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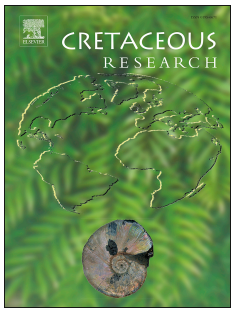

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A hypertrophied ungual phalanx from the lower Barremian of Spain: implications for the diversity and palaeoecology of Spinosauridae (Theropoda) in Iberia

José M. Gasca[1*], Ignacio Díaz-Martínez[2], Miguel Moreno-Azanza[3], José I. Canudo[4] and Antonio Alonso[4]

[1]*CONICET-Museo Provincial de Ciencias Naturales "Profesor Dr. Juan A. Olsacher", Zapala, 8340 Neuquén, Argentina. jmgaska@hotmail.com;*

[2]*CONICET-Instituto de Investigación en Paleobiología y Geología, Universidad Nacional de Río Negro, General Roca, Río Negro, Argentina, inaportu@hotmail.com;*

[3]*GeoBioTec, Departamento de Ciências da Terra. Faculdade de Ciências e Tecnologia, FCT, Universidade Nova de Lisboa, 2829-526. Caparica, Portugal. Museu da Lourinhã, mmazanza@fct.unl.pt;*

[4]*Grupo Aragosaurus-IUCA (http://www.aragosaurus.com). Universidad de Zaragoza. E-50009 Zaragoza, Spain. jicanudo@unizar.es; talonso@unizar.es*

[*]Corresponding author. Mail: jmgaska@hotmail.com

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Abstract

An enlarged theropod manual ungual (CSC1-4) from the *Weald* facies of Spain is described. The claw was found in the fossil locality of Caña Seca 1, Teruel province, within the El Castellar Formation of early Barremian (Early Cretaceous) in age. CSC1-4 is morphologically closer to megalosauroids than to any other theropod clade bearing enlarged manual claws and shows the greatest similarity to the manual ungual of digit I of *Baryonyx walkeri.* Both CS1-4 and this taxon share a particularly enlarged, elongated and transversely wide manual claw. CSC1-4, however, differs from *Baryonyx´*s ungual in having less curvature, a straight dorsal edge in the proximal part, slightly more width above the grooves than below, and a certain asymmetry, with the lateral face more flattened. Taking into account the paleogeographic and temporal context, these considerations suggest that they are closely related but distinct spinosaurid taxa.

The presence of an enlarged manual claw in spinosaurids has been invoked as an anatomical feature typically associated with scavenging and hunting habits, as well as digging behaviour. The spinosaurid record from the Barremian of the Iberian Peninsula shows that members of this clade favored freshwater environments with some marine influence in this part of Europe.

Key words: El Castellar Formation, Megalosauroidea, *Baryonyx*, Lower Cretaceous, Teruel.

1. Introduction

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Megalosauroidea forms a clade of large-bodied theropod dinosaurs whose presence in the Lower Cretaceous of Europe is limited to the specialized clade of Spinosauridae (e.g., Charig and Milner, 1986; Buffetaut, 2007; Canudo et al., 2008; Mateus et al., 2011). Spinosaurids have been described as “crocodile mimics”, being predominantly fish-eating predators with a semi-aquatic lifestyle (Sereno et al., 1998; Rayfield et al., 2007; Amiot et al., 2010; Ibrahim et al., 2014). They were a highly specialized group with a craniodental morphology clearly distinct from other carnivorous dinosaurs (e.g., Sereno et al., 1998; Rayfield et al., 2007; Hendrickx et al., 2016; Vullo et al., 2016). *Baryonyx walkeri*, first recovered from the Barremian of England, is the best known spinosaurid taxon hitherto and the only known species of Spinosauridae from Europe (Charig and Milner, 1986). The holotype of *Baryonyx* consists of a partial skeleton including partial skull and postcranium (Charig and Milner, 1986, 1997). Along with its crocodile-like skull, *Baryonyx* also stands out in having a hypertrophied manual ungual of digit I, which is the meaning of its genus name. Such enlarged thumb claw also appears to be present in other spinosaurid taxa such as *Suchomimus tenerensis* (Sereno et al., 1998) and possibly *Spinosaurus aegyptiacus* (Ibrahim et al., 2014). Several taxa of large-bodied tetanurans also developed enlarged manual ungual phalanges (see Fig. 1), including the megalosaurid *Torvosaurus* (Galton and Jensen, 1979), the allosauroid *Chilantaisaurus* (Benson and Xu, 2008), all megaraptorids (Porfiri et al., 2014) and the tyrannosauroid *Dryptosaurus* (Brusatte et al., 2011). Noteworthy among more derived theropods is the gigantic size of the forelimbs of *Deinocheirus*, terminating in powerful yet poorly recurved claws (Osmólska and Roniewicz, 1970; Lautenschlager, 2014).

Remains referred to *Baryonyx* are also known from the Lower Cretaceous of Portugal and Spain, though they mostly consist of dental material (e.g., Torcida et al., 1997; Fuentes Vidarte et al., 2001; Mateus et al., 2011). The most complete specimen comes

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from the Barremian Papo Seco Formation of Portugal and includes both cranial and postcranial material (Buffetaut, 2007; Mateus et al., 2011). The Portuguese material was referred to the species *Baryonyx walkeri* by Mateus et al. (2011) based on the combination of shared dental characters, in spite the fact that some postcranial differences, considered to be the result of intraspecific variation by these authors, occur. In addition to the presence of *Baryonyx walkeri* in Iberia, several different tooth morphotypes have been reported, implying the presence of more than one spinosaurid taxon for some authors (e.g., Alonso and Canudo, 2016), although the scarcity of associated postcranial material makes testing this hypothesis a challenge.

This paper aims to describe an enlarged theropod manual ungual recently discovered in an outcrop from the *Weald* facies of Spain. This new specimen is compared in details with those from other theropods. The implications of this new specimen for our understanding of spinosaurid diversity are also discussed.

2. Geological and Palaeontological Context

The manual ungual CSC1-4 was recovered from the fossil locality of Caña Seca 1 in the municipality of Gúdar, Teruel province, Spain (Fig. 2). The study area is located in the northeastern part of the Iberian Chain. The latter was developed during the Palaeogene as a result of the Alpine inversion of the Mesozoic Iberian Rift System (e.g., Salas et al., 2001). The Caña Seca 1 fossil site is part of the El Castellar Formation and is palaeogeographically located within the Galve sub-basin, in the western part of the Maestrazgo Basin (Fig. 2A). This basin forms part of the Iberian Rift System and was developed during a rifting phase that commenced at the end of the Jurassic and lasted until the mid-Albian (Salas et al., 2001). The Upper Jurassic-Lower Cretaceous stratigraphy of the Galve sub-basin, summarized by Aurell et al. (2016), includes a syn-

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rift sequence of predominantly continental-transitional series corresponding to *Weald* facies. The carbonate-lutitic shallow-lacustrine-palustrine facies represented by the El Castellar Formation across the entire Galve sub-basin were deposited during the latest Hauterivian-earliest Barremian (Aurell et al., 2016), and are equivalent to the K1.4 sequence of the sequential stratigraphic model for the Maestrazgo Basin (Salas et al., 2001). Given the presence and predominance of the charophyte *Atopochara trivolvis triquetra* within the charophyte assemblage, the fossil site of Caña Seca 1 is dated to the early Barremian (Riveline, 1996; Canudo et al., 2012).

The stratigraphic series of the Mesozoic outcrops northwest to the village of Gúdar, where Caña Seca 1 is located, (Fig. 2C) begins with the late Tithonian-middle Berriasian Aguilar del Alfambra Formation, which is around 400m thick (Aurell et al., 2016). The overlying Galve Formation, dated to the late Berriasian-Hauterivian? in age, comprises a 20-30 meters thick succession of red lutites with decametric burrowed sandstones and a conglomeratic level in its middle part. Above this, the El Castellar Formation is 60m thick and has a lower level of discontinuous white sandstone up to 5m thick, with cross-bedding and lateral accretion geometries. The rest of the unit is dominated by alternating brown-yellow marls and burrowed skeletal limestones, where some vertebrate fossil sites have been found (Gasca et al., 2012).

The fossiliferous level of Caña Seca 1 (Fig. 2C) is located in the lower part of the El Castellar Formation and comprises a 5m-thick level of grey marls just above the basalmost detritic deposits of the El Castellar Formation. These grey marls bear dark-grey and ochre mottling, carbonate nodules and bioturbation, which is characteristic of shallow lacustrine-palustrine conditions (Meléndez et al., 2009), as usually seen in other vertebrate fossil sites of the El Castellar Formation (e.g., Cuenca-Bescós et al., 2014). The fossil assemblage of Caña Seca 1 is composed of microremains as well as isolated

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vertebrate macrofossils. This fossil content consists of ostracod shells, charophytes (*Globator maillardii trochiliscoides* and *Atopochara trivolvis triquetra utriculi*), coprolites and eggshell fragments along with vertebrate bony remains (Gasca et al., 2012). Based on the identified remains of teeth, bones and scales, the faunal list of the vertebrate assemblage comprises chondrichthyans (*Hybodus*), osteichthyans (Semionotiformes, Amiiformes, *Archodonichthys*), lissamphibians, chelonians (Solemydidae), dinosaurs (Ornithopoda and Theropoda) and crocodylomorphs (Atoposauridae, cf. *Bernissartia* and Goniopholididae). The dinosaur remains recovered from the fossiliferous bed are scarce. They consist of an isolated dorsal vertebra from an undetermined iguanodontian ornithopod, a caudal centrum from a tetanuran theropod bearing pleurocentral fossae on its lateral side, and the manual claw here studied. A small isolated ilium from an undetermined coelurosaur was also found dozens of metres away (Gasca et al., 2012).

3. Material and Methods

The fossil claw CSC1-4 (Fig. 3 and 4) was collected by surface prospecting during the 2010 fieldwork campaign by the Aragosaurus-IUCA research team of the University of Zaragoza. Other fossil specimens from the same fossil locality were recovered by surface collection or screen washing (microfossils) between 2008 and 2011. Additional items from the El Castellar Formation mentioned in this paper (see Table 1: numbers MOAL-1/1, SM-2/D1, BNA2-7, SUE1-2, VES4-1) were recovered during the same fieldwork campaign. These fossil materials are deposited in the Natural History Museum of the University of Zaragoza (Museo de Ciencias Naturales de la Universidad de Zaragoza; Canudo, 2017).

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The anatomical nomenclature of theropod unguals follows Charig and Milner (1997) and Agnolin and Chiarelli (2010). The phylogenetic framework for Tetanurae followed in this work is based on the results obtained by Rauhut et al., (2016) who performed a phylogenetic analysis on a revised version of the datamatrix of Carrano et al. (2012). For the purpose of comparison, the manual unguals of *Baryonyx walkeri* (NHMUK R9951) *Suchomimus tenerensis* (NHMUK R16013, casts) and *Allosaurus fragilis* (NHMUK R10868, cast) deposited in the Natural History Museum (NHMUK, London, United Kingdom) were examined first-hand (Fig. 5). Figured silhouettes of the claws from other theropod taxa were redrawn from the bibliography (see Fig. 1).

A tridimensional model of the theropod claw was generated through photogrammetry (see Supplementary Online Material). CSC1-4 was digitized using the software Agisoft PhotoScanTM (version 0.8.5.1423), following the methodology of Mallison and Wings (2014). Photos were taken using a Panasonic DMC-TZ7 digital camera to compile a 360° digital reconstruction of the specimen. Two separate chunks were produced of the dorsal and ventral surfaces (using 78 and 50 photographs respectively), maintaining considerable overlap at the sides. These were generated using an 8-core workstation with 32GB RAM.

4. Systematic Palaeontology

Dinosauria Owen 1842

Theropoda Marsh 1881

Megalosauroidea Fitzinger 1843

Spinosauridae Stromer 1915

Aff. *Baryonyx* sp.

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Material, locality and age: CSC1-4, a left manual ungual claw (digit I?) from the Caña Seca 1 fossil locality, municipality of Gúdar, Teruel province, Spain. El Castellar Formation, lower Barremian (Lower Cretaceous).

Description and comparison

CSC1-4 is a large and elongated ungual phalanx preserving much of its length, with only the proximoventral and distal portions missing (Fig. 3). The preserved portion of the claw has a proximodistal length of 190 mm, a lateromedial width of 64 mm and a dorsoventral height of 100 mm in its maximum dimensions. The ungual is estimated to reach over 220 mm in length. Recent damage due to aerial exposure in the outcrop has caused the loss of the distal part by breakage, partial discoloration and slight weathering of the fossil surfaces. Bone modification by taphonomic processes includes moderate weathering of the claw, being difficult to quantify a precise stage due to the masking effect produced by recent erosion. The proximal articular surface was largely covered by carbonated matrix when the fossil was found, allowing the degree of bone modification to be ascertained after preparation of the fossil by mechanical techniques (Fig. 3A). This part of the bone was particularly altered during the biostratinomic phase as a result of weathering and perhaps other processes (i.e., consumption by scavenger organisms), affecting in part the preservation of the original morphology, especially in the area of the flexor tubercle.

The proximal articular surface bears a dorsoventrally oriented ridge that is slightly offset medially, as in other theropods (e.g., *Dryptosaurus*, Brusatte et al., 2011). As preserved, the dorsoventral height of the proximal articular surface seems to be roughly similar to its width (Fig. 3A). Although its original shape is not well preserved, the flexor tubercle seems to be prominent, as in other basal tetanurans (e.g., *Baryonyx*,

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191 *Allosaurus*: Fig. 5). The asymmetry of the claw CSC1-4 is also shown by the medial
192 side being slightly more flattened than the lateral, unlike in *Baryonyx* which has more
193 symmetrical unguals.
194 The outline of CSC1-4 in profile (i.e., lateral and medial views) is fairly straight in the
195 proximal part of the dorsal edge, unlike the outline of other large manual claws
196 belonging to theropods. This outline is convex in baryonychine spinosaurids (Fig. 1)
197 and concave in the manual ungual of some megaraptorans (e.g., *Australovenator*; White
198 et al., 2012) and possibly *Spinosaurus* (Russel, 1996; Ibrahim et al., 2014). It also
199 differs from derived coelurosaurs in which the articular facet exceeds the ungual blade
200 in height, giving the appearance of a dorsal depression between the articular facet and
201 the claw blade (Rauhut and Werner, 1995). Otherwise, the gradual tapering of the
202 ungual is similar to other basal tetanurans (e.g., *Baryonyx*) but differs from that of
203 compsognathids such as *Juravenator*, whose manual claws taper abruptly around their
204 midpoints (Chiappe and Göhlich, 2010).
205 A well-defined, vascular groove runs along both the lateral and medial surfaces just
206 ventral to the mid-height of the phalanx and parallel to the ventral margin. One,
207 possibly two foramina can be observed within these grooves (Fig. 4). These foramina
208 are rarely mentioned in the literature (e.g., Pérez-Moreno et al., 1993) but are at least
209 present in the ungual I of the *Baryonyx* holotype.
210 The transverse section is oval in outline, becoming progressively more circular towards
211 the tip. The dorsal and ventral edges are lateromedially rounded unlike megaraptoran
212 allosauroids, which bear claws with a sharp ventral edge (e.g., White et al., 2015). The
213 dorsal portion of the section, above the grooves, is slightly broader: 45 mm wide above
214 the grooves versus 43 mm below, measured at a mid-length section. This contrasts with
215 the unguals of primitive theropods and allosauroids (Pérez-Moreno et al., 1993:

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character 22), which are broader ventral to the grooves. This is also slightly different from the unguals of spinosaurids such as *Baryonyx*. However, the relevance of this feature in CSC1-4 must be taken cautiously given the poor state of preservation.

5. Discussion

The identification of the claw CSC1-4 as a theropod manual ungual rather than a pedal ungual is based on several features, such as a proximal articular surface that is dorsoventrally tall and shows a marked median keel, an oval transverse cross-section, and a strong curvature (Agnolin and Chiarelli, 2009).

The asymmetry in the proximal articular surface (i.e., a dorsoventral ridge slightly offset medially) is used to identify CSC1-4 as a left ungual. Given its large size, the attribution of CSC1-4 to digit I is the most probable option according to the criteria previously followed by other authors in identifying disarticulated claws (e.g., Galton and Jensen, 1979; Charig and Milner, 1997; Benson and Xu, 2008). However, the claw of digit two in at least *Suchomimus* appears to be very large too, and almost as large as CSC1-4 (see Fig. 5), ,so the fact that the latter might also belong to digit II cannot be ruled out. The estimated total length of CSC1-4 is about 220mm, which is slightly less than digit I unguals but clearly greater than the length of digit III of *Baryonyx* and *Suchomimus* (see Fig. 5).

The known manual unguals of non-tetanuran theropods such as those of the ceratosaurians *Limusaurus*, *Masiakasaurus* and *Noasaurus* clearly differ from CSC1-4. *Noasaurus* differs in that its bizarre claw bears a median ventral ridge (Agnolin and Chiarelli, 2009: fig. 1A), whereas those of *Masiakasaurus* differ in their lower curvature and the reduction of the flexor tubercle (Carrano et al., 2002: fig. 12). In *Limusaurus*, the unguals are mediolaterally expanded at their proximal end but differ in being short,

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stout and small (Xu et al., 2009). Furthermore, the loss of manual unguals has been suggested in some abelisaurids (Agnolin and Chiarelli, 2009).

The tetanuran clades Megalosauroidea and Allosauroidea includes large-bodied taxa with enlarged forelimbs and hypertrophied claws (Benson et al., 2012). However, the presence of enlarged and proximally wide manual unguals has only been reported in megalosauroids (*sensu* Carrano et al., 2012). Carrano et al. (2012: character 259) reported a character which describes the relative length, and thus size, of manual ungual I based on the length:height ratio. By this criterion, enlarged claws are present at least in the megalosaurs *Torvosaurus*, *Suchomimus* and *Baryonyx* and in the megaraptoran *Megaraptor* (Carrano et al., 2012). Despite lacking the distal end, the total length of CSC1-4 can be estimated by comparison with better-preserved specimens (see Fig. 5A), allowing it to be identified as an enlarged claw comparable with those of other theropods (Fig. 1). The estimated proximodistal length:dorsoventral height ratio is 2.2 in CSC1-4, which is similar to that of *Baryonyx*, *Suchomimus*, *Deinocheirus* or *Fukuiraptor* (2.2-2.3) and lesser than that of *Torvosaurus*? (2.4), *Chilantaisaurus* (2.5), *Dryptosaurus* (2.6), and *Spinosaurus?* and *Megaraptor* (3.2; see Fig. 1;). Other megalosauroids (e.g., *Dubreuillosaurus*, 2.1) and allosauroids (e.g., *Sinraptor*, 1.9; *Allosaurus*, 2.0) show lower ratios (see Fig. 1).

The manual claws of neovenatorids (including megaraptorans) and the first manual ungual of some spinosaurids are similarly enlarged and elongated relative to those of other non-coelurosaurian theropods (Benson and Xu, 2008). However, megaraptorans (e.g., *Australovenator*, *Fukuiraptor*, *Megaraptor*) and *Chilantaisaurus* bear transversely narrow claws (Carrano et al., 2012: character 260; Porfiri et al., 2014: character 141), which are therefore very different from CSC1-4. The hypertrophied manual claws and modified manus of neovenatorids (mostly megaraptorans) represent an unusual

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morphological adaptation among carnivorous dinosaurs (e.g., White et al., 2015). Some manual unguals in *Australovenator* and *Fukuiraptor* also differ in having asymmetrical lateral grooves and a well-developed ridge on the ventral margin (Porfiri et al., 2014: characters 144 and 145).

The case of *Chilantaisaurus* from the Cretaceous of Mongolia is paradigmatic; it has been recovered as a derived member of both Allosauroidea and Megalosauroidea (Benson and Xu, 2008). *Chilantaisaurus* shares certain features with some megalosauroids: an enlarged and elongated first manual ungual and a suprastragalar buttress that has been modified to a vertical ridge (Benson and Xu, 2008). In fact, Allain et al. (2012) considered *Chilantaisaurus* to be a member of Spinosauridae after adding this taxon to their matrix. Pursuing further this approach, they highlighted that, among large theropods, an enlarged manual digit I ungual had only been reported in the 'spinosaurids' *Baryonyx*, *Suchomimus* and *Chilantaisaurus* (Allain et al., 2012). However, later phylogenetic analyses by other authors place *Chilantaisaurus* within Allosauroidea, more specifically within the clade of neovenatorid carcharodontosaurians as the sister taxon of megaraptorans (Carrano et al., 2012; Rauhut et al., 2016). Unlike Spinosauridae, the ungual claw of *Chilantaisaurus* is clearly more laterally compressed (see Benson and Xu, 2008: fig. 2C), supporting an affinity with megaraptorans.

Allosauroids such as *Allosaurus* (Madsen, 1976; Pérez-Moreno et al., 1993) and *Sinraptor* (Currie and Zhao, 1993: fig. 20) also differ in the lateral compression of their unguals, which is less important than in megaraptorans but greater than in spinosaurids. This difference may not be obvious (see Fig. 5G2), but it adds to the more strongly curved nature of the claw in *Allosaurus* than in spinosaurids (Charig and Milner, 1997). Other allosauroids such as carcharodontosaurids can be differentiated by the presence of

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291 claws that are almost as high (proximally) as long (Rauhut and Werner, 1995).
292 Carcharodontosaurids such as *Mapusaurus* bear manual unguals that are distinctive in
293 having asymmetrical positioning of the lateral grooves (see Coria and Currie, 2006: fig.
294 25).
295 Basal coelurosaurs bearing proportionally large manual unguals such as *Juravenator*,
296 *Sinosauropteryx* and *Tanycolagreus* (Porfiri et al., 2014: character 48) differ in the
297 morphology and the smaller size of their unguals in absolute terms, the latter reflecting
298 their small body size. The claw morphology of *Juravenator* is characteristic in being
299 very high proximally and tapering abruptly around the midpoint (Chiappe and Göhlich,
300 2010). The claws in *Sinosauropteryx* and *Tanycolagreus* (Currie and Chen, 2001;
301 Carpenter et al., 2005) are significantly less curved than in spinosaurids. Tyrannosaurids
302 (e.g., *Tyrannosaurus*, *Albertosaurus*) differ in having a flexor tubercle reduced to a
303 small convexity (Porfiri et al., 2014: character 143) and shallower vascular grooves
304 (Benson et al., 2012). Other derived coelurosaurs bearing powerful enlarged manual
305 claws are the therizinosaurs, but their claws are wholly different in their lesser curvature
306 and the abruptly tapering morphology of the proximal end (e.g., *Deinocheirus*,
307 Osmólska and Roniewicz, 1970; Lautenschlager, 2014).
308 Without ruling out other affinities completely, the ungual phalanx CSC1-4 can be
309 reliably related to Megalosauroidea. A large ungual phalanx from the Upper Jurassic
310 Morrison Formation was referred to *Torvosaurus* (Galton and Jensen, 1979: fig. 1M).
311 This element (BYU 2020) was found isolated in another fossil locality far from the
312 *Torvosaurus* type locality. Later it was suggested that this manual ungual might actually
313 be referable to Spinosauridae, this being the oldest known occurrence of the group
314 (Allain et al., 2012). Apart from the uncertainty of its assignment to *Torvosaurus*, the
315 megalosauroid affinity of the claw BYU 2020 seems clear in the light of features such

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316 as the degree of curvature, which is similar to that of *Baryonyx* and clearly less than in
317 other coeval large-sized theropods such as *Allosaurus* (see Fig. 1).
318 Further comparison between CSC1-4 and BYU 2020 requires first-hand examination of
319 the latter. Other megalosauroids such as *Dubreuillosaurus* (Allain, 2005) and possibly
320 *Megalosaurus* (Owen, 1849: plate 32 in vol. II) bear less enlarged manual claws, with
321 lower ratios of length:height (roughly 2.1 in both taxa) and width:height (0.42 estimated
322 in *Megalosaurus*). Taking into account the stratigraphical context and their shared
323 morphological features, the inclusion of CSC1-4 within Spinosauridae is the most
324 plausible scenario.
325 The preserved segment of the dorsal edge of CSC1-4 is gently curved, similar to
326 *Suchomimus* and to a lesser extent than in *Baryonyx* (Fig. 5) and in BYU 2020 (Galton
327 and Jensen, 1979). The straight profile of the dorsal edge at its proximalmost end in
328 CSC1-4 is different from all the others. CSC1-4 bears greatest similarity to the manual
329 ungual of digit I of *Baryonyx walkeri* (Charig and Milner, 1986, 1997). They share
330 general features such as being enlarged, elongated and transversely wide. The
331 lateromedial width:dorsoventral height ratio in CSC1-4 (0.64) is higher than in
332 *Baryonyx* and *Suchomimus* (0.56) and these values are in turn higher than in other
333 theropods (e.g., *Chilantaisaurus*, 0.36; *Allosaurus*, 0.47; *Deinocheirus*, 0.49; *Sinraptor*,
334 0.50; *Dryptosaurus*, 0.55).
335 On the other hand, ungual CSC1-4 differs from that of *Baryonyx walkeri* in having a
336 little less curvature, a straight dorsal edge in the proximal part, slightly more width
337 above the grooves than below –comparing the section at mid-length–, and a certain
338 asymmetry, with the lateral face more flattened. These considerations suggest that they
339 were closely related but distinct spinosaurid taxa, which is in agreement with their close
340 palaeogeographical and temporal proximity. The open nomenclature aff. *Baryonyx* sp. is

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used here to highlight the close affinity of the ungual CSC1-4 with the contemporary spinosaurid *Baryonyx walkeri*, from the Barremian of Europe. Nevertheless, at least the same degree of morphological similarity is present between CSC1-4 and the slightly younger African spinosaurid *Suchomimus*.

Additional spinosaurid material from the El Castellar Formation

Other localities from the El Castellar Formation have also yielded spinosaurid material. Isolated teeth are the most common spinosaurid material from this formation (Sánchez-Hernández et al., 2007; Gasca et al., 2008, 2009; Table 1; Fig. 6), yet two middle caudal vertebrae have also been recovered from two different localities respectively located in Aliaga (Fig. 6B) and Miravete de la Sierra.

The isolated crowns from the El Castellar Formation are weakly labiolingually compressed, and bear mesial and distal carinae as well as apicobasal ridges on both labial and lingual sides. MOAL-1/D1 (Fig. 6A) and BNA-2/7 from Aliaga and Mora de Rubielos, respectively, belong to the same tooth morphotype as the teeth from the coeval La Cantalera 1 fossil site of the Blesa Formation and referred to Baryonychinae (Alonso and Canudo, 2016).

SM-2/D1 from Miravete de la Sierra represents another tooth morphotype characterized by the absence of mesial denticles (Gasca et al., 2009: fig. 4A). The crown also bears a split distal carina, which is probably the result of a pathological condition, as reported in other theropod teeth (e.g., Candeiro and Tanke, 2008). Specimen MPG PX-23 from Galve was confusingly described and figured by Sánchez-Hernández et al. (2007), and it is difficult to ascertain whether it is a baryonychine tooth. The specimen is attributed to Baryonychinae due to the presence of minute denticles on the distal carina, whereas the mesial carina is unserrated. However, the tooth does not possess the flutes characteristic

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of spinosaurid teeth (e.g., Alonso and Canudo, 2016), and the number of denticles per mm is not provided. Some authors have pointed out the existence of a baryonychine morphotype without denticles on the mesial carina, as stated above (Canudo and Ruiz-Omeñaca, 2003; Infante et al., 2005). Specimen MPG PX-23 seems to belong to a different tooth morphotype characterized by the absence apicobasal ridges. As a whole, the teeth from the El Castellar Formation appear to be different from those of *Baryonyx walkeri* as the latter bear apicobasal ridges only on the lingual side. Furthermore, the morphotypes from the El Castellar Formation seem to indicate the presence of more than one spinosaurid representative. However, this proposal cannot be definitively addressed with the currently available specimens, given that heterodonty may be an alternative, equally plausible explanation.

Two other fossil localities from the El Castellar Formation have provided postcranial material assignable to Spinosauridae. SUE1-2 (Fig. 6B) and VES4-1 are two vertebral centra belonging to the middle caudal series, which are quite similar to the caudal vertebrae of the Portuguese specimen ML1190 from the Barremian Papo Seco Formation of Portugal, referred to *Baryonyx walkeri* (Mateus et al., 2011). They are amphicoelous, and the posterior face is more shallowly concave. The anterior and posterior faces of the centra have a characteristic subrectangular outline, being as high as wide. The chevron facets are well visible, mainly on the ventroposterior margin of the centrum. The ventral face of the centrum has two parallel ridges between which a deep and wide longitudinal groove extends along the midline.

The ungual phalanx CSC1-4 described in detail in this work is an isolated but informative occurrence of Spinosauridae. In the absence of more complete specimens, CSC1-4 is the only postcranial fossil from the lower Barremian El Castellar Formation apart from the isolated vertebrae mentioned just above. The fragmentary nature of the

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vertebrate record is the general taphonomic pattern of the El Castellar Formation (e.g., Sánchez-Hernández et al., 2007; Gasca et al., 2009; Cuenca-Bescós et al., 2014). Given this context, each fossil occurrence is relevant in order to reconstruct the El Castellar Formation biota as a whole. Regarding theropods, the presence of spinosaurids contributes to a diverse biota from El Castellar Formation biota, together with allosauroids (Buscalioni and Sanz, 1984; Gasca et al., 2012) and coelurosaurians (see Ruiz-Omeñaca et al., 2004).

Approach to the palaeoecological significance of the presence of spinosaurids

Spinosaurs were a major component of the theropod faunas in the Early Cretaceous of Iberia. The presence of spinosaurids has been confirmed in several localities in the Maestrazgo Basin, including the Barremian units of El Castellar, the Blesa Formation (Canudo et al., 2010; Alonso et al., 2016), the Mirambel Formation (Infante et al., 2005; Gasca et al., 2014), and the Papo Seco Formation (Mateus et al., 2011); the upper Barremian Morella Formation (Canudo et al., 2008); and the upper Hauterivian-Aptian series from the Cameros Basin (Torcida et al., 1997; Fuentes Vidarte et al., 2001). This contrasts with the absence of spinosaurids or any other megalosaurid theropods in La Huerguina Formation (Serranía de Cuenca Basin, southern Iberian Range; Barremian), in which a large diversity of theropods is present (Buscalioni et al., 2008; Ortega et al., 2012). The intensive palaeontological surveys in this formation over the last 30 years have yielded several large-bodied theropods in the same environment (e.g., the carcharodontosaurid *Concavenator*, Ortega et al., 2012). This suggests that the absence of megalosauroid theropods is not a sampling or taphonomic bias, but characterizes the palaeoecosystem of La Huerguina Formation.

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A recent analysis of the environmental preferences of allosauroids and megalosauroids in the Jurassic indicates that the former preferred inland environments, whereas the latter are more common in nearshore environments (Rauhut et al., 2016). On the other hand, megalosauroid theropods, represented by the spinosaurids, were positively associated with coastal palaeoenvironments in the Cretaceous whereas carcharodontosaurids and abelisaurids were more closely associated with terrestrial palaeoenvironments during the same period (Sales et al., 2016).

Both groups of large-sized theropods (i.e., carcharodontosaurid allosauroids and spinosaurid megalosauroids) are present in the palustrine-lacustrine deposits of the El Castellar Formation as well as in other coeval units of the Maestrazgo Basin, such as the Blesa Formation (Canudo et al., 2010; Alonso et al., 2016) and the Mirambel Formation (Infante et al., 2005; Gasca et al., 2014). The sedimentary record of the El Castellar Formation corresponds rather to inland environments, but these are located palaeogeographically close to coastal zones. Furthermore, an ostreid-bearing limestone bed from the uppermost part of the El Castellar Formation has been identified in the Gúdar area, showing a certain degree of marine influence and confirming its proximity to the sea. A coastal influence is more in evidence in some horizons in the Mirambel and Blesa Formations (Canudo et al., 2010; Gasca et al., 2017). On the other hand, La Huerguina Formation is a genuine inland wetland, with no marine influence (Buscalioni and Poyato-Ariza, 2016).

A large number of anatomical features in spinosaurids clearly indicates a very different mode of prey capture and processing from other theropods, with a tendency to focus on aquatic prey items (Hone and Holtz, 2017). A piscivorous diet has been suggested for spinosaurid megalosauroids on the basis of jaw as well as tooth morphology and stomach contents (e.g., Charig and Milner, 1997; Ibrahim et al., 2014; Hendrickx et al.,

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2016). But direct evidences have shown on two instances that spinosaurid were also feeding on ornithischians (Charig & Milner, 1997) and pterosaurs (Buffetaut et al., 2004) as well. Furthermore, on the basis of the oxygen isotopic composition of their phosphatic remains, Amiot et al. (2010) revealed that spinosaurs had semiaquatic lifestyles. This research shed light on niche partitioning among large predatory dinosaurs, so that the likely piscivorous diet and aquatic habits of spinosaurids may have allowed them to coexist with other large theropods such as carcharodontosaurids and abelisaurids by reducing competition for food and territory (Amiot et al., 2014). The fossil record of the Iberian Peninsula also supports the fact that spinosaurs preferred freshwater environments with a certain degree of marine influence.

Approach to the palaeoecological significance of the manual claw morphology in spinosaurids

The morphological study of ungual phalanges in animals is of particular importance since variations are associated with different life styles, activities such as locomotion and hunting, as well as ecology and habits (Pike and Maitland, 2004; Birn-Jeffery et al., 2012; Lautenschlager, 2014). They can be expected to show different morphological adaptations according to the type of substrate and the way in which they are applied to it (Macleod and Rose, 1993).

In theropod dinosaurs, the shape and size of pedal unguals have been related with grasping (see Becerra et al., 2016), perching (see Manning et al., 2009), digging (e.g., Simpson et al., 2010), wading and climbing (Glen and Bennett, 2007). Nevertheless, the function of manual unguals has received less interest (Lautenschlager, 2014). Ostrom (1969) and Currie and Chen (2001), for example, proposed that *Deinonychus* and *Sinosauropteryx* used their claws for grasping their prey. Lautenschlager (2014) pointed

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out that some therizinosaur taxa used their claws in a generalist fashion, whereas other taxa were functionally adapted for using the claws as grasping hooks during foraging. Even the single manual ungual of the alvarezsaurid *Linhenykus* has been related with digging behaviour (Xu et al., 2010).

Many ideas have been proposed on the functional morphology and the mode of life of spinosaurids (e.g., Charig and Milner, 1997; Rayfield et al., 2007; Ibrahim et al., 2014; Hendrickx et al., 2016; Vullo et al., 2016), but the presence of an enlarged manual claw has been left largely out of account. A scavenging habit has been suggested for *Baryonyx* on the basis of the massively developed forelimbs with huge claws, which would be ideal for breaking into a carcass (Kitchener, 1987). However, it has usually been argued that they had a diet consisting mainly of fish (Charig and Milner, 1997). These authors considered the enlarged manual claws of *Baryonyx* to be a powerful offensive weapon. They presented this spinosaurid as mainly a fish-eater, although fishing would not be its only source of food, and pointed out that it may well have been both an active predator (using its powerful forelimbs and claws rather than its jaws and teeth) and/or an opportunistic scavenger (Charig and Milner, 1997). In their discussion, Charig and Milner (1997) note that: "*The characters of the fore-limb and manus suggest that the forelimbs of Baryonyx were exceptionally powerful, the fore-arm being capable of exerting great force at the wrist when extended. (…)The enlarged claws could also have been used for 'gaffing', i.e. hooking or flipping fishes out of the water as is done today by grizzly bears.*"

Many extant (anteaters, pangolins, moles, armadillos, etc.) and extinct mammals (ground sloths, glyptodonts, palaeanodonts, etc.) also present hypertrophied manus claws (see Rose and Emry, 1983) and all of them share the ecological habit of being

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diggers. Digging is a behaviour that has only recently been explored in dinosaurs (see Fearon and Varricchio, 2015 and references therein).

Hildebrand (1985) proposed three basic types of limb-based digging mechanics used by mammals: scratch digging, humeral rotation and hook-and-pull. The first two are characteristic of fossorial animals (i.e., animals adapted to digging and living underground) that use their short, robust forelimbs and hypertrophied manual ungual phalanges to build their burrows (Kley and Kearney, 2007). Fearon and Varricchio (2015) studied the forearm of the basal ornithopod *Oryctodromeus cubicularis*, which was found in a burrow, and concluded that it produced burrows by scratch digging. By contrast, hook-and-pull digging is not typically used for burrowing, but for food gathering (Fearon and Varricchio, 2015). Hook-and-pull digging is a two-step process: 1) the enormous, curved claws of the forefoot are hooked into a preexisting crack, crevice or hole; and 2) the digits are strongly flexed and the forefoot is pulled back toward the body. Anteaters use this technique when foraging to rip holes into termite mounds, ant hills and rotting logs (Kley and Kearney, 2007). Senter (2005) suggested that animals that use hook-and-pull digging must have one huge manual ungual that is larger than the others, and an enlarged digit capable of enough flexion to reach the palm (Hildebrand, 1985). The *Baryonyx* holotype includes some manual digit elements, and the ungual of the first digit is notably larger than the others (Charig and Milner, 1997). Moreover, it preserves a well-developed flexor tubercle. In the light of the above discussion, we suggest that the hypertrophied manual ungual CSC1-4, as well as that of other spinosaurids, could be associated with hook-and-pull digging behaviour. In their recent review of Spinosauridae, Hone and Holtz (2017) point out that the short, robust nature of the limb with an enlarged olecranon in combination with enlarged unguals is a feature held in common with animals that engage in scratch-digging and hook-and-pull

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digging. The authors suggest that the relatively narrow width of the enlarged ungula and the lack of a spade-like spread to the limbs imply that it was used for digging into harder substrates rather than moving large quantities of softer materials. Hone and Holtz (2017) propose that the hypertrophied manual ungual of spinosaurids could have served them to dig up nests, dig for water or reach certain prey items. Another hypothesis would be to help them raise their prey from the ground. In this sense, Russell (1996) points out that lungfish bones have been found close to *Spinosaurus* remains in Morocco. On the other hand, Ibrahim et al. (2014) hypothesized that elongate manual phalanges and less recurved, manual unguals likely referable to *Spinosaurus* (Russell, 1996: fig. 24) possibly used in gaffing and slicing aquatic prey. Nevertheless, whether used for hooking or flipping fishes (Charig and Milner, 1997), for opportunistic scavenging (Kitchener, 1987) or for digging, such skill involves the same bone movements: hooking with large curved claws into a substrate, carcass or a living animal; flexing; and pulling back toward the body. To further explore the functional morphology of the spinosaurid manus claw, future research should focus on an analysis of the forearm and pectoral girdle as a whole. Morphometric and Finite Element analyses of these elements may shed light on the relative contributions of the three postulated behaviours in shaping the powerful claw of spinosaurid dinosaurs.

6. Conclusion

The record of an isolated large manual claw in the El Castellar Formation yields new evidence on the common presence of spinosaurids within the vertebrate communities of the Barremian of southwestern Europe (i.e., Iberia). It also provides new data on the presence of a second spinosaurid taxon apart from *Baryonyx walkeri*, reinforcing the

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information from the tooth record which already pointed to the coexistence of various spinosaurid species in the Barremian of Europe.

This claw is the only postcranial spinosaurid fossil from the lower Barremian El Castellar Formation apart from two isolated vertebrae, and it is highly relevant for reconstructing the diversity of this fossil biota. Within Theropoda, the presence of spinosaurids in the El Castellar Formation is thus added to that of other large-sized tetanurans such as allosauroids as well as several coelurosaurians.

The record of spinosaurids from the Barremian of the Iberian Peninsula shows that this theropod group preferred freshwater environments with a certain degree of marine influence in this part of Europe.

In spite of the fact that studies of function are poorly developed in manual unguals, the presence of an enlarged manual claw in spinosaurids has been invoked as an anatomical feature that could be useful in various palaeoecological scenarios – i.e., for scavenging and/or as an offensive weapon – but recently the option of its use in digging behaviour has also been considered.

Supplementary Online Material

A tridimensional model of the theropod claw CSC1-4 generated by photogrammetry.

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819

820 FIGURE CAPTIONS

821 Figure 1. Size comparison of scale of theropod manual claws in profile. Claws are
822 aligned from their proximodorsal corners, whereas each claw is oriented so that the line
823 between the dorsoproximal corner and the distal tip is horizontal.
824 Figure 2. Geographical and geological setting of Caña Seca 1 fossil locality (Gúdar,
825 Teruel province, Spain), modified from Gasca et al. (2012). A. Palaeogeographical
826 location within the Maestrazgo Basin. B. Detailed geographical location near the village
827 of Gúdar. C. Stratigraphic section of the studied outcrop.
828 Figure 3. Manual ungual CSC1-4 in proximal (A), medial (B), lateral (C), distal (D) and
829 dorsal (E) views. Abbreviations: laf – lateral articular facet, maf – medial articular facet,
830 ft – flexor tubercle.
831 Figure 4. CSC1-4, close-up of the medial side showing the presence of foramina on the
832 vascular groove.
833 Figure 5. Manual claws (original fossil or cast), examined first-hand, of spinosaurid (A-
834 F) and allosaurid theropods (G). A. CSC1-4 in medial (A1), dorsal (A2) and lateral (A3)
835 view. B-C. *Baryonyx walkeri*, ungual I in medial (B1), lateral (B2) and dorsal (B3)
836 views and ungual of digit II or III in dorsal (C1), medial (C2) and lateral (C3) views. D-
837 F. *Suchomimus tenerensis*, ungual I in medial (D1), lateral (D2) and dorsal (D3) views,
838 ungual II (E) and III (F) in medial view. G. *Allosaurus*, profile (G1) and dorsal (G2)
839 view.

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840 Figure 6. Some additional spinosaurid fossils from the El Castellar Formation. A. Tooth
841 MOAL-1/1 in mesial (A1), lateral (A2) and adapical (A3) views. B. Caudal centrum
842 SUE 1-2 in dorsal (B1), left lateral (B2) and posterior (B3) views.
843 Table 1. Spinosaurid record of the El Castellar Formation (lower Barremian, Teruel
844 province, Spain).
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Number	Material	Fossil locality	Municipality	Reference
MPG PX-23	Tooth	"PX outcrop"	Galve	Sánchez-Hernández et al., 2007
MOAL-1/1	Tooth	Molino Alto 1	Aliaga	Gasca et al., 2008
SM-2/D1	Tooth	Senda Miravete 2	Miravete de la Sierra	Gasca et al., 2009
BNA2-7	Tooth	Barranco de las Navas 2	Mora de Rubielos	This work
SUE1-2	Middle caudal centrum	Suertes 1	Miravete de la Sierra	This work
VES4-1	Middle caudal centrum	Valdespino 4	Aliaga	This work
CSC1-4	Manual claw	Caña Seca 1	Gúdar	This work

Table 1. Fossil remains of Spinosauridae from the El Castellar Formation.

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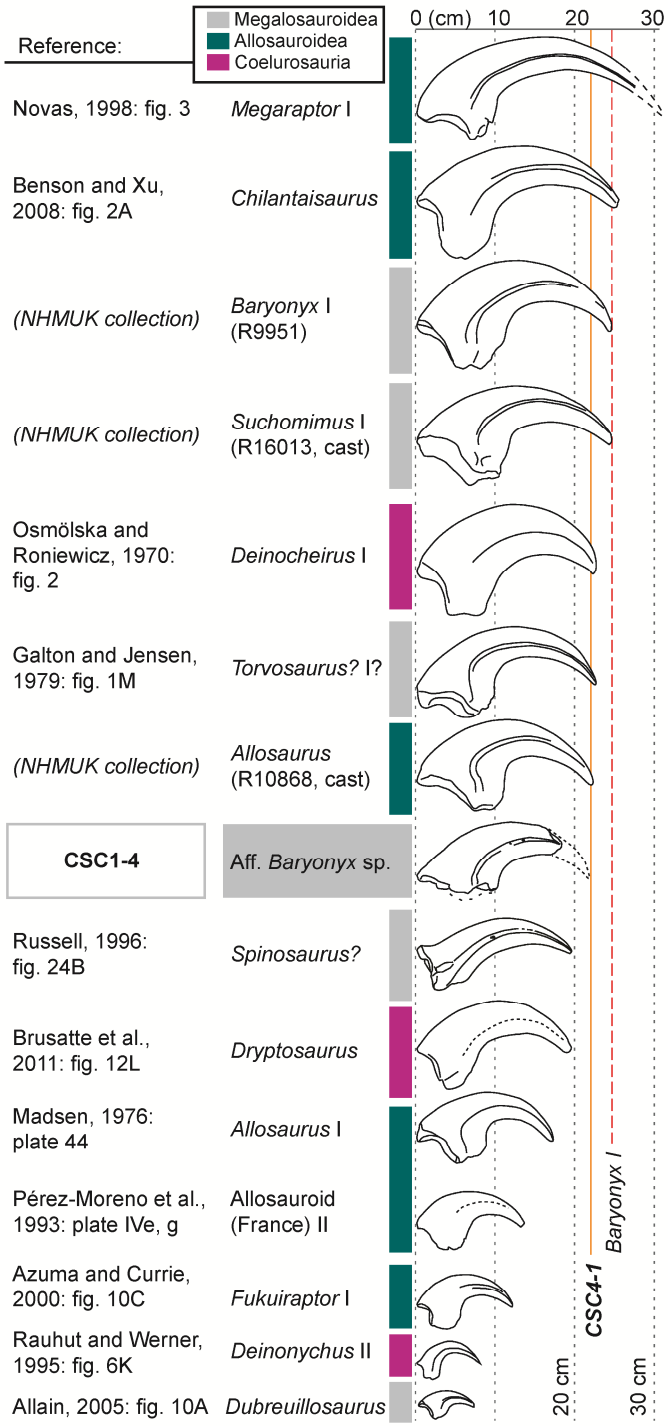

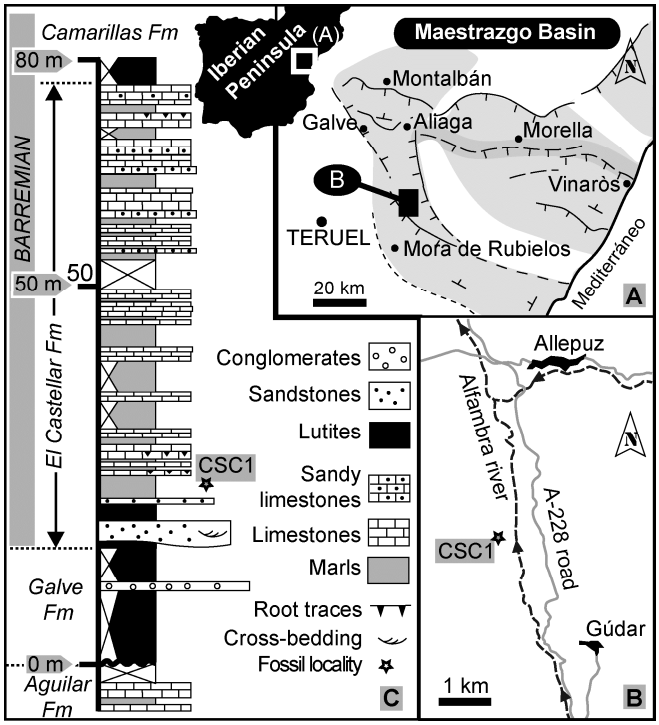

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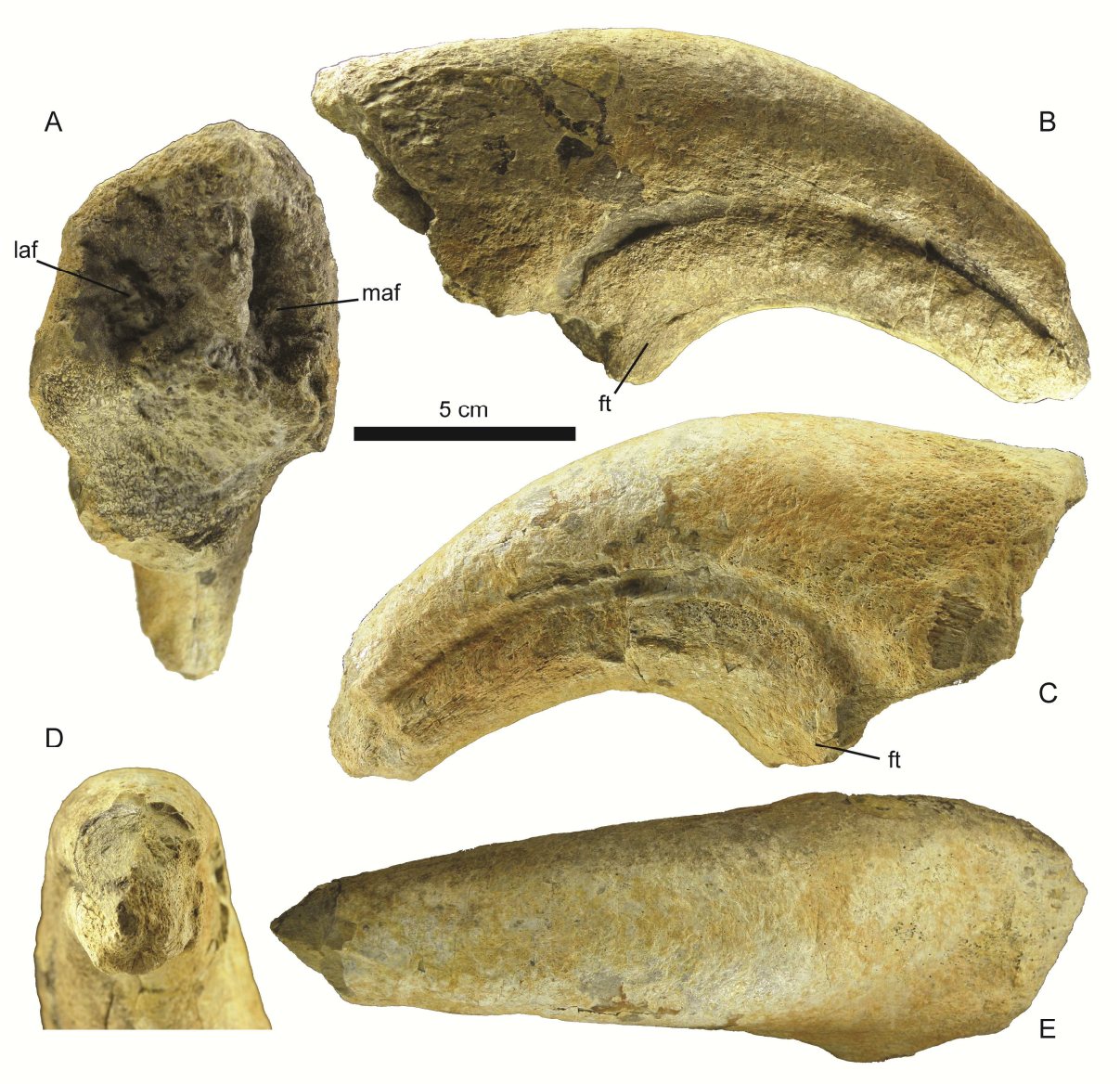

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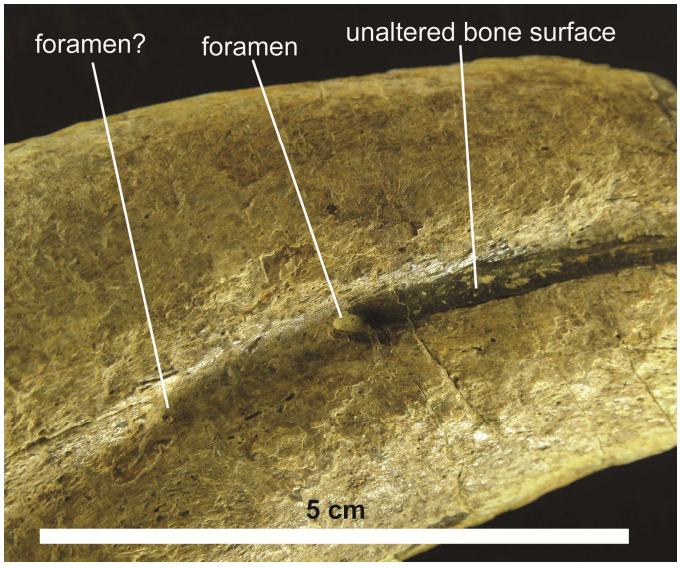

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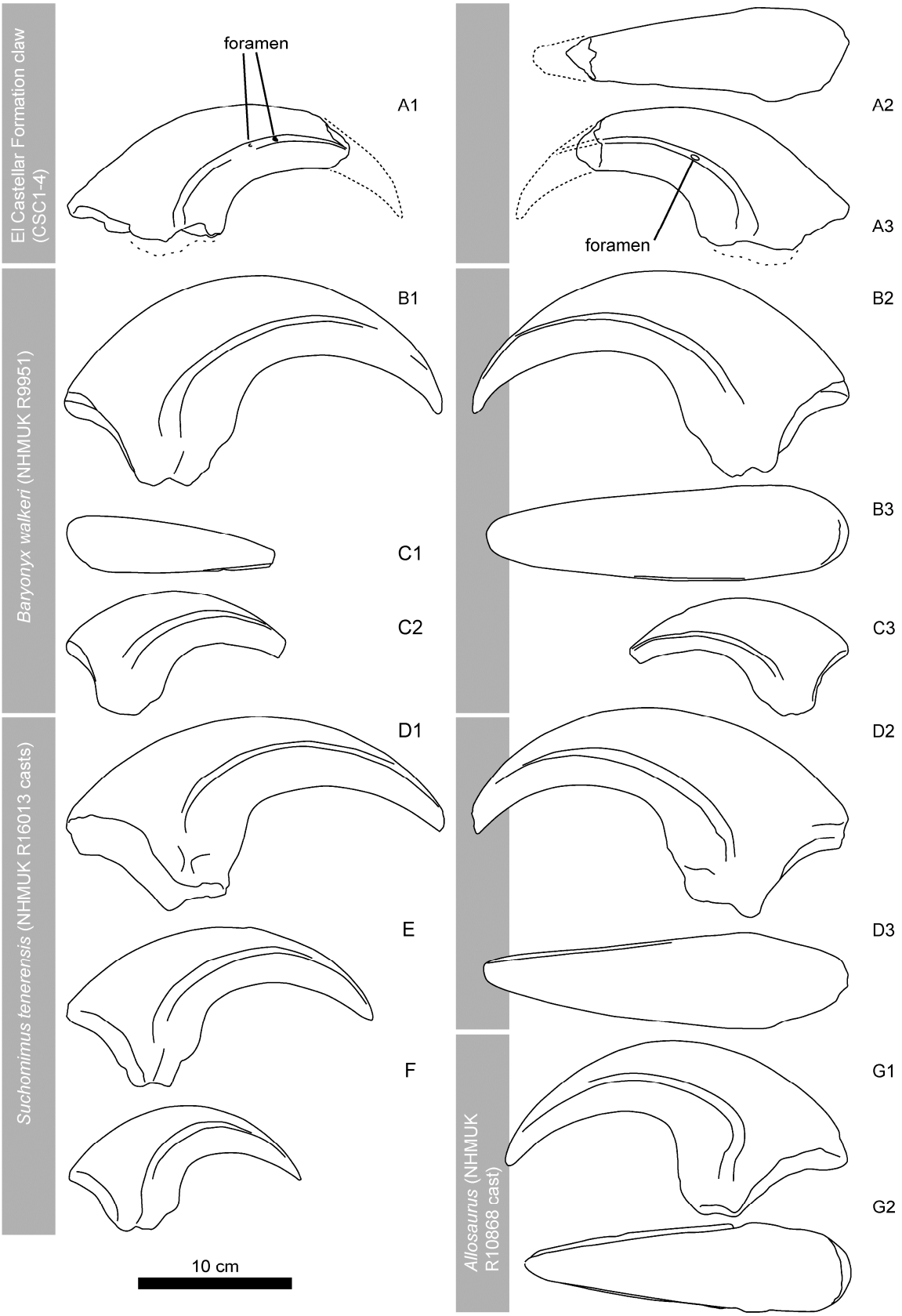
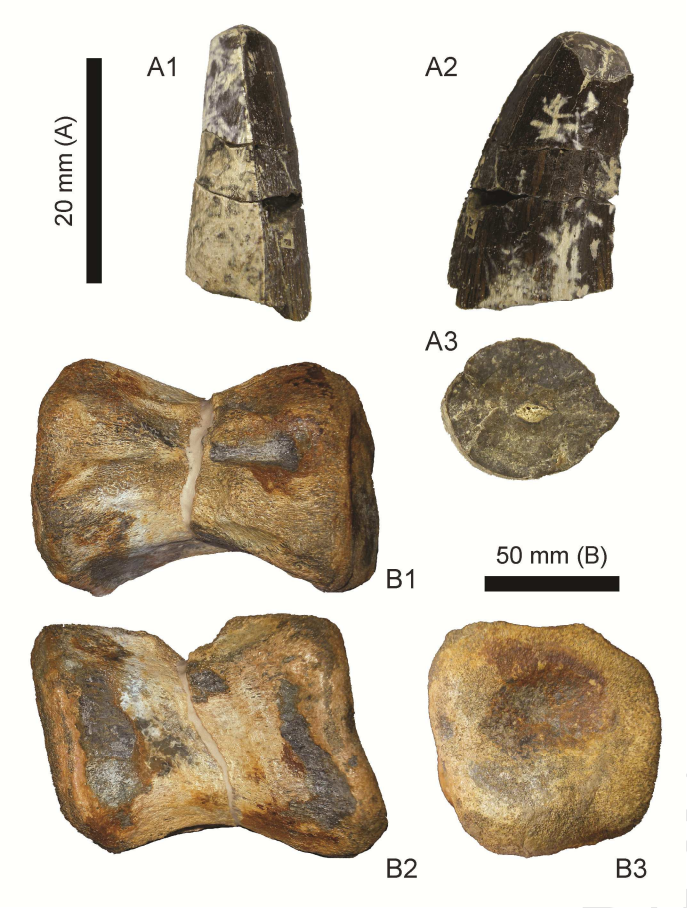

El Castellar Formation claw (CSC1-4)
foramen
A1
A2
A3
foramen
Baryonyx walkeri (NHMUK R9951)
B1
B2
B3
C1
C2
C3
Suchomimus tenerensis (NHMUK R16013 casts)
D1
D2
E
D3
F
Allosaurus (NHMUK R10868 cast)
G1
G2
10 cm



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