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Feather diversity in the Barremian (Early Cretaceous) of Las Hoyas, Spain

Diversité des plumes dans le Barrémien (Crétacé inférieur) de Las Hoyas, Espagne

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ABSTRACT

The preservation of feathers is a rare phenomenon in the fossil record. In this study, we report 11 isolated feathers from the Early Cretaceous of the Konservat-Lagerstätte of Las Hoyas, Spain. Most of them are preserved as a carbonised thin layer, but there are also imprints. The specimens are relatively small, and unambiguously correspond to body contour feathers, although it is very difficult to match them to a particular taxon (among avian or non-avian theropods). Among the fossils, there is an almost complete remige, a well-preserved fragment of a possible ornamental rectrice feather, and possibly a semiplume. Furthermore, some specimens appear to have different colour patterns, such as stripes or patches.

Mots clés :
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RÉSUMÉ

La préservation des plumes est un phénomène rare dans le registre fossile. Dans cette étude, 11 plumes isolées provenant du Crétacé inférieur du Konservat-Lagerstätte de Las Hoyas (Espagne) sont décrites. La plupart des plumes sont préservées sous forme de pellicule carbonée, d'autres étant visibles sous forme d'empreinte. Les spécimens sont de petit taille et correspondent certainement à des plumes de contour du corps. Il est, en revanche, difficile de les attribuer à un quelconque taxon (parmi les théropodes aviens ou non-aviens). Une rémige sub-complète, un fragment bien préservé attribuable à une rectrice d'ornement, ainsi qu'une semi-plume probable ont été reconnus parmi ces fossiles. De plus, quelques spécimens semblent présenter différents *patterns* de coloration, tels que des bandes ou des taches.

1. Introduction

Fossil feathers have been reported from worldwide-distributed geological formations ranging in age from the

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Late Jurassic to the Pleistocene (Kellner, 2002). The Barremian fossil Lagerstätte of Las Hoyas has yielded a rich floral and faunal continental assemblage (Escaso et al., 2005; Sanz et al., 1988a). The most significant taphonomic features of the vertebrate specimens found in these laminated deposits are their completeness (i.e., fully articulated skeletons) and exquisite preservation (e.g., mineralization of soft tissue) (Briggs et al., 1997; Ortega et al., 2010). However, the Las Hoyas beds also contain a few isolated vertebrate remains, such as teeth, ribs, feathers and fish scales. Sanz et al. (1988b) reported the first isolated feather (LH-367) together with the description of the first almost complete enantiornithine bird from this site (i.e., *Iberomesornis romerali*). Thereafter, new fossil feathers from Las Hoyas were reported associated with two new genera of enanthionithines, *Concornis lacustris* and more visibly in *Eoalulavis hoyensis* (Sanz and Buscalioni, 1992; Sanz et al., 1996). Kellner (2002) described an isolated flight feather from the site, and more recently two long feathers were described in a pellet containing several skeletal remains (Sanz et al., 2001). In this article, we report 11 new isolated feathers unearthed from Las Hoyas, a number so far possibly only comparable to that reported from the La Pedrera site at El Montsec (Lleida), another Spanish Konservat-Lagersttäte of similar age (Lacasa-Ruíz, 1985).

2. Geological and palaeoenvironmental setting

The Las Hoyas subbasin is located in the Serranía de Cuenca (La Huérguina Formation, Upper Barremian), southwestern Iberian ranges, eastern Spain (Fregenal-Martínez and Meléndez, 2000). The sequence including the Las Hoyas fossiliferous deposits is composed of laminated limestone and rare marlstone levels. These deposits were produced in the context of a continental (freshwater) subtropical carbonate wetland that overlays a low-relief karstic terrain (Buscalioni et al., 2008). The Las Hoyas biota mainly consists of obligate aquatic organisms (e.g., osteichthyan fishes, decapod crustaceans, belostomid insects, charophytes, the aquatic plant *Montsechia*) (Buscalioni et al., 2008). The amphibious forms (i.e. lissamphibians, turtles and crocodiles) are much less abundant, and the facultative ones (i.e. terrestrial/arboreal forms such as insects, lizards and basal birds) are rather rare. Large animals such as dinosaurs are exceptional in the assemblage, and correspond to the incidental ecological category (Buscalioni and Fregenal-Martínez, 2006). The terrestrial macroflora is dominated by conifers (Cheirolepidiaceae) and ferns (Mantoniacea and Schizaeaceae) (Escaso et al., 2005).

3. Anatomical descriptions

The material described here consists of 11 isolated feathers with different preservations and morphologies, and it is all housed in the paleontological collection of the Museo de las Ciencias de Castilla-La Mancha (MCCM). The description is subdivided by the type of preservation; namely, carbonised residues (corresponding to the majority) and inprintations. The description of feather morphology follows Lucas and Stettenheim (1972).

All the specimens belong to the Armando Díaz Romeral collection (ADRM PL) or Las Hoyas (LH) collection of the Museo de las Ciencias de Castilla-La Mancha (MCCM), in which they are housed.

3.1. Feathers preserved as carbonised traces

ADRM PL 110 (Fig. 1A) is 11.1 mm long and its maximum width is 4.9 mm. The calamus is not preserved but the barbs are visible, well developed, and quite tightly connected. The rachis is only visible in the middle of the feather, where the width is less than 0.5 mm. The apical third of the feather appears to be naturally curved (i.e., not due to preservation). In the latter area of the feather, there are relatively large patches of lighter tone, which contrast with the overall darker tone of the rest of the barbs, suggesting the preservation of coloration pattern.

LH 23740 (Fig. 1B) is preserved in slab and counter-slab, each one differently preserved. It is a slender and notably symmetric feather 22.6 mm long and 5.9 mm wide (maximal width). It is well preserved, and though it is missing the calamus, it presents symmetrically arranged barbs, angled obliquely relative to the rachis. The rachis is remarkably thin and becomes invisible near the middle of the feather. There is a wide and brownish stripe that crosses perpendicularly the apical third of the feather, which is visible in the two slabs. The overall good preservation of this feather suggests that this stripe could be a patch of different colour.

LH 15980 (Fig. 1C) is an impression of a 19.5 mm long and 12.3 mm wide feather. The material is not completely prepared but it is visible that it preserves a small portion of the calamus. The rachis tapers towards the apex, and near the base its maximal width is 0.8 mm. Despite the poor preparation, many of the thin barbs are visible. The latter change their orientation becoming nearly perpendicular to the rachis along the centre of the feather, making it notably wider than most of the rest of the specimens in the collection. However, the preservation does not help to conclude if this morphology is due to preservation or intrinsic to the morphology of the feather. Likewise, the colour of this feather is brown instead of black, crossed by lighter stripes, but the preservation does not allow asserting whether these stripes represent a different colour patterning or simply diagenetic bias.

LH 2162 (Fig. 1D) is also present in two slabs. It is a 10.9 mm long and 6.4 mm maximum width feather (measurable only in one slab). The barbs are very well preserved, making it visible that they are not tightly packed. The rachis is thin and is more visible in the counters-slab. The barbs show a clear gradient of yellowish to dark-brown colour from the base to the top of the feather.

LH 27135 (Fig. 1E) is preserved in two slabs, and unfortunately the calamus is totally missing (broken in extraction). Measuring from the exposed base of the feather to the apex it is 22.0 mm long, with a vane maximally 6.9 mm wide. The preservation of one side of the feather is very good, and it is possible to see the barbs well, and even some barbules. On the opposite side of the vane, the barbs are more compact, and their disposition suggests an apparent asymmetry of the feather. This may be a preservational artefact (it could be as if one of the sides of the feather was slightly

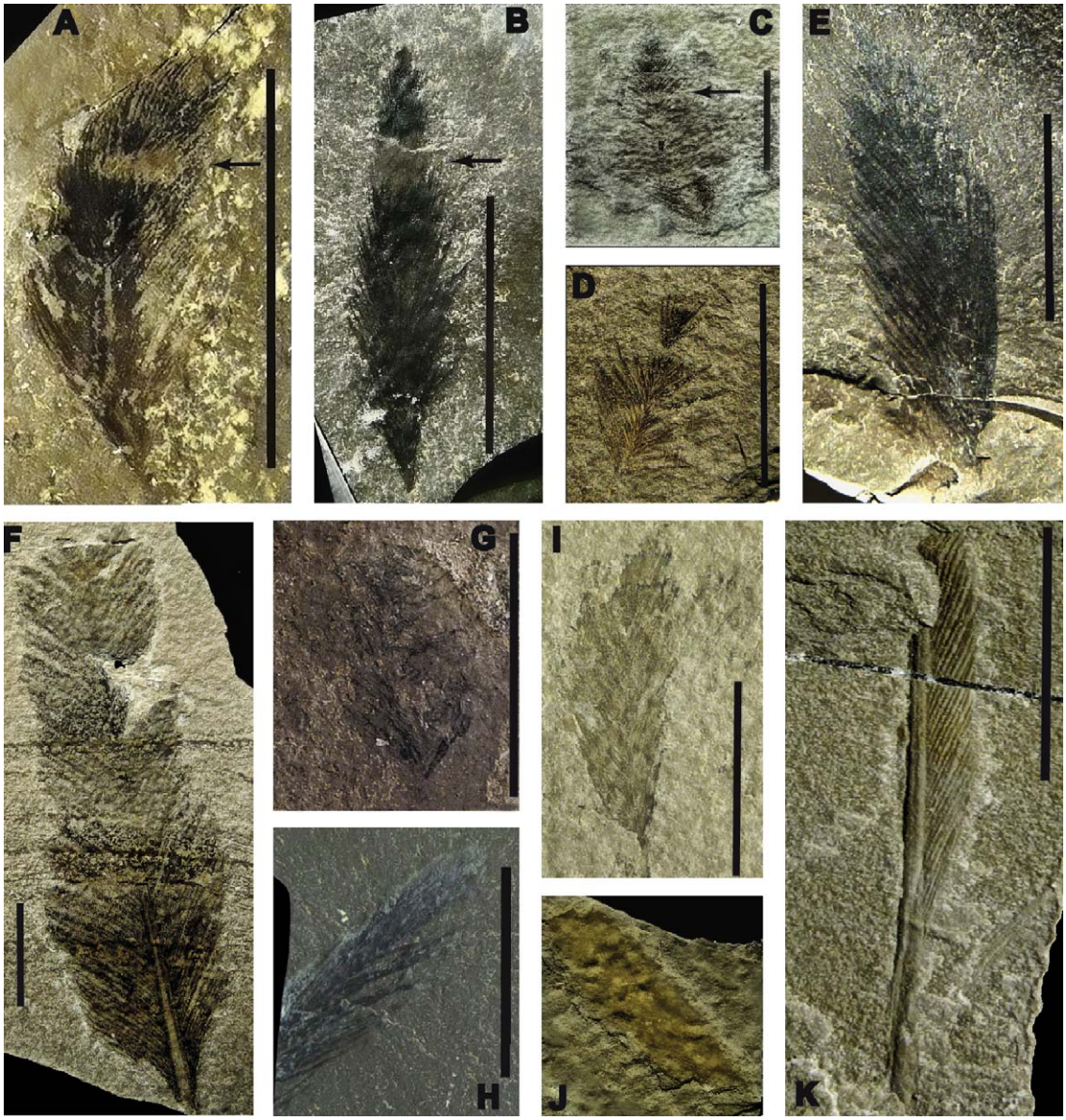

Fig. 1. Fossil feathers from Las Hoyas described in this study. A, ADRM PL 110. B, LH 23740. C, LH 15980. D, LH 2162. E, LH 27135. F, LH 3000. G, LH 26460. H, LH 26209. I, LH 23279. J, LH 29781. K, LH14224. Arrows point to tonal patches that could indicate differences in colour pattern. Scale bars: 10 mm.
Fig. 1. Plumes fossiles de Las Hoyas décrites dans cette étude. A, ADRM PL 110. B, LH 23740. C, LH 15980. D, LH 2162. E, LH 27135. F, LH 3000. G, LH 26460. H, LH 26209. I, LH 23279. J, LH 29781. K, LH 14224. Les flèches indiquent la position des taches pouvant correspondre à des différences de couleur ou de ton. Barres d'échelle : 10 mm.

folded towards the opposite side). Because of this, the very thin rachis of the feather is nearly invisible. The feather is homogeneously black.

LH 3000 (Fig. 1F) is a large feather well preserved in two slabs (ca. 60 mm long and 18 mm wide). The calamus is lacking but the rachis is perfectly visible, such that it is wider at the base (1.3 mm) and tapers towards the apex third of the total length of the feather. A long grove running laterally along the proximal third of the rachis is quite visible, possibly indicating that the feather is exposed ventrally. The vane is pennaceous and the barbs are perfectly visible in the proximal third of the feather, but due to preservation they start to fade at the middle of the feather towards the apex. The vane is quite symmetrical but this may be a preservational artefact. The fact that it is large, possibly stiff (thick calamus) and pennaceous indicates that this is a remige. Although its colour tends to be black there are tinted patches along the entire feather. However, these may likely be diagenetic, produced by the infiltrations clearly distinguishable in the rock.

There are other carbonised specimens in the collection: LH 26460 (Fig. 1G), a very poorly preserved feather, small (8.7 mm long, and 5.4 maximal width) which is interesting because it is comparable to a semiplume from the

El Montsec (see Lacasa-Ruíz, 1985: pp. 229, Fig. 1.5), and a well preserved but very fragmentary feather LH 26209 (Fig. 1H).

3.2. Feathers preserved as imprint traces

LH 23279 (Fig. 1I) is preserved in two slabs, and its morphology is strikingly similar to that of LH 27135 described above (Fig. 1E). However, in this specimen (18.1 mm long and 5.1 mm in maximal width) the calamus is preserved, although poorly, and the rachis is visible. The latter is fairly thin (less that 0.5 mm) and it fades toward the middle of the feather. It is difficult to determine whether the vanes are homogeneously pennaceous or more plumaceous at the base in these two feathers (i.e., if they are body contour feathers or semiplumes).

LH 29781 (Fig. 1J) is a small fragment (18.9 mm in length, maximal width 4.2 mm) and its preservation is relatively poor. LH 14224 (Fig. 1K) is a three-dimensionally preserved fragment in two slabs. Its measurable length is 23.1 mm though unfortunately this measurement is an underestimation since a great part of the feather, the totality of one side of the vane, remains underneath the sediment. Nevertheless, the rachis is perfectly visible, thick and long, likely extending along the entire feather and tapering only very slightly from one end to the other. Interestingly, the rachis preserves what appears to be a long lateral groove that reaches near the prospective apex of the feather. The barbs are neatly preserved, are relatively long and thick, and they are all characteristically stacked parallel and running oblique (ca. 17°) along almost the entire rachis. All these features indicate that the feather possibly was quite stiff, and therefore could be a tail rectrice, perhaps ornamental.

4. Discussion

4.1. Taphonomy

Like the fossil feathers from the great majority of localities elsewhere (Davis and Briggs, 1995), most of the Las Hoyas feathers are outnumbered by carbonaceous residues. Although this preservation was often interpreted as a sign of the presence of degrading bacteria (Wuttke, 1983), it has recently been demonstrated that the preservation of these carbon residues is aided by the presence of eumelanin-contaning melanosomes in the feathers (Vinther et al., 2008). Melanosomes are lysosome-like organelles inside melanocytes (the pigment cells) (Marks and Seabra, 2001), and eumelanosomes are those melanosomes containing black melanin. These particular melanosomes have a very high preservation potential because eumelanin is more resistant to chemical degradation than other colour melanins (Liu and Simon, 2003).

However, the fact that in Las Hoyas there are also imprints possibly does not imply a differential preservation than that of carbon residues. Rather, loss of melanosomes can be a subsequent diagenetic phase whereby these lithified structures have been washed away (Vinther et al., 2008). Interestingly, LH 27135 and LH 23279 (Fig. 1E and 1I, respectively) are nearly identical feathers with completely different preservation, the former a carbonaceous residue and the latter an imprint, which thus substantiates this hypothesis. Given that the characterization of feather preservational patterns is still developing (Li et al., 2010; Vinther et al., 2010; Zhang et al., 2010), comparatively studying the ultra-structural patterning of these feathers from Las Hoyas could not only contribute further insight about this complex taphonomic phenomenon, but also to explain the meaning of the observed tonal patches in certain specimens (ADRM PL 110, LH 23740 and LH 15980).

4.2. Palaeobiology

In the last decade of the 20th century, 77% of fossil avian fauna was determined by fossil feathers (Davis and Briggs, 1995), because feathers were considered a key characteristic of birds. However, today feasibly assigning any of the studied feathers to a particular taxon is more difficult because feathers have been documented in most non-avian coelurosaurian theropod groups (Xu et al., 2010). For instance, even non-avian maniraptorans had closed pennaceous, symmetrical feathers that resemble modern flight feathers (Norell et al., 2002; Prum and Brush, 2002). This notwithstanding, the average size of the studied feathers is relatively small (22.1 mm in length), indicating that the feathers belonged to relatively small animals, a characteristic of Las Hoyas fauna (Buscalioni et al., 2008) and, in particular, of the small sized basal birds well known to have inhabited the Las Hoyas paleoecosystem (enantiornithine birds). However, none of the feathers here described match the morphology of the feathers preserved in *C. lacustris* or *E. hoyensis* (Sanz and Buscalioni, 1992; Sanz et al., 1996), implying that so far they cannot be confidently addressed to any particular avian or non-avian theropod taxon.

Feathers are typically classified according to their external morphology into three groups, most of which nevertheless encompasses a continuum of forms, rather than discrete natural types (Lucas and Stettenheim, 1972). Developmental biologists have demonstrated that this continuum of morphologies reflects a series of stage-by-stage logic that matches feather morphogenesis (Prum, 1999, 2005). New findings of fossil dinosaurs in China have suggested that feather morphological diversity has decreased from the Mesozoic (i.e., the range of feather-like structures was larger than that displayed by modern birds; Xu et al., 2010). In spite of the large amount of isolated remains from Las Hoyas, all these can be arguably grouped to previously known morphotypes of contour feathers (body contour, remiges and rectrices, and perhaps two semiplumes). However, the recent discovery of quill-knobs in the ulna (structures related to the insertion of remiges in the ulna) in a medium-sized carcharodontosaurian theropod (Allosauroidea) from Las Hoyas (Ortega et al., 2010) hints that more discoveries from the site may shed new light in the developmental and evolutionary history of feathers and its homologues. Interestingly, besides the impact of colour patterning in avian life-styles, studies in modern birds suggest that ambient light partially drives the evolution of colour signals at community scale (Gomez and Théry, 2004). Thus, the ultra-structure of colour patterning of the feathers from Las Hoyas (melanosomes) could pro-

vide information about the palaeoenvironment inhabited by these avian and non-avian theropods.

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