Concavenator corcovatus Ortega, Escaso, Sanz, 2010

(Dinosauria: Carcharodontosauridae)

Ejemplar MCCM-LH 6666 (holotipo)

Cretácico Inferior (Barremiense). Hace unos125 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 paleohumedal 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.

LETTERS

A bizarre, humped Carcharodontosauria (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 Carcharodontosauria[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

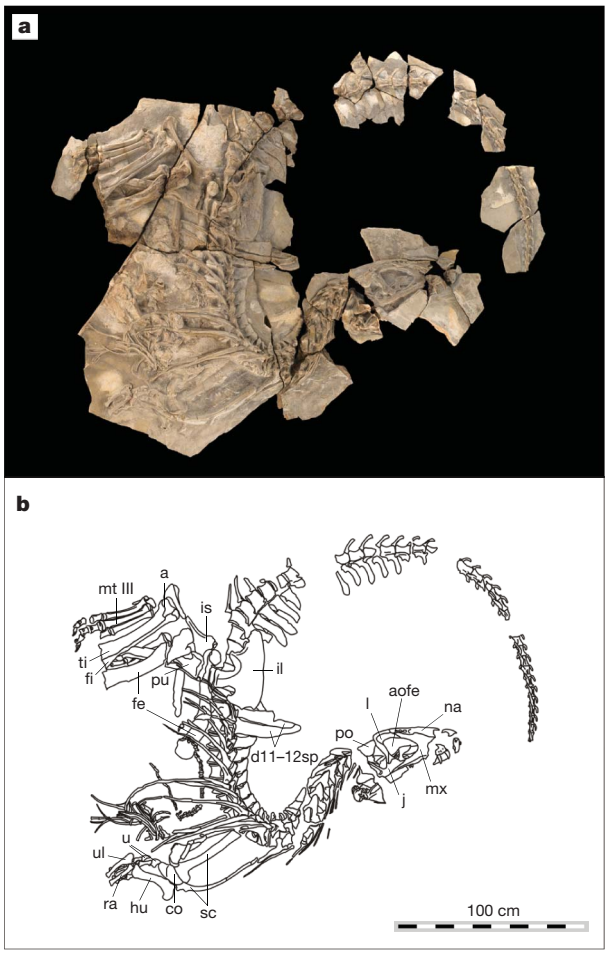

Figure 1 | Holotype of *Concavenator corcovatus*. Specimen MCCM-LH 6666 from the Lower Cretaceous series (Barremian stage) of Las Hoyas (Cuenca, Spain). **a**, Photograph under visible light. **b**, Schematic interpretation of the exposed right side of the skeleton. a, astragalus; aofe, antorbital fenestra; co, coracoid; d11–12sp, neural spines of the eleventh and twelfth dorsal vertebrae; fe, femur; fi, fibula; hu, humerus; il, ilium; is, ischium; j, jugal; l, lacrimal; mt III, third metatarsal; mx, maxilla; na, nasal; po, postorbital; pu, pubis; ra, radius; sc, scapula; ti, tibia; u, ungual phalanx; ul, ulna.

[1]Grupo de Biología, Departamento de Física Matemática y de Fluidos, Facultad de Ciencias, Universidad Nacional de Educación a Distancia, Paseo Senda del Rey 9, 28040 Madrid, Spain. [2]Unidad de Paleontología, Departamento de Biología, Facultad de Ciencias, Universidad Autónoma de Madrid, Cantoblanco, 28049 Madrid, Spain.

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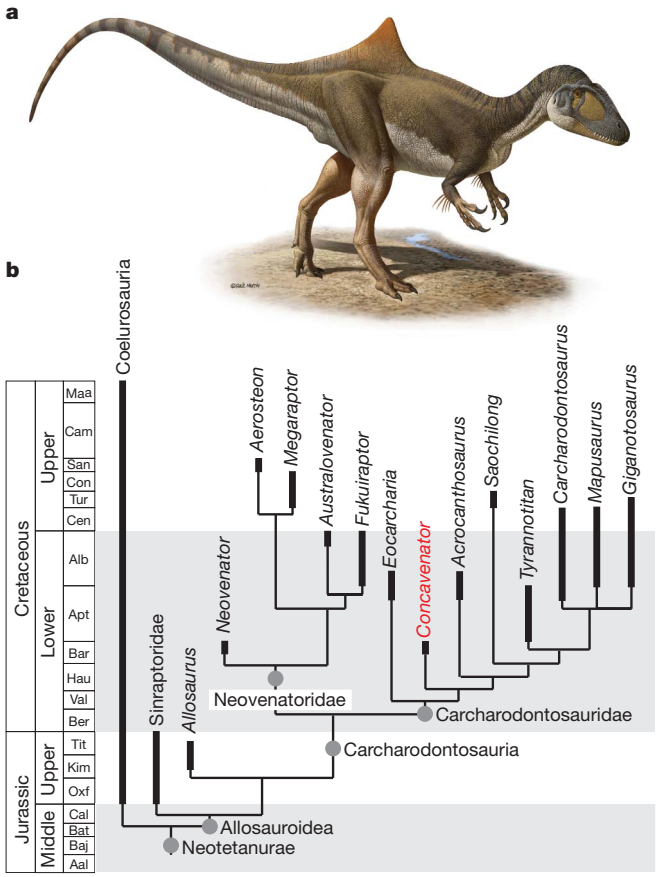

Figure 2 | Time-calibrated reduced consensus of the phylogeny of Neotetanurae theropods. a, Hypothetical flesh reconstruction of *Concavenator corcovatus*. **b**, The phylogeny resulting from a parsimony analysis of the data matrix[6] in which *Concavenator* is incorporated (see Supplementary Information). 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 proximomedially inclined femoral head. Our analysis agrees with recent hypotheses[6] in considering that Carcharodontosauria is basally split into Carcharodontosauridae and Neovenatoridae[6]. 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; Cen, Cenomanian; Alb, Albian; Apt, Aptian; Bar, Barremian; Hau, Hauterivian; Val, Valanginian; Ber, Berriasian; Tit, Tithonian; Kim, Kimmeridgian; Oxf, Oxfordian; Cal, Callovian; Bat, Bathonian; Baj, Bajocian; Aal, Aalenian.

postorbital brow occupying one-third of the orbit; tall neurapophyses of the eleventh and twelfth dorsal vertebrae (five times the height of the centra); relatively high, cranially directed neurapophyses of the second and third caudal vertebrae; and a small, thorn-like caudal process at the base of each neurapophysis of the proximal caudal vertebrae. In addition, *Concavenator* presents a unique combination of characters: the heavily rugose (wrinkled) dorsal surface of the nasal bone, shared with more derived carcharodontosaurids[8] and abelisaurids[9]; the anterior end of the jugal bone posterior to the internal antorbital fenestra; the thick dorsoventral anterior process of the lacrimal bone; light rugosity on the lacrimal horn; no fenestra on the lacrimal bone; the anteriormost point of the lateral lamina of the ventral process in the lacrimal situated dorsal to the mid-height of the ventral process, with a distinct rugose patch on the lateral surface; no suborbital process on the lacrimal bone; weak enamel wrinkles on teeth adjacent to the carinae that do not extend across the labial and lingual tooth surfaces, (shared with *Tyrannotitan* and carcharodontosaurines[10]); no crown recurvature, (shared with carcharodontosaurines[10]); accessory centrodiapophyseal lamina on the transverse processes of the posterior dorsal vertebrae, (shared with baryonychines[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 tyrannosaurs[12]).

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 nasal bone exhibit a rugose dorsal margin. The nasal bone shows four lateral recesses below its dorsal rim, the posterior ones connected by a mid-line 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 carcharodontosaurines 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 centra. There are 13 dorsal vertebrae without pleurocoels, unlike in most tetanurans[8]. The length of the neurapophyses of the eleventh and twelfth dorsal vertebrae (Fig. 3b) exceeds five times the height of the centra. The neural spines of the sacral and first caudal vertebrae are low, below the dorsal rim of the ilium. Neural spines of the anterior caudal vertebrae are relatively tall and the second to the fifth anterior caudal vertebrae have small, thorn-like anterior and posterior processes. The anterior process is retained along with the whole available tail, as in *Allosaurus*[13].

The left scapulocoracoid is exposed in medial view, and the right one is exposed in ventral view. The scapular blade is long, having parallel borders and no distal expansion, unlike *Neovenator*[4] and *Acrocanthosaurus*[1]. The forelimbs are short (42% of the hindlimb length). The ulna has a prominent olecranon and a series of low bumps placed along a posterolateral crest (Fig. 4a, b). These bumps correspond topographically to, and are morphologically similar to, feather quill knobs, and we consider them homologous to those present in many birds (Fig. 4c), as well as in other derived maniraptorans, such as *Velociraptor mongoliensis*[11]. 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*[4], and unlike derived carcharodontosaurids without a distal boot, such as *Giganotosaurus*[14] and *Mapusaurus*[15]. 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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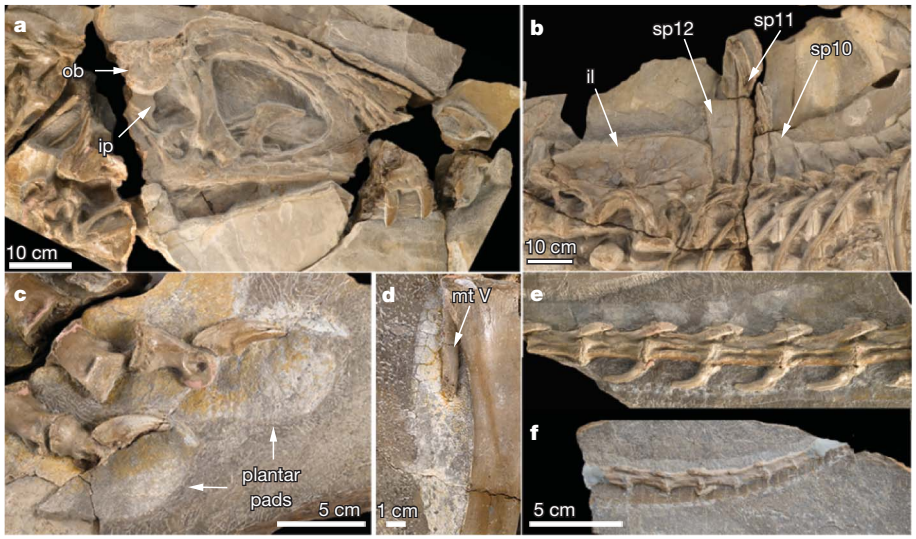

Figure 3 | Details of the holotype of *Concavenator corcovatus*. Specimen MCCM-LH 6666 from the Lower Cretaceous series (Barremian stage) of Las Hoyas (Cuenca, Spain). **a**, Lateral view of the skull. **b**, Middle part of the axial skeleton showing the distribution of the height of the neural spines of vertebrae around the pelvic region. **c**, Detail of distal phalanx of the right foot showing impressions of plantar pads and corneous sheaths of the ungual bones. **d**, Impressions of hexagonal scales associated with the fifth metatarsal. **e**, Distal portion of the tail vertebrae showing a body outline. **f**, Distal portion of the tail vertebrae showing a body outline and the disposition of some rectangular scales. il, ilium; ip, intraorbital process; ob, orbital brow; mt V, fifth metatarsal; sp10–12, neural spines of the tenth–twelfth dorsal vertebrae.

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 present[16–18]. 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 neurapophyses are relatively common in dinosaurs[19–22]; among theropods, they are well known in spinosaurids, carcharodontosaurids and some undetermined tetanurans[23–26]. However, none of these has elongated neurapophyses restricted to two presacral dorsal vertebrae (Figs 1b, 2b). The elongated neurapophyses have been largely thought to be support structures for thermoregulation, energy storage or even display[27], 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 *Tianyulong*[28] and the ceratopsian *Psittacosaurus*[29]. 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 follicle[18,30]. 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.

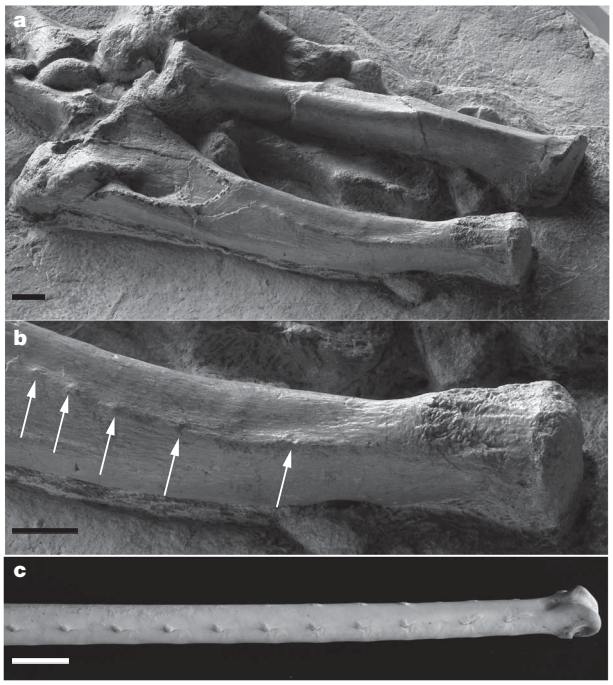

Figure 4 | Forearm of *Concavenator corcovatus*. Specimen MCCM-LH 6666 from the Lower Cretaceous series (Barremian stage) of Las Hoyas in Cuenca, Spain. **a**, Forearm (radius and ulna) of *Concavenator corcovatus*. **b**, Detail of the posterolateral crest showing a series of feather quill knobs (arrows mark the available five elements of the series). **c**, Dorsal view of the ulna of an extant turkey vulture (*Cathartes* sp.). Scale bars, 1 cm.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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