



Identification of a large anguimorph lizard (Reptilia, Squamata) by an articulated hindlimb from the upper Maastrichtian (Upper Cretaceous) of Basturs-1 (Lleida, Spain)

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ABSTRACT

Appendicular remains of squamate reptiles are barely described in the fossil record due to their low preservational potential and generally poor diagnostic information. Not many squamate fossil individuals preserve appendicular bony elements, these being mainly restricted to the rare articulated specimens found in a limited number of localities with specific conditions that favor exceptional preservation. Detailed descriptions of these bones, especially tarsals and metatarsals, are thus scarce in the literature due to the lesser relevance given to these elements in most anatomical descriptions. In this study we analyze an unpublished fossil specimen from the Maastrichtian of Basturs-1 (Lleida, Catalonia, Spain) corresponding to several articulated appendicular pes bones of a possible member of Varaniformes. We also provide detailed insights on the anatomy of the tarsalia and metatarsalia, particularly in anguimorphs. The fossil specimen here described, with an estimated snout-vent length (SVL) of ~581 mm, reveals the putative varaniform from Basturs-1 as one of the largest Mesozoic terrestrial lizards, and possibly the largest from the European fossil record. Previous observations of an association between large lizards and dinosaur nesting sites are further supported by the find of this giant form in a locality known for the presence of numerous dinosaur eggs.

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1. Introduction

The squamate fossil record from the Maastrichtian (uppermost Cretaceous) of Europe includes representatives of Iguania, “Scincomorpha”, Anguimorpha, Ophidia and Gekkota (Folie and Codrea, 2005; Pereda-Suberbiola, 2009; Bolet Mercadal, 2014; Bolet, 2017; Marmi et al., 2014; Csiki-Sava et al., 2015; Blanco et al., 2015, 2016; Ortega et al., 2015; Blanco, 2017). European Maastrichtian anguimorphs contain anguids (e.g. Blain et al., 2010), but most have been referred to groups included in the old conception of “Varanoidea”. In this view of squamates interrelationships, based on morphological data (e.g. McDowell and Bogert, 1954; Pregill et al., 1986; Caldwell, 1999; Conrad, 2008; Gauthier et al., 2012), helodermatids and varanids were closely related, and the term “Varanoidea” was

used to group them as well as related extinct taxa. Gao and Norell (1998) used the term in a more restrictive sense, consisting in the most recent common ancestor of *Telmasaurus* and Varanidae, and all its descendants. Conrad (2008) and Conrad et al. (2011a) used the term Varaniformes for the group containing forms closer to *Varanus* than to *Heloderma* or mosasaurs. In contrast to Conrad (2008), Conrad et al. (2011a) recovered “Varanoidea” as paraphyletic in their combined evidence analysis of anguimorph relationships, in agreement with molecular phylogenetic analyses that consider *Shinisaurus* as more closely related to *Varanus* than *Heloderma*. We here refer to Varaniformes sensu Conrad (2008), and use the term “Varanoidea” informally for those fossils whose attribution was made under the old definition of the term, and are too incomplete to support their attribution to either monsteraurs (*Heloderma* plus its stem) or varaniforms. All of this is further complicated by the uncertain position of mosasauroforms, which have been considered as “varanoids” (e.g. Estes et al., 1988; Conrad,

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2008; Conrad et al., 2011a), pythonomorphs (a clade consisting in mosasaurs plus snakes, see Lee, 1997; Lee and Caldwell, 2000 and Reeder et al., 2015), or recovered in a stem-ward position outside Anguimorpha (stem “scleroglossans” in Gauthier et al., 2012). Note, however, that mosasauriforms are only tangentially considered here, basically for discarding mosasauriform affinities of the fossil described, and for considering their distribution in the paleogeographic figures. Terrestrial “varanoids” have been reported from the Upper Cretaceous of Europe (e.g. Buffetaut et al., 1997; Laurent et al., 2002; Houssaye et al., 2013a; Rage, 2013; Ortega et al., 2015), although material is too fragmentary to provide an assignation to either monstrosaur or varaniforms. Iberian fossils referred to “varanoids” include taxa ranging from the Barremian or Aptian to the Maastrichtian, being mosasaurs (then considered to be “varanoids”, but see above) the most abundant group (Bardet et al., 1999, 2006, 2013a,b; Pereda-Suberbiola et al., 2015) (Fig. 1). Regarding Iberian terrestrial “varanoids”, they include *Arcanosaurus ibericus* (vertebrae from the Barremian or Aptian of Salas de los Infantes, Burgos) and some other indeterminate forms (vertebrae from the upper Campanian or lower Maastrichtian of Lo Hueco, in Cuenca, and Aveiro and Viso, in Portugal; and upper Maastrichtian of Albaina, Treviño County) (Antunes and De Broin, 1988; Vullo et al., 2009; Houssaye et al., 2013b; Ortega et al., 2015; Pereda-Suberbiola et al., 2015).

Here we report a previously undescribed specimen attributable to Anguimorpha composed of several articulated appendicular bones, referred as an indeterminate archosaur by López-Martínez (2000), from the Maastrichtian site of Basturs-1 (Lleida, Catalonia, Spain; Fig. 2), which is tentatively assigned to a large member of Varaniformes.

Anatomical abbreviations. *dt*, distal tarsal; *lpt*, lateral plantar tubercle; *mpt*, medial plantar tubercle; *mt*, metatarsal; *op*, outer process.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; CAS, California Academy of Sciences, San Francisco, California, USA; CT, Ankara University, department of Engineering Geology, Cestepe, Turkey; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; GNM, Simon Janashia Museum of Georgia, Georgian National Museum, Tbilisi, Georgia; IGM, Institute of Geology, Mongolian Academy of Sciences, Ulaan Bataar, Mongolia; IRScNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; KNM, Kenya National Museum, Nairobi, Kenya; LGPUT, Laboratory of Geology and Palaeontology of the University of Thessaloniki, Thessaloniki, Greece; MÁFI, Magyar Állami Földtani Intézet (Hungarian Geological Institute), Budapest, Hungary; MCD, Museu de la Conca Dellà, Lleida, Spain; MCSNT, Museo Civico di Storia Naturale di Trieste, Italy; MNCN, Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; MNHN AC, Anatomie Comparée, Muséum National d'Histoire naturelle, Paris, France; MPUR, Museo Paleontologico dell'Università di Roma, Lazio, Italy; MSNM, Museo di Storia Naturale di Milano, Italy; NCSM, North Carolina Museum of Natural Sciences, North Carolina, USA; NHMUK, Natural History Museum of London, UK; RPI, Ravin de la Pluie locality, acronym of the collections of the LGPUT; TMM, Texas Memorial Museum (The University of Texas at Austin), Austin, Texas, USA; UANL-FCT, Universidad Autónoma de Nuevo León, Facultad de Ciencias de la Tierra, Linares, Nuevo León, Mexico; UCM MACV, Museo de Anatomía Comparada de Vertebrados, Universidad Complutense de Madrid, Madrid, Spain; UF, University of Florida, Gainesville, USA; UMMZ, University of Michigan Museum of Zoology, Michigan, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA; ZPAL, Zakład Paleobiologii, Polska Akademia Nauk (Paleobiological Institute, Polish Academy of Sciences), Warsaw, Poland.

2. Materials and methods

A total of 161 specimens belonging to both extinct and extant lepidosaurs were considered for the comparative study performed here. Some of the specimens corresponding to extant species were studied firsthand in the MACV, MNCN, and MNHN collections. The information for the other extant specimens considered here was obtained from the online platforms GBIF (Global Biodiversity Information Facility (<https://www.gbif.org/>)), iDigBio (Integrated Digitized Biocollections (<https://www.idigbio.org/>)) and the 3D simulator MorphoSource (<https://www.morphosource.org/>). Information about fossil individuals was mainly obtained from the papers in which those individuals were originally described (see [Supplementary information 1 in Appendix A](#)).

Based on previous works (see Borsuk-Białynicka, 2018 and references therein), the following measurements were obtained using previously defined criteria: hooking angle of the fifth metatarsal (*ha*), corresponding to the angle between the long axis of the metatarsal and a line perpendicular to the articular facet for the fourth distal tarsal; lateral plantar tubercle angle (*lpt_z*), corresponding to the angle between this tubercle in relation to the medial plantar tubercle and the outer process; inflexion angle (*inf*), relating to the bending of the long axis in the plantar-dorsal plane; angulation, considering the geometric shape of the fifth metatarsal in proximal view; distal tarsal proportion (*dtIV/dtIII*), considering the fourth/third distal tarsal ratio in maximum preaxial-postaxial length. The *ha*, *lpt_z*, *inf* and *dtIV/dtIII* were all measured with the software Avizo 7.1®. The shape and size of the third and fourth distal tarsals and fifth metatarsal, as well as positions of tubercles in the latter, were the morphological traits considered in this study to compare between species and clades.

In order to obtain the complete appendicular 3D model, and the 3D models of each skeletal element, the specimen was processed in the Non-destructive Techniques Laboratory of the Museo Nacional de Ciencias Naturales, in Madrid, where it was CT-scanned to provide the 3D model according to the following technical parameters: 160 kV, 62 μA, 0.625 thick copper filter, 0.127-pixel size, 900 projections. The files obtained (DCM and tiff files) were processed using the software Avizo 7.1® in through the axes XY, XZ and YZ. Both the bone material and the sediment were reconstructed on the 3D model separately, so that the latter could be virtually removed. Finally, the surface of the specimen as a whole was generated.

3. Systematic paleontology

Squamata Oppel, 1811
Anguimorpha Fürbringer, 1900
?Varaniformes Conrad, 2008

?Varaniformes gen. et sp. indet (Figs. 3–5)

Material. MCD-8827, an articulated left hindlimb, preserving two complete tarsals and four metatarsals (Figs. 3–5), the *mtV* being the only complete of them.

Locality and Horizon. Basturs-1 fossil site (Fig. 2), uppermost Cretaceous (Maastrichtian). Tremp Synclinal, Lleida, Catalonia, Spain (López-Martínez, 2000; Csiki-Sava et al., 2015; Gaete et al., 2015; Fondevilla et al., 2018, 2019).

Description. MCD-8827 measures 7.06 cm in its maximum length and 3.11 cm in its maximum width. Six articulated bony elements can be identified: two distal tarsals (the third and the fourth) and four metatarsals (from the second to the fifth) (Fig. 3A–F). Metatarsals from the second to the fourth lack their distal parts (Fig. 3A–F), so their total original length is unknown (see Table 1), and the fifth metatarsal is completely preserved (Fig. 3A–F).

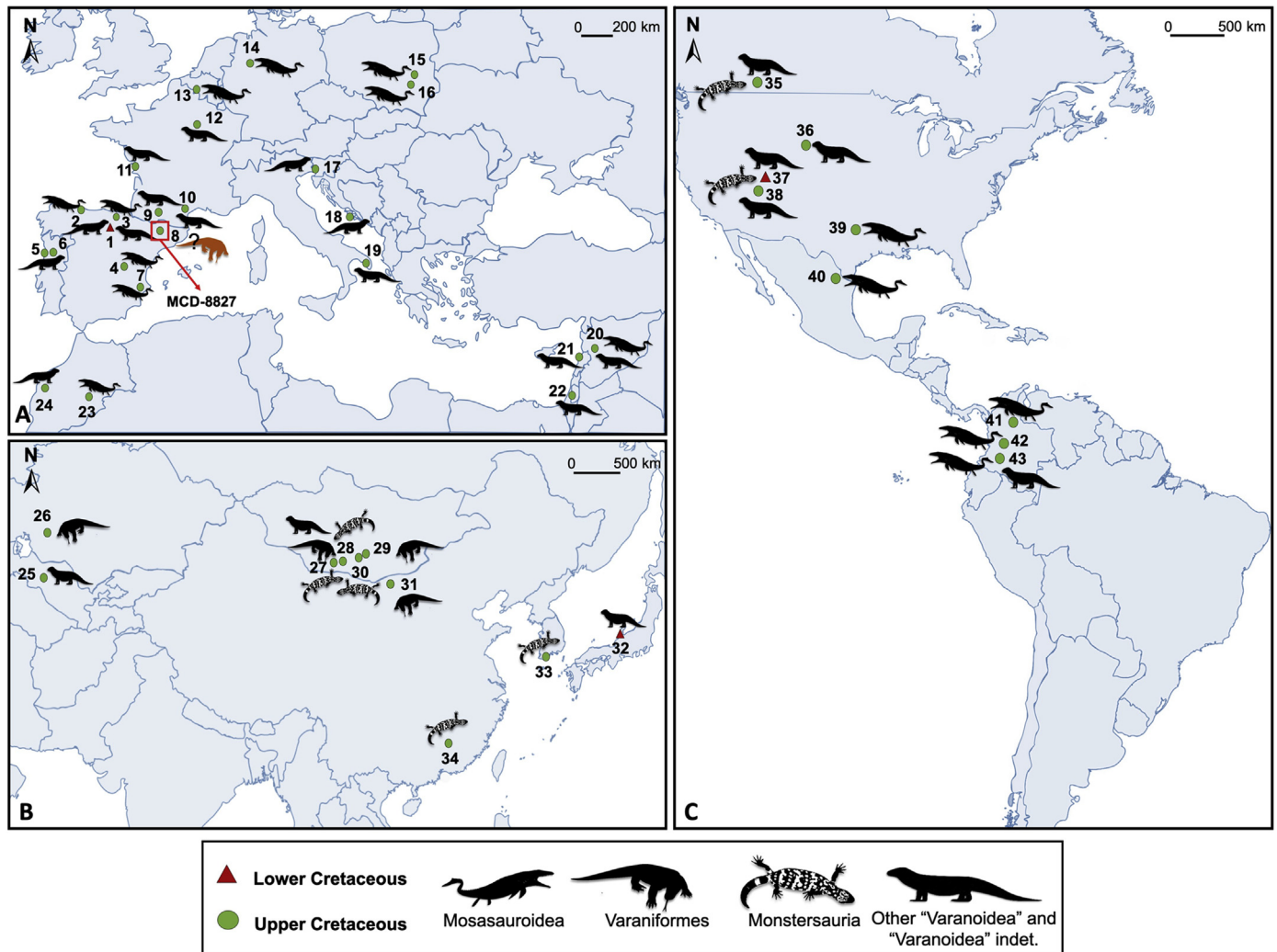


Fig. 1. Main localities of the “varanoid” fossil taxa compiled for this study and fossil specimen MCD-8827, corresponding to a partial left pes attributable to ?Varaniformes from the Maastrichtian of Basturs-1 (Lleida, Spain). “Varanoidea” geographical range during the Cretaceous showing a main distribution throughout the supercontinent Laurasia. A, European, North African and middle East localities: 1, Salas de los Infantes, Viajete Site (Burgos, Spain) (Barremian–Aptian); 2, La Cabaña Formation (Asturias, Spain) (upper Cenomanian); 3, Castillo-Lasarte (Álava, Spain) (upper Campanian) and Albaina, Laño quarry (Condado de Treviño, Burgos, Spain) (upper Maastrichtian); 4, Lo Hueco (Cuenca, Spain) (upper Campanian–lower Maastrichtian); 5, Aveiro (Portugal) (upper Campanian–lower Maastrichtian); 6, Viso (Portugal) (upper Campanian–lower Maastrichtian); 7, Font de la Carrasca Quarry, Castalla (Alicante, Spain) (upper Maastrichtian); 8, Basturs-1 (Lleida, Catalonia, Spain) (Maastrichtian); 9, Auzas Marls (France) (upper Maastrichtian); 10, Cruzy (Hérault) and Montsérét (Corbières) (France) (upper Campanian–lower Maastrichtian); 11, Madame Island (France) (upper Cenomanian); 12, Sainte-Maure (Indre-et-Loire, France) (middle Turonian); 13, Mesvin (Hainault, Belgium); 14, DIMAC quarry, Hesselstal Formation (Germany) (lowermost Turonian); 15, Piotrawin (Poland) (upper Campanian) and Nasitów (Poland) (upper Maastrichtian); 16, Maruszów (Poland) (upper Maastrichtian); 17, Komen (Slovenia) (upper Cenomanian); 18, Hvar Island (Croatia) (upper Cenomanian); 19, Nardò (Lecce, Puglia, Italy) (upper Campanian, lower Maastrichtian); 20, Charquieih, Khneifiss, Bardeh and Soukhneih (Syria) (Maastrichtian); 21, Hakei (Lebanon) (lower–middle Cenomanian); 22, Judean Hills (Israel) (upper Cenomanian–lower Turonian); 23, Goulmima (Er-Rachidia, Morocco) (lower Turonian); 24, Yousseoufia (Morocco) (Maastrichtian). B, Asian localities: 25, Dzharakuduk (Uzbekistan) (Turonian/Coniacian); 26, Zhirkindek (Kazakhstan) (Turonian–Coniacian); 27, Khermeen-Tsav and Hirmin Tsav (Gobi Desert, Mongolia) (Santonian–Campanian and ?middle Campanian); 28, Khulsan, Ukhua Tolgod and Uuden Sair (Gobi Desert, Mongolia) (?upper Santonian/?lower Campanian, ?middle Campanian, upper Campanian); 29, Shabarakh Usu (Gobi Desert, Mongolia) (Santonian–Campanian); 30, Tögrökgiin Shiree (Gobi Desert, Mongolia) (?middle Campanian); 31, Bayan Mandahu (Urad Houqi, Inner Mongolia, China) (middle Campanian); 32, Kuwajima (Honshu, Japan) (Berriasian–Valanginian); 33, Boseong, (Chollanam-do, South Korea) (Campanian); 34, Nankang (Jiangxi, China) (Maastrichtian); C, American localities: 35, Milk River Area (Alberta, Canada) (Campanian); 36, Lance Formation (Wyoming) (Maastrichtian); 37, Emery County (Utah, USA) (Albian–Cenomanian); 38, Kaiparowits Formation (Utah, USA) (Campanian); 39, Cedar Hill (Dallas County, Texas) (middle Turonian); 40, Vallecillo (Nuevo León State, Mexico) (lower Turonian); 41, Lebrija (Colombia) (lower Coniacian); 42, Coello (Colombia) (Campanian); 43, The Upper Magdalena Valley (Colombia) (Turonian). Data according to Gilmore (1928, 1943), Arambourg (1952), Estes (1964), Borsuk-Biatynicka (1984), Nessov (1981), Antunes and De Broin (1988), Rage (1989), Norell et al. (1992, 2008), Alifanov (1993), Cifelli and Nydam (1995), Gao and Hou (1996), Lingham-Soliar (1996), Buffetaut et al. (1997), Dal Sasso and Pinna (1997), Norell and Keqin (1997), Bardet et al. (1999, 2000, 2003, 2006, 2013a, b), Keqin and Norell (2000), Nydam (2000, 2013), Kordikova et al. (2001), Peng et al. (2001), Laurent et al. (2002), Machalski et al. (2003), Pierce and Caldwell (2004), Rage and Néraudeau (2004), Bell and Polcyn (2005), Haber and Polcyn (2005), Evans et al. (2006), Smith and Buchy (2008), Vullo et al. (2009), Houssaye et al. (2010), Palci and Caldwell (2010), Conrad et al. (2011b), Páramo-Fonseca (2011), Mo et al. (2012), Houssaye et al. (2013a, b), Yi and Norell (2013), Ortega et al. (2015), Park et al. (2015), Pereda-Suberbiola et al. (2015), Paparella et al. (2018), Smith et al. (2019).

The fourth distal tarsal in MCD-8827 is rhomboidal in shape and is slightly longer in its preaxial-postaxial axis than in its proximal-distal axis (Fig. 3B–C). This bony element articulates medi-odistally with the third distal tarsal through a small contact surface (Fig. 3C). The fourth distal tarsal also contacts the fourth metatarsal

posterodistally and the fifth metatarsal posteroproximally through a larger surface (Fig. 3C). Proximally, in its inner surface, the fourth distal tarsal bears a distinct *tongue-in-groove* concavity (Fig. 3B–C red arrows) which we interpret as the articular facet for the astragalocalcaneum. The third distal tarsal is smaller in size, nearly

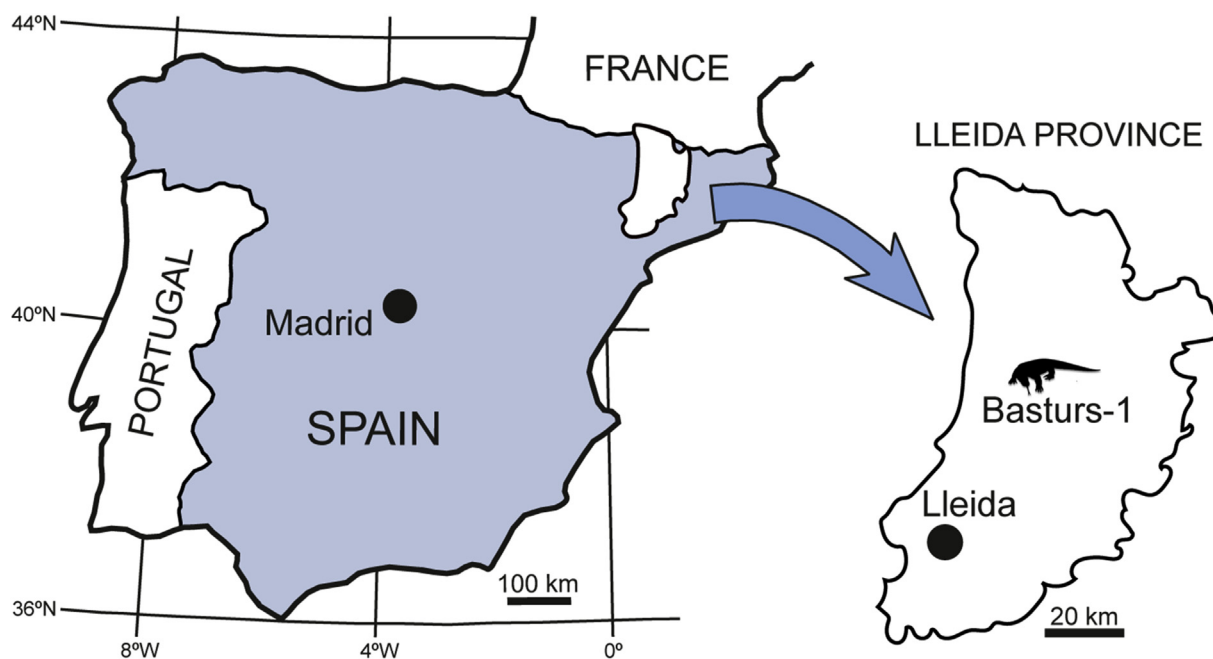


Fig. 2. Geographical location of the Maastrichtian fossil site of Basturs-1 (Lleida, Spain) where the fossil specimen MCD-8827, corresponding to a partial left pes attributable to ? Varaniformes, was found. The geographical coordinates of the site, 42° 10' 15.128" N, 1° 1' 1.315" E, were obtained from the georeferenced map corresponding to Gaete et al. (2015: fig. 2).

half the width of the fourth distal tarsal (Fig. 3C). This bony element is slender and more elongated than the fourth distal tarsal, with a posterior process directed towards the plantar surface (Figs. 4C–D, 5A). The third distal tarsal articulates with the fourth distal tarsal at its proximal-most facet. Moreover, this element articulates anterodistally with the second metatarsal, posterodistally with the third metatarsal and with the fourth metatarsal through its most posteroproximal facet (Figs. 3B–C, 5A). The position of the third distal tarsal is noteworthy in that it lies between the second and the third metatarsals, contacting them by means of a wedge-like distal tip (Figs. 3B–C, 5A).

The second metatarsal articulates proximally through its postaxial facet with the anterodistal facet of the third distal tarsal and with the third metatarsal posteroproximally (Fig. 3B–C). The third metatarsal articulates anteroproximally with the third distal tarsal and with the fourth metatarsal posteroproximally. Both the second and the third metatarsals bear moderately developed proximal epiphyses (Fig. 3B–C). The fourth metatarsal articulates with the fourth distal tarsal through its proximal-most facet and, in its anteroproximal facet, a distinct contact with the third distal tarsal occurs and bears a better developed epiphysis than the second and third metatarsals (Fig. 3B–C). The fifth metatarsal articulates proximally with the fourth distal tarsal and, despite contacting the fourth metatarsal, there is no direct articulation between the latter with the fifth metatarsal (Figs. 3B–C, E–F, 5A). The fifth metatarsal bears a partially eroded outer process (Figs. 4A–B, 5A–B), the base of which is preserved. Despite this partial preservation, its base demonstrates that it was distinct and well developed (Fig. 5C). Ventrally, the fifth metatarsal possesses two well developed tubercles and a slightly elevated area corresponding to the base of the outer process (Fig. 5C). The lateral plantar tubercle is elongated, robust and has a rounded ovoid tip that extends close to the medial plantar tubercle. The medial plantar tubercle also bears a rounded ovoid tip that is less robust (Fig. 5C). The outer process is distally placed from both plantar tubercles and seems less prominent than both lateral and medial plantar tubercles (Fig. 5C). The fifth metatarsal is proportionally more robust than the other metatarsals. It

has a moderately long longitudinal axis (Fig. 4A–B), and it bears a well-developed proximal head with squarish contours, isolated from the rest of the metatarsal and so setting up a 'long-necked' configuration (Fig. 5A–C). The fifth metatarsal is distinguished by its double angulation, here referred as 'hooking angle' and 'inflexion angle' (Fig. 5C, E). Metatarsals from two to four have rounded cross-sections and are laterally flattened (Fig. 3E–F) with a distinct dorsal-plantar development (Fig. 4C–D), most noticeable on the fourth metatarsal.

The hooking angle (ha) and the inflexion angle (inf) are 122.4° and 120° respectively (see Table 1 and Supplementary information 2 in Appendix B). The angle of the lateral plantar tubercle in relation to the other two (lpt_x) is estimated to be about 82.6° due to preservation issues (see Table 1 and Supplementary information 2 in Appendix B). Angulation in MCD-8827 results in it being sub-pentagonal in shape (Fig. 5D). The fourth distal tarsal is roughly twice the width of the third (dtIV/dtIII) (Fig. 3C, see Table 1).

4. Discussion

4.1. Systematic assignment of MCD-8827

Identification of MCD-8827 as a member of Squamata. MCD-8827 shows two characters considered synapomorphies of Squamata, allowing its attribution to this clade: presence of a distinct 'tongue-in-groove' articular surface on the fourth distal tarsal for the astragalocalcaneum (Fig. 3B–C) (Brinkman, 1979; Rewcastle, 1980; Estes et al., 1988; Gauthier et al., 1988; Reynoso, 1998, 2000; Evans and Wang, 2005, 2010; Conrad, 2006a; Sullivan, 2010; Conrad et al., 2011b); and presence of a specialized fifth metatarsal with double angulation and well developed plantar tubercles (Fig. 5C, E) (Estes et al., 1988; Carroll and DeBraga, 1992; Reynoso, 2000; Evans, 2003; Conrad and Norell, 2007; Jerez, 2012).

A fourth-third distal tarsal proportion of roughly two, as documented in this study and others (Rieppel, 1992; Conrad, 2006a; Rieppel and Grande, 2007; Smith and Buchy, 2008; Evans and

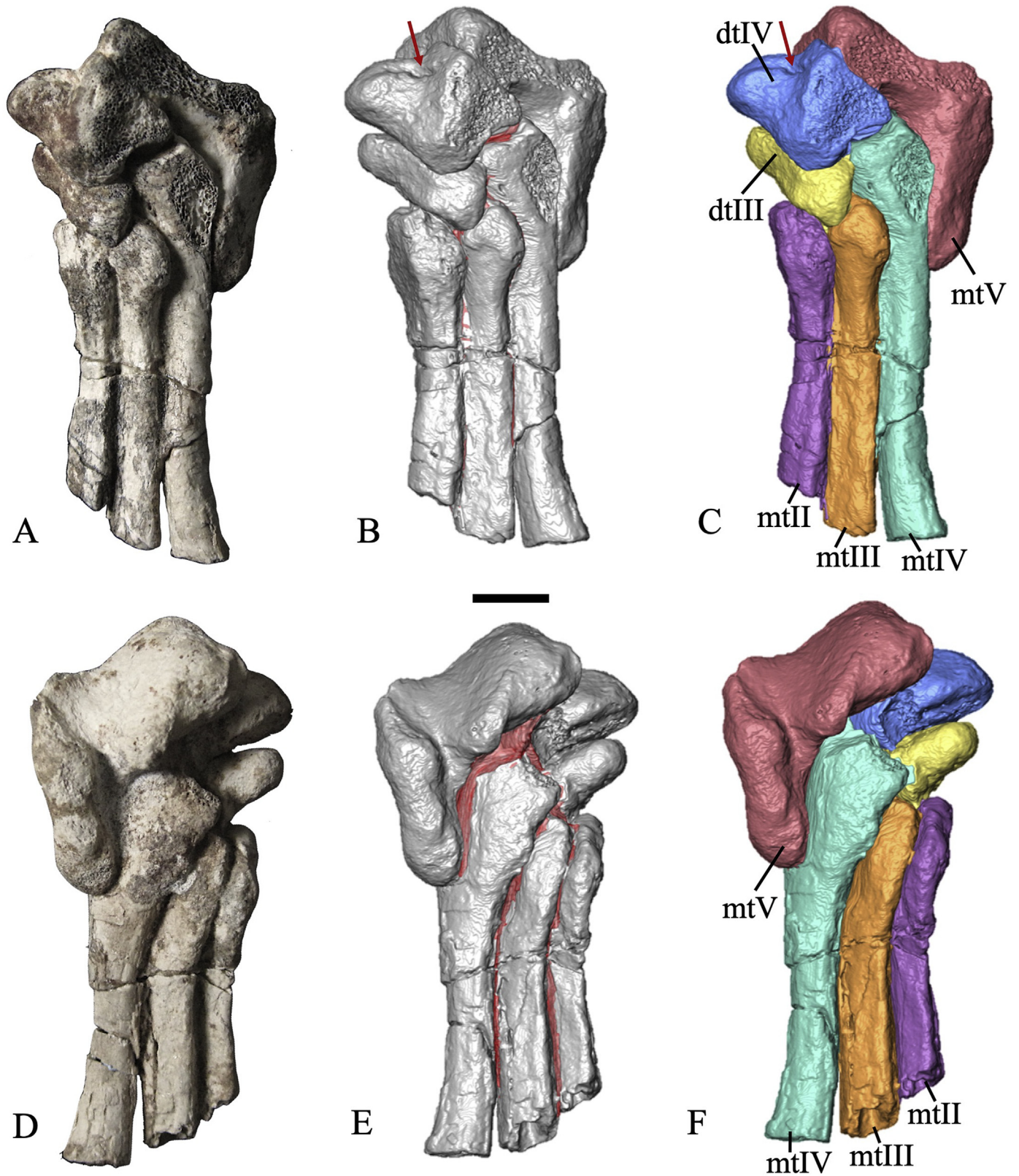


Fig. 3. Original material and digital reconstruction of MCD-8827 fossil specimen, corresponding to a partial left pes attributable to ?Varaniformes, from the Maastrichtian of Basturs-1 (Lleida, Spain). Original material (A, D) and reconstructed 3D model from CT-Scan (B–C, E–F) before (B, E) and after (C, F) surrounding matrix was removed (transparent red) in dorsal (A–C) and plantar views (D–F). Arrows indicate the *tongue-in-groove* articulation of *dtIV* exclusive of Squamata. Scale bar: 10 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

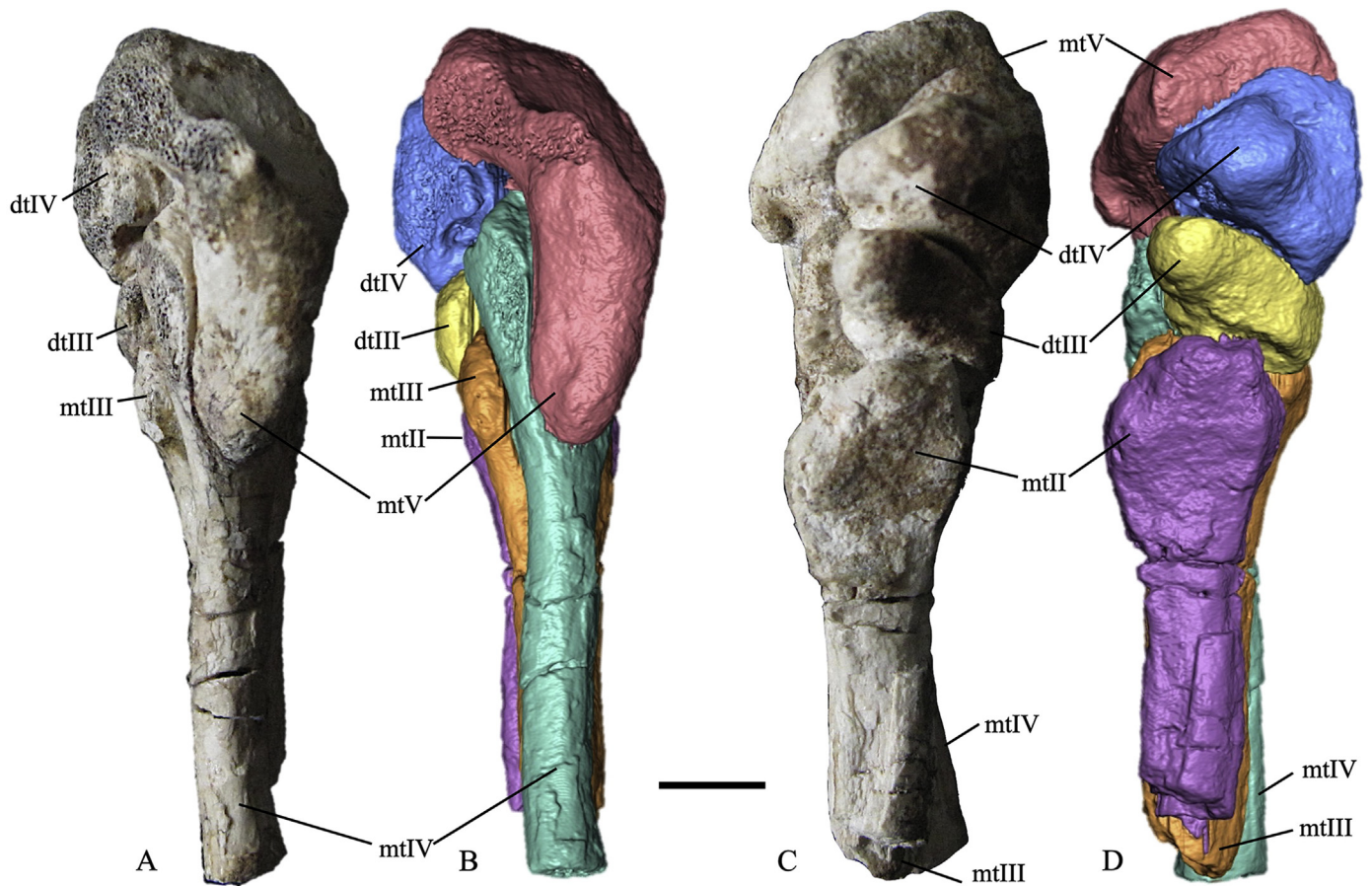


Fig. 4. Original material and digital reconstruction of MCD-8827 fossil specimen, corresponding to a partial left pes attributable to ?Varaniformes, from the Maastrichtian of Basturs-1 (Lleida, Spain). Original material (A, C) and reconstructed 3D model (B, D) in left lateral (outer face) (A–B) and right lateral (inner face) (C–D) views. Scale bar: 10 mm.

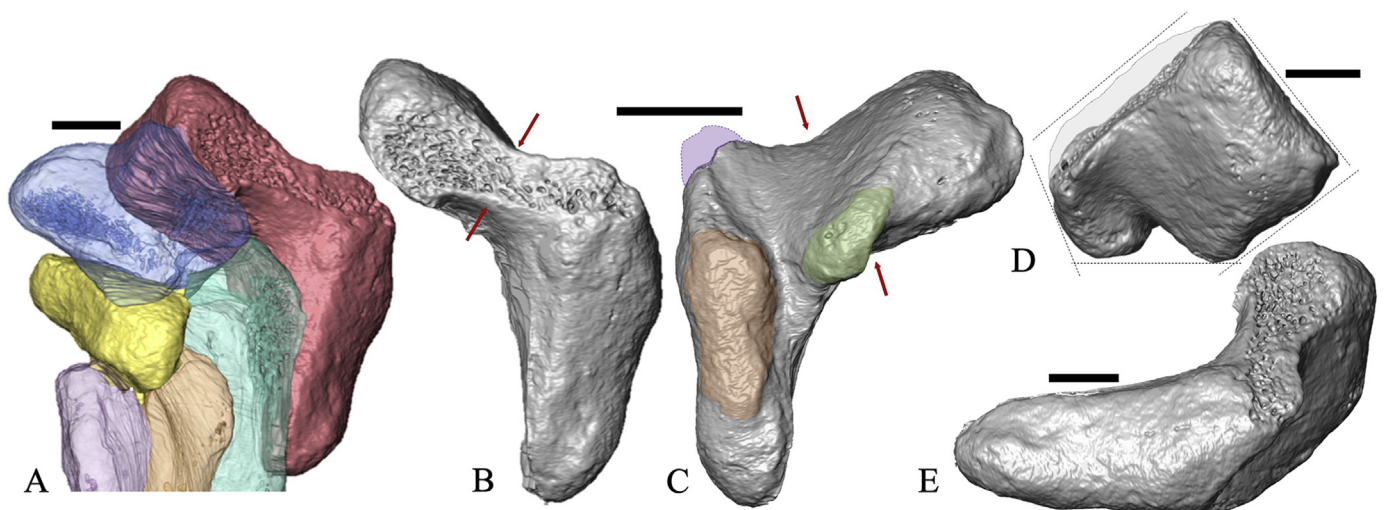


Fig. 5. Reconstruction of the articulations and morphology of the metatarsal V of MCD-8827, corresponding to a partial left pes attributable to ?Varaniformes, from the Maastrichtian of Basturs-1 (Lleida, Spain). A, main articulations shown between tarsal and metatarsal elements with *mtV*, where the transparent elements represent those which articulate with the latter. B–E, general morphology of *mtV* shown in dorsal (B), plantar (C), proximal (D) and lateral views (E). Arrows indicate the long-necked hooked *mtV* configuration typical of Lepidosauromorpha. Plantar tubercles: *lpt* (orange); *mpt* (green); *op* (purple). Scale bars: A, E, 6 mm; B, C, 10 mm; D, 7 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Wang, 2010; Conrad et al., 2011b), can be recognized as exclusive to Squamata (Table 2), being also shared by MCD-8827 (Table 1). In this sense, the *Sphenodon punctatus* specimens analysed in this

study show a fourth-third distal tarsal proportion of approximately three (see Table 2). This was also observed in the *S. punctatus* specimens analysed in other works (e.g. Brinkman, 1979; Benton,

Table 1

Tarsal and metatarsal measures of fossil specimen MCD-8827, corresponding to a partial left pes attributable to ?Varaniformes, from the Maastrichtian of Basturs-1 (Lleida, Spain). Length measures of metatarsals II-IV are not representative of the actual element length since they are fragmented in their distal part. Hooking (ha), inflexion (inf) and lateral plantar tubercle (lpt_z) angles were only measured in *mtV*.

Measures	Anatomical element				
	<i>mtII</i>	<i>mtIII</i>	<i>mtIV</i>	<i>mtV</i>	<i>dtIV/dtIII</i>
Radius (cm)	0.52	0.68	0.8	0.57	—
Length (cm)	4.05	4.42	5.55	2.68	—
ha (°)	—	—	—	122.4	—
inf (°)	—	—	—	120	—
lpt _z (°)	—	—	—	82.6	—
Proportion	—	—	—	—	1.83

Table 2

Tarsal and metatarsal V measure ranges in the Lepidosauria taxa analysed in the study. The table shows a summary of the main values obtained for the hooking angle (ha) and the proportion between the *dtIV* and *dtIII* (*dtIV/dtIII*) from the lepidosaur specimens here studied (see [Supplementary information 2 in Appendix B](#)).

Measures	Taxon				Sphenodontia
	Squamata				<i>Sphenodon</i>
	Iguania	Anguimorpha	Scincoidea	Lacertoidea	
<i>MtV</i> ha (°)	130.1–?142.1	119.4–136.6	131–142	?134–145	115.1
<i>dtIV/dtIII</i>	1.94–2.09	?1.75–2.22	1.99–2.04	1.90–2	2.93–3

1985; Gauthier et al., 1988). This character, along with a rounded centrally placed lateral plantar tubercle, unique for *S. punctatus*, in combination with a moderately developed outer process, and a poorly developed medial plantar tubercle (none of them shared with the Basturs-1 specimen analysed here), differentiates the fifth metatarsal of *S. punctatus* from that of the squamates (see Fig. 6A,G) (Brinkman, 1979; Gauthier et al., 2012; Regnault et al., 2016; Borsuk-Białynicka, 2018).

Comparison of MCD-8827 with the squamate clade Gekkota. The fossil specimen MCD-8827 differs from Gekkota in having a slender and elongated fifth metatarsal with a “pedunculated” lateral plantar tubercle capped with an ovoid-rounded protuberance. In contrast, the gekkotan condition shows a rather short fifth

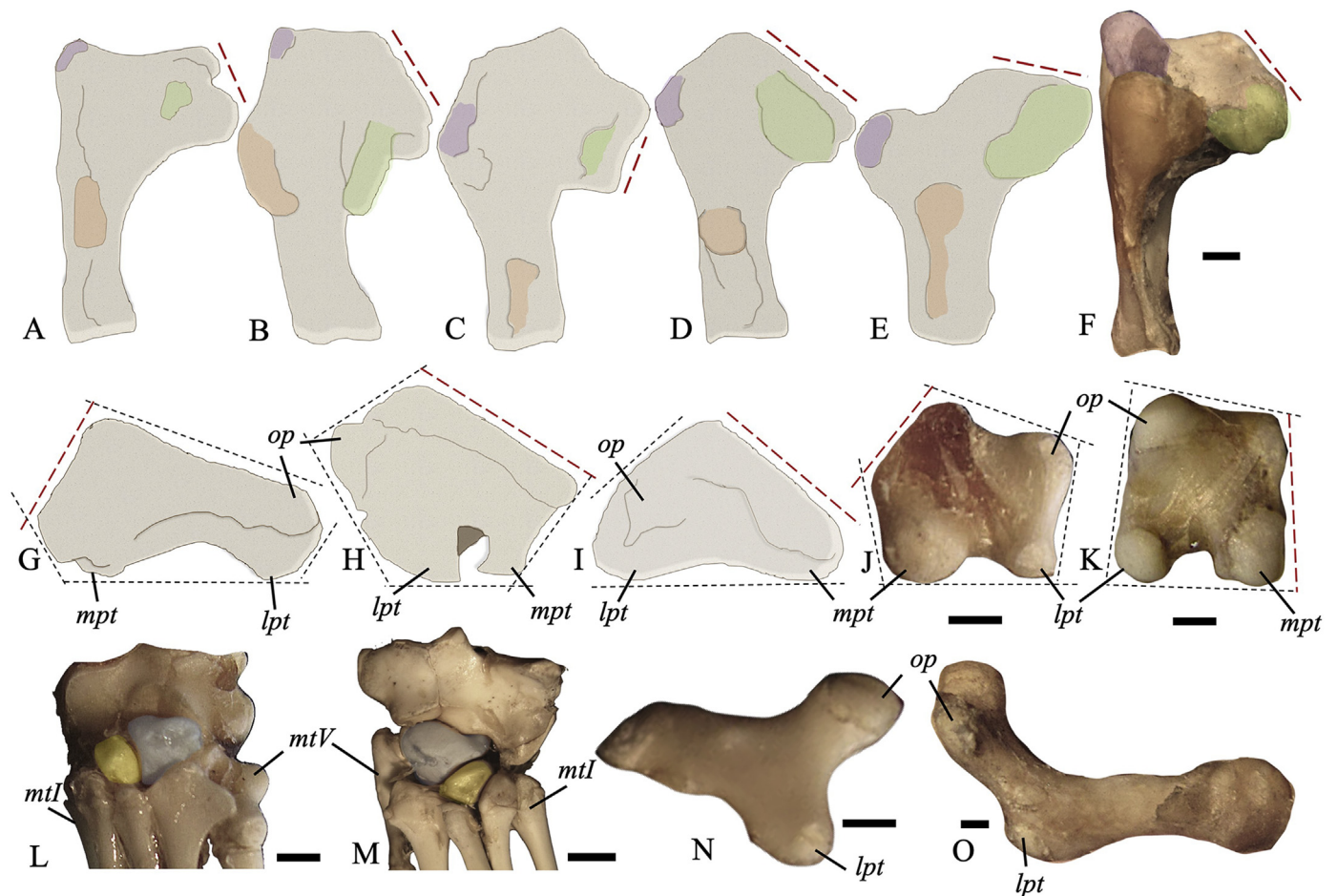


Fig. 6. Tarsal and metatarsal traits in some lepidosaur taxa examined in this study. A–F, morphology of the tubercles of the *mtV*; G–K, angulation in proximal view, the upper margin corresponding to the dorsal region; L–M, *dtIV/dtIII* proportion; and N–O, inflexion angle in some species of Lepidosauria: *Sphenodon punctatus* (A, G), *Amblyrhynchus cristatus* (B), *Shinisaurus crocodilurus* (C, I), *Xenosaurus rectocollaris* (D), *Heloderma horridum* (E), *Varanus bengalensis* (F, M), *H. suspectum* (J, L, N), *Iguana iguana* (H), *V. rudicollis* (K), *V. griseus* (O). Plantar tubercles: *lpt* (orange); *mpt* (green); *op* (purple). *DtIII* (yellow) y *dtIV* (blue). Dashed lines in red represent the articular facet for *dtIV*. Drawings not to scale. Scale bars: F, K, L, 2 mm; J, N, O, 1 mm; M, 4 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

metatarsal with a rather bulbous and “non-pedunculated” tubercle (see Daza and Bauer, 2012; Scherz et al., 2017), and raised plantar tubercles, really close to the articulation facet and between each other (Russel et al., 1997; Scherz et al., 2017). Gekkotans tend to acquire a symmetrical foot as a result of a shorter fourth metatarsal compared to the third one (Russel et al., 1997; Simões et al., 2016), a condition that cannot be confirmed in MCD-8827 due to the fragmentary state of these bony elements. Additionally, in gekkotans the proximal head of the fourth metatarsal is extremely broadened so that the angle between the shafts of the third and fifth metatarsal increases and, consequently, the imbrication amongst the metatarsals is proximally reduced (Daza and Bauer, 2012; Simões et al., 2016). This condition is not shared with MCD-8827 since the third metatarsal proximally overlaps a great portion of the fourth (Figs. 3, 5A).

Comparison of MCD-8827 with the squamate clades Scincoidea and Lacertoidea. The scincoids *Cordylus angolensis*, *C. cordylus*, *C. namakuiyus*, *C. phonolithos*, *Corucia zebrata*, *Ctenotus schomburgkii*, *Egernia whitii*, *Smaug barbertonensis*, *S. giganteus* and *Tribolonotus* sp. and the lacertoids *Ameiva ameiva*, *Ecleopopus gaudichaudii*, *Heterodactylus imbricatus*, *Leposoma scincoides*, *Micrablepharus maximiliani*, *Placosoma cordylinum* and *Takydromus sexlineatus* (as members of their corresponding clades for which observations were obtained) tend to have a stout proximal head of the fifth metatarsal which, in ventral view, is notably widened (see fig. 6 in Jerez, 2012, and fig. 5 in Černánský and Smith, 2019). MCD-8827, however, has a fifth metatarsal with the proximal part resulting in a well-developed head that is somehow elongated towards and behind the fourth distal tarsal (Fig. 5A). Moreover, in these two clades the medial plantar tubercle tends to be situated apart from the outer process and, together with the lateral plantar tubercle, they develop in a dorsal-plantar plane in a “heel-like” manner (see fig. 11F in Müller, 2001; fig. 4 –*Amphiglossus ornaticeps* plate, central image– in Miralles et al., 2015; fig. 7C in Talanda, 2018; and fig. 5 in Černánský and Smith, 2019), and with moderate developed apophyses of the tubercles. In contrast, MCD-8827 bears two plantar tubercles that are more longitudinally developed, relatively closer to each other and with bigger ovoid apophyses.

Comparison of MCD-8827 with the squamate clade Iguania. The fossil specimen MCD-8827 differs from the members of Iguania in having a fifth metatarsal morphology presenting well-developed, ovoid-rounded tubercles and a protuberant outer process (Fig. 5C), in contrast to the iguanian condition where the outer process is barely developed and the plantar tubercles tend to acquire a more elongated shape with the medial plantar tubercle, usually the most developed, generally resulting in a ‘downward-pointing’ structure (e.g. *Bronchocela cristatella* or *Sceloporus undulatus*). This feature is much more evident in the species within the family Iguanidae (e.g. *Amblyrhynchus cristatus*, *Ctenosaura similis* or *Iguana iguana*) (see Brinkman, 1979, 1980; Borsuk-Białynicka, 2018; and Fig. 6B, H in this work).

Comparison of MCD-8827 with the squamate clade Borioteiioidea. The clade Borioteiioidea (or Polyglyphanodontia sensu Gauthier et al., 2012) includes large fossil taxa (e.g. *Polyglyphanodon*, *Gilmoreteius*) occasionally represented by skeletons preserving hindlimb elements. The three specimens of *Polyglyphanodon sternbergi* described by Gilmore (1942) (USNM 15568, USNM 15816 and USNM 15817) preserve the entire foot (see fig. 36 in Gilmore, 1942). However, the pes of these specimens are preserved and illustrated in dorsal view and the fifth metatarsal is not described in detail, hence, no anatomical features of the plantar tubercles could be compared. Nonetheless, some features could be compared: the specimen USNM 15568 possesses a “flattened” fourth distal tarsal (referred as “tarsale 4” in Gilmore, 1942) that acquires a slightly

overlying position upon the third distal tarsal (see fig. 36 in Gilmore, 1942). MCD-8827, instead, has a rhomboidal fourth distal tarsal that lies completely upon the third distal tarsal (Fig. 5A). Additionally, the proximal head in the fifth metatarsal of the three specimens mentioned of *P. sternbergi* is not as developed as in MCD-8827. Besides, the specimen USNM 15568 has measures for all the five metatarsals, showing a *mtIV/mtV* ratio of 2.77, which is apparently higher than that estimated for MCD-8827 (about 2.07).

On the other hand, the Yale Peabody Museum specimen of *Polyglyphanodon sternbergi* (YPM VP 003230) preserves the fifth metatarsal in both dorsal and ventral views. In dorsal view, the fifth metatarsal also shows a less developed proximal head than that of the fifth metatarsal of MCD-8827. In ventral view, the fifth metatarsal of *P. sternbergi* bears two distinct rounded and ‘not-pedunculated’ plantar tubercles that resemble those of the teiid *Ameiva ameiva*, but with the medial plantar tubercle situated right in the edge of the articular facet with the fourth distal tarsal and, thus, differing as well from those of MCD-8827.

A specimen of *Gilmoreteius* (*Macrocephalosaurus*) *chulsanensis* (ZPAL-I/14) preserving the hindlimb was described in detail by Sulimski (1975). The foot is illustrated both in dorsal and ventral views. In dorsal view, the third distal tarsal lies completely lateral to the fourth distal tarsal unlike in *Polyglyphanodon sternbergi* (YPM VP 003230) and the fossil specimen from Basturs-1 (MCD-8827). The fourth distal tarsal is subrectangular in shape (see fig. 11A₁–A₂ in Sulimski, 1975) rather than rhomboidal as in MCD-8827 (Fig. 3A–C). As in *P. sternbergi*, the proximal head of the fifth metatarsal is not as developed as in MCD-8827. In ventral view, the fifth metatarsal of ZPAL-I/14 is illustrated as bearing a distinct lateral plantar tubercle which seems ‘not-pedunculated’ and a medial plantar tubercle hardly developed, thus differing from the fossil specimen MCD-8827 (Fig. 5C). Besides, the *mtIV/mtV* ratio in ZPAL-I/14 (*G. chulsanensis*) is 2.90, which is much higher than that estimated for the fossil specimen MCD-8827 from Basturs-1 (about 2.07).

Comparison of MCD-8827 with the squamate clade Mosasauriformes. European mosasauriforms preserving the tarsus include *Acteosaurus tommasinii* from the upper Cenomanian of Komen (Slovenia) and *Primitivus manduriensis* from the upper Campanian/lower Maastrichtian of Nardò (Italy). MCD-8827 differs from *A. tommasinii* in the hooked fifth metatarsal, which in the latter has a hookless configuration (Palci and Caldwell, 2010). MCD-8827 shares with *P. manduriensis* a fifth metatarsal with a proximal expanded head, but the latter differs from MCD-8827 in having a slightly curved fifth metatarsal which is notably shorter (1.04 cm; Paparella et al., 2018) than that of MCD-8827 (2.68 cm) making a *mtIV/mtV* ratio of 1.05, at least half the value estimated for MCD-8827 (2.07). Forms from other continents include the lower/middle Cenomanian *Aphanizocnemus lebanensis* of Hakel (Lebanon) and the lower Turonian *Vallecillosaurus donrobertoi* of Nuevo León (Mexico). MCD-8827 differs from *A. lebanensis* in the fifth metatarsal, which is not hooked in the latter, and in the dorso-ventral compression of metatarsals (Dal Sasso and Pinna, 1997), these two traits being characteristic of aquatic forms (mosasauriforms) (DeBraga and Carroll, 1993; Dal Sasso and Pinna, 1997; Lee et al., 2016; Paparella et al., 2018; Goncalves Augusta, 2019). MCD-8827, in contrast, presents metatarsals that are laterally flattened (Fig. 4). MCD-8827 differs from *V. donrobertoi* in the placement of the third and fourth distal tarsals, these elements being situated one after the other in the latter and not lying one upon each other as it occurs in MCD-8827; in the less pronounced inflexion of the fifth metatarsal; and, finally, in the length of the fifth metatarsal, shorter (1.01 cm) (Smith and Buchy, 2008) than in MCD-8827, making a *mtIV/mtV* ratio of 1.7 (in contrast to that of MCD-8827, with an estimated minimal value of 2.07).

Comparison of MCD-8827 with the squamate clade Anguimorpha. MCD-8827 shares with the pes of Anguimorpha the presence of a fifth metatarsal with well-developed medial and lateral plantar tubercles, the latter being elongated; the elongated condition of the metatarsal long axis (e.g. Evans and Wang, 2005; Conrad, 2006a; see Fig. 5C); and a hooking angle lower than 137° (see Table 2). Within anguimorphs, MCD-8827 differs from the xenosaurids (e.g. *Xenosaurus grandis* and *X. rectocollaris*) in the mediolaterally positioned lateral plantar tubercle, and in the outwards inclination of its “peduncle” (see fig. 9B in Conrad, 2006a and Fig. 6D in this work). Both *X. grandis* and *X. rectocollaris* have a wider hooking angle (135°) than MCD-8827 (122.4°) (see Supplementary information 2 in Appendix B).

The shinisaurid *Shinisaurus crocodilurus* has a fifth metatarsal with a moderate outer process and a lateral plantar tubercle placed next to the articular condyle of the metatarsal (Fig. 6C, I) (Conrad, 2006a,b; Bhullar, 2011; Conrad et al., 2011b). The fifth metatarsal of the Eocene shinisaurid *Bahndwivici ammoskius*, from Wyoming (USA), resembles that of *S. crocodilurus* in having a lateral plantar tubercle placed distally, near the articular condyle (Conrad, 2006b), as well as a medial plantar tubercle and outer process similar in shape and placement to those found in *S. crocodilurus*, hence differing from MCD-8827.

The anguoids *Abronia graminea*, *Diploglossus millepunctatus*, *Elgaria coerulea* and *Mesaspis moreletii* have a fifth metatarsal with a moderate outer process, a medial plantar tubercle slightly bigger than the lateral plantar tubercle, somehow intermediate between helodermatids and varanids (see below), and a well-developed proximal head of the fifth metatarsal. On the contrary, MCD-8827 has a fifth metatarsal with a medial plantar tubercle not bigger than the lateral plantar tubercle, a bigger development of the proximal head and a smaller hooking angle (122.4°) than the anguoids above mentioned (133° – 136.6°).

Rieppel and Grande (2007) mentioned a fifth metatarsal bearing an “expanded head with squarish contours” as a character that the varanid *Saniwa ensidens* shares with other “varanoids”. However, other anguimorphs here studied show a similar configuration (e.g. *Abronia graminea*, *Mesaspis moreletii* or *Xenosaurus rectocollaris*). Similarly, MCD-8827 resembles the pes of helodermatids and varanids in having these squarish contours along with well-developed plantar tubercles generally placed close to each other (Figs. 5C, 6E–F) (see Rieppel and Grande, 2007). However, note that, because current molecular and combined phylogenies regard shinisaurids as more closely related to varanids than to helodermatids (e.g. Conrad et al., 2011a; Wiens et al., 2012; Burbrink et al., 2019), the similarities between helodermatids and varanids noted above cannot be regarded as indicative of shared ancestry.

Large fossil anguimorphs include members of Monstersauria (*Heloderma* plus its stem), Varaniformes (Varanidae plus its stem), and indeterminate “varanoids”, the latter term traditionally used for forms more similar to *Heloderma* and *Varanus* than to other anguimorphs, although the group is now considered as polyphyletic (see above and also Burbrink et al., 2019). Regarding “Varanoidea”, no anatomical comparison between MCD-8827 and the fossil “varanoids” of the Iberian Peninsula is possible due to the lack of tarsal/metatarsal elements preservation in those specimens. However, some European and non-European monstersaurs and varaniforms preserve tarsal/metatarsal elements to be compared with the fossil specimen of Basturs-1 (see section *Extinct species* of Supplementary information 1 in Appendix A).

Regarding monstersaurs, MCD-8827 differs from the extant helodermatids *Heloderma horridum* and *H. suspectum* in their fifth metatarsal with an enlarged medial plantar tubercle that expands reaching most of the surface of the articular facet with the fourth distal tarsal, and which is much bigger in comparison with the

lateral plantar tubercle and the outer process (Fig. 6E; see also Conrad, 2006a,b). In both *H. horridum* and *H. suspectum* the third and fourth distal tarsals are placed one after another (Fig. 6L), the hooking angles are around 130° and the inflexion angles are pretty acute (81.6° and 88° respectively), therefore, differing from MCD-8827.

The middle Campanian *Gobiderma pulchrum* of Tögrökgiin Shiree (Mongolia) also shares the ‘helodermatid’ condition of the position of the distal tarsals (one settled after the other). Nevertheless, its fifth metatarsal has a distally placed lateral plantar tubercle (Conrad et al., 2011b), which is much smaller in length (less than 1 cm), differing from MCD-8827 in this regard. However, the reported fifth metatarsal that “is only slightly shorter than II and IV” is not evident in the provided figure (see fig. 51A in Conrad et al., 2011b). It is finally important to note that not all phylogenetic analyses recovered *G. pulchrum* as a monstersaur. Gauthier et al. (2012) recovered it on the stem of a monophyletic “Varanoidea”, whereas in Reeder et al. (2015) it was placed, together with *Aiolosaurus oriens* and *Estesia mongoliensis*, as sister to varanids. The pes of *Palaeosaniwa canadensis* (Monstersauria) from the Upper Cretaceous of Canada is known (Balsai, 2001), but has not been described in detail, and comparison is thus not possible.

Regarding varaniforms, MCD-8827 more closely resembles this group rather than monstersaurs in: *Varanus*-like plantar tubercles similar in their ovoid shape and relative position; a medial plantar tubercle similar in size to that of the lateral plantar tubercle (Figs. 5C, 6F) (see also Rewcastle, 1980; Conrad, 2006a); and the relative positions of the third and fourth distal tarsals in MCD-8827, shared with *Varanus* spp., whose fourth distal tarsals always lie completely upon the third distal tarsals (Figs. 5A, 6M) (see also Owen, 1866; Goodrich, 1942; Benton, 1985; Brinkman, 1979, 1980; Lee et al., 2016). Additional features help in tipping the balance towards varaniform against monstersaur affinities. MCD-8827 more closely resembles varaniforms than helodermatids in having: a hooking angle of 122.4° , which falls within the range obtained for *Varanus* and *Lanthanotus* specimens examined in this study (between 119.4° and 122.6° , the latter value corresponding to *Lanthanotus*) and out of the range of *Heloderma horridum* and *H. suspectum* (about 130°) (see Supplementary information 2 in Appendix B; see also Rieppel, 1980; Conrad, 2006a); and an inflexion angle of 120° closer to the range of *Varanus* spp. than to *Heloderma* spp. (81° – 88°) (see Supplementary information 2 in Appendix B). MCD-8827 also differs from the extant members of *Heloderma* in the morphology of the fifth metatarsal in lateral view, where the inflexion and the lateral plantar tubercle is less pronounced (*Varanus*-like) (Figs. 5E, 6O) rather than acute and protuberant, as in *H. horridum* and *H. suspectum* (Fig. 6N) (see also Lee, 1997; Conrad, 2006b; Borsuk-Białynicka, 2018).

Despite MCD-8827 resembling the general morphology of the varanid pes, the fossil specimen clearly shows some features that differ from the extant *Varanus*: it differs from the extant members of *Varanus* in its inflexion angle, 120° in MCD-8827, being wider in the species of *Varanus* (approximately 140°) (see Supplementary information 2 in Appendix B; and Lee, 1997; Borsuk-Białynicka, 2018); in the third distal tarsal, which in *Varanus* spp. acquires a subtriangular shape (Fig. 6M) (see Brinkman, 1979, 1980; Goodrich, 1942; Lee et al., 2016) whereas in MCD-8827 is elongated and with a pointing-backwards process (Fig. 5A); in the angulation, with a signature trapezoidal shape in the *Varanus* specimens here analysed (Fig. 6K) (see “angulation” in Borsuk-Białynicka, 2018) but with a subpentagonal shape in MCD-8827 (Fig. 5D); and in the reduction of the proximal articulation area of the fifth metatarsal, this element not being in contact along its axis with the fourth metatarsal in *Varanus* (Owen, 1866; Brinkman, 1980; Rieppel, 1980; Estes et al., 1988; Lee, 1997; Rieppel and Grande, 2007; Sullivan,

2010; El-Bakry et al., 2013; Borsuk-Białynicka, 2018), while in MCD-8827 these two elements maintain a close contact between each other (Figs. 3A–F, 5A). Besides, MCD-8827 also differs from the closest extant relative of *Varanus*, *Lanthanotus borneensis*, in the lateral plantar tubercle, which in the latter is placed distally, near the articulation condyle of the fifth metatarsal (Rieppel, 1980, 1992; Lee, 1997; Conrad, 2006a; Conrad et al., 2011b).

With regards to fossil forms, no other Cretaceous varaniform than the Santonian or Campanian *Telmasaurus grangeri* specimen (AMNH 6643), described by Gilmore (1943), preserves tarsal or metatarsal elements, but these elements were not described in detail and the preservation of such elements hinder their description. In the Cenozoic, the European *Paranecrosaurus feisti* and the North American *Saniwa ensidens* both preserve pes bones. The lower Eocene *S. ensidens* specimen FMNH PR2378 presents a pes typical of Varanidae (Rieppel and Grande, 2007), thus sharing with *Varanus* the absence of a much bigger medial plantar tubercle and a fourth distal tarsal completely lied upon third distal tarsal, and differing from MCD-8827 in their subtriangular third distal tarsal without pointing-backwards process mentioned above. The *P. feisti* specimens HLMD-Me 13709 and SMF-ME 10954 share a similar configuration of the articulation between the metatarsal V and the distal tarsal IV with MCD-8827, due to the first of these bones extends further back the latter (see Fig. 5A in this work and fig. 24A–B in Smith and Habersetzer, 2021). Moreover, *P. feisti* and MCD-8827 share features such as the relative position of the third distal tarsal with respect to the fourth one (the latter lied upon the first one), the configuration of both the lateral plantar tubercle and the outer process, and the grade of inflexion of the fifth metatarsal. Nonetheless, MCD-8827 differs from *P. feisti* in the shape of the fourth distal tarsal in ventral view (being U-shaped in *P. feisti*; see information about the “Pohl-Perner specimen” in the Appendix 3B of Smith and Habersetzer, 2021), and in the morphology of the third distal tarsal (being subtriangular and without pointing-backwards process in *P. feisti*). In the Iberian Neogene, Varanidae is represented by *Varanus marathonensis* (Delfino et al., 2013; Georgalis et al., 2017; Ivanov et al., 2017; Villa et al., 2018) for which elements of the tarsus have not been yet described.

Considering all the characters available in the fossil specimen of Basturs-1 here studied and discussed above, it is assigned to Anguimorpha and tentatively referred to Varaniformes.

4.2. Biogeographic implications for the Cretaceous squamate record

The fossil record of large sized squamates in the Cretaceous is dominated by mosasauriforms (mosasaurs and related taxa, see Fig. 1). This aquatic radiation (Bardet et al., 2003; Haber and Polcyn, 2005; Evans et al., 2006) culminated in the successful mosasaurs, which greatly expanded during the Late Cretaceous (Fig. 1A, C) (Lingham-Soliar, 1996; Bardet et al., 1999, 2000, 2003, 2006, 2013a,b; Machalski et al., 2003; Pierce and Caldwell, 2004; Rage and Néraudeau, 2004; Bell and Polcyn, 2005; Smith and Buchy, 2008; Vullo et al., 2009; Páramo-Fonseca, 2011; Makádi et al., 2012; Pereda-Suberbiola et al., 2015; Paparella et al., 2018; Smith et al., 2019). Among terrestrial squamates, large taxa include borioiteioids (e.g. *Polyglyphanodon*), monstersaurs and varaniforms. The two latter groups would include forms related to helodermatids and varanids respectively, plus a suite of forms traditionally referred as “varanoids” that cannot be attributed to one or the other. These were already present by the Lower Cretaceous record (Fig. 1) with forms such as *Arcanosaurus ibericus* from the Barremian or Aptian of Spain (Houssaye et al., 2013b), and indeterminate taxa from the Aptian and Albanian of Mongolia and USA (Alifanov, 1993; Cifelli and Nydam, 1995). The earliest clear record of Monstersauria is *Primaderma nessovi* from the Albanian or

Cenomanian of USA (Nydam, 2000; Pianka et al., 2004; Yi and Norell, 2013; Alifanov, 2018), whereas the earliest varaniforms recorded are not older than Coniacian or Santonian/Campanian in age (Borsuk-Białynicka, 1984; Rage and Auge, 1993; Kordikova et al., 2001; Pianka et al., 2004). The fossil record seems to indicate an Asian origin for Varanidae and a North American origin for Helodermatidae, the latter originating from an Asian monstersaur-like form (Fig. 1B) (Pregill et al., 1986; Averianov and Danilov, 1997; Alifanov, 2000; Nydam, 2000; Bhullar and Smith, 2008; Arida and Böhme, 2010; Smith and Gauthier, 2013; Mead et al., 2015).

MCD-8827 falls within a geologic time range (Maastriichtian) when monstersaurs, varaniforms, and indeterminate related forms were relatively common components of the Laurasian fauna. Nonetheless, varaniforms have not been confidently identified at that time in Europe, since the oldest confirmed records in the continent pertain to *Saniwa orsmaelensis* (lower Eocene of Belgium; Dollo, 1923) and *Paranecrosaurus feisti* (middle Eocene of Germany; Stritzke, 1983). Some of the specimens traditionally assigned to “Varanoidea” could potentially represent varaniforms, but none of them is complete enough to warrant an unambiguous identification. Varaniforms are known from the Upper Cretaceous of Mongolia (e.g. *Cherminotus longifrons*, *Saniwides mongoliensis*; *Telmasaurus grangeri*), Kazakhstan and China, as shown in Fig. 1B (Gilmore, 1943; Borsuk-Białynicka, 1984; Alifanov, 1993, 2000; Clos, 1995; Gao and Hou, 1996; Kejin and Norell, 2000; Kordikova et al., 2001; Fitch et al., 2006; Norell et al., 2008; Conrad et al., 2012). Some authors have referred fossils from the Santonian or Campanian and Turonian or Coniacian of Mongolia and Kazakhstan (Asia) to *Saniwa* and close forms (Alifanov, 1993; Kordikova et al., 2001, respectively). If correct, this taxon would be the only varaniform present both before and after the Cretaceous–Paleogene boundary, since no other forms present in the uppermost Cretaceous have been recovered from the Paleocene (Longrich et al., 2012; Nydam, 2013). However, these specimens are, due to their fragmentary nature, best regarded as indeterminate varaniforms. To date, MCD-8827 represents the sole specimen tentatively attributable to a varaniform lizard in the Basturs-1 fossil site. The information gathered exclusively from this fragmentary specimen, altogether with the scarce information on appendicular fossil material from this clade in the Upper Cretaceous of Europe, do not allow more accuracy in the determination.

4.3. Size estimation of the individual from Basturs-1

The most striking feature of MCD-8827 is its large size. Although the fragmentary nature of the specimen precludes an accurate estimation of the SVL of the taxon, a tentative approximation can be calculated. According to DeMar et al. (2017), the largest Mesozoic terrestrial fossil squamate would be *Chianghsia nankangensis*, an Upper Cretaceous monstersaur from China (Mo et al., 2012) with an approximate SVL of 1000 mm. Park et al. (2015), however, reported the even larger taxon *Asprosaurus bibongriensis*. Unfortunately, no comparison is possible between these taxa and MCD-8827 because of the lack of shared elements among those preserved. A slightly smaller size specimen has been reported for the North American putative monstersaur *Palaeosaniwa canadensis* (~850 mm) but, although hindlimbs are known (Balsai, 2001) they have not been described in detail and again comparison is not possible. The estimated SVL of MCD-8827, as calculated from *mtV* length, would be comprised between that of these large monstersaurs and the borioiteioid *Polyglyphanodon sternbergi* from the Upper Cretaceous of North America, with an estimated SVL of 450 mm. A regression line calculated from the *mtV* length and SVL of 29 fossil and extant squamates, allowed to predict a SVL of 580.96 mm for MCD-8827 (Fig. 7). According to the minimum SVL value of 600 mm

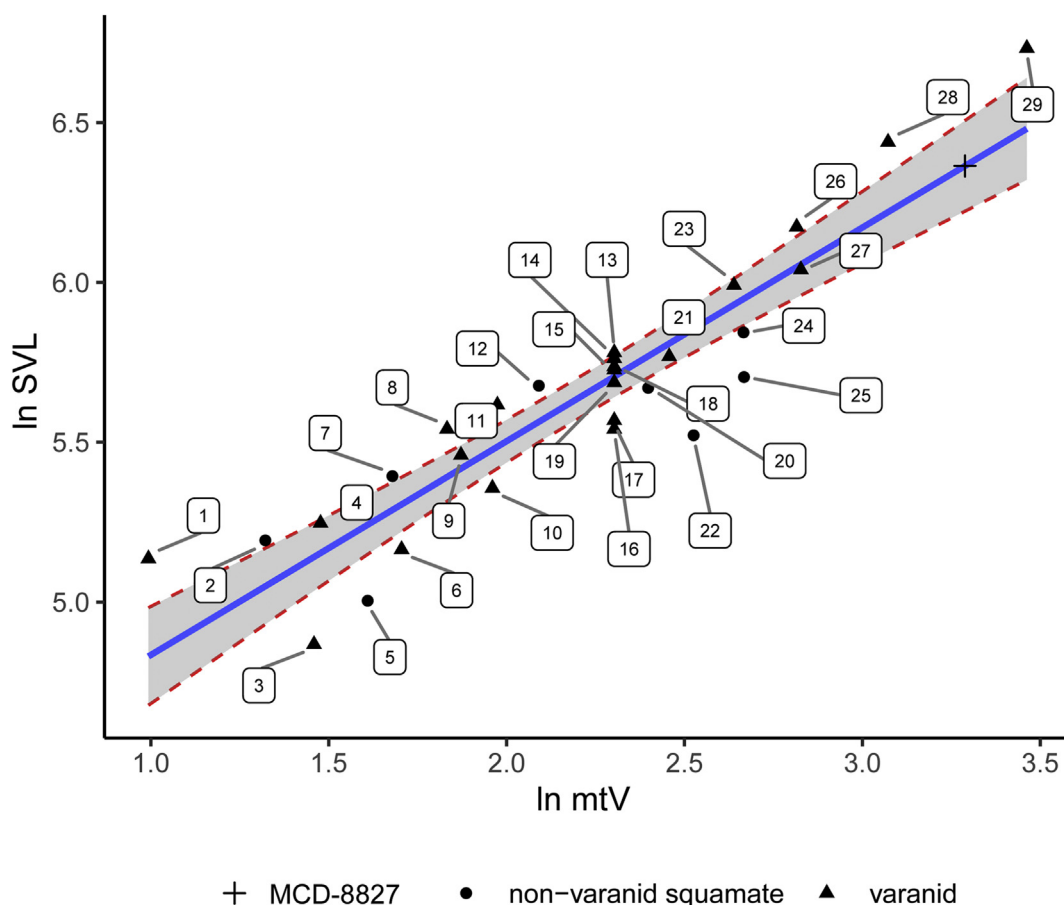


Fig. 7. Size estimate for the fossil specimen of Basturs-1 (MCD-8827) based on comparisons of the \ln of the mtV length across a selection of 29 fossil and extant squamates. MCD-8827, whose mtV is almost 27 mm, is represented by a “cross” symbol, and corresponds with an estimated SVL of 581 mm. Numbers correspond to: 1, *Varanus dumerilii* (YPM-HERR 012148); 2, *Lanthanotus borneensis* (FMNH-134698); 3, *V. exanthematicus* (YPM-HERR 019119); 4, *V. acanthurus* (FMNH-97862); 5, *Sauromalus varius* (YPM-HERR 019215); 6, *V. jobiensis* (YPM-HERR 011074); 7, *Heloderma suspectum* (AC-1966-100); 8, *V. prasinus* (YPM-HERR 010328); 9, *V. beccarii* (YPM-HERR 013267); 10, *V. salvator* (YPM-HERR 011064); 11, *V. beccarii* (YPM-HERR 011899); 12, *H. suspectum* (YPM-HERR 016818); 13, *V. dumerilii* (YPM-HERR 011038); 14, *V. exanthematicus* (YPM-HERR 013940); 15, *V. exanthematicus* (YPM-HERR 011063); 16, *V. rudicollis* (YPM-HERR 011144); 17, *V. bengalensis* (YPM-HERR 011028); 18, *V. salvator* (MNCN-13818); 19, *V. prasinus* (YPM-HERR 011747); 20, *Macrocephalosaurus chulsanensis* (ZPAL MgR-I/14); 21, *V. salvator* (YPM-HERR 011043); 22, *S. varius* (YPM-HERR 019217); 23, *Saniwa ensidens* (USNM PAL 617520); 24, *Hydrosaurus pustulatus* (YPM-HERR 016563); 25, *H. pustulatus* (YPM-HERR 014869); 26, *V. varius* (YPM-HERR 016800); 27, *S. ensidens* (FMNH PR2378); 28, *S. ensidens* (FMNH PR2380); 29, *V. komodoensis* (TMM-M-17921).

specified by Conrad et al. (2012), the Basturs-1 specimen would be close to the minimum size for being considered a giant terrestrial lizard. However, note that other lizards traditionally regarded as giant, like large fossil forms of *Gallotia* from the Canary Islands, are much smaller than this, with a maximum SVL of 500 mm (Barahona et al., 2000), the largest extant “giant” species being about 232 mm in SVL. The largest size ever achieved by a terrestrial lizard would correspond to the extinct *Varanus priscus* (SVL >2000 mm), followed by the extant *Varanus komodoensis* (SVL ~1500 mm), sizes according to Conrad et al. 2012. Note, however, that the fossil giant taxon is not included in the regression line because we do not have access to specimens for which both the mtV length and the SVL are known. A SVL of ~581 mm probably situates the form from Basturs-1 as the largest terrestrial lizard from the European fossil record and contributes to our limited knowledge on the diversity and paleoecology of Iberian Upper Cretaceous lizards.

As a final note, large sized Upper Cretaceous anguimorphs like the North American *Palaeosaniwa canadensis* and the Asian *Asprosaurus bibongiensis*, *Chianghsia nankangensis* and *Estesia mongoliensis* have been all found close to dinosaur eggs (Gilmore, 1928; Norell et al., 1992; Mo et al., 2012; Park et al., 2015), suggesting they might represent nest raiders (Park et al., 2015). The locality of

Basturs-1 is a relevant European dinosaur egg site (e.g. De Lapparent, 1958; Sander et al., 1998), so this specimen seems to represent yet another example of an interesting association between large anguimorphs and dinosaur egg sites. Basturs-1 fossil record is dominated by titanosaur sauropod eggs (attributable to *Megaloolithus*), although it has also yielded an articulated skeleton tentatively referred to a lizard, fragmentary teeth of crocodiles and bones of adult and juvenile dinosaurs (López-Martínez, 2000). The putative lizard was interpreted as a potential nest raider (López-Martínez, 2000), but has never been described. It is, however, much smaller in size than the specimen described herein, suggesting that these specimens do not belong to the same taxon. Moreover, according to its size, MCD-8827 is more likely to represent an example of nest raider lizard than the small skeleton. According to Riera et al. (2009), the lithology found at Basturs-1 corresponds to a medium to very coarse grain sandstone, and the interpreted paleoenvironment is of beach, barrier and delta. The nearby locality of Basturs Poble does not contain eggs, but it is extremely rich in hadrosaur bones and has occasionally yielded theropod dinosaur and crocodile remains. This site contains mixed very fine-to coarse-grained sandstone, microconglomerates and conglomerates interpreted as a meandering fluvial channel

environment. It is thus possible that changes in the recorded fauna across these localities were indeed influenced by changes in the depositional setting and environment, and reflect true compositional differences.

5. Conclusions

Here we report an articulated fossil specimen from the Upper Cretaceous (Maastrichtian) of Basturs-1 (Lleida, Spain) corresponding to a partial left pes of a lizard. Generally, studies concerning fossil squamates have been focused mainly on cranial and vertebral elements, with less attention given to tarsal and metatarsal elements (Georgalis et al., 2018). Material of the pes is rare, often badly preserved, and/or the descriptions are poorly detailed. The conservative nature of limb morphology in squamates (Fabrezi et al., 2007; Sen et al., 2017; Georgalis et al., 2018) possibly contributes to the limited taxonomic value of these elements, but the potential for identifying fossils on the basis of tarsal morphology has been poorly explored. These elements (with the possible exception of the astragalocalcaneum) have been of limited help in characterising the different groups of squamates.

Some characters of MCD-8827 (e.g. proximal head of the fifth metatarsal with squarish contours, plantar tubercles and outer process pretty developed in an ovoid-rounded shape, lateral plantar tubercle generally placed proximally to the medial plantar tubercle and the outer process) would support its attribution to the traditional “Varanoidea”. However, in the current classification, where *Heloderma* is not closer to *Varanus* than *Shinisaurus* is, these characters are interpreted as convergences, and thus cannot be used to support a relationship to either varaniformes or monstrosauria. A few other characters (e.g. absence of an enlarged medial plantar tubercle occupying the majority of the articulation facet, fourth distal tarsal completely lied upon the third distal tarsal and a hooking angle closer to 140°), however, seem to support a closer affinity of the specimen studied here to *Varanus* than to *Heloderma* or *Shinisaurus* and, accordingly, it is tentatively assigned to Varaniformes. This form is the largest terrestrial squamate so far known from the European fossil record, and is among the largest squamates from the worldwide Mesozoic record. Moreover, it represents an additional record of a large anguimorph associated to a dinosaur nesting site. A more precise identification is hampered by the current limited knowledge of tarsus elements morphologies in many extant groups and, particularly, for fossil forms.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2021.105094>.