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RAPID COMMUNICATION

An articulated hindlimb of a basal iguanodont (Dinosauria, Ornithopoda) from the Early Cretaceous Las Hoyas Lagerstätte (Spain)

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Abstract

An isolated, fully articulated hindlimb of a basal iguanodont from the Spanish Las Hoyas Lagerstätte is described. It probably belonged to a juvenile or subadult individual. Despite some slight differences, anatomical features, as well as the late Barremian age of this specimen, would suggest that it belongs to *Mantellisaurus atherfieldensis*. The exquisite preservation of this specimen provides information on the foot anatomy of basal iguanodonts. This is the first report of a non-theropod dinosaur from Las Hoyas. From a palaeoecological point of view, this discovery indicates that potential prey of the carcharodontosaurian theropod *Concavenator* were present at Las Hoyas, thus complementing our knowledge of the trophic structure of this Early Cretaceous palaeocommunity.

Keywords: Cretaceous, Barremian, Iguanodontia, Las Hoyas Lagerstätte, Spain.

1. Introduction

The Early Cretaceous Las Hoyas Lagerstätte is famous for its rich and diverse wetland assemblage including numerous plant, invertebrate and vertebrate taxa (Sanz *et al.* 1988, 2001; Fregenal-Martínez & Meléndez, 2000; Escaso, Sanz & Ortega, 2005; Buscalioni & Fregenal-Martínez, 2010). In this upper Barremian locality, tetrapods are mostly articulated and occasionally preserve soft tissue and histological structures (Briggs *et al.* 1997; Gupta *et al.* 2008; Bailleul *et al.* 2011). The tetrapods found at Las Hoyas belong to Salientia, Caudata, Albanerpetontidae, Scincomorpha, Chelonia, Pterosauria, Crocodyliformes, and Dinosauria (including Aves) (Buscalioni & Fregenal-Martínez, 2010). Most of the recorded species are small-sized forms (ranging from 5 to 30 cm in total length), except for the dinosaur and pterosaur taxa. Small (subadult to adult) individuals are largely dominant in the assemblage, whereas large ones are exceptional. Considering that body size plays a relevant role in the ecology of wetlands (van der Valk, 2006), the large species have been interpreted as incidental, i.e. species occasionally found in wetlands (Buscalioni & Fregenal-Martínez, 2006, 2010). Pterosaurs are known from isolated teeth, and a fragmentary skull and mandible. They have been referred to as indeterminate istiodactylids and ornithocheirids (Vullo *et al.* 2009), and a new tapejarid taxon, *Europejara olcadesorum*, was recently erected (LH-9413; Vullo *et al.* 2012). The non-avian dinosaur record is composed of footprints and two species each known from a single individual: the ornithomimosaur *Pelecanimimus polyodon* (LH-7777; Pérez-Moreno *et al.* 1994), and the carcharodontosaur *Concavenator corcovatus* (LH-6666; Ortega, Escaso & Sanz, 2010). Dinosaur and crocodile footprints are concentrated at the base of each unit, and they are associated with facies from drier periods (Buscalioni & Fregenal-Martínez, 2010). The Las Hoyas dinosaur footprints are frequently distorted and were produced by rather large theropods (Vullo *et al.* 2009).

Here, we describe an exquisitely preserved specimen with integument impressions. The fossil is an isolated but fully articulated lower hindlimb of a medium sized iguanodontian ornithopod. This discovery represents the first clear occurrence of an ornithischian dinosaur at Las Hoyas and complements the palaeoecological reconstruction and trophic network of this ancient wetland.

2. Description

The material studied (specimen LH-30677 housed in the Museo de las Ciencias de Castilla-La Mancha, Cuenca) consists of an incomplete but fully articulated right hindlimb (Figs. 1, 2; see Table 1 for measurements). The femur is missing, as well as the proximal extremities of both the tibia and fibula. While the latter two bones are exposed in anterior view, all pes elements (i.e. tarsals, metatarsals, and phalanges) are visible in ventral view. The phalangeal formula of this tridactyl pes is clearly recognizable: 0-3-4-5-0. The maximal length of the foot is about 32 cm.

The tibia shaft is slightly crushed anteroposteriorly, and the distal extremity is hidden by the overlying metatarsals. The calcaneum is in contact with the distal end of the fibula. The ventral surface is convex. The astragalus is fully hidden. Two flat, oval-shaped bones adjacent to the proximal ends of the metatarsals III and IV are probably the distal tarsals III and IV,

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Table 1. Measurements (in mm) of hindlimb elements of LH-30677

	length	maximal width
tibia	385*	59
fibula	330*	40
metatarsal I	?	?
metatarsal II	130	30
phalanx II-1	60	25
phalanx II-2	30	24
phalanx II-3	40	25
metatarsal III	170	40
phalanx III-1	60	42
phalanx III-2	15	40
phalanx III-3	20	33
phalanx III-4	50	35
metatarsal IV	140	40
phalanx IV-1	45	32
phalanx IV-2	10	30
phalanx IV-3	10	28
phalanx IV-4	11	24
phalanx IV-5	40	22

*Preserved lengths

Figure 1. (Colour online) Iguanodont hindlimb (LH-30677) from the upper Barremian of Las Hoyas (La Huérguina Formation, Cuenca), tentatively referred to *Mantellisaurus atherfieldensis*. Scale bar equals 10 cm.

respectively. Four metatarsals are present (I–IV). Although most of the metatarsal I is hidden, this bone is notably reduced when compared to the functional II–IV metatarsals. The first metatarsal shows a stylus-like shape, and distally reaches the middle part of the metatarsal II. The metatarsal II is the shortest of the three functional metatarsals. The proximal articular surface has a rectangular outline with concave medial and straight lateral edges. In ventral view, the shaft is compressed. The shaft of metatarsal II curves gently medially towards its distal end. The proximal end of the metatarsal II anteriorly overlaps that of the metatarsal III with a tab of bone on the craniomedial margin. The metatarsal III is the longest and most robust bone of the metatarsus, being 30 % and 20 % longer than metatarsals II and IV, respectively. It displays a strong ventral crest developed from the proximal extremity to the middle of the medial border, and a median crest that reaches the distal articulation. The proximal crest delimits a medial surface where the metatarsal II is ventrally lying, while the metatarsal III anteriorly overlaps the proximal end of the metatarsal IV. The shaft of the metatarsal IV is robust, and shows a slight lateral curvature. The metatarsal IV bears a proximal medial crest, and the proximal articular surface extends lateromedially.

The proximal phalange is the largest one in all three digits. The proximal phalange of the digit II has an elongate rectangular shape, while those of the digits III and IV are more robust. More distal phalanges become progressively shorter before culminating in the pedal unguals. The unguals are relatively elongate with a blunt, rounded distal extremity. Some slight brownish integument impressions are preserved around the digits II, III and IV. However, no scale-like structures can be observed. Examination of the specimen under ultraviolet light reveals two types of integumentary structures: (1) whitish structures at the ungual tips which may correspond to the hoof-like claws; and (2) dark structures around each digit which may correspond to the toe pads.

3. Discussion and conclusions

The fossil record of basal iguanodonts (i.e. non-hadrosaurid members of Iguanodontia; McDonald, 2012*a*) is well documented in the Early Cretaceous of Western Europe, with most of the material coming from England (Norman, 2011), Belgium (Norman, 1980), Germany (Norman, 1987), France (Martin & Buffetaut, 1992) and Spain (for an exhaustive review of the Spanish occurrences, see Ruiz-Omeñaca, Canudo & Cuenca-Bescós, 1998). Until recently, almost all iguanodontian remains found in the Early Cretaceous of Europe had been assigned to the classic genus *Iguanodon*. At present, this group has an intricate taxonomy because of the erection of several new genera and species during the last five years: *Mantellisaurus* Paul, 2007; *Dollodon* Paul, 2008; *Owenodon* Galton, 2009; *Barilium* Norman, 2010 (objective senior synonym of *Torilion* Carpenter & Ishida, 2010); *Hypselospinus* Norman, 2010 (objective senior synonym of *Wadhurstia* Carpenter & Ishida, 2010); *Proplanicoxa* Carpenter & Ishida, 2010; *Sellacoxa* Carpenter & Ishida, 2010; *Kukufeldia* McDonald, Barrett & Chapman, 2010 and *Delapparentia* Ruiz-Omeñaca, 2011. According to Norman (2011) and McDonald (2012*b*), *Iguanodon bernissartensis* and *Mantellisaurus atherfieldensis* are the only two taxa of large-bodied iguanodonts present in the Barremian–Aptian of Belgium and England, *Dollodon bampingi* being considered a junior synonym of the latter by these authors.

Concerning the foot anatomy of basal iguanodonts such as *Iguanodon* and *Mantellisaurus*, there are only a few detailed descriptions of associated, sometimes fully articulated, pes elements. The holotypic material of *Mantellisaurus atherfieldensis* (NHMUK R5764) includes almost all pes elements (Hooley, 1925; Norman, 1986, 2011). The Bernissart specimen assigned to *Mantellisaurus atherfieldensis* (IRNSB 1551) also provides information on the foot anatomy of this taxon. The well-preserved, articulated specimen NHMUK R1829 from the Barremian of the Isle of Wight, referable to *Mantellisaurus atherfieldensis* (Norman, 2011), was originally described by Owen (1858*a*, *b*) then re-figured by Naish & Martill (2001) as *Iguanodon* sp. Another well-preserved specimen (NHMUK R28685), also from the Barremian of Isle of Wight, was described by Hulke (1882) as *Iguanodon seelyi*, a junior synonym of *Iguanodon bernissartensis* following Norman (2011) and McDonald (2012*b*). The foot anatomy of *Iguanodon bernissartensis* is also well-known on the basis of the material from Bernissart, especially thanks to the description of the holotype IRNSB 1534 by Norman (1980).

As underlined by Norman (2011), the hindlimb bones, including the lower leg elements, are not particularly distinctive. However, some differences can be noted between *Mantellisaurus* and *Iguanodon* regarding the size, proportion, and morphology of the various pes bones. The large species *Iguanodon bernissartensis* has a foot made of robust

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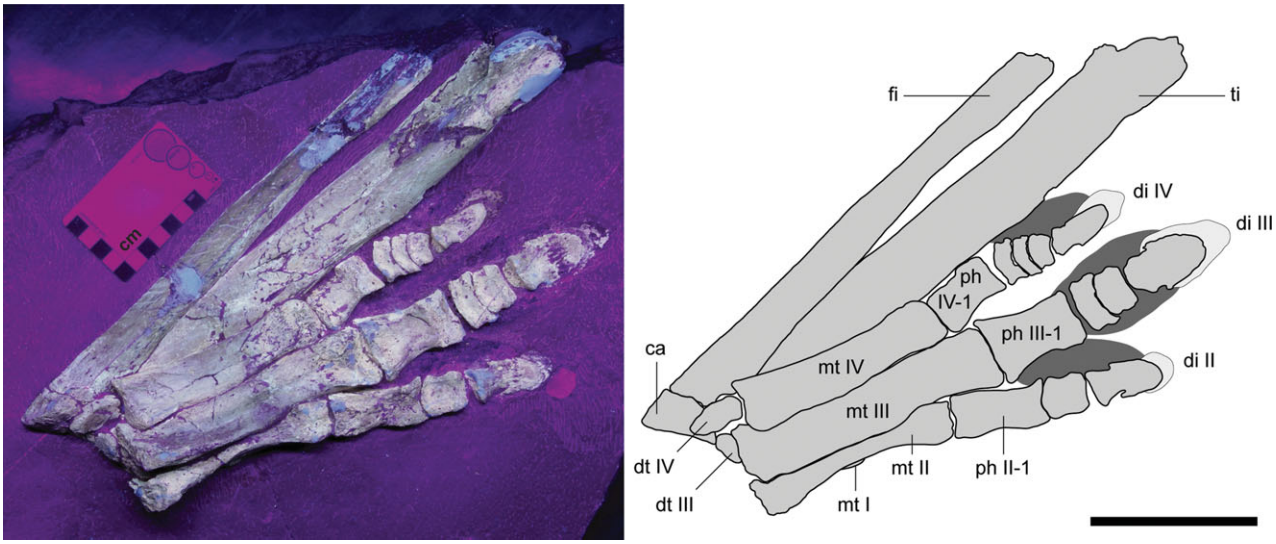

Figure 2. (Colour online) LH-30677 under ultraviolet light, and interpretative line drawing. Imprints of claws and toe pads are represented in light and dark grey, respectively. Abbreviations: ca – calcaneum; di – digit; dt – distal tarsal; fi – fibula; mt – metatarsal; ph – phalanx; ti – tibia. Scale bar equals 10 cm.

elements. The metatarsal I is reduced and laterally flattened. The length of the metatarsal III ranges from 270 to 350 mm among the specimens from Bernissart (Norman, 1980), this length roughly corresponds to 1.5 to 2 times the value observed in the Las Hoyas specimen. The smaller taxon *Mantellisaurus atherfieldensis* has a more gracile foot, with more slender bones. The metatarsal I (preserved in NHMUK R1829) is narrow and has a rod-like shape, similar to the condition observed in LH-30677. In *Mantellisaurus atherfieldensis*, the metatarsal III is 280 mm in length. The phalangeal formula and the way in which the metatarsals II to IV are arranged in LH-30677 are the same as those in *Mantellisaurus* and *Iguanodon*. Until more material is recovered, the Las Hoyas iguanodont is tentatively assigned to *Mantellisaurus atherfieldensis* because of the relative proportions of the foot. However, some slight differences can be noted in the Las Hoyas specimen: the foot is more lightly built; the metatarsal IV is relatively enlarged in relation to the narrow metatarsal II; and the unguals are relatively small compared to other phalanges. Such differences may be ontogenetic, but could also suggest that the Las Hoyas iguanodont represents a new, smaller taxon.

The specimen LH-30677 was collected *in situ* from a taphonomically controlled area named 'Magenta'. The fossil was apparently isolated and was showing the top part of the metatarsal III embedded in a thick (~7 cm) slab. Although no additional material has been recovered from around this specimen to date, the rest of the skeleton might be preserved in the still unexcavated part of the 'Magenta' area. This hindlimb was probably separated from the fleshy carcass and was buried before it could be scattered. Complete to sub-complete isolated limbs remaining in articulation and preserved more or less far away from the rest of the skeleton (or inversely a nearly complete articulated skeleton missing some limbs, e.g. the crocodyliform *Susisuchus* from the Cretaceous Crato Formation in Brazil; Salisbury *et al.* 2003) are relatively frequent in the fossil record. This kind of preservation, corresponding to the taphonomic subclass IIB defined by Holz & Barberena (1994), often occurs when subaerial processes lead to mummification (i.e. dehydrated carcasses). Mummification is not unusual at Las Hoyas (e.g. the albanerpetontid *Celtedens*; McGowan & Evans, 1995) and that phenomenon might be linked to the occurrence of some extreme temperatures during the warm and dry seasons (Buscalioni & Fregenal-Martínez, 2010).

More or less well-preserved iguanodont remains are not rare in lower stratigraphic sequences (Rambla de Las Cruces I) of the La Huérguina Formation (Buscalioni *et al.* 2008). Some isolated vertebrae and a femur were reported from the nearby locality of Buenache de la Sierra (see Ruiz-Omeñaca, Canudo & Cuenca-Bescós, 1998). LH-30677 represents the first discovery of an ornithopod dinosaur in the Las Hoyas limestone and the third non-avian dinosaur body fossil. As mentioned above, the only occurrences of non-avian dinosaurs at Las Hoyas correspond to a few medium-sized dinosaur footprints (15 to 35 cm in length) and two well-preserved skeletons, corresponding to 2–2.5 m (*Pelecanimimus*) and 6 m (*Concavenator*) long animals. The Las Hoyas iguanodont would correspond to an individual about 5.5 to 6 m long. This bias (i.e. the very low relative abundance of medium to large-sized animals) has also been noted for the Late Jurassic locality of Guimarota (Martin, 2000), suggesting that heavy dinosaurs probably avoided the soft substrate of such a coastal palaeoenvironment. The Las Hoyas deposits have been interpreted as a rather isolated carbonate shallow subtropical lake located in a complex wetland system (Buscalioni & Fregenal-Martínez, 2010). Thus, a similar hypothesis can be applied for the muddy palaeoenvironment of Las Hoyas. This rareness supports the notion of facultative to incidental categories, i.e. organisms that may be found in wetlands and in the terrestrial surrounding environments, or only occasionally found, respectively (Buscalioni & Fregenal-Martínez, 2010). Thus, considering the Las Hoyas iguanodont as a facultative organism is not surprising considering the large number of terrestrial plants (e.g. ferns and conifers mostly represented by *Weichselia* and *Frenelopsis*, respectively) present in that palaeoecosystem (Gomez *et al.* 2001). Lastly, an ornithopod dinosaur such as *Mantellisaurus* may have represented a valuable prey item for the top predator *Concavenator*, thus fulfilling the reconstruction of the trophic chain of this ancient ecosystem.

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