*Concavenator corcovatus* Ortega, Escaso, Sanz, 2010  
(Dinosauria: Carcharodontosauridae)  
Ejemplar MCCM-LH 6666 (holotipo)  
Cretácico Inferior (Barremiense). Hace unos 125 millones de años  
Las Hoyas (La Cierva, Cuenca)  
El único ejemplar conocido hasta la fecha del dinosaurio carnívoro *Concavenator corcovatus* ("el cazador jorobado de Cuenca") vivió hace unos 125 millones de años en el paleohumedral de Las Hoyas. Este fósil representa el ejemplar más completo de un dinosaurio carcarodontosaurio, dado que ha conservado la mayor parte de su esqueleto e incluso impresiones de la piel. *Concavenator* presentaba dos características especialmente singulares: una pequeña joroba formada justo por delante de la cadera y el desarrollo de unas estructuras en la piel de los brazos que podrían estar relacionadas con las plumas que actualmente presentan las aves.
A bizarre, humped Carcharodontosaurus (Theropoda) from the Lower Cretaceous of Spain

Francisco Ortega 1, Fernando Escaso 1,2 & José L. Sanz 2

Carcharodontosaurs were the largest predatory dinosaurs, and their early evolutionary history seems to be more intricate than was previously thought. Until recently, carcharodontosaurs were restricted to a group of large theropods inhabiting the Late Cretaceous Gondwanan land masses 1,2, but in the last few years Laurasian evidence 3–5 has been causing a reevaluation of their initial diversification 6. Here we describe an almost complete and exquisitely preserved skeleton of a medium-sized (roughly six metres long) theropod from the Lower Cretaceous series (Barremian stage) Konservat-Lagerstätte of Las Hoyas 7 in Cuenca, Spain. Cladistic analysis supports the idea that the new taxon Concavenator corcovatus is a primitive member of Carcharodontosaurus 6, exhibiting two unusual features: elongation of the neurapophyses of two presacral vertebrae forming a pointed, hump-like structure and a series of small bumps on the ulna. We think that these bumps are homologous to quill knobs present on some modern birds; the knobs are related to the insertion area of follicular ligaments that anchor the roots of the flight feathers (remiges) to the arm. We propose that Concavenator has integumentary follicular structures inserted on the ulna, as in modern birds. Because scales do not have follicles, we consider the structures anchored to the Concavenator arms to be non-scale skin appendages homologous to the feathers of modern birds. If this is true, then the phylogenetic bracket for the presence of non-scale skin structures homologous to feathers in theropod dinosaurs would be extended to the Neotetanurae, enlarging the scope for explaining the origin of feathers in theropods.

The recent interpretation of the theropod dinosaur Neovenator salerii from the Barremian stage of the Isle of Wight, UK, as a basal neovenatorid carcharodontosaurian 6 seems to relate the early evolutionary history of this traditionally Gondwanan group to the Lower Cretaceous of Europe. In the same way, we describe an exquisitely preserved skeleton of a new carcharodontosaurian, Concavenator corcovatus gen. et sp. nov., from the Lower Cretaceous Konservat-Lagerstätte of Las Hoyas in Cuenca, Spain 7. This fossil represents the most complete individual of a carcharodontosaurian theropod, and, to our knowledge, the first one in which direct and indirect evidence of integumentary structures is reported.

Theropoda Marsh, 1881
Allosauroidea Marsh, 1878
Carcharodontosauria Benson, Brusatte and Carrano, 2010
Concavenator corcovatus Ortega, Escaso and Sanz gen. et sp. nov.

Etymology. Concavenator from Conca (Latin), for the Spanish province of Cuenca, and venator (Latin), a hunter; corcovatus (Latin), refers to the hump-like structure formed by the elongation of two presacral vertebrae.

Holotype. Specimen MCCM-LH 6666 at Museo de las Ciencias de Castilla-La Mancha, Cuenca, Spain, a nearly complete and articulated skeleton (Fig. 1).

Horizon and locality. Las Hoyas site 7. Calizas de La Huérguina Formation, Upper Barremian (Lower Cretaceous); La Cierva township, Cuenca, Spain.

Diagnosis. A carcharodontosaurian 6 (Fig. 2) having four recesses, three of them connected, on the nasal bones; a large, rounded, thickened...
and carcharodontosaurines\(^9\); no crown recurvature, (shared with carcharodontosaurines\(^9\)); accessory centrodioaphyseal lamina on the transverse processes of the posterior dorsal vertebrae, (shared with baryonychinae\(^8\)); the prominent rugose distal tubercle on the ischium (part of the hip bone); quill knobs in the posterolateral margin of the ulna, (shared with derived maniraptorans\(^11\)); and the preacetabular blade of the ilium having a convex ventral portion of the cranial edge and hook-like ventral process, (shared with tyrannosaurids\(^8\)).

**Description.** The specimen is embedded into lithographic limestone with its right side mainly exposed. The surrounding sediment has multiple impressions that discouraged further preparation, and thus some characters are not accessible. The skull (Fig. 3a) of Concavenator is nearly complete, but the snout and the occipital region are not well preserved. The anterior portion of the antorbital fossa has one or two maxillary recesses. The lacrimal and dorsal surface of the ilium bone exhibit a rugose dorsal margin. The nasal bone shows four lateral recesses below its dorsal rim, the posterior ones connected by a midline groove. A large, rugose and robust postorbital brow overhangs the dorsal rim of the orbit, occupying one-third of the orbital height. The ventral ramus of the postorbital has a relatively large, nearly triangular and blunt intraorbital process that differs from the more distally placed process of Acrocanthosaurus and carcharodontosaurids as well as the small and rugose process of Eocarcharia\(^10\). The frontal does not participate in the orbit, as in carcharodontosaurids, abelisaurids and the largest tyrannosaurids. The maxillary teeth are transversely compressed. They have convex mesial and straight distal carinae, with small denticles. Like Eocarcharia, they do not have high-relief enamel wrinkles, and thus differ from most other carcharodontosaurids\(^10\). There are ten cervical vertebrae with pleurocoels in the posterior centrum. There are 13 dorsal vertebrae without pleurocoels, unlike in most tetanurans\(^6\).

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The long axis of the femoral head is less dorsomedially directed than in derived carcharodontosaurids without a distal boot, such as Giganotosaurus\(^4\) and Mapusaurus\(^3\). The partially exposed right manus is elongated (65% of the length of the whole forearm). The two exposed manual claws are short, stout and proximally tall.

The pelvis is orthopubic. The iliac blade is short and low. The dorsal portion of the cranial margin of the preacetabular blade has a concave dorsal contour and a convex ventral portion in the cranial edge. It also has a conspicuous hook-like ventral process, as in tyrannosaurids\(^12\). The iliac articular surface is deeply concave in Concavenator. The ischiatic process of the ischium has a visible distal boot-like expansion, as in Neovenator\(^*,1*\), and unlike derived carcharodontosaurids without a distal boot, such as Giganotosaurus\(^4\) and Mapusaurus\(^3\). The long axis of the femoral head is less dorsomedially directed than in derived carcharodontosaurids. The tibia is stout and large. The metatarsals are large and robust, contrasting with the small dimensions of the foot, especially the pedal unguals. The third metatarsal is the longest; the second and fourth metatarsals are nearly equal in length.

Some delicate integumentary structures are preserved. We interpret some impressions under the pedal digits as remnants of plantar pads (Fig. 3c), and the ungual phalanges are associated with the impression of corneous sheaths. Large and small integumentary polygonal scales

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**Figure 2** Time-calibrated reduced consensus of the phylogeny of Neotetanurae theropods. *a* Hypothetical flesh reconstruction of Concavenator corcovatus. *b* The phylogeny resulting from a parsimony analysis of the data matrix in which Concavenator is incorporated (see Supplementary Information). If poorly represented carcharodontosaurian taxa are considered, Concavenator is located either as the sister group to the remaining Carcharodontosauria or as a basal carcharodontosaurian, but on removing the less informative taxa, Concavenator stands unequivocally as the most basal Carcharodontosauridae. Concavenator possesses two unambiguous synapomorphies of Carcharodontosauria: a deeply concave iliac articular surface on the ischia and a proxiomedially inclined femoral head. Our analysis agrees with recent hypotheses in considering that Carcharodontosaurus is basally split into Carcharodontosauridae and Neovenatoridae. Two cranial synapomorphies would place Concavenator within Carcharodontosauridae: the lacrimal-postorbital contact and a large curving flange in the jugal process on the postorbital. Maa, Maastrichtian; Cam, Campanian; San, Santonian; Con, Coniacian; Tur, Turonian; Gen, Cenomanian; Alb, Albian; Apt, Aptian; Bar, Barremian; Hau, Haurtivian; Val, Valanginian; Ber, Berriasian; Tit, Tithonian; Kim, Kimmeridgian; Oxf, Oxfordian; Cal, Callovian; Bat, Bathonian; Baj, Bajocian; Aal, Aalenian.
are visible in the metatarsal area of the ankle region (Fig. 3d). An almost continuous impression delimiting the distal caudal outline is extended both dorsally and ventrally to the vertebral series (Fig. 3e). On the ventral side, the impression of three nearly quadrangular scales is associated with each vertebra (Fig. 3f). The scale diversity shown by Concavenator is quite similar to that of some present-day Neornithes (modern birds), in which reticulate, scutate and scutella scales are present16–18. The former correspond to the footpads. Scutate scales are rectangular and are situated on the anterior metatarsal area and the dorsal digit zone. Scutella scales are placed lateral to the scutate scales; they are smaller but also rectangular in outline.

Probably the most conspicuous features of Concavenator are the hypertrophied neural spines on the eleventh and twelfth dorsal vertebrae. Elongated neapophyses are relatively common in dinosauroids and some undetermined tetanurans23–26. However, none of these has elongated neapophyses restricted to two presacral dorsal vertebrae (Figs 1b, 2b). The elongated neapophyses have been largely thought to be support structures for thermoregulation, energy storage or even display27, but the abrupt, tall and cranio-caudally short singular structure of Concavenator has no analogous structures, and its function is unclear.

The presence of ulnar quill knobs is also noteworthy. Ulnar quill knobs are structures on the periosteum that are exclusively related to follicular ligaments that anchor the roots of the remiges (flight feathers) to the bone. Because scales do not have follicles, we consider the quill knobs on the posterolateral side of the Concavenator ulna (Fig. 4b) to indicate the presence of non-scale skin appendages in a similar position to that of the remiges of modern birds and, therefore, homologous to them.

Recent findings have reported the presence of filamentous tubular integumentary structures in ornithischian dinosaurs such as the heterodontosaurid Tianyulong28 and the ceratopian Psittacosaurus29. The debate about the homology between these structures and bird feathers is open. If ornithischian tubular filaments are a kind of feather, they are an evolutionary novelty in dinosaurs, and their presence is expected in non-maniraptoran theropods such as Concavenator. If they are not a type of feather, Concavenator marks the most primitive presence of non-scale skin appendages in the theropod lineage, placing them at the node Neotetanurae. The simplest hypothesis about the ulnar Concavenator skin appendages is that they are short, rigid filaments (Fig. 2). However, it is possible that they might have had barb ridges, because these structures appear before the formation of the follicle18,30. In any case, Concavenator shows that the combination of scale and non-scale skin appendages exhibited in present-day poultry was already present in large theropod dinosaurs 130 million years ago.

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LETTERS

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206


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