

magma chamber and t is the residence time. For the 1973 Heimaey magmas, both these expressions give an identical residence time of 20 ± 15 years (Fig. 2).

Combining the ^{238}U -series data presented here with previous results from Vestmannaeyjar leads to the following model for magma evolution in this system. At the time of the alkali basalt eruption at Surtsey in 1963, similar basalts were also emplaced at 15–20 km depth in the crust beneath Heimaey. The crust there was relatively cold, as indicated by its low geothermal gradient³⁰, causing rapid cooling and rapid crystal fractionation of the injected alkali basalt, to form hawaiite and mugearite. The differentiated magma resided in the chamber for about 10 years, during which volatile accumulation led to overpressure in the upper part of the magma chamber and provoked the 1973

Heimaey eruption.

The origin of ^{210}Pb – ^{226}Ra – ^{230}Th disequilibria in Vestmannaeyjar magmas remains unclear, but the decreasing disequilibria with magma differentiation^{4,25,31} are probably inherited from the parental basaltic magmas. An instantaneous radium enrichment during basalt genesis could explain the observed ^{210}Pb – ^{226}Ra – ^{230}Th disequilibria in the 1963 basalt from Surtsey. But this enrichment could be due to partial mantle melting with $D_{\text{Ra}} < D_{\text{Pb}} \approx D_{\text{Th}} < D_{\text{U}}$ only if the basaltic melt erupted immediately after formation. This study shows that magma differentiation effects on radioactive disequilibria must be assessed before ascribing them to partial melting only, and that magma chamber residence time may often be of the order of only a few years or decades. □

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An Early Cretaceous bird from Spain and its implications for the evolution of avian flight

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AVIAN flight is one of the most remarkable achievements of vertebrate evolution, yet there is little evidence of its early phases. Specimens of *Archaeopteryx* shed important (albeit controversial) light on this evolutionary phenomenon, but the large morphological (and almost certainly functional) gap between *Archaeopteryx* and modern avians remained virtually empty until recently. Here we report a new, exquisitely preserved, bird from the Lower Cretaceous Konservat-Lagerstätte of Las Hoyas (Cuenca, Spain) which provides evidence for the oldest known alula (bastard wing). Crustacean remains found inside its belly also provide the oldest direct evidence of feeding habits in birds. The new specimen has numerous synapomorphies with the Enantiornithes, but its unique sternal morphology, along with other autapomorphies in the furcula and vertebral centra, support the recognition of a new enantiornithine taxon, *Eoalulavis*

hoyasi. The combination in *Eoalulavis* of a decisive aerodynamic feature, such as the alula, with the basic structures of the modern flight apparatus indicates that as early as 115 million years ago, birds had evolved a sophisticated structural system that enabled them to fly at low speeds and to attain high manoeuvrability.

Fossil birds of the Early Cretaceous of Las Hoyas are among the most informative for understanding the early evolutionary history of birds. Two avian taxa have been described to date: the basal ornithothoracine *Iberomesornis*^{1,2} and the enantiornithine *Concornis*^{3,4}. A new and well-preserved bird provides important evidence about the early stages of the evolution of flight.

Aves L., 1758

Ornithothoraces Chiappe and Calvo, 1994

Enantiornithes Walker, 1981

Eoalulavis hoyasi, gen. et sp. nov.

Etymology. *Eos* (Greek): dawn; *alula* (Latin): bastard wing; and *avis* (Latin): bird; because it provides the oldest evidence of an alula; *hoyasi* (from the Spanish word Hoyas): referring to where it was found.

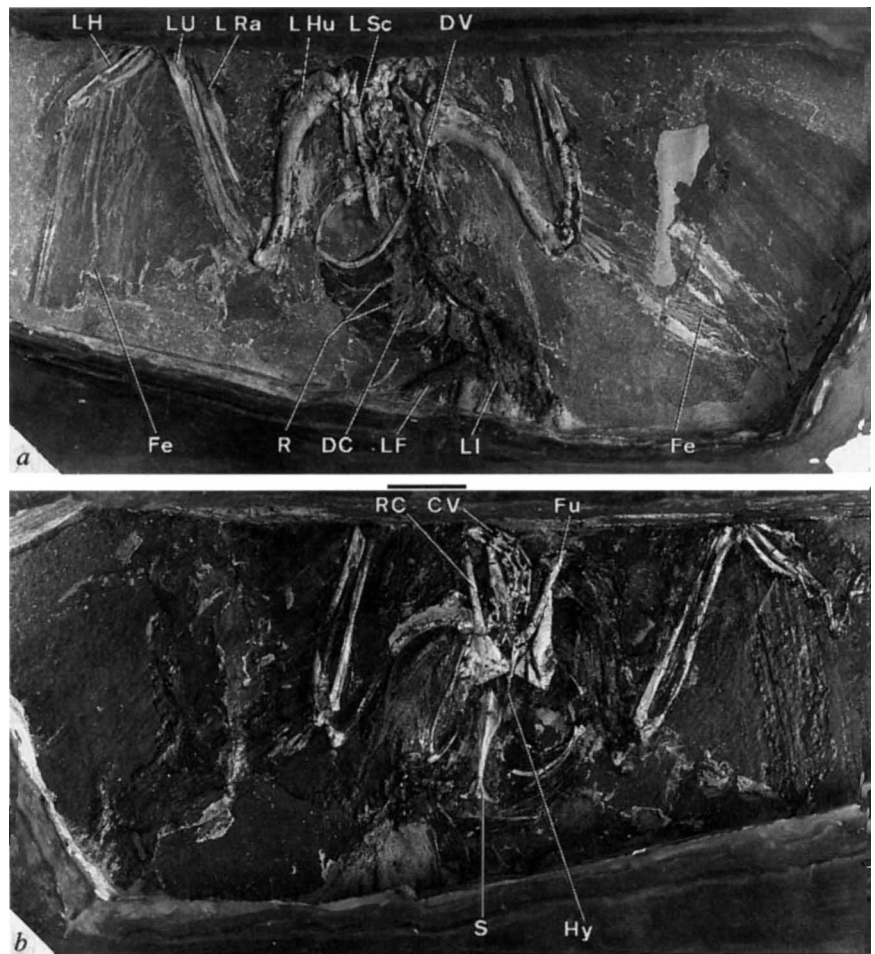
Holotype. See Fig. 1.

Horizon and locality. Las Hoyas fossil site, La Cierva township, province of Cuenca, Spain. Calizas de La Huérguina Formation, Late Barremian (Early Cretaceous)⁵.

Diagnosis. See Fig. 2.

Eoalulavis has a skeletal wingspan of about 17 cm, roughly the size of a goldfinch (*Carduelis carduelis*). The cervical and dorsal centra have deep lateral excavations. Neither uncinat processes nor gastralia are present. The robust furcula has an interclavicular angle of about 45°. Its hypocleidium is extremely long (~77% of the rami) and compressed. The elongated strut-like coracoid has a subtriangular dorsal fossa converging towards a supracoracoid nerve foramen, which opens into a medial groove. Its sternal third

FIG. 1 Holotype specimen (LH 13500 a/b; Las Hoyas Collection, Museo de Cuenca, Cuenca, Spain) of *Eoalulavis hoyasi* (provisionally housed in the Unidad de Paleontología of the Universidad Autónoma de Madrid, Spain) LH 13500 is preserved between a slab and a counterslab. Slabs were prepared with formic acid after embedding them in a frame of transparent polyester resin²³. LH 13500a (dorsal view, a) contains 15 vertebrae (five of them are cervicals), both scapulae, left coracoid and proximal half of the right one, the furcula and its hypocleidium, several ribs, nearly complete left wing and right wing except of the hand, portions of left ilium, proximal end of left femur, and sacrum. The counterslab (LH 13500b, ventral view, b) includes seven vertebrae (five of them are cervicals), both coracoids, proximal end of left scapula, complete furcula and sternum, several ribs, left wing, and humerus and ulna–radius of right wing. Feathers and digestive contents are preserved in both slabs. Although the sternum appears to be only partially ossified, the degree of ossification of the articular surfaces of the remaining elements, as well as the complete ossification of the furcula, which normally ossify late in ontogeny, suggests that this specimen does not represent an early ontogenetic stage. Note that caudal to the ninth preserved vertebra, the specimen is preserved as a mould (copied by the plastic resin) of the diagenetic dissolution of bones. Despite the fact that the bones were accurately moulded, little information can be retrieved from them. Scale bar represents 1 cm. Abbreviations: CV, cervical vertebrae; DC, digestive contents; DV, dorsal vertebrae; Fe, feathers; Fu, furcula; Hy, hypocleidium; LF, left femur; LH, left hand; LHu, left humerus; LI, left ilium; LRa, left radius; LU, left ulna; LSc, left scapula; R, ribs; RC, right coracoid; S, sternum.



is strongly convex laterally, although becoming distally straight. The scapular blade is straight with a sharp end. The well-developed acromion is roughly depressed, somewhat perpendicular to the blade. The morphology of the sternum is unique within dinosaurs (see diagnosis in Fig. 2, and Fig. 3). The lateral margins are smooth and well-defined, lacking either facets for the articulation of the ribs or the coracoids. The humerus has a prominent and cranioventrally projected bicapital area. Its ventral tubercle is caudally projected and separated from the head by the capital incision. Both pneumatic foramen and fossa are absent. The humeral distal end is craniocaudally compressed with transversely oriented condyles. The humerus–ulna length ratio is roughly 88%. The ulnar shaft is twice as wide as the radial one, and the ulna has a weak olecranon and an elongated, strong scar for the bicapital muscle. The radius has a caudal, longitudinal groove and a distinct bicapital tubercle. The hand–ulna length ratio is about 58%. The major metacarpal is shorter than the minor one and is not fused to it distally. The alular and major digits have two and three phalanges, respectively; the distal phalanges are small claws.

Feathers are conspicuous in both slabs (Figs 1 and 4a). Body feathers are visible around the humeri and thoracic girdle. Flight feathers are preserved connected to the distal portion of the wing. Eight primary remiges are preserved, although they are missing in the proximal two thirds of the major metacarpal. Seven secondary remiges attach to the proximal ulnar extremity and one to its distal end. The alular digit has at least one small feather attached to its proximal phalanx. The rachis of this feather is not visible, but its barbs are placed symmetrically. Undoubtedly, this feather corresponds to the alula, or bastard wing.

The skeletal morphology of *Eoalulavis* exhibits a large number

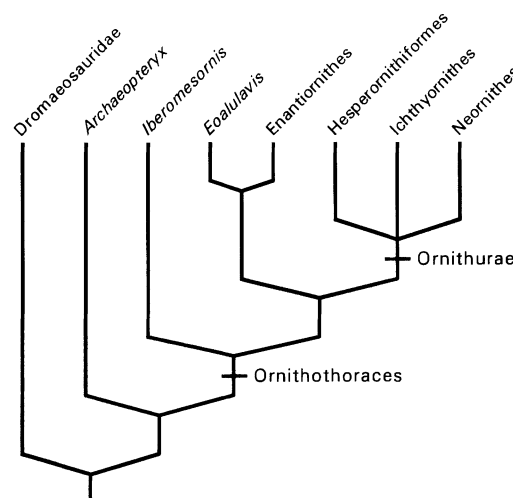
of derived characters used to diagnose the Enantiornithes (Fig. 2), a distinct group of volant ornithothoracine birds distributed world-wide during the Cretaceous^{6,7}. Despite the fact that *Eoalulavis* is easily identifiable as a member of the Enantiornithes, its precise interrelationships must await a comprehensive phylogenetic study of this speciose group (Fig. 2).

At the Las Hoyas Konservat-Lagerstätte, soft tissues are frequently preserved. Examples include both isolated and adhered feathers (such as *Concornis*³), as well as other epidermal remains (like in the ornithomimosaur *Pelecanimimus*⁸ or the albanerperontid *Celtesedens*⁹). *Eoalulavis* provides another striking example. In the holotype, in addition to feathers, digestive contents have been found. Scattered organic particles are preserved within a limonitic mass in the thoracic cavity (Fig. 1). Some of these particles are identifiable as crustacean exoskeletal elements, providing the oldest direct evidence of trophic habits in birds (the only other mesozoic case is that of Late Cretaceous *Baptornis*¹⁰). This evidence suggests that *Eoalulavis* had aquatic feeding habits, an interpretation congruent with previous considerations of the Las Hoyas birds as water-related (although not strictly aquatic) inhabitants³.

Specimens with preserved feathers are rare in the fossil record. Even rarer are those in which feathers are arranged in a natural position. In *Eoalulavis*, five and three primaries are attached to the phalanges and the major metacarpal, respectively, and eight secondaries are connected to the ulna. Most remarkable is the preservation of the alula in its natural position (Fig. 4a). This feather constitutes the oldest known alula (it is not preserved in *Concornis* and *Iberomesornis*).

The occurrence of an alula in this early bird sheds significant light on the evolution of avian flight. The alula is essential in

FIG. 2 Phylogenetic analysis. Nelsen consensus cladogram (two most parsimonious trees were obtained) resulted from the analysis of the data matrix, using the implicit enumeration option of the Hennig 86 (ref. 24) program (consistency index, 0.85; retention index, 0.86; length, 100). To establish the relationships of *Eoalulavis* to other basal birds we have scored this taxon in the data-matrix used in ref. 4. We modified this matrix as follows: (1) Dromaeosauridae is the single outgroup; (2) *Patagopteryx* has been excluded from the analysis; (3) *Concornis* has been included within Enantiornithes; (4) Characters 2 (maxillary process of premaxilla forming most of the facial margin) and 5 (osseous external naris considerably larger than antorbital fenestra) in Enantiornithes have been coded as 0 (primitive state), on the basis of new data. *Eoalulavis* and the Enantiornithes are unambiguously united by derived states 72 (prominent bicapital crest of humerus, cranioventrally projected), 74 (convex lateral margin of coracoid), 75 (supracoracoid nerve foramen of coracoid opening into an elongate furrow medially and separated from the medial margin by a thick bony bar), 76 (strong lateral grooves on the bodies of dorsal vertebrae), 77 (parapophyses located in the central part of the bodies of dorsal vertebrae), 83 (lateral face of the humeral bicapital crest with a small fossa for muscular attachment) and 84 (furcula laterally excavated). Derived characters 73 (convex lateral cotyle of ulna, separated from the olecranon by a groove), 78 (caudal projection of the lateral border of the distal end of the femur), 79 (wide and bulbous medial condyle of tibiotarsus), 80 (metatarsal IV significantly smaller than metatarsals II and III) and 81 (trochlea of metatarsal II broader than trochlea of metatarsals III and IV) are ambiguous synapomorphies of these two clades. The position of *Eoalulavis* with respect to the Enantiornithes must not be taken as a sister-group relationship. The present data simply support the placement of *Eoalulavis* on the enantiornithine branch. A comprehensive analysis of this clade will be provided



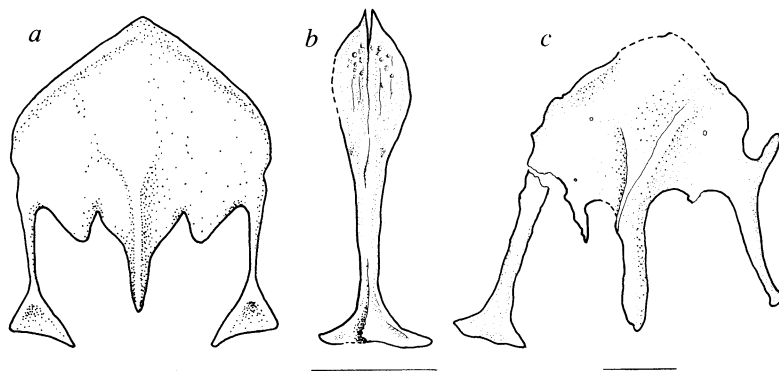
elsewhere. *Eoalulavis* is diagnosed by the presence of cervical and dorsal laminar, keel-like vertical centra; undulated ventral surface of furcula; distal end of humerus with thick, caudally projected ventral margin; several small tubercles on the distal, caudal surface of the minor metacarpal; depressed, lanceolate sternum, with foot-like caudal expansion, and a faint carina; and a deep, rostral cleft in the sternum.

modern birds for low-speed flight and manoeuvrability. To decrease their speed while maintaining lift on the wings, birds must increase the angle of attack of their wings (Fig. 4b). This leads to an increase in drag. There is a limit to the angle of attack, for when the angle is large the wing stalls: turbulent eddies develop over the dorsal surface of the wings, and lift drops dramatically so that the bird can no longer fly. The alula, which acts as a slot on the medial leading edge of the wing, serves to delay stall and to allow the wing to continue to generate lift even at very high angles of attack. The alula lifts automatically when pressure above the wing drops, and in most birds is used only in very slow flight, take off and landing¹¹⁻¹³.

Eoalulavis is the most primitive bird found with an alula. The fact that this structure is absent in the well-preserved, feathered wings of the Berlin and Eichstätt specimens of *Archaeopteryx* suggests that this may reflect the Urvogel's actual condition. There has been much debate about the aerodynamic capability of *Archaeopteryx*, but no consensus has been achieved other than the acceptance that it was able to perform some sort of flight^{6,14-19}.

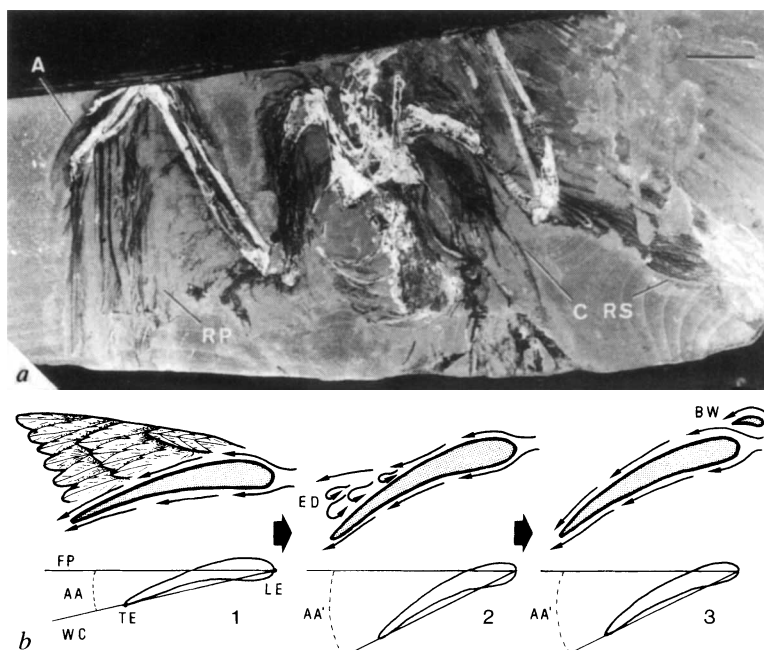
If the alula was truly absent, *Archaeopteryx* may have had aerodynamic constraints during low speed flights²⁰, unless it eventually possessed an alternative means of performing this kind of flight. Furthermore, *Archaeopteryx* lacks most modern skeletal structures usually correlated with an enhanced flying ability. It lacks a strut-like coracoid, a rigid carpometacarpus and a pygostyle, and it retains proportions between wing elements typical of its flightless, non-avian theropod relatives^{21,22}. Indeed, the basic design of the modern flight apparatus is first known for the basalmost ornithothoracine birds such as the Early Cretaceous *Iberomesornis*^{1,2}. Structural disparity between *Archaeopteryx* and basal ornithothoracines indicates important differences in their ability to fly. In *Eoalulavis*, an advanced skeletal design of the flight apparatus is consorted with a novel element in feather function. This suggests that basal ornithothoracines had substantially improved their flight capabilities. *Eoalulavis* demonstrates that as early as 115 million years ago, birds had developed a sophisticated structural complex allowing them to perform low-speeds flights and accurate manoeuvrability control. □

FIG. 3 Comparisons between the sternum of *Eoalulavis* and that of other Enantiornithes. Scale bars represent 5 mm. a, Sternum of *Cathayornis yandica* (modified from ref. 25) in ventral view. b, Sternum of *Eoalulavis hoyasi* in ventral view. c, Sternum of *Concornis lacustris* (modified from ref. 4) in ventral view. The sternum of *Eoalulavis* stands out among the sterna of other enantiornithines because it is remarkably narrow and it possesses only a faint ventral keel. This condition, which may suggest a reduced volume of flight musculature, contrasts with the many other features indicating aerodynamic skills. Nevertheless, the tall coracoids could have been connected to the robust furcula by a coraco-clavicular membrane providing an extensive area for the origin of the flight musculature, a condition previously suggested for *Archaeopteryx*²⁶. Moreover, the absence of sternal facets for the articulation with the coracoids suggests that the preserved bone may be the remnant of a larger cartilaginous structure which may have provided additional area for the origin of the flight muscles (there is increasing evidence for the existence of a widely unossified large sternum in early birds, including *Archaeopteryx*). Even if so, we believe that the caudal expansion and the rostral notch of the sternum



represent its actual shape. Hence these features are considered here as autapomorphies of *Eoalulavis*. The extremely long hypocleidium presumably fits into the rostral sternal notch, providing further strength to the thoracic girdle.

FIG. 4 a, Ultraviolet induced fluorescence photograph (before preparation). Most of the isolated feathers from Las Hoyas are preserved as carbonized traces, the most common type of feather preservation in the fossil record²⁷. Nevertheless, the feathers of *Eoalulavis* are usually highlighted (like some bones) by limonite and, occasionally, by pyroluxite. *Eoalulavis* lacks a true carpometacarpus, as the distal ends of the major and minor metacarpals are not fused to each other. It is not possible to verify the condition of the wrist. Despite the conclusions of ref. 19, the absence of a true carpometacarpus does not seem to preclude active flight, considering the presence in *Eoalulavis* of an alula and other advanced skeletal features. Scale bar represents 1 cm. Abbreviations: A, alula; C, body feathers; RP, primary remiges; RS: secondary remiges. b, Schematic drawing of a cross section of a wing with (1) a small angle of attack, (2) a large angle of attack without an alula, and (3) a large angle of attack with an extended alula. Abbreviations: AA, angle of attack; AA', increased AA; BW, alula or bastard wing; ED, eddying; FP, flight path; LE, leading edge; TE, trailing edge; WC, wing chord. Modified from ref. 28.



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Humic substances as electron acceptors for microbial respiration

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HUMIC substances are heterogeneous high-molecular-weight organic materials which are ubiquitous in terrestrial and aquatic environments. They are resistant to microbial degradation¹ and thus are not generally considered to be dynamically involved in microbial metabolism, especially in anoxic habitats. However, we show here that some microorganisms found in soils and sedi-

ments are able to use humic substances as an electron acceptor for the anaerobic oxidation of organic compounds and hydrogen. This electron transport yields energy to support growth. Microbial humic reduction also enhances the capacity for microorganisms to reduce other, less accessible electron acceptors, such as insoluble Fe(III) oxides, because humic substances can shuttle electrons between the humic-reducing microorganisms and the Fe(III) oxide. The finding that microorganisms can donate electrons to humic acids has important implications for the mechanisms by which microorganisms oxidize both natural and contaminant organics in anaerobic soils and sediments, and suggests a biological source of electrons for humics-mediated reduction of contaminant metals and organics.

In a study on the effect of various Fe(III) chelators on anaerobic benzene degradation in petroleum-contaminated aquifers, it was found that humic acids stimulated benzene degradation better than any of the synthetic chelators evaluated². Synthetic chelators stimulate benzene degradation by solubilizing Fe(III) oxides and thus making Fe(III) more available to benzene-oxidizing Fe(III)-reducing bacteria^{3,4}. The superiority of the humic acids over synthetic chelators such as nitrilotriacetic acid (NTA) was surprising because although humic acids can chelate Fe(III)⁵, they do not