species and five indeterminate family-based taxa) separated into 20 monophyletic or paraphyletic group measured for 12 variables (CBL, CBW, CH, AL, MCL, MCW, MSL, LAF, LIF, CA, MDL, DDL; see Table 1). As noted in Hendrickx et al. (2020a), Young et al. (2019) and Hendrickx et al. (2020b) incorrectly use the abbreviation DCL and DDC for DDL. Due to inconsistencies between authors when measuring dinosaur tooth crowns (Hendrickx et al. 2020b), a second analysis was conducted on a reduced dataset restricted to measurements previously taken by a single author using a consistent measuring protocol. This reduced dataset includes 594 teeth belonging to 72 theropod taxa separated into 20 monophyletic or paraphyletic groups.

In sum, clade- and genus-level discriminant function analyses were conducted on both the whole and reduced pan-theropodan datasets. These datasets were subject to an additional round of clade- and genus-level analyses where the absence of denticles was considered inapplicable (no denticles = ”?”).

Spinosaurid-only datasets

In order to assess the morphospace occupied by each spinosaurid specimen, additional discriminant function analyses were conducted on the raw morphometric data from Hendrickx et al. (2020b) focussing only on Spinosauridae. HASMG G369a was thus added to a dataset that included teeth from *Baryonyx*, cf. *Suchomimus*, *Irritator*, "*Sinopliosaurus fusuiensis*" and "*Suchosaurus cultridens*", as well as teeth referred to cf. Baryonychinae (XMDFEC V10010) and various indeterminate Spinosaurinae (the specimens and their associated data are compiled from Hendrickx et al. (2020b); see supplementary information). Only teeth from *Baryonyx*, *Irritator*, “*Suchosaurus*” and “*Sinopliosaurus*” are from holotype specimens. We follow Hendrickx et al. (2015a) in performing two analyses in Past4 where all morphometric variables of interest (n=35) were included in the first instance, followed by an analysis were ratio variables (MAVG, DAVG, CBR, CHR, MCR, MEC, DSDI, CA, CDA, CMA and CAA) were excluded; CDA is derived from two ratio variables (Buckley et al., 2012) and thus also excluded from this second analysis. The variables “transverse undulations” and “interdenticular sulci” were excluded from both analyses as the former contained qualitatively described data whilst the presence of the latter is not a character associated with spinosaurid dentition (Hendrickx et al. 2019). Alternative versions of variables (i.e. CA2, DAVG2), based on the measurements, were also excluded so as not to inflate the dataset.

As in Hendrickx et al. (2015a), measurements were not log-transformed. Missing or uncertain data were coded as “?”, whilst characters with an uncertain data range were averaged (e.g. the value 11.5 was used for the “11 or 12” lingual flutes scored for “*Suchosaurus*” NHMUK PV R36536). Data prefaced with a greater or less than sign were arbitrarily adjusted by plus or minus one point respectively (i.e. “>5” was changed to “6”). Data scored as “absent” or “not applicable” (represented by a dash) were replaced with the value zero. The “absent?” data point for the lingual flutes of cf. *Suchomimus* specimen UC G73-3 was changed to “?” given the uncertainty of the interpretation. These changes are compiled with the supplementary information.

A second round of analyses was undertaken, based on a reduced spinosaurid sample excluding the *nomina dubia* “*Suchosaurus*” (NHMUK PVR 36536) and “*Sinopliosaurus fusuiensis”* (IVPP V4793.1), as well as cf. Baryonychinae (XMDFEC V10010) given suggestions this specimen does not represent a spinosaurid taxon (see also below) (Buffetaut et al. 2019; Katsuhiro & Yoshikazu 2017; Soto et al. 2020). The remaining spinosaurids were subjected to the same analyses described above (i.e. one DFA using all variables and another excluding ratio variables).

Cluster analysis

Cluster analyses were also performed in Past4 on the different pan-theropodan datasets mentioned above. Hierarchical clustering with a Paired group algorithm and Neighbour joining clustering were used, rooting the tree with the final branch, whilst selecting Euclidean distances as the similarity index.

Table 1 Measurements of the reconstructed HASMG G369a used in the morphometric analyses. Measurements in millimetres (mm) and crown angle in degrees (º). Asterisk (*) marks measurements derived from reconstructed, rather than observed, crown height (see main text).

Crown base length (CBL)	8.16
Crown base width (CBW)	7.03
Crown height (CH)*	17.2
Apical length (AL)	?

Midcrown length (MCL)*	5.67
Midcrown width (MCW)*	4.54
Mesial serrated carina length (MSL)	?
Number of labial flutes (+1) (LAF)	7 (8)
Number of lingual flutes (+1) (LIF)	5 (6)
Crown angle (CA)	74
Mesial denticle length (MDL)	?
Distal denticle length (DDL)	0.171

Results

Systematic Palaeontology

DINOSAURIA Owen (1842)
THEROPODA Marsh (1881)
TETANURAE Gauthier (1986)
SPINOSAURIDAE Stromer (1915)

Spinosauridae gen. and sp. indet.

Description

Orientation

The slight distal recurvature of the crown means that HASMG G369a can be oriented along its mesiodistal axis but the labiolingual axis is less clear. A basal depression, ordinarily lingually situated in theropods (Hendrickx et al. 2015b), is absent on either side of HASMG G369a. This crown subunit may appear planar in some theropods (Hendrickx et al. 2015b), but this is also not the case in HASMG G396a. The crown does, however, display slight labiolingual curvature when viewed distally, and we use this feature to differentiate the lingual and labial surfaces.

Condition

HASMG G369a comprises a near-complete crown (lacking its apex) associated with the basal portion of the root. The enamel is largely well preserved on the labial surface excepting a small chip apically. Large parts of the enamel on the lingual surface however have been worn. The preserved mesial carina has been abraded in several places, such that only two short sections remain: one just above the cervix and the other located mesiocentrally; the denticles – where preserved – appear slightly worn. The distal carina is more complete, with wear mainly affecting the apical-most portion.

Crown

HASMG G369a is a conidont crown with a lenticular cross section at the cervix and at mid-crown (Fig. 2A–B); as such, the crown is weakly labiolingually compressed (CBR: 0.86). The crown is not particularly large (preserved CH: 13.2mm; reconstructed CH: 17.2mm) and only moderately elongated (preserved CHR: 1.68; reconstructed CHR: 2.1).

The mesial and distal carinae are both denticulated (Fig. 2C–D, Fig. 3), lacking adjacent concave surfaces. The former is straight, undivided, and not notably developed, and is positioned largely centrally on the mesial profile. Whilst the basalmost portion has been chipped off (see above), what remains suggests the mesial carina almost certainly reached the cervix. The distal carina is slightly diagonally oriented, and as mentioned above, trending towards the labial side basally. It too is not markedly developed and lacks any twisting of splitting. It extends basally past the cervix a short distance. The apical extent of either carina cannot be determined for this specimen.

The crown displays weak distal recurvature in labiolingual views (Fig. 2A). Its mesial profile is weakly convex, whilst the distal profile is almost straight for the majority of its preserved length. The apex is almost centrally positioned. When viewed distally (Fig. 2D), the crown also possesses minor lingual curvature, with the apex closer to the lingual side. Both the labial and lingual crown surfaces are convex.

The cervix assumes a parabolic morphology on the better-preserved labial side of the crown, such that the basalmost extent of the enamel occurs roughly centrally (Fig. 2E). The equivalent features, or relative extent of the enamel on the lingual side, cannot be reliably ascertained due to preservation. However, the extent of the enamel on the mesial and distal surfaces appears largely similar.

Denticles

The denticles (Fig. 3) of the mesial carina are best preserved at mid-crown, although some incipiently visible ones are also observed at the basalmost preserved portion of the carina. Those of the distal carina are present across a large extent but are worn distoapically and between the distocentral and distobasal portion of the crown.

There are approximately 7 denticles per millimetre on both the mesial and distal carinae at midcrown. These are typically mesiodistally longer than apicobasally tall and are oriented perpendicularly relative to their respective carina. Their external margins are flattened, giving them a horizontally subrectangular appearance in lateral view. The interdenticular spaces are relatively broad and well developed, though the interdenticular diaphyses are not easily recognised, perhaps due to preservation. The mesial and distal denticles at midcrown are approximately the same size (denticle size density index (DSDI): 1), and interdenticular sulci are not observed on either carina. The more complete distal carina also reveals a regular variation in denticle size; this attribute can also be extended to those sections preserved on the mesial carina.

The basalmost segments of the carinae are also denticulated. However, those present mesially are difficult to measure and describe, being visible only under certain light conditions and orientations. Those situated distobasally appear to extend to the cervix (if not just beyond the latter) and are generally similar to those of the midcrown, being smaller and slightly more numerous per millimetre.

Ornamentations

The crown is ornamented, possessing weakly developed flutes, of which seven (possibly eight) are present on the lingual side and five on the labial one (Fig. 2A, E). Those adorning the latter surface are less prominent. Transverse and marginal undulations appear absent. The crown possesses veined enamel texture basally, which is particularly fine near the cervix and whose grooves/ridges are generally apicobasally oriented barring those that curve towards the carina. More apically however, the texture becomes irregular (Fig. 2F–H).

Cladistic Analysis

The results of the various cladistic analyses, detailed below, are summarised in Table 1. Full versions of the recovered trees are available in the supplementary information.

Whole Dentition Dataset

Two MPTs of 1318 steps were recovered following the constrained search on the whole dentition dataset (CI=0.204097, RI=0.451360). HASMG G369a either assumed a position outside the baryonychine + spinosaurine clade or at the base of Spinosaurinae; the latter position was supported by a single synapomorphy: a slightly convex mesial margin (Ch. 73:1). Accordingly, the strict consensus recovered HASMG G369a in a polytomous Spinosauridae alongside Baryonychinae and Spinosaurinae (Fig. 4A), with the clade supported by numerous synapomorphies. Of these, HASMG G69a shared: 1) weak labiolingual compression of the crown with a CBR exceeding 0.75 (Ch. 70:2), 2) subcircular basal cross-section of the crown (Ch. 76:0), 3) over 30 distocentral denticles per 5mm (Ch. 89:0), 4) fluted enamel surfaces present on both labiolingual surfaces (Ch. 111:2) and 5) veined enamel texture (Ch. 121:3). The unconstrained search on the whole dentition dataset initially returned 248 MPTs of 1074 steps (CI=0.250466, RI=0.578975). This increased to 87576 MPTs following the round of TBR. The strict consensus is largely unresolved and predominantly formed by two large polytomies containing well over 25 OTUs each. Few traditional clades can be recognised but those present include Spinosauridae and Abelisauridae. The strict consensus nevertheless recovered HASMG G369a within a polytomous Spinosauridae alongside Baryonychinae and Spinosaurinae.

A reduced consensus was achieved following the pruning of 23 wildcard OTUs (*Limusaurus* (juvenile), *Masiakasaurus*, *Indosuchus, Chilesaurus*, *Piatnitzkysaurus*, *Sciuruminus*, *Eustretospondylus*, *Afrovenator*, *Dubreillosaurus*, *Duriavenator*, *Sinraptor*, *Allosaurus*, *Orkoraptor, Acrocanthosaurus*, *Aorun, Guanlong*, *Eotyrannus*, *Raptorex*, *Gorgosaurus*, *Alioramus, Daspletosaurus,, Tyrannosaurus* and *Ornitholestes*) identified via the iterPCR function (Fig. 4B). As above, HASMG G369a is again recovered in a polytomous Spinosauridae alongside Spinosaurinae and Baryonychinae, which is supported by several synapomorphies; those present in HASMG G369a are: 1) the basalmost denticle on the mesial carina of lateral teeth extending to the base of the crown or slightly above the cervix (Ch. 82; see comment in the "Cladistic analysis" section above), 2) basalmost serration on the distal carina situated below the cervix (Ch. 85), and 3) flutes present on both labial and lingual surfaces (Ch. 111).

Crown-based Dataset

The unconstrained search on the crown-based dataset initially recovered 244 MPTs of 648 steps (CI=0.251543, RI=0.62139). The additional round of TBR returned over 99999 trees found (overflow). The strict consensus produced a huge polytomy incorporating the vast majority of OTUs including HASMG G369a (see supplementary information for the full result). HASMG G369a was one of 74 OTUs acting as wildcard taxa (the others include: *Daemonosaurus*, *Eodromaeus*, *Eoraptor*, *Dracovenator*, *Coelophysis*, *Liliensternus*, *Dilophosaurus*, *Ceratosaurus*, *Genyodectes*, *Berberosaurus*, *Masiakasaurus, Kryptops*, *Rugops*, *Abelisaurus*, *Aucasaurus*, *Arcovenator*, *Chenanisaurus*, *Indosuchus*, *Majungasaurus*, *Skorpiovenator*, *Piatnitzkysaurus*, *Marshosaurus*, *Monolophosaurus*, *Sciuriminus*, *Eustreptospondylus*, *Afrovenator*, *Dubreuillosaurus*, *Duriavenator*, *Megalosaurus*, *Torvosaurus*, *Baryonyx*, *Suchomimus*, *Irritator*, *Spinosaurus*, *Erectopus*, *Sinraptor*, *Allosaurus*, *Neovenator*, *Fukuiraptor*, *Australovenator*, *Megaraptor*, *Orkoraptor*, *Acrocanthosaurus*, *Eocarcharia*, *Carcharodontosaurus*, *Giganotosaurus*, *Mapusaurus*, *Bicentenaria*, *Aorun*, *Zuolong*, *Proceratosaurus*, *Guanlong*, *Dilong*, *Compsognathus*, *Ornitholestes, Haplocheirus*, *Eshanosaurus*, *Falcarius*, *Jianchangosaurus*, *Segnosaurus*, *Erlikosaurus*, *Incisivosaurus*, *Halszkaraptor*, *Sinornithosaurus*, *Graciliraptor*, *Dromaeosaurus*, *Bambiraptor*, *Tsaagan*, *Velociraptor*, *Sinusonasus*, *Zanabazar*, *Troodon* and *Archaeopteryx*).

Table 1 Summary of the cladistic analyses, describing the position of HASMG G369a in Newick format..

Dataset	**Position**	**Constrained**	**Unconstrained**	
			Strict Consensus	**Reduced Consensus**
Whole dentition	Lateral	(HASMG G369a, Spinosaurinae, Baryonychinae)	(HASMG G369a, Spinosaurinae, Baryonychinae)	(HASMG G369a, Spinosaurinae, Baryonychinae)
Crown only	Lateral	–	Polytomy with majority of theropod OTUs	n/a

Discriminant Function Analysis

Pan-theropodan datasets

The analyses conducted on the whole dataset (Fig. 5), regardless of whether the absence of denticles was considered inapplicable or not, consistently classified HASMG G369a as a spinosaurid (clade-level analyses) or referred the tooth to the baryonychine spinosaurid *Suchomimus* (genus-level analyses) (Table 2). Reclassification rates (RR) are, however, generally low, ranging between 59.37–62.07%. Similarly, the reduced datasets based on single-author measurements classified HASMG G369a as a spinosaurid and as *Suchomimus* in the respective analyses (again, with low RR between 59.19–63.74%).

Table 2 Results of the discriminant function analyses on the various iterations of the pan-theropodan dataset, with HASMG G369a treated as an unknown taxon.

Dataset	**Discriminant Function Analysis**		**Reclassification Rate (RR)**	
	Clade level	**Genus level**	**Clade level (%)**	**Taxon level (%)**
Whole dataset	Spinosauridae	*Suchomimus*	61.02	61.17
Whole dataset (no denticles = ?)	Spinosauridae	*Suchomimus*	62.07	59.37
Reduced dataset	Spinosauridae	*Suchomimus*	59.36	63.74
Reduced dataset (no denticles = ?)	Spinosauridae	*Suchomimus*	59.19	60.37

Dataset	**Clade level**		**Genus level**		**Clade level (Eigenvalue)**		**Taxon level (Eigenvalue)**	
	PC1 (%)	**PC2 (%)**	**PC1 (%)**	**PC2 (%)**	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
Whole dataset	51.01	19.8	41.04	21.56	5.71	2.22	18.38	9.65
Whole dataset (no denticles = ?)	50.2	19.04	42.87	17.08	5.79	2.20	18.01	7.18
Reduced dataset	57.1	21.9	41.07	24.72	12.19	4.67	24.99	15.04
Reduced dataset (no denticles = ?)	54.27	22.94	41.4	25.66	10.98	4.64	23.75	14.72

Spinosaurid-only datasets

The DFA results for the spinosaurid-only morphometric datasets (Table 3) consistently classified HASMG G369a as a non-*Baryonyx* spinosaurid. Reclassification rates are very high (98.18–100%), especially in comparison to the pan-theropodan datasets used above, with HASMG G369a classified as cf. *Suchomimus* in the majority of analyses (PC1 63.73–84.32%, PC2 14.84–26.12%). Interestingly, the results from the dataset including all spinosaurids and all variables classified HASMG G369a as "*Suchosaurus*" (PC1 72.53%, PC2 20.03%), which is also known from the Hastings Group.

Table 3 Results of the discriminant function analyses on the various iterations of the spinosaurid-only dataset, with HASMG G369a treated as an unknown taxon.

Dataset	**Discriminant Function Analysis**	**Reclassification Rate (RR) (%)**
All spinosaurid dataset	*"Suchosaurus"*	98.28
All spinosaurid dataset no ratios	*Suchomimus*	98.28
Reduced spinosaurid dataset	*Suchomimus*	100
Reduced spinosaurid dataset no ratios	*Suchomimus*	98.18

Dataset	**Taxon level**		**Taxon level (Eigenvalue)**	
	PC1 (%)	**PC2 (%)**	**Axis 1**	**Axis 2**
All spinosaurid dataset	72.53	20.03	89.905	24.824
All spinosaurid dataset no ratios	63.73	26.12	40.277	16.506
Reduced spinosaurid dataset	84.32	14.84	73.009	12.846
Reduced spinosaurid dataset no ratios	82.02	17.34	36.934	7.807

Visualisation of the DFA plots also shows that spinosaurid teeth are readily differentiable based on the data from Hendrickx et al. (2020b) (Figs. 6 and 7): spinosaurine and baryonychine taxa occupy different morphospace areas, whilst *Baryonyx* and cf. *Suchomimus* do not overlap in any iteration of the analyses. This suggests that *Baryonyx* and cf. *Suchomimus* teeth are morphologically distinct. Whether this impacts discussions regarding the congeneric status of the two taxa remains to be seen, especially given the non-cranial nature of the *Suchomimus* holotype skeleton (Carrano et al. 2012; Sereno et al. 1998). Also of note is the tendency for "*Suchosaurus*" to cluster closely with the cf. *Suchomimus* morphospace in the analyses containing all spinosaurid specimens, whilst "*Sinopliosaurus*" plotted close to the morphospace occupied by spinosaurine teeth.

As an aside, the isolated specimen XMDFEC V10010 from the Santonian (Late Cretaceous) Majiacun Formation of China, referred to Baryonychinae by Hone et al. (2010), does not cluster closely or share morphospace with any spinosaurid taxon in the DFA analyses of the spinosaurid sample. To explore this further, we tested the specimen using discriminant function and cluster analyses on the "whole", "personal" and "large crown" pan-theropodan datasets from Hendrickx et al. (2020b), treating XMDFEC V10010 as an unknown taxon. These results are presented in full in the supplementary information and are briefly discussed below.

Cluster Analysis

The cluster analyses based on the pan-theropodan dataset (Table 4, supplementary information), regardless of the method employed (i.e. hierarchical vs. neighbour joining), unanimously support spinosaurid affinities of HASMG G369a. Almost all results recover the crown as a sister taxon to *Suchomimus*, except for the Neighbour joining analysis performed on the whole dataset (no denticles = "?"), where it is recovered as sister to a clade containing *Irritator* + *Suchomimus*.

Table 4 Results of the cluster analyses on the various iterations of the pan-theropodan datasets, with HASMG G369a treated as an unknown taxon.

Dataset	**Cluster Analysis**	
	Hierarchical clustering	**Neighbour joining**
Whole dataset	*Suchomimus*	*Suchomimus*
Whole dataset (no denticles = ?)	*Suchomimus*	*Suchomimus+Irritator*
Reduced dataset	*Suchomimus*	*Suchomimus*
Reduced dataset (no denticles = ?)	*Suchomimus*	*Suchomimus*

Discussion

Affinities of HASMG G369a and the Diversity of British Spinosaurids

The results from the cladistic, discriminant and cluster analyses clearly support the spinosaurid affinities of HASMG G369a. HASMG G369a shares multiple dental characters in common with spinosaurids, including a sub-circular outline, fluted enamel ornamentation and veined enamel texture, extension of the mesial carina to the cervix and a centrally positioned distal carina (Hendrickx et al. 2019).

Of particular note is the finding that HASMG G369a (its wildcard status within the crown-only phylogenetic analyses excepting) failed to associate with *Baryonyx* in any data run. This further supports previous arguments that the Wealden Supergroup contains multiple spinosaurid lineages (Barker et al. 2021; Buffetaut 2010; Naish 2011; Naish & Martill 2007). These results also suggest that the spinosaurid diversity within the Wealden Supergroup reflects the situation of coeval Iberian localities, which appear to have contained a more diverse spinosaurid fauna than previously assumed (Isasmendi et al. 2020; Malafaia et al. 2020; Mateus & Estraviz-López 2022).

The dentition of *Ceratosuchops* and *Riparovenator* were not scored for this analysis due to poor preservation; however, future work should aim to use cladistic and discriminant methods on spinosaurid crowns found in known strata within the Wealden Supergroup in order to further assess the diversity of its spinosaurids. It would be of particular interest to examine isolated spinosaurid teeth from the Upper Weald Clay Formation, in order to test whether these can be confidently referred to *Baryonyx*. Revisiting coeval Lower Cretaceous localities from Iberia may also be useful given the widespread presence of spinosaurids in these deposits (Malafaia et al. 2020); several morphometric-based (PCA and DFA) analyses have already been undertaken on

Iberian spinosaurid crowns (the results of which also hint at high spinosaurid diversity) (Alonso & Canudo 2016; Alonso et al. 2018; Isasmendi et al. 2020). However, cladistic analyses are recommended (if not preferred) for the identification of isolated theropod teeth (Hendrickx et al. 2020b), although some alternative machine learning techniques (e.g. decision trees) may be attractive tools with which to assess morphometric data from isolated theropod teeth (Wills et al. 2021). It should be noted that performing cladistic analyses on single teeth can be time consuming: each individual tooth in a batch of “unknown” specimens has to be tested separately, or appropriately grouped into morphotypes (Hendrickx et al. 2020b). This is further exacerbated by the difficulty distinguishing the position of isolated spinosaurid teeth (Hendrickx et al. 2015b); whilst we believe a lateral position for HASMG G369a is a more likely origin (see above), spinosaurid samples could alternatively be tested in both positions.

Another potential technique for investigating spinosaurid diversity in the Wealden Supergroup is to conduct specimen-level phylogenetic analyses using Bayesian methods and incorporating stratigraphical information, a method inspired by Cau (2017). As an aside, histological studies of baryonychine-type teeth may also provide insight into replacement patterns in these earlier forms, given the unusually rapid rate observed in Cenomanian spinosaurines (Heckeberg & Rauhut 2020).

Comparative Anatomy

The large number of minute denticles recalls the condition present in baryonychine spinosaurids (Hendrickx et al. 2019). The presence of minute denticles on both carinae most recalls the situation of other British spinosaurid crowns, including those of *Baryonyx* (Charig & Milner 1997), *Riparovenator* (Barker et al. 2021), and BEXHM 1995.485 (Barker, pers. obs; Charig & Milner (1997) misreported the accession number of this specimen as “BEXHM 1993.485”); the carinae of *Ceratosuchops* are poorly preserved and its dentition will be revisited elsewhere, but denticles are present on some distal carinae at least. The denticles of the “*Suchosaurus cultridens*” type specimen (NHMUK PV R36536) are difficult to discern but this is probably due to wear (Buffetaut 2010). Nevertheless, HASMG G369a differs from some Iberian spinosaurid teeth where a baryonychine dental morphotype lacking mesial denticles has been reported (Isasmendi et al. 2020).

Sporadic variation in denticle size is noted in baryonychines and is particularly developed in *Baryonyx* and *Iberospinus* (Hendrickx et al. 2019; Mateus & Estraviz-López 2022). In contrast, those of cf. *Suchomimus* change more gradually and sporadic variation in denticle size is mainly observed on the basal portions of the teeth (Hendrickx et al. 2019). Those of the preserved mesial dentition of *Riparovenator* are similarly regular (Barker, pers. obs.), as are baryonychine teeth from the Barremian–lower Aptian Cameros Basin of Spain (Isasmendi et al. 2020). HASMG G369a mirrors the latter specimens in this regard, with the more complete distal carina possessing a largely gradual change of denticle size.

Although damaged in its basal portion, the mesial carina likely reaches or terminates very near the cervix in HASMG G369a, as is common for spinosaurids generally (Hendrickx et al. 2019).

However, a few spinosaurid crowns, notably from Lower Cretaceous Iberian deposits, do display shorter carinae that extend over only half or two-thirds of the crown height (Canudo et al. 2008; Hendrickx et al. 2019; Isasmendi et al. 2020). A similar feature is also seen in *Iberospinus* (Mateus & Estraviz-López 2022). Charig & Milner (1997) described the carinae of BEXHM 1995.485 as failing to reach the cervix, however it would appear that the carinae have been chipped in places, and what remains basally seems to extend past the cervix.
Fluted enamel is typical of spinosaurid crowns (Hendrickx et al. 2019), and some have noted that these tend to be more numerous and better developed on the lingual surface (Buffetaut 2012), further corroborating the orientation of the specimen proposed above. Those present on HASMG G369a, whilst generally weakly developed, are nevertheless in the range of several other spinosaurids: *Baryonyx* and cf. *Suchomimus* average around 6–7 flutes (range 4–8 and 2–10 respectively), whilst an average of 7–8 flutes are observed in *Irritator* (range 5–10) (Hendrickx et al. 2019). A similar range (3–9 flutes) has been observed in spinosaurid crowns from Lower Cretaceous Iberian localities (Ruiz-Omeñaca et al. 2005). However, the number of flutes in HASMG G369a differs from "*Suchosaurus*" (10–12 flutes) and several spinosaurines (17–20 flutes) (Hendrickx et al. 2019). The presence of flutes on both sides of the tooth also makes HASMG G369a different from *Baryonyx walkeri* (where the flutes are almost entirely lingually located) , and is instead similar to the condition present in *Ceratosuchops*, *Riparovenator*, "*Suchosaurus*" and cf. *Suchomimus*.

Other forms of enamel ornamentation, such as the transverse undulations observed in some *Baryonyx* (NHMUK PV R9951), *Iberospinus* (ML1190) and cf. *Suchomimus* crowns (e.g. MNN G67-1), or the marginal undulations present in *Baryonyx*, *Irritator* (SMNS 58022), cf. *Suchomimus* (e.g. MNN G35-9) and indeterminate Brazilian spinosaurines (Hendrickx et al. 2019; Hendrickx et al. 2020b; Medeiros 2006), are absent in HASMG G369a. Similarly, HASMG G369a shares with spinosaurids a lack of interdenticular sulci (Hendrickx et al. 2019).
The enamel texture of HASMG G369a is unusual in that two morphotypes are present: a veined textured basally and a more irregular texture apically. The former is common in spinosaurids and synapomorphic for the clade: it is present in *Baryonyx* (NHMUK PV R9951), *Iberospinus* (ML 1190) and various cf. *Suchomimus* crowns (e.g. MNN G35-9) (Hendrickx et al. 2019). Veined enamel texture is also present in *Ceratosuchops inferodios* (IWCMS 2014.95.5) and *Riparovenator milnerae* (IWCMS. 2014.95.6) (Barker, pers. obs.). Indeed, HASMG 639a also possesses the strong basal curvature of the veined texture towards the adjacent carinae, which is characteristic of the clade (Hendrickx et al. 2019; Mateus et al. 2011). However, an irregular enamel texture has so far only been reported for some *Irritator* crowns among spinosaurids (Hendrickx et al. 2019).

Differences in dental characters have been used to discuss the taxonomy of isolated spinosaurid teeth (Fanti et al. 2014; Richter et al. 2013), however the utility of several traits has been questioned (Hendrickx et al. 2016). Tooth-bearing spinosaurid bones often lack erupted in-situ teeth, rendering variation between teeth within a complete tooth row poorly understood. Where teeth can be assigned to a single individual, as in the *Baryonyx walkeri* holotype NHMUK PV R9951, variation in ornamentation is documented (Hendrickx et al. 2016). Theropod dentition is also known to vary ontogenetically (Hendrickx et al. 2019) and it remains possible that differences in spinosaurid crown ornamentation may reflect ontogeny or tooth position more than phylogenetic position (Hendrickx et al. 2016).

Spinosaurid teeth are sometimes confused for those of crocodyliforms (Bertin 2010; Buffetaut 2010; Hone et al. 2010; Sánchez-Hernández et al. 2007), and the latter are well represented and taxonomically diverse in the Purbeck Group and Wealden Supergroup of southern England (Benton & Spencer 1995; Salisbury 2002; Salisbury & Naish 2011). The crocodyliform fauna recovered from the Hastings Group is dominated by goniopholidids but also includes atoposaurids, bernissartiids and indeterminate mesoeucrocodylians and eusuchians (Salisbury & Naish 2011). However, we can confidently dismiss a crocodyliform origin for HASMG G396a based on several lines of evidence.

Numerous “ridges” (i.e. flutes) ornament the enamel of goniopholidid and pholidosaurid crowns; in *Goniopholis* and *Pholidosaurus* for instance, these are well defined and closely packed (Allain et al. 2022; de Andrade et al. 2011; Martin et al. 2016; Owen 1840–1845; Owen 1878; Owen 1879), whereas those of HASMG G369a are fewer and poorly defined. Interestingly, Owen (1840–1845) drew attention to the differences present between enamel ornamentation of “*Suchosaurus cultridens*” relative to that of *Goniopholis*. Smooth carinae are observed in goniopholidids generally, although false-ziphodont serrations are present in some taxa (e.g. *G. kiplingi*) (de Andrade et al. 2011; Puértolas-Pascual et al. 2015; Salisbury et al. 1999). The latter are clearly distinguishable from the true denticles of HASMG G369a. Similarly, the mesial and distal carinae of pholidosaurids such as *Pholidosaurus* lack denticles, and can barely be differentiated from the flutes on the enamel surface (Martin et al. 2016). HASMG G396a is evidently not referable to atoposaurids, due both to the small size (<1m) of representative taxa (e.g. *Theriosuchus*) (Schwarz & Salisbury 2005) and their distinctive distal dentition (Salisbury & Naish 2011; Young et al. 2016). Fluted, conical teeth are present in the mesial dentition of bernissartiids, but these are also represented by small (<1m) taxa (Martin et al. 2020; Sweetman et al. 2015). In addition, their mesial teeth lack serrations and possess incipient cervical constriction (Martin et al. 2020; Norell & Clark 1990). The short, rounded posterior crowns of bernissartiids are also obviously incompatible with the conidont morphology of HASMG G369a (Martin et al. 2020; Norell & Clark 1990; Sweetman et al. 2015). In conclusion, we can reject with confidence the possibility that HASMG G369a might be considered referable to Crocodyliformes.

The British Spinosaurid Record and Biogeography of Early Spinosaurids

Most British spinosaurid skeletal (i.e. non-dental) material has been recovered from the Barremian strata of Surrey (Upper Weald Clay Formation) and the Isle of Wight (Wessex Formation and base of the Vectis Formation) (Barker et al. 2021; Barker et al. 2022; Charig & Milner 1986; Charig & Milner 1997; Martill & Hutt 1996; Milner 2003). However, spinosaurid teeth are relatively common throughout the Wealden Supergroup (Fowler 2007; Turmine-Juhel et al. 2019). While this is well known, the extent of the British spinosaurid record, and how it compares to that of other localities globally, has yet to be rigorously analysed.

The spinosaurid crown BEXHM 1995.485 is briefly described by Charig & Milner (1997) as originating from the “Ashdown Sand (Hauterivian)” near Bexhill in East Sussex, which Milner (2003) considered to be the earliest record of Spinosauridae. The term “Ashdown Sands” is now defunct (Hopson et al. 2008), having been introduced by Drew (1861) before being formalised to Ashdown Formation by Rawson (1992). The latter is now considered late Berriasian to early Valanginian in age (Hopson et al. 2008). More recently, Turmine-Juhel et al. (2019) described and figured two poorly preserved crowns (BEXHM 2019.49.251 and BEXHM 2019.49.253) which they referred to *Baryonyx* sp. All three teeth were found from the same site – the Pevensey Pit at Ashdown Brickworks (Turkey Road, Bexhill-on-Sea; J. Porter and D. Brockhurst, pers. comms., 2022) – where the only exposures are of the Valanginian Wadhurst Clay Formation (Turmine-Juhel et al. 2019). BEXHM 1995.485 therefore cannot be Hauterivian or from the Ashdown Formation, contra Charig & Milner (1997) and Milner (2003).

Modern interest in spinosaurids has resulted in the discovery of several Wealden Supergroup teeth in collections of crocodylomorph material housed in various institutions (Buffetaut 2007; Buffetaut 2010; Fowler 2007; Milner 2003). However, the historic nature of many of these specimens impacts our ability to identify their precise stratigraphic position. Fowler (2007) described a pair of spinosaurid crowns within a collection of goniopholidid teeth (NHMUK PV R1901) from the “Wealden” of Hastings, a provenance which would make them Valanginian or possibly Berriasian. Elsewhere, Bertin (2010), following Lydekker (1888), listed a “*Suchosaurus cultridens*” crown (NHMUK PV R635) as originating from the Berriasian-Valanginian “Hastings Sands” of Sandown. Older works suggested that the “Hastings Sands” were represented on the Isle of Wight (White 1921). However, the oldest exposed Wealden Supergroup strata on the Isle of Wight are from the entirely Barremian upper portion of the Wessex Formation (Radley & Allen 2012b; Sweetman 2011) and this specimen is thus likely Barremian in age.
It would thus appear that the oldest British spinosaurid material is definitively Valanginian in age, with Berriasian occurrences remaining a possibility for some specimens of undetermined provenance. In comparison, the oldest specimens from Iberia – the other European hotspot for spinosaurid remains – are late Hauterivian in age (Malafaia et al. 2020). Fowler (2007) described and figured a “saurian” tooth (DCM-G95a) potentially recovered from the Purbeck Group of Swanage (Dorset, UK), which possesses several spinosaurid characters such as fluted enamel ornamentation. However, it is not dissimilar from plesiosaur tooth crowns (Fowler 2007) and is indeed most likely from a marine reptile (D. Fowler pers. comms., 2022).

Alleged Jurassic spinosaurid teeth have been reported from Tanzania (Buffetaut 2012) and Niger (Serrano-Martínez et al. 2015; Serrano-Martínez et al. 2016). However, similarities with other theropod clades (notably ceratosaurs and megalosaurids) have been noted and doubts have been cast on the identification of these specimens (Hendrickx et al. 2019; Soto et al. 2020). An additional putative spinosaurid tooth – initially compared with the above mentioned Tanzanian material – has been described from the Jurassic of France (Vullo et al. 2014). Insufficient data exists to regard this identity as secured and, like the above Tanzanian “spinosaurid” specimens, it is probable that this tooth is also non-spinosaurid. Thus, whilst Spinosauridae likely evolved during the Jurassic (Barker et al. 2021; Carrano et al. 2012), definitive Jurassic material pertaining to the group remains elusive. Moreover, associated discussion regarding the early evolution of spinosaurid teeth, with a proposed gradual acquisition of adaptations towards piscivory (Buffetaut 2012; Serrano-Martínez et al. 2015; Serrano-Martínez et al. 2016), are best considered speculative pending further data (Hendrickx et al. 2019; Soto et al. 2020).

A small, conidont crown (LPUFS 5737) from the Berriasian–Valanginian of Brazil (Sales et al. 2017) may represent one of the oldest spinosaurid occurrences globally. Additional spinosaurine teeth, as well as specimens referred to Baryonychinae (e.g. LPUFS 5870) or regarded as indeterminate spinosaurids (e.g. LPUFS 5871), have also been recently recovered from the locality (Aragão 2021; Lacerda et al. 2023). We note that the identification of these specimens is based on (sometimes limited) qualitative data and would benefit from additional support generated using cladistic, discriminant and cluster analyses, as advocated for isolated theropod teeth in general (Hendrickx et al. 2020b). Nevertheless, evidence for spinosaurids in deposits of Berriasian–Valanginian age could complicate the biogeographic scenario proposed for the clade by Barker et al. (2021), as independently suggested by Lacerda et al. (2023). Barker et al. (2021) regarded Europe as the ancestral region but did not include specimens known from isolated teeth. As a result, alternative biogeographical scenarios include earlier instances of dispersal from the proposed European ancestral area, or a different ancestral area altogether.

Spinosaurid persistence in the Late Cretaceous and status of specimen XMDFEC V10010

The results of the discriminant function analyses (supplementary information) show that XMDFEC V10010 does not associate with Spinosauridae when classified at either the clade or genus level. At the clade-level, the specimen was consistently classified as an allosauroid (Metriacanthosauridae or Allosauridae; reclassification rates = 54.46–62.12%; PC1 37.97–57.88%, PC2 19.11–31.01%), regardless of the dataset or whether serrations were considered inapplicable. At the genus-level, the allosauroid signal was retained, with the tooth most commonly referred to Early Cretaceous *Erectopus*, a tetanuran previously referred to Allosauroidea (and possibly Metriacanthosauridae) (Carrano et al. 2012). XMDFEC V10010 was also referred to the megalosauroid *Condorraptor* and the abelisaurid *Skorpiovenator* in some genus-level DFAs. Reclassification rates in the genus level analyses were generally similar to those at the clade level analyses, and ranged between 57.4–63.68%.
The cluster analyses using the hierarchical clustering option consistently recovered XMDFEC V10010 as the sister taxon to an indeterminate abelisaurid. Similarly, the neighbour-joining option also commonly recovered the tooth as sister to an indeterminate abelisaurid, with several analyses of the whole dataset also recovering XMDFEC V10010 as a sister taxon to Abelisauridae indet.+*Fukuiraptor*.

The conflicting signals produced by the above quantitative analyses on XMDFEC V10010 are perhaps expected given that the dentition of Metriacanthosauridae and Allosauridae are considered the closest to that of Abelisauridae (Hendrickx et al. 2020b), although these allosauroid clades are not known from the Late Cretaceous (Carrano et al. 2012). In comparison, abelisaurids were successful and diverse during the Late Cretaceous but are poorly represented in Asian deposits (outside of India) (Carrano & Sampson 2008; Delcourt 2018). Their teeth are nevertheless relatively diagnostic; however, the dental characters that unite Abelisauridae involve the shape of the premaxillary and maxillary alveoli (which are unknown for XMDFEC V10010) or relate to the morphology of the denticles (which are somewhat worn in XMDFEC V10010; Hone et al., 2010) (Hendrickx et al. 2019; Hendrickx et al. 2020b). Cladistic analyses of XMDFEC V10010 based on first hand examination of the specimen would be beneficial, and we refrain from referring the tooth to a theropod clade without this additional line of evidence. However the quantitative evidence presented herein corroborates previous suggestions that XMDFEC V10010 cannot be referred to Spinosauridae (Buffetaut et al. 2019; Katsuhiro & Yoshikazu 2017; Soto et al. 2020). With the Patagonian late Cenomanian-early Turonian tooth referred to Spinosauridae in Salgado et al. (2009) also likely from a different theropod lineage (Soto et al. 2020), the youngest definitive spinosaurid remains appear to come from Cenomanian deposits of Africa (Benyoucef et al. 2022; Ibrahim et al. 2020b; Sereno et al. 2022).

Assuming the reinterpretation of the above-mentioned Chinese and Patagonian specimens is correct, the potential extinction of Spinosauridae around the Cenomanian–Turonian boundary (CTB) remains poorly understood (Candeiro et al. 2017). This time interval coincides with the peak Cretaceous greenhouse climate and a major marine transgression, and a marine extinction event has been documented (Kerr 2014; Sepkoski 1986). However, studies of the faunal changes in terrestrial, freshwater and brackish water environments during this transition are rare, and available data from North America suggests these faunas were not (a few taxa excepting) overly affected (Benson et al. 2013; Eaton et al. 1997). Spinosaurids are not definitively known from the Mesozoic of North America, however, and it may be that results inferred from these deposits may not be applicable elsewhere. Moreover, as theropods that have been positively associated with costal palaeoenvironments (Sales et al. 2016), it is interesting to speculate upon the impact of the CTB marine transgression on available spinosaurid habitat, and certainly warrants further consideration as a potential driver of their apparent extinction.

Conclusions

An isolated spinosaurid tooth crown HASMG G369a cannot be referred to *Baryonyx* based on the results of multiple quantitative and qualitative analyses, and further supports suggestions that multiple spinosaurid taxa are present within the Wealden Supergroup. Although the precise provenance of HASMG G369a could not be ascertained with certainty, it is among the oldest spinosaurid remains found in Britain and is probably Valanginian in age. Indeed, while the oldest definitive British spinosaurid material comes from this stage, Berriasian occurrences cannot be completely ruled out for some specimens. Future work should look to apply cladistic and discriminant methods on spinosaurid crowns from known strata within the Wealden Supergroup, which may help further assess the British diversity of the clade and provide information on the dental evolution of these atypical theropods.

Following the general consensus that Jurassic spinosaurid material is currently unknown, and that previously referred material represent other theropod clades (see above), a literal interpretation of the fossil record highlights Western Europe as a key region for early spinosaurid evolution, given the wealth of (albeit largely fragmentary) Early Cretaceous material. However, the presence of isolated spinosaurid teeth from the Berriasian-Valanginian of Brazil suggests that early spinosaurids were more spatially widespread, and underlines the palaeobiogeographical importance of fragmentary specimens. As such, alternative biogeographic scenarios regarding the place of origin and early movements of the clade should be examined. Meanwhile, evidence for post-Cenomanian spinosaurid persistence is not supported based on quantitative reinterpretation of dental material previously referred to the clade, and the lack of spinosaurid remains in the latter stages of the Cretaceous hints at an extinction event around the Cenomanian-Turonian boundary.

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Institutional Abbreviations

BEXHM, Bexhill Museum, Bexhill, UK;
DCM, Dorset County Museum, Dorchester, UK;
HASMG, Hastings Museum and Arts Gallery, Hastings, UK;
IWCMS, Dinosaur Isle Museum (Isle of Wight County Museum Services) Sandown, Isle of Wight;
IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China;
LUPFS, Laboratorio de Paleontologia of the Universidade Federal de Sergipe, São Cristóvao, Brazil;
ML, Museu de Lourinhã, Lourinhã, Portugal;
MNEMG, Maidstone Museum, Kent, UK;
MNN, Musée National du Niger, Niamey, Republic of Niger;
NHMUK, Natural History Museum, London, UK;
SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany;
XMDFEC, Xixia Museum of Dinosaur Fossil Eggs of China, Xixia, China.

References

Allain R, Vullo R, Rozada L, Anquetin J, Bourgeais R, Goedert J, Lasseron M, Martin JE, Pérez-García A, and De Fabrègues CP. 2022. Vertebrate paleobiodiversity of the Early Cretaceous (Berriasian) Angeac-Charente Lagerstätte (southwestern France):

implications for continental faunal turnover at the J/K boundary. *Geodiversitas* 44:683-752.

Allain R, Xaisanavong T, Richir P, and Khentavong B. 2012. The first definitive Asian spinosaurid (Dinosauria: Theropoda) from the early cretaceous of Laos. *Naturwissenschaften* 99:369-377.

Alonso A, and Canudo JI. 2016. On the spinosaurid theropod teeth from the early Barremian (Early Cretaceous) Blesa Formation (Spain). *Historical Biology* 28:823-834.

Alonso A, Gasca J, Navarro-Lorbés P, Rubio C, and Canudo J. 2018. A new contribution to our knowledge of the large-bodied theropods from the Barremian of the Iberian Peninsula: the “Barranco del Hocino” site (Spain). *Journal of Iberian Geology* 44:7-23.

Amiot R, Buffetaut E, Lécuyer C, Fernandez V, Fourel F, Martineau F, and Suteethorn V. 2009. Oxygen isotope composition of continental vertebrate apatites from Mesozoic formations of Thailand; environmental and ecological significance. *Geological Society, London, Special Publications* 315:271-283.

Amiot R, Buffetaut E, Lécuyer C, Wang X, Boudad L, Ding Z, Fourel F, Hutt S, Martineau F, and Medeiros MA. 2010a. Oxygen isotope evidence for semi-aquatic habits among spinosaurid theropods. *Geology* 38:139-142.

Amiot R, Wang X, Lécuyer C, Buffetaut E, Boudad L, Cavin L, Ding Z, Fluteau F, Kellner AW, and Tong H. 2010b. Oxygen and carbon isotope compositions of middle Cretaceous vertebrates from North Africa and Brazil: ecological and environmental significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* 297:439-451.

Aragão PRL. 2021. Dentes fósseis de arcossauros da Formação Feliz Deserto (Cretáceo Inferior), Bacia de Sergipe-Alagoas Bachelors. Universidade Federal de Sergipe.

Arden TMS, Klein CG, Zouhri S, and Longrich NR. 2019. Aquatic adaptation in the skull of carnivorous dinosaurs (Theropoda:Spinosauridae) and the evolution of aquatic habits in spinosaurids. *Cretaceous Research* 93:275-284. 10.1016/j.cretres.2018.06.013

Barker CT, Hone DW, Naish D, Cau A, Lockwood JA, Foster B, Clarkin CE, Schneider P, and Gostling NJ. 2021. New spinosaurids from the Wessex Formation (Early Cretaceous, UK) and the European origins of Spinosauridae. *Scientific Reports* 11:1-15.

Barker CT, Lockwood JA, Naish D, Brown S, Hart A, Tulloch E, and Gostling NJ. 2022. A European giant: a large spinosaurid (Dinosauria: Theropoda) from the Vectis Formation (Wealden Group, Early Cretaceous), UK. *PeerJ* 10:e13543.

Barrett P, Benson R, and Upchurch P. 2010. Dinosaurs of Dorset: Part II, the sauropod dinosaurs (Saurischia, Sauropoda) with additional comments on te theropods. *Proceedings of the Dorset Natural History and Archaeological Society* 131:113-126.

Batten DJ. 2011. Wealden Geology. In: Batten DJ, ed. *English Wealden Fossils*. London: The Palaeontological Association, 7-14.

Beevor T, Quigley A, Smith RE, Smyth RS, Ibrahim N, Zouhri S, and Martill DM. 2021. Taphonomic evidence supports an aquatic lifestyle for *Spinosaurus*. *Cretaceous Research* 117:104627.

Benson RB. 2010. A description of *Megalosaurus bucklandii* (Dinosauria: Theropoda) from the Bathonian of the UK and the relationships of Middle Jurassic theropods. *Zoological Journal of the Linnean Society* 158:882-935.

Benson RBJ, and Barrett P. 2009. Dinosaurs of Dorset: part I, the carnivorous dinosaurs (Saurischia, Theropoda). *Proceedings of the Dorset Natural History and Archaeological Society* 130:133-147.

Benson RBJ, Mannion PD, Butler RJ, Upchurch P, Goswami A, and Evans SE. 2013. Cretaceous tetrapod fossil record sampling and faunal turnover: Implications for biogeography and the rise of modern clades. *Palaeogeography, Palaeoclimatology, Palaeoecology* 372:88-107. https://doi.org/10.1016/j.palaeo.2012.10.028

Benton MJ, Bouaziz S, Buffetaut E, Martill D, Ouaja M, Soussi M, and Trueman C. 2000. Dinosaurs and other fossil vertebrates from fluvial deposits in the Lower Cretaceous of southern Tunisia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 157:227-246.

Benton MJ, and Spencer PS. 1995. *Fossil reptiles of Great Britain*. Dordrecht: Springer.

Benyoucef M, Läng E, Cavin L, Mebarki K, Adaci M, and Bensalah M. 2015. Overabundance of piscivorous dinosaurs (Theropoda: Spinosauridae) in the mid-Cretaceous of North Africa: The Algerian dilemma. *Cretaceous Research* 55:44-55.

Benyoucef M, Pérez-García A, Bendella M, Ortega F, Vullo R, Bouchemla I, and Ferré B. 2022. The" mid"-Cretaceous (Lower Cenomanian) Continental Vertebrates of Gara Samani, Algeria. Sedimentological Framework and Palaeodiversity. *Frontiers in Earth Science* 10:927059.

Bertin T. 2010. A catalogue of material and review of the Spinosauridae. *PalArch's Journal of Vertebrate Palaeontology* 7:1-39.

Bouaziz S, Buffetaut E, Ghanmi M, Jaeger J-J, Martin M, Mazin J-M, and Tong H. 1988. Nouvelle decouvertes de vertebres fossiles dans l'Albien du Sud tunisien. *Bulletin de la Société géologique de France* 4:335-339.

Brooks K. 2008. Pierre Teilhard de Chardin 1881-1955. *Hastings & District Geological Society Journal* 14:30–33.

Buffetaut E. 2007. The spinosaurid dinosaur *Baryonyx* (Saurischia, Theropoda) in the Early Cretaceous of Portugal. *Geological Magazine* 144:1021–1025.

Buffetaut E. 2010. Spinosaurs before Stromer: early finds of spinosaurid dinosaurs and their interpretations. In: Moody RTJ, Buffetaut E, Naish D, and Martill DM, eds. *Dinosaurs and Other Extinct Saurians: A Historical Perspective*. London: The Geological Society of London, 175–188.

Buffetaut E. 2012. An early spinosaurid dinosaur from the Late Jurassic of Tendaguru (Tanzania) and the evolution of the spinosaurid dentition. *Oryctos* 10:1-8.

Buffetaut E, and Ingavat R. 1986. Unusual theropod dinosaur teeth from the Upper Jurassic of Phu Wiang, northeastern Thailand. *Revue de Paléobiologie* 5:217-220.

Buffetaut E, Martill D, and Escuillié F. 2004. Pterosaurs as part of a spinosaur diet. *Nature* 430:33-33.

Buffetaut E, and Ouaja M. 2002. A new specimen of *Spinosaurus* (Dinosauria, Theropoda) from the Lower Cretaceous of Tunisia, with remarks on the evolutionary history of the Spinosauridae. *Bulletin de la Société géologique de France* 173:415-421.

Buffetaut E, Suteethorn S, Suteethorn V, Tong H, and Wongko K. 2019. Spinosaurid teeth from the Lower Cretaceous of Ko Kut, eastern Thailand. *Annales de Paléontologie* 105:239-243.

Buffetaut E, Suteethorn V, Tong H, and Amiot R. 2008. An Early Cretaceous spinosaurid theropod from southern China. *Geological Magazine* 145:745-748.

Candeiro CRA, Brusatte SL, and de Souza AL. 2017. Spinosaurid dinosaurs from the Early Cretaceous of North Africa and Europe: fossil record, biogeography and extinction. *Anuário do Instituto de Geociências* 40:294-302.

Canudo JI, Gasulla JM, Gómez-Fernández D, Ortega F, Sanz JL, and Yagüe P. 2008. Primera evidencia de dientes aislados atribuidos a Spinosauridae (Theropoda) en el Aptiano inferior (Cretácico Inferior) de Europa: Formación Arcillas de Morella (España). *Ameghiniana* 45:649-662.

Carrano MT, Benson RB, and Sampson SD. 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* 10:211–300.

Carrano MT, and Sampson SD. 2008. The phylogeny of ceratosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* 6:183-236.

Cau A. 2017. Specimen-level phylogenetics in paleontology using the Fossilized Birth-Death model with sampled ancestors. *PeerJ* 5:e3055.

Charig AJ, and Milner AC. 1986. *Baryonyx*, a remarkable new theropod dinosaur. *Nature* 324:359-361.

Charig AJ, and Milner AC. 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin-Natural History Museum Geology Series* 53:11-70.

Congleton JD. 1990. Vertebrate paleontology of the Koum Basin, northern Cameroon, and archosaurian paleobiogeography in the Early Cretaceous. Southern Methodist University.

Cope JCW. 2007. Drawing the line: the history of the Jurassic—Cretaceous boundary. *Proceedings of the Geologists' Association* 119:105-117.

Dal Sasso C, Maganuco S, Buffetaut E, and Mendez MA. 2005. New information on the skull of the enigmatic theropod *Spinosaurus*, with remarks on its size and affinities. *Journal of Vertebrate Paleontology* 25:888-896. 10.1671/0272-4634(2005)025[0888:NIOTSO]2.0.CO;2

de Andrade MB, Edmonds R, Benton MJ, and Schouten R. 2011. A new Berriasian species of Goniopholis (Mesoeucrocodylia, Neosuchia) from England, and a review of the genus. *Zoological Journal of the Linnean Society* 163:S66-S108.

Delcourt R. 2018. Ceratosaur palaeobiology: new insights on evolution and ecology of the southern rulers. *Scientific Reports* 8:1-12.

Drew F. 1861. On the succession of the beds in the Hastings sands of the southern portion of the weald. *Quarterly Journal of the Geological Society of London* 17:217-286.

Eaton JG, Kirkland JI, Howard Hutchison J, Denton R, O'Neill RC, and Michael Parrish J. 1997. Nonmarine extinction across the Cenomanian-Turonian boundary, southwestern Utah, with a comparison to the Cretaceous-Tertiary extinction event. *Geological Society of America Bulletin* 109:560-567.

Evers SW, Rauhut OW, Milner AC, McFeeters B, and Allain R. 2015. A reappraisal of the morphology and systematic position of the theropod dinosaur *Sigilmassasaurus* from the “middle” Cretaceous of Morocco. *PeerJ* 3:e1323.

Fabbri M, Navalón G, Benson RB, Pol D, O’Connor J, Bhullar B-AS, Erickson GM, Norell MA, Orkney A, and Lamanna MC. 2022. Subaqueous foraging among carnivorous dinosaurs. *Nature* 603:852-857.

Fanti F, Cau A, Martinelli A, and Contessi M. 2014. Integrating palaeoecology and morphology in theropod diversity estimation: a case from the Aptian-Albian of Tunisia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 410:39-57.

Fowler D. 2007. Recently rediscovered baryonychine teeth (Dinosauria: Theropoda): New morphologic data, range extension & similarity to *Ceratosaurus*. *Journal of Vertebrate Paleontology* 27:76A-76A.

Gauthier J. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of sciences* 8:1-55.

Goloboff PA, and Catalano SA. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32:221-238.

Goloboff PA, and Szumik CA. 2015. Identifying unstable taxa: efficient implementation of triplet-based measures of stability, and comparison with Phyutility and RogueNaRok. *Molecular phylogenetics and evolution* 88:93-104.

Hammer Ø, Harper DA, and Ryan PD. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4:9.

Hasegawa Y, Buffetaut E, Manabe M, and Y T. 2003. A possible spinosaurid tooth from the Sebayashi formation (Lower Cretaceous), Gunma, Japan. *Bulletin of Gunma Museum of Natural History* 7:1-6.

Hassler A, Martin J, Amiot R, Tacail T, Godet FA, Allain R, and Balter V. 2018. Calcium isotopes offer clues on resource partitioning among Cretaceous predatory dinosaurs. *Proceedings of the Royal Society B: Biological Sciences* 285:20180197.

Heckeberg NS, and Rauhut OW. 2020. Histology of spinosaurid dinosaur teeth from the Albian-Cenomanian of Morocco: Implications for tooth replacement and ecology. *Palaeontologia Electronica* 23:a48.

Hendrickx C, and Mateus O. 2014. Abelisauridae (Dinosauria: Theropoda) from the Late Jurassic of Portugal and dentition-based phylogeny as a contribution for the identification of isolated theropod teeth. *Zootaxa* 3759.

Hendrickx C, Mateus O, and Araújo R. 2015a. The dentition of megalosaurid theropods. *Acta Palaeontologica Polonica* 60:627-642.

Hendrickx C, Mateus O, and Araújo R. 2015b. A proposed terminology of theropod teeth (Dinosauria, Saurischia). *Journal of Vertebrate Paleontology* 35:e982797.

Hendrickx C, Mateus O, Araújo R, and Choiniere J. 2019. The distribution of dental features in non-avian theropod dinosaurs: Taxonomic potential, degree of homoplasy, and major evolutionary trends. *Palaeontologia Electronica* 22.

Hendrickx C, Mateus O, and Buffetaut E. 2016. Morphofunctional Analysis of the Quadrate of Spinosauridae (Dinosauria: Theropoda) and the Presence of Spinosaurus and a Second Spinosaurine Taxon in the Cenomanian of North Africa. *PLOS ONE* 11.

Hendrickx C, Stiegler J, Currie PJ, Han F, Xu X, Choiniere JN, and Wu X-C. 2020a. Dental anatomy of the apex predator *Sinraptor dongi* (Theropoda: Allosauroidea) from the Late Jurassic of China. *Canadian Journal of Earth Sciences* 57:1127-1147.

Hendrickx C, Tschopp E, and d. Ezcurra M. 2020b. Taxonomic identification of isolated theropod teeth: the case of the shed tooth crown associated with *Aerosteon* (Theropoda: Megaraptora) and the dentition of Abelisauridae. *Cretaceous Research* 108:104312.

Holtz TR. 1998. Spinosaurs as crocodile mimics. *Science* 282:1276-1277.

Holtz TR, Molnar RE, and Currie PJ. 2004. Basal Tetanurae. In: Weishampel DB, Dodson P, and Osmólska H, eds. *The Dinosauria*. Berkley and Los Angeles, California: University of California Press, 71-110.

Hone D, Xu X, and Wang D. 2010. A probable baryonychine (Theropoda: Spinosauridae) tooth from the Upper Cretaceous of Henan Province, China. *Vertebrata PalAsiatica* 48:19–26.

Hone DWE, and Holtz Jr TR. 2021. Evaluating the ecology of *Spinosaurus*: Shoreline generalist or aquatic pursuit specialist? *Palaeontologia Electronica* 23:a03.

Hopson P, Wilkinson I, and Woods M. 2008. A stratigraphical framework for the Lower Cretaceous of England. British Geological Survey Research Report, Explanation of Sheets 320 and 321.

Howitt F. 1964. Stratigraphy and structure of the Purbeck inliers of Sussex (England). *Quarterly Journal of the Geological Society* 120:77-113.

Ibrahim N, Maganuco S, Dal Sasso C, Fabbri M, Auditore M, Bindellini G, Martill DM, Zouhri S, Mattarelli DA, and Unwin DM. 2020a. Tail-propelled aquatic locomotion in a theropod dinosaur. *Nature* 581:67-70.

Ibrahim N, Sereno PC, Dal Sasso C, Maganuco S, Fabbri M, Martill DM, Zouhri S, Myhrvold N, and Iurino DA. 2014. Semiaquatic adaptations in a giant predatory dinosaur. *Science* 345:1613-1616.

Ibrahim N, Sereno PC, Varricchio DJ, Martill DM, Dutheil DB, Unwin DM, Baidder L, Larsson HC, Zouhri S, and Kaoukaya A. 2020b. Geology and paleontology of the Upper Cretaceous Kem Kem Group of eastern Morocco. *ZooKeys* 928:1-216.

Isasmendi E, Sáez-Benito P, Torices A, Navarro-Lorbés P, and Pereda-Suberbiola X. 2020. New insights about theropod palaeobiodiversity in the Iberian Peninsula and Europe: Spinosaurid teeth (Theropoda, Megalosauroidea) from the Lower Cretaceous of La Rioja (Spain). *Cretaceous Research* 116:104600.

Katsuhiro K, and Yoshikazu TYaH. 2017. Second discovery of a spinosaurid tooth from the Sebayashi Formation (Lower Cretaceous), Kanna Town, Gunma Prefecture, Japan. *Bull Gunma Mus Natu Hist* 21:1-6.

Kerr AC. 2014. 4.18 - Oceanic Plateaus. In: Holland HD, and Turekian KK, eds. *Treatise on Geochemistry (Second Edition)*. Oxford: Elsevier, 631-667.

Lacerda MB, de Andrade MB, Sales MA, Aragão PR, Vieira FS, Bittencourt JS, and Liparini A. 2023. The vertebrate fossil record from the Feliz Deserto Formation (Lower Cretaceous), Sergipe, NE Brazil: paleoecological, taphonomic, and paleobiogeographic implications. *Cretaceous Research*:105463.

Lake RD, and Shepard-Thorn ER. 1987. *Geology of the country around Hastings and Dungeness: Memoir for 1:50,000 Geological Sheets 320 and 321 (England and Wales)*. London: British Geological Survey

Le Loeuff J, Metais E, Dutheil DB, Rubino JL, Buffetaut E, Lafont F, Cavin L, Moreau F, Tong H, and Blanpied C. 2010. An Early Cretaceous vertebrate assemblage from the Cabao Formation of NW Libya. *Geological Magazine* 147:750-759.

Lydekker R. 1888. Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History). Part I. In: History) BMN, editor. London. p 309.

Maisch MW. 2016. The nomenclatural status of the carnivorous dinosaur genus Altispinax v. Huene, 1923 (Saurischia, Theropoda) from the Lower Cretaceous of England. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*:215-219.

Malafaia E, Gasulla J, Escaso F, Narvaéz I, and Ortega F. 2020. An update of the spinosaurid (Dinosauria: Theropoda) fossil record from the Lower Cretaceous of the Iberian Peninsula: distribution, diversity, and evolutionary history. *Journal of Iberian Geology* 46:431-444.

Marsh OC. 1881. Principal characters of American Jurassic dinosaurs, part V. *American Journal of Science*:417-423.

Martill DM, and Hutt S. 1996. Possible baryonychid dinosaur teeth from the Wessex Formation (Lower Cretaceous, Barremian) of the Isle of Wight, England. *Proceedings of the Geologists' Association* 107:81-84.

Martin JE, Raslan-Loubatié J, and Mazin J-M. 2016. Cranial anatomy of *Pholidosaurus purbeckensis* from the Lower Cretaceous of France and its bearing on pholidosaurid affinities. *Cretaceous Research* 66:43-59.

Martin JE, Smith T, Salaviale C, Adrien J, and Delfino M. 2020. Virtual reconstruction of the skull of *Bernissartia fagesii* and current understanding of the neosuchian–eusuchian transition. *Journal of Systematic Palaeontology* 18:1079-1101.

Mateus O, Araujo R, Natário C, and Castanhinha R. 2011. A new specimen of the theropod dinosaur *Baryonyx* from the early Cretaceous of Portugal and taxonomic validity of *Suchosaurus*. *Zootaxa* 2827.

Mateus O, and Estraviz-López D. 2022. A new theropod dinosaur from the early cretaceous (Barremian) of Cabo Espichel, Portugal: Implications for spinosaurid evolution. *PLOS ONE* 17:e0262614.

McCurry MR, Evans AR, Fitzgerald EM, McHenry CR, Bevitt J, and Pyenson ND. 2019. The repeated evolution of dental apicobasal ridges in aquatic-feeding mammals and reptiles. *Biological Journal of the Linnean Society* 127:245-259.

Medeiros MA. 2006. Large theropod teeth from the Eocenomanian of northeastern Brazil and the occurrence of Spinosauridae. *Revista brasileira de Paleontologia* 9:333-338.

Milner AC. 2002. Theropod dinosaurs of the Purbeck limestone group, Southern England. *Special Papers in Palaeontology* 68:191-202.

Milner AC. 2003. Fish-eating theropods: a short review of the systematics, biology and palaeobiogeography. Actas de las II Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno: Salas de los Infantes (Burgos, España), septiembre de 2001: Caja de Burgos. p 129-138.

Milner HB. 1922. The geology of the country around Heathfield, Sussex: With report of excursion to heathfield, brightling, netherfield and robertsbridge. Saturday, June 4th, 1921. *Proceedings of the Geologists' Association* 33:142-151.

Naish D. 2003. A definitive allosauroid (Dinosauria; Theropoda) from the Lower Cretaceous of east Sussex. *Proceedings of the Geologists' Association* 114:319-326.

Naish D. 2011. Theropod dinosaurs. In: Batten DJ, ed. *English Wealden Fossils* London: The Palaeontological Association, 526-559.

Naish D, and Martill DM. 2007. Dinosaurs of Great Britain and the role of the Geological Society of London in their discovery: basal Dinosauria and Saurischia. *Journal of the Geological Society* 164:493–510.

Naish D, and Sweetman SC. 2011. A tiny maniraptoran dinosaur in the Lower Cretaceous Hastings Group: evidence from a new vertebrate-bearing locality in south-east England. *Cretaceous Research* 32:464-471.

Norell MA, and Clark JM. 1990. A reanalysis of *Bernissartia fagesii*, with comments on its phylogenetic position and its bearing on the origin and diagnosis of the Eusuchia. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 60:115-128.

Owen R. 1840–1845. *Odontography; or, A treatise on the comparative anatomy of the teeth; their physiological relations, mode of development, and microscopic structure, in the vertebrate animals*. London: Hippolyte Baillière.

Owen R. 1842. Report on British Fossil Reptiles Part II. Reports of the meetings of the British Association for the Advancement of Science. London: R. and JE Taylor. p 61–204.

Owen R. 1878. Monograph on the fossil Reptilia of the Wealden and Purbeck Formations, Supplement VIII: Crocodilia (*Goniopholis*, *Petrosuchus* and *Suchosaurus*). *Palaeontographical Society Monographs*:1–15.

Owen R. 1879. Monograph on the fossil Reptilia of the Wealden and Purbeck Formations, Supplement IX: Crocodilia (*Goniopholis*, *Brachydectes*, *Nannosuchus*, *Theriosuchus* and *Nuthetes*). *Palaeontographical Society Monographs* 33:1–19.

Pol D, and Escapa IH. 2009. Unstable taxa in cladistic analysis: identification and the assessment of relevant characters. *Cladistics* 25:515-527.

Puértolas-Pascual E, Canudo J, and Rabal-Garcés R. 2015. Exceptional crocodylomorph biodiversity of "La Cantalera" site (lower Barremian; Lower Cretaceous) in Teruel, Spain.

Radley JD, and Allen P. 2012a. The Wealden (non-marine Lower Cretaceous) of the Weald sub-basin, southern England. *Proceedings of the Geologists' Association* 123:245-318.

Radley JD, and Allen P. 2012b. The Wealden (non-marine Lower Cretaceous) of the Wessex Sub-basin, southern England. *Proceedings of the Geologists' Association* 123:319-373.

Rauhut OW, and Pol D. 2019. Probable basal allosauroid from the early Middle Jurassic Cañadón Asfalto Formation of Argentina highlights phylogenetic uncertainty in tetanuran theropod dinosaurs. *Scientific Reports* 9:1–9.

Rawson PF. 1992. The Cretaceous. In: Duff PMD, and Smith AJ, eds. *Geology of ENgland and Wales*. London: The Geological Society 355-388.

Richter U, Mudroch A, and Buckley LG. 2013. Isolated theropod teeth from the Kem Kem beds (early Cenomanian) near Taouz, Morocco. *Paläontologische Zeitschrift* 87:291-309.

Ruiz-Omeñaca JI, Canudo JI, Cruzado-Caballero P, Infante P, and Moreno-Azanza M. 2005. Baryonychine teeth (Theropoda: Spinosauridae) from the Lower Cretaceous of La Cantalera (Josa, NE Spain). *Kaupia* 14:59-63.

Sales MA, Lacerda MB, Horn BL, de Oliveira IA, and Schultz CL. 2016. The "χ" of the matter: Testing the relationship between paleoenvironments and three theropod Clades. *PLOS ONE* 11:e0147031.

Sales MA, Liparini A, de Andrade MB, Aragão PR, and Schultz CL. 2017. The oldest South American occurrence of Spinosauridae (Dinosauria, Theropoda). *Journal of South American Earth Sciences* 74:83-88.

Sales MAF, and Schultz CL. 2017. Spinosaur taxonomy and evolution of craniodental features: Evidence from Brazil. *PLOS ONE* 12:e0187070. 10.1371/journal.pone.0187070

Salgado L, Canudo JI, Garrido AC, Ruiz-Omenaca JI, García RA, Marcelo S, Barco JL, and Bollati R. 2009. Upper Cretaceous vertebrates from El Anfiteatro area, Río Negro, Patagonia, Argentina. *Cretaceous Research* 30:767-784.

Salisbury SW. 2002. Crocodilians from the Lower Cretaceous (Berriasian) Purbeck Limestone Group of Dorset, southern England. *Special Papers in Palaeontology: Life And Environments In Purbeck Times* 68:121-144.

Salisbury SW, and Naish D. 2011. Crocodilians. In: Batten DJ, ed. *English Wealden Fossils*. London: The Palaeontological Association, 305-369.

Salisbury SW, Willis PM, Peitz S, and Sander PM. 1999. The crocodilian *Goniopholis simus* from the Lower Cretaceous of north-western Germany. *Special Papers in Palaeontology* 60:121-148.

Sánchez-Hernández B, Benton MJ, and Naish D. 2007. Dinosaurs and other fossil vertebrates from the Late Jurassic and Early Cretaceous of the Galve area, NE Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 249:180-215.

Sanguino F. 2020. Isolated archosaur teeth from Las Hoyas (Barremian, Cuenca, Spain) and the challenge of discriminating highly convergent teeth. *Journal of Iberian Geology* 46:223-251.

Schindelin J, Arganda-Carreras I, Frise E, Kaynig V, Longair M, Pietzsch T, Preibisch S, Rueden C, Saalfeld S, and Schmid B. 2012. Fiji: an open-source platform for biological-image analysis. *Nature methods* 9:676-682.

Schwarz D, and Salisbury SW. 2005. A new species of Theriosuchus (Atoposauridae, Crocodylomorpha) from the late Jurassic (Kimmeridgian) of Guimarota, Portugal. *Geobios* 38:779-802.

Sepkoski JJ. 1986. Phanerozoic Overview of Mass Extinction. Berlin, Heidelberg: Springer Berlin Heidelberg. p 277-295.

Sereno PC, Beck AL, Dutheil DB, Gado B, Larsson HC, Lyon GH, Marcot JD, Rauhut OW, Sadleir RW, and Sidor CA. 1998. A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. *Science* 282:1298-1302.

Sereno PC, Myhrvold N, Henderson DM, Fish FE, Vidal D, Baumgart SL, Keillor TM, Formoso KK, and Conroy LL. 2022. *Spinosaurus* is not an aquatic dinosaur. *eLife* 11:e80092. 10.7554/eLife.80092

Serrano-Martínez A, Ortega F, Sciscio L, Tent-Manclús JE, Bandera IF, and Knoll F. 2015. New theropod remains from the Tiourarén Formation (? Middle Jurassic, Niger) and their bearing on the dental evolution in basal tetanurans. *Proceedings of the Geologists' Association* 126:107-118.

Serrano-Martínez A, Vidal D, Sciscio L, Ortega F, and Knoll F. 2016. Isolated theropod teeth from the Middle Jurassic of Niger and the early dental evolution of Spinosauridae. *Acta Palaeontologica Polonica* 61:403-415.

Shu'an J, Pei Z, and Daolin L. 2022. New materials of the Early Cretaceous spinosaurid (Theropoda) teeth of Napai Basin, Fusui County, Guangxi. *Geological Bulletin of China* 41:1509-1515.

Smith JB, Vann DR, and Dodson P. 2005. Dental morphology and variation in theropod dinosaurs: implications for the taxonomic identification of isolated teeth. *The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology: An Official Publication of the American Association of Anatomists* 285:699-736.

Sone M, Hirayama R, He TY, Yoshida M, and Komatsu T. 2015. First dinosaur fossils from Malaysia: spinosaurid and ornithischian teeth. The 2nd International Symposium on Asian Dinosaurs (ISAD2015) Program and Abstract, Bangkok, 19–20 November 2015:

Nakhorn Ratchasima Rajabhat University and Department of Mineral Resources …. p 18.

Soto M, Toriño P, and Perea D. 2020. *Ceratosaurus* (Theropoda, Ceratosauria) teeth from the Tacuarembó Formation (Late Jurassic, Uruguay). *Journal of South American Earth Sciences* 103:102781.

Stromer E. 1915. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharîje Stufe (unterstes Cenoman). 3. Das Original des Theropoden *Spinosaurus aegyptiacus* nov. gen., nov. spec. . *Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, Mathematisch-physikalische Klasse Abhandlung* 28:1-32.

Sues HD, Frey E, Martill DM, and Scott DM. 2002. *Irritator challengeri*, a spinosaurid (Dinosauria : Theropoda) from the Lower Cretaceous of Brazil. *Journal of Vertebrate Paleontology* 22:535-547. Doi 10.1671/0272-4634(2002)022[0535:Icasdt]2.0.Co;2

Sweetman SC. 2011. The Wealden of the Isle of Wight. In: Batten DJ, ed. *English Wealden Fossils*. London: The Palaeontological Association, 52-78.

Sweetman SC, Pedreira-Segade U, and Vidovic SU. 2015. A new bernissartiid crocodyliform from the Lower Cretaceous Wessex Formation (Wealden Group, Barremian) of the Isle of Wight, southern England. *Acta Palaeontologica Polonica* 60:257-268.

Taquet P. 1984. Une curieuse spécialisation du crâne de certains Dinosaures carnovores du Crétacé: le museau long et étroit des Spinosauridés. *Comptes-rendus des séances de l'Académie des sciences Série 2, Mécanique-physique, chimie, sciences de l'univers, sciences de la terre* 299:217-222.

Topley W. 1875. *The Geology of the Weald (parts of the Counties of Kent, Surrey, Sussex, and Hants)*. London: HM Stationery Office.

Turmine-Juhel P, Wilks R, Brockhurst D, Austen PA, Duffin CJ, and Benton MJ. 2019. Microvertebrates from the Wadhurst Clay Formation (Lower Cretaceous) of Ashdown Brickworks, East Sussex, UK. *Proceedings of the Geologists' Association* 130:752-769.

von Huene F. 1923. Carnivorous saurischia in Europe since the Triassic. *Bulletin of the Geological Society of America* 34:449-458.

Vullo R, Abit D, Ballevre M, Billon-Bruyat J-P, Bourgeais R, Buffetaut E, Daviero-Gomez V, Garcia G, Gomez B, and Mazin J-M. 2014. Palaeontology of the Purbeck-type (Tithonian, Late Jurassic) bonebeds of Chassiron (Oléron Island, western France). *Comptes Rendus Palevol* 13:421-441.

White HJO. 1928. *The Geology of the Country Near Hastings and Dungeness*. London: Memoirs of the Geological Survey England.

White O. 1921. *A Short Account of the Geology of the Isle of Wight*. London: Memoirs of the Geological Survey.

Wills S, Underwood CJ, and Barrett PM. 2021. Learning to see the wood for the trees: machine learning, decision trees, and the classification of isolated theropod teeth. *Palaeontology* 64:75-99.

Wongko K, Buffetaut E, Khamha S, and Lauprasert K. 2019. Spinosaurid theropod teeth from the red beds of the Khok Kruat formation (Early Cretaceous) in Northeastern Thailand. *Tropical Natural History* 19:8-20.

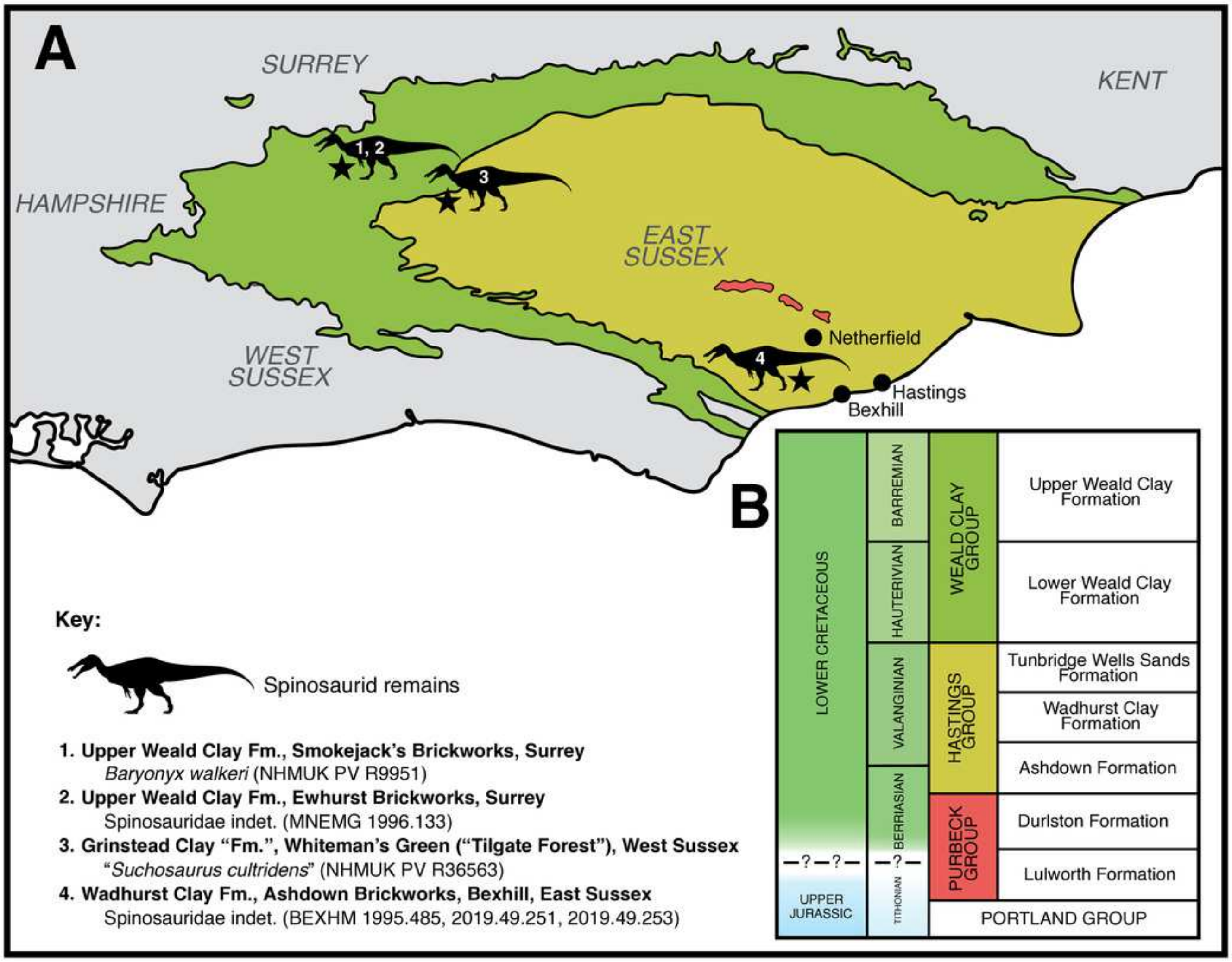
Young CM, Hendrickx C, Challands TJ, Foffa D, Ross DA, Butler IB, and Brusatte SL. 2019. New theropod dinosaur teeth from the Middle Jurassic of the Isle of Skye, Scotland. *Scottish Journal of Geology* 55:7-19.

Young MT, Tennant JP, Brusatte SL, Challands TJ, Fraser NC, Clark ND, and Ross DA. 2016. The first definitive Middle Jurassic atoposaurid (Crocodylomorpha, Neosuchia), and a discussion on the genus *Theriosuchus*. *Zoological Journal of the Linnean Society* 176:443-462.

Figure 1

Geological context of the Lower Cretaceous deposits of southeast England, focussing on the Purbeck Group and Wealden Supergroup.

(A) Schematic geology of the Lower Cretaceous deposits of the Weald Sub-basin (southeast England), highlighting published spinosaurid finds (Charig and Milner, 1997, Salisbury and Naish, 2011, Turmine-Juhel et al., 2019). Based on Austen and Batten (2018: Fig. 2). Note that various additional spinosaurid teeth are known from the region but remain undescribed in detail (Fowler, 2007). (B) Simplified stratigraphic column of the Weald Group in southeast England, based on Batten and Austen (2011: Fig. 3.2). Note that the Grinstead Clay Formation, which subdivides the Tunbridge Wells Sands Formation in Batten and Austen (2011) and from which the "*Suchosaurus cultridens*" type specimen was discovered (Salisbury and Naish, 2011), is downgraded to a member of the latter formation in other works Hopson et al. (2008) and has not been included in this column. Spinosaurid silhouette courtesy of Dan Folkes (CC-BY 4.0).


A
SURREY
KENT
HAMPSHIRE
EAST SUSSEX
WEST SUSSEX
1, 2
3
4
Netherfield
Hastings
Bexhill
B
LOWER CRETACEOUS
UPPER JURASSIC
BARREMIAN
HAUTERIVIAN
VALANGINIAN
BERRIASIAN
TITHONIAN
—?—?—
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WEALD CLAY GROUP
HASTINGS GROUP
PURBECK GROUP
Upper Weald Clay Formation
Lower Weald Clay Formation
Tunbridge Wells Sands Formation
Wadhurst Clay Formation
Ashdown Formation
Durlston Formation
Lulworth Formation
PORTLAND GROUP
Key:
Spinosaurid remains
1. Upper Weald Clay Fm., Smokejack's Brickworks, Surrey
Baryonyx walkeri (NHMUK PV R9951)
2. Upper Weald Clay Fm., Ewhurst Brickworks, Surrey
Spinosauridae indet. (MNEMG 1996.133)
3. Grinstead Clay "Fm.", Whiteman's Green ("Tilgate Forest"), West Sussex
"*Suchosaurus cultridens*" (NHMUK PV R36563)
4. Wadhurst Clay Fm., Ashdown Brickworks, Bexhill, East Sussex
Spinosauridae indet. (BEXHM 1995.485, 2019.49.251, 2019.49.253)

Figure 2

Isolated tooth HASMG G369a.

(A) lingual, (B) basal, (C) mesial, (D) distal and (E) labial view. (F–G) Close up of the enamel texture on the labial tooth surface. Abbreviations: ca, carina; ce, cervix; co, crown; ent, enamel texture; flu, flute; puc, pulp cavity (infilled); ro, root. Scale bars (A–E): 10mm, (F–G): 1mm.

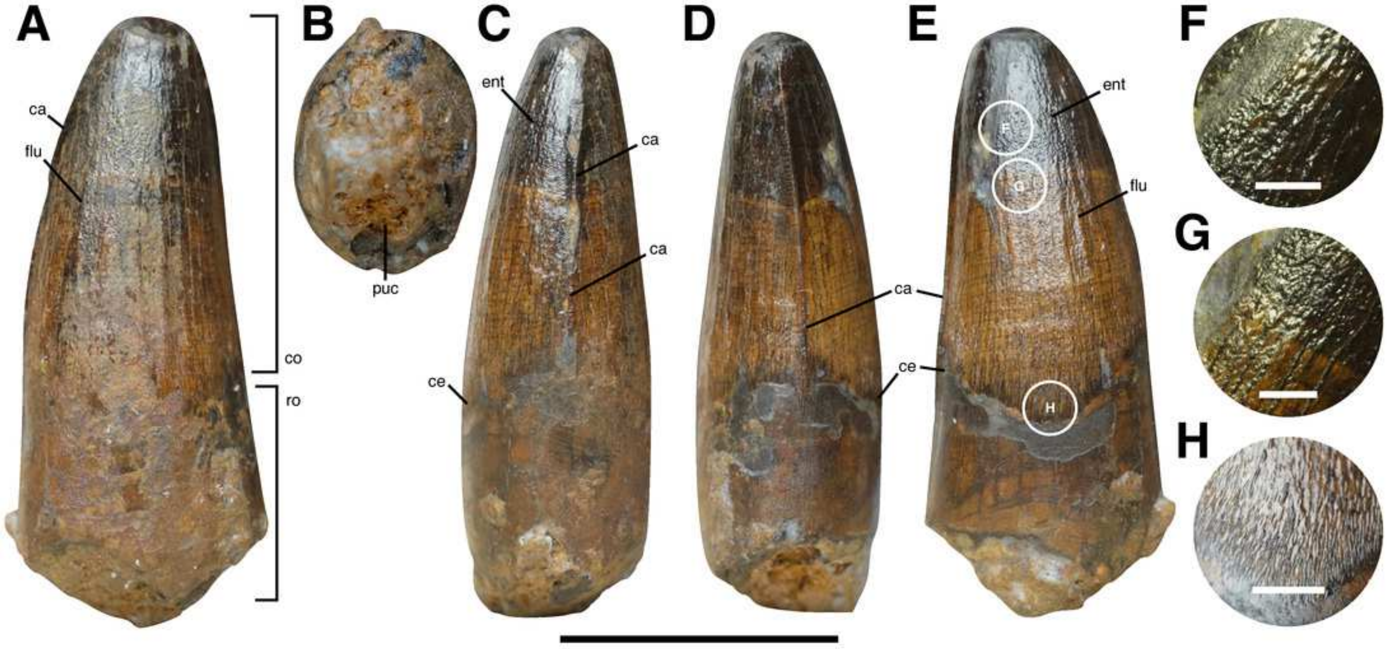
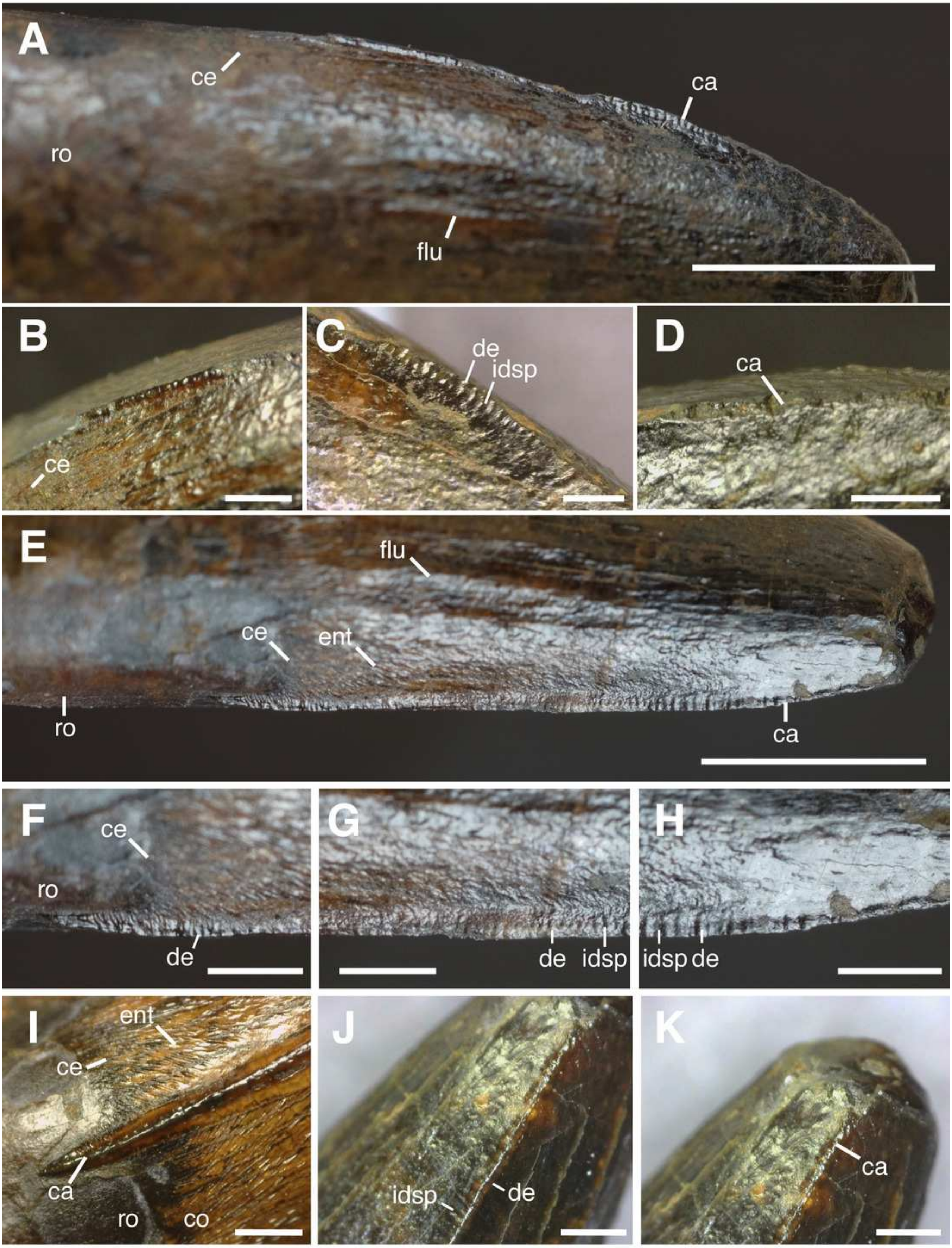


Figure 3

Close up of carinae and denticles of HASMG G369a.

Mesial carina in (A) lateral view. Close up of mesial carina in (B) mesiobasal, (C) mesiocentral and (D) mesioapical views. Distal carina in (E–H) lateral and (I–J) distal views. Close up of (F) distobasal carina, G) distocentral carina, H) distoapical carina. Abbreviations: flu, ca, carina; ce, cervix; co, crown; de, denticle; ent, enamel texture; flute; idsp, interdenticular space; ro, root. Scale bars: (A, E) 5mm, (B–D, F–K) 1mm.


A
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G
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Figure 4

Results of the phylogenetic analyses.

(A) Strict consensus of the analysis using the whole dataset under constrained conditions. (B) Reduced consensus of the unconstrained analysis using the whole dataset. Numbers at nodes indicate Bremer supports values. Full results can be found in the supplementary information.

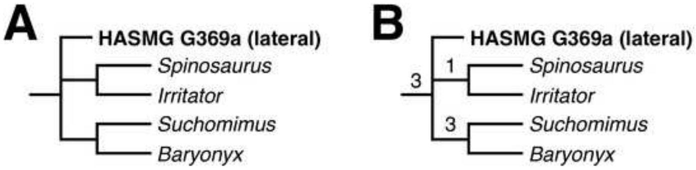
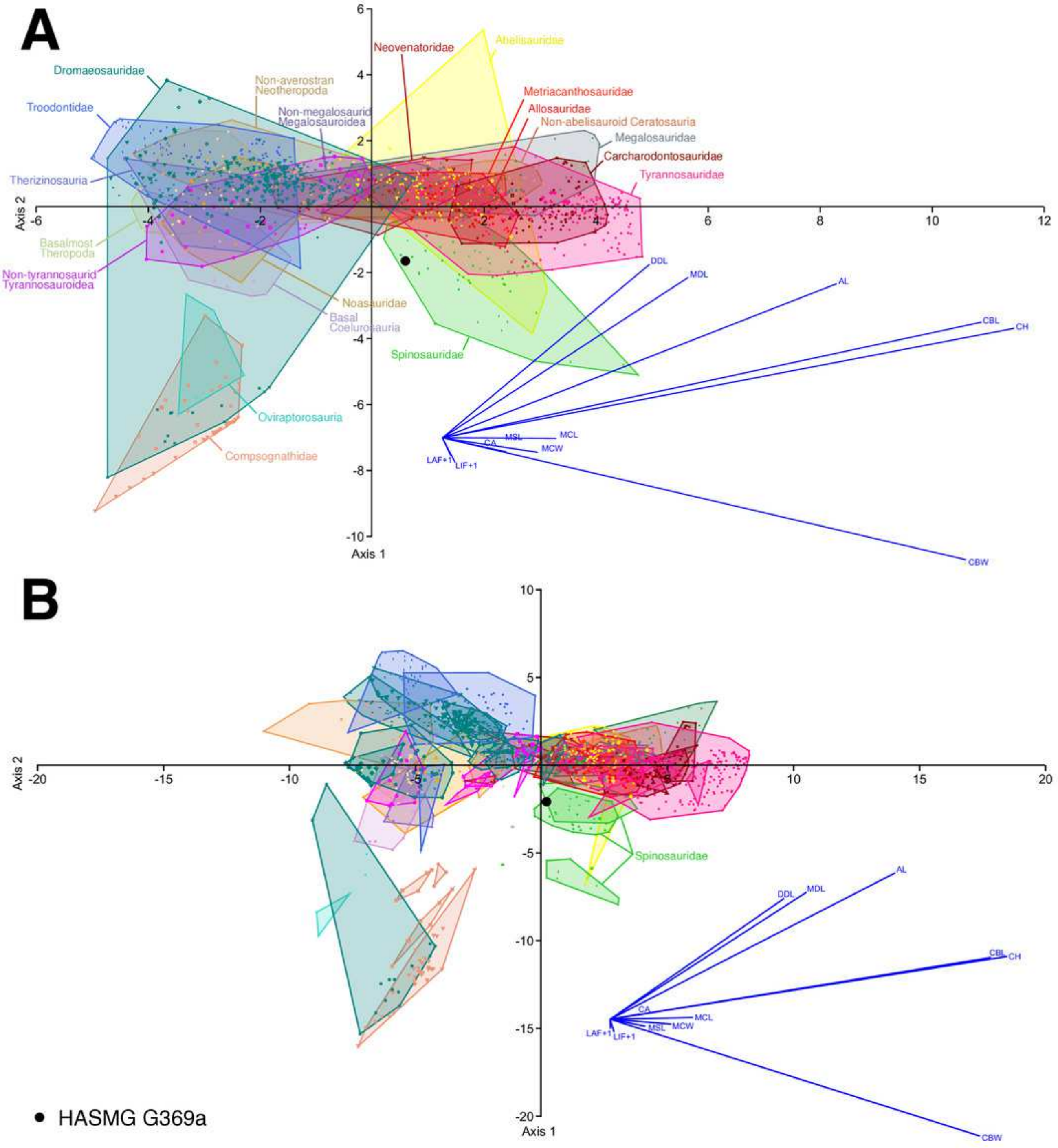


Figure 5

Select results of the discriminant function analysis of the pan-theropodan dataset plotted along the first two canonical axes of maximum discrimination in the dataset.

(A) clade level analysis (Eigenvalue of Axis 1=5.7073, which accounts for 51.01% of the total variation; Eigenvalue of Axis 2=2.2155, which accounts for 19.8% of the total variation) and (B) taxon level analysis (Eigenvalue of Axis 1=18.377, which accounts for 41.04% of the total variation; Eigenvalue of Axis 2=9.6544, which accounts for 21.56% of the total variation), on the whole dataset consisting of 1335 crowns belonging to 89 taxa (i.e., 84 species and five indeterminate family-based taxa) separated into 20 monophyletic or paraphyletic groups. 61.02% and 61.17% of the theropod specimens were correctly classified to their respective groups and taxa, with HASMG G369a (black dot) respectively classified as a spinosaurid and *Suchomimus*at the clade and taxon-level. Abbreviations: AL, apical length; CA, crown angle; CBW, crown base width; CH, crown height; DDC, distal denticle length; LAF+1, number of labial flutes plus one; LIF+1, number of lingual flutes plus one; MCL, mid-crown length; MCW, mid-crown width; MDL, mesial denticle length.


A
Dromaeosauridae
Troodontidae
Therizinosauria
Non-averostran Neotheropoda
Non-megalosaurid Megalosauroidea
Neovenatoridae
Abelisauridae
Metriacanthosauridae
Allosauridae
Non-abelisauroid Ceratosauria
Megalosauridae
Carcharodontosauridae
Tyrannosauridae
Basalmost Theropoda
Non-tyrannosaurid Tyrannosauroidea
Noasauridae
Basal Coelurosauria
Spinosauridae
Oviraptorosauria
Compsognathidae
Axis 2
Axis 1
6
4
2
-2
-4
-6
-8
-10
-6
-4
-2
2
4
6
8
10
12
DDL
MDL
AL
CBL
CH
MSL
MCL
CA
MCW
LAF+1
LIF+1
CBW
B
Axis 2
Axis 1
10
5
-5
-10
-15
-20
-20
-15
-10
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5
10
15
20
Spinosauridae
AL
DDL
MDL
CBL
CH
CA
MCL
MSL
MCW
LAF+1
LIF+1
CBW
● HASMG G369a

Figure 6

Graphical results of the discriminant analyses using a spinosaurid-only dataset comprised of 59 teeth from 7 taxa (*Baryonyx*, cf. *Suchomimus*, *Irritator*, Spinosaurinae indet., cf. Baryonychinae, “*Suchosaurus*”, “*Sinopliosaurus*”)

(A) Results of the analysis including all variables (PC1 72.53, PC2 20.03; Eigenvalue of axis 1: 89.905, axis 2: 24.824; reclassification rate = 98.28%), where HASMG G369a was referred to “*Suchosaurus*”. (B) Results of the analysis excluding ratio variables (PC1 63.73, PC2 26.12; Eigenvalue of axis 40.277, axis 2: 16.506; RR = 98.28%), where HASMG G369a was referred to cf. *Suchomimus*. Abbreviations: see (Hendrickx et al., 2015b) and (Richter et al., 2013). Silhouette credits: Scott Hartman/Phylopic.

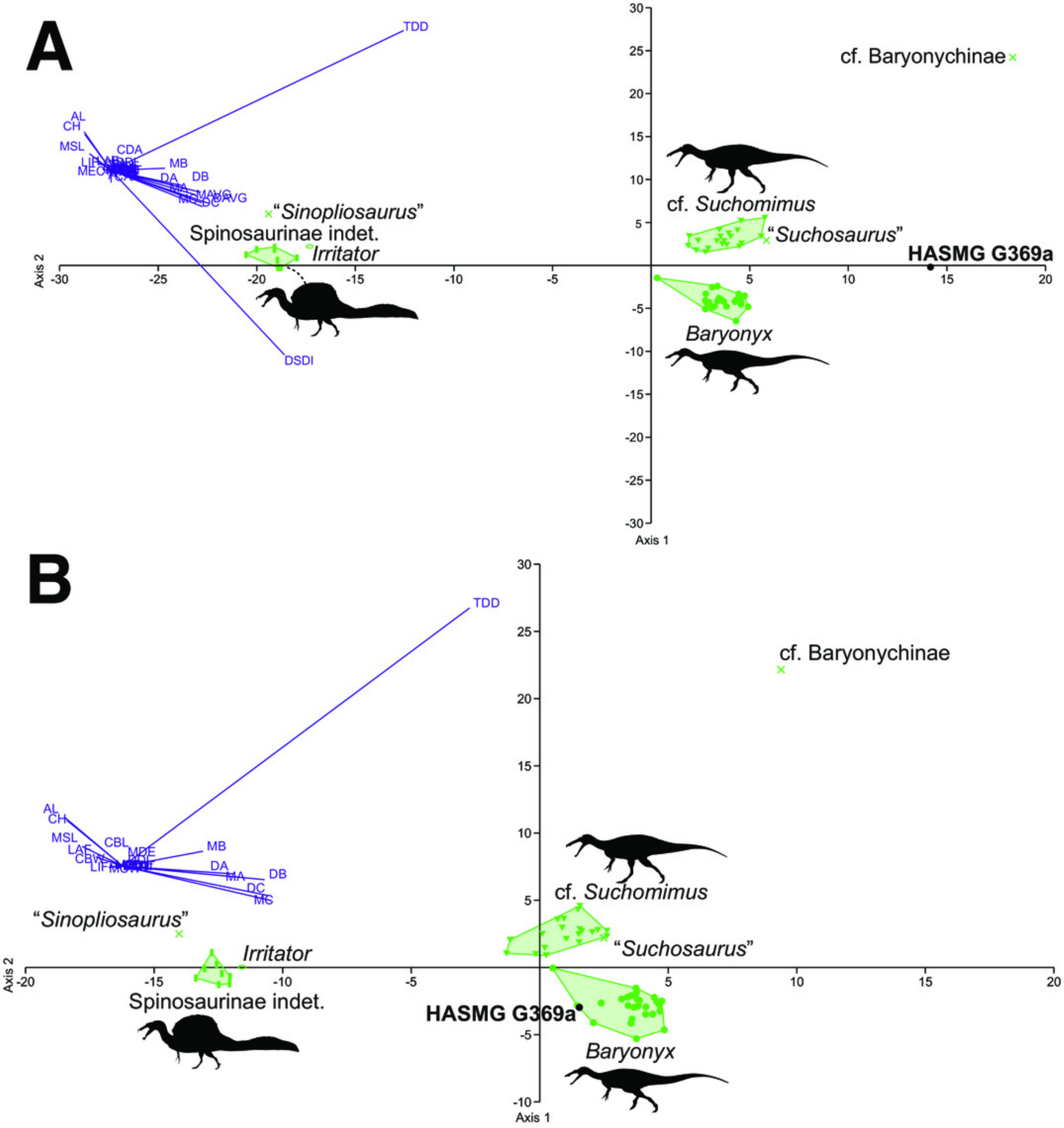
A
TDD
AL
CH
MSL
CDA
MB
DB
DA
MA
MAVG
DAVG
MC
DC
MEC
DSDI
“Sinopliosaurus”
Spinosaurinae indet.
Irritator
cf. Baryonychinae
cf. Suchomimus
“Suchosaurus”
HASMG G369a
Baryonyx
30
25
20
15
10
5
-5
-10
-15
-20
-25
-30
-30
-25
-20
-15
-10
-5
5
10
15
20
Axis 1
Axis 2
B
TDD
AL
CH
MSL
CBL
LAF
CBW
LIF
MCW
MDE
MB
DA
MA
DB
DC
MC
“Sinopliosaurus”
Irritator
Spinosaurinae indet.
cf. Baryonychinae
cf. Suchomimus
“Suchosaurus”
HASMG G369a
Baryonyx
30
25
20
15
10
5
-5
-10
-20
-15
-10
-5
5
10
15
20
Axis 1
Axis 2

Figure 7

Graphical results of the discriminant analyses using a spinosaurid-only dataset comprised of 56 teeth from 4 taxa (*Baryonyx*, cf. *Suchomimus*, *Irritator*, Spinosaurinae indet.), including HASMG G369a as an unknown taxon.

(A) Results of the analysis including all variables (PC1 84.32, PC2 14.84; Eigenvalue of axis 1: 73.009, axis 2: 12.846; reclassification rate = 100%), where HASMG G369a was referred to cf. *Suchomimus*. (B) Results of the analysis excluding ratio variables (PC1 82.02, PC2 17.34; Eigenvalue of axis 36.934, axis 2: 7.807; RR = 98.18%), where HASMG G369a was referred to cf. *Suchomimus*. Abbreviations: see (Hendrickx et al., 2015b) and (Richter et al., 2013). Silhouettes credit: Scott Hartman/Phylopic.

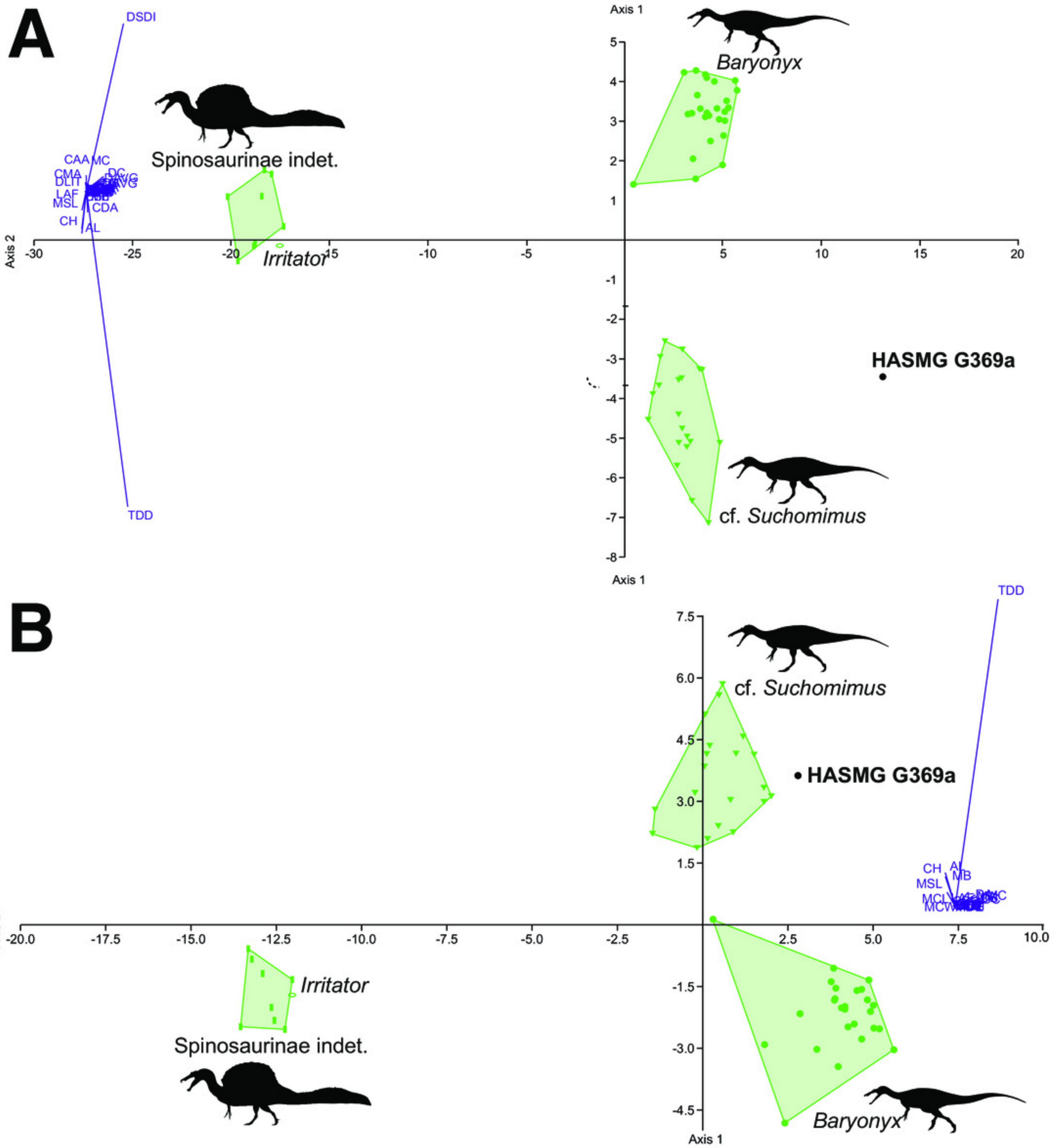
A
DSDI
CAA
MC
CMA
DLIT
DC
AVG
LAF
MSL
CDA
CH
AL
TDD
Spinosaurinae indet.
Irritator
Baryonyx
cf. *Suchomimus*
HASMG G369a
Axis 1
Axis 2
5
4
3
2
1
-1
-2
-3
-4
-5
-6
-7
-8
-30
-25
-20
-15
-10
-5
5
10
15
20
B
TDD
CH
AL
MB
MSL
MCL
MCW
MC
cf. *Suchomimus*
HASMG G369a
Irritator
Spinosaurinae indet.
Baryonyx
Axis 1
Axis 2
7.5
6.0
4.5
3.0
1.5
-1.5
-3.0
-4.5
-20.0
-17.5
-15.0
-12.5
-10.0
-7.5
-5.0
-2.5
2.5
5.0
7.5
10.0

Table 1(on next page)

Measurements of the reconstructed HASMG G369a used in the morphometric analyses.

Measurements in millimetres (mm) and crown angle in degrees (º). Asterisk (*) marks measurements derived from reconstructed, rather than observed, crown height (see main text).

Crown base length (CBL)	8.16
Crown base width (CBW)	7.03
Crown height (CH)*	17.2
Apical length (AL)	?
Midcrown length (MCL)*	5.67
Midcrown width (MCW)*	4.54
Mesial serrated carina length (MSL)	?
Number of labial flutes (+1) (LAF)	7 (8)
Number of lingual flutes (+1) (LIF)	5 (6)
Crown angle (CA)	74
Mesial denticle length (MDL)	?
Distal denticle length (DDL)	0.171

Table 2(on next page)

Summary of the cladistic analyses, describing the position of HASMG G369a in Newick format.

Dataset	**Tooth Position**	**Constrained**	**Unconstrained**	
			Strict Consensus	**Reduced Consensus**
Whole dentition	Lateral	(HASMG G369a, Spinosaurinae, Baryonychinae)	(HASMG G369a, Spinosaurinae, Baryonychinae)	(HASMG G369a, Spinosaurinae, Baryonychinae)
Crown only	Lateral	–	Polytomy with majority of theropod OTUs	n/a

1

Table 3(on next page)

Results of the discriminant function analyses on the various iterations of the pan-theropodan dataset, with HASMG G369a treated as an unknown taxon.

Dataset	**Discriminant Function Analysis**		**Reclassification Rate (RR)**		**Clade level**		**Genus level**		**Clade level (Eigenvalue)**		**Genus level (Eigenvalue)**	
	Clade level	**Genus level**	**Clade level (%)**	**Taxon level (%)**	**PC1 (%)**	**PC2 (%)**	**PC1 (%)**	**PC2 (%)**	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
Whole dataset	Spinosauridae	*Suchomimus*	61.02	61.17	51.01	19.8	41.04	21.56	5.71	2.22	18.38	9.65
Whole dataset (no denticles = ?)	Spinosauridae	*Suchomimus*	62.07	59.37	50.2	19.04	42.87	17.08	5.79	2.20	18.01	7.18
Reduced dataset	Spinosauridae	*Suchomimus*	59.36	63.74	57.1	21.9	41.07	24.72	12.19	4.67	24.99	15.04
Reduced dataset (no denticles = ?)	Spinosauridae	*Suchomimus*	59.19	60.37	54.27	22.94	41.4	25.66	10.98	4.64	23.75	14.72

Table 4(on next page)

Results of the discriminant function analyses on the various iterations of the spinosaurid-only dataset, with HASMG G369a treated as an unknown taxon.

Dataset	**Discriminant Function Analysis**	**Reclassification Rate (RR) (%)**	**Taxon level**		**Taxon level (Eigenvalue)**	
			PC1 (%)	**PC2 (%)**	**Axis 1**	**Axis 2**
All spinosaurid dataset	*"Suchosaurus"*	98.28	72.53	20.03	89.905	24.824
All spinosaurid dataset no ratios	*Suchomimus*	98.28	63.73	26.12	40.277	16.506
Reduced spinosaurid dataset	*Suchomimus*	100	84.32	14.84	73.009	12.846
Reduced spinosaurid dataset no ratios	*Suchomimus*	98.18	82.02	17.34	36.934	7.807

1

Table 5(on next page)

Results of the cluster analyses on the various iterations of the pan-theropodan datasets, with HASMG G369a treated as an unknown taxon.

Dataset	**Cluster Analysis**	
	Hierarchical clustering	**Neighbour joining**
Whole dataset	*Suchomimus*	*Suchomimus*
Whole dataset (no denticles = ?)	*Suchomimus*	*Suchomimus+Irritator*
Reduced dataset	*Suchomimus*	*Suchomimus*
Reduced dataset (no denticles = ?)	*Suchomimus*	*Suchomimus*