

*Science Progress* (2002), 85 (2), 113–130

## The birds from Las Hoyas

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*Information on the first steps of the avian evolutionary history has dramatically increased during the last few years. The fossil record provides a general view of the morphological changes of the avian flight apparatus from non-volant ancestors (non-avian theropod dinosaurs) to the first derived fliers of the Early Cretaceous. The Las Hoyas bird record includes three genera: Iberomesornis, Concornis and Eoalulavis. This fossil material has yielded information about the early avian evolutionary history. These Early Cretaceous birds (some 120 Myr old) had a wingbeat cycle and breathing devices similar to those of extant birds. The function of the rectricial fan was also similar. In the evolutionary transition from cursorial ancestors to derived fliers it is possible to verify a trend to increase lift. Primitive wing aspect ratio morphotypes were elliptical ones, other derived morphotypes appeared, for example, in the Neornithes (extant birds). Some primitive fliers, like the Las Hoyas genus Eoalulavis, had an alula (feathers attached to the first digit of the hand) similar to that of present day birds, indicating braking and manoeuvring skills similar to those of their extant relatives. Primitive avian life habits are poorly understood. Some evidence from the Las Hoyas bird record indicates that Early Cretaceous birds were present in the trophic chains.*

*Keywords: avian evolutionary history*



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## Introduction

Some 120 million years ago (Early Cretaceous) a shallow lake existed in the Serranía de Cuenca (East–Central Spain). The sediments of this paleolake, known as Las Hoyas, consist of rhythmically fine-grained laminated limestones preserving such delicate structures as dinosaur muscle tissues, gut contents or feathers<sup>1,2</sup> (Figure 1). The Las Hoyas limestones have yielded a diverse flora and fauna emerging from both aquatic and terrestrial biota. The floral assemblage includes charophytes, bryophytes, filicales, bennettitales, gnetales, coniferales and angiosperms. Animal remains belong to bivalves, gastropods, crustaceans, insects, myriapods, bony fishes, albanerpetontids, anurans, urodelans, turtles, lizards, crocodiles, dinosaurs and birds<sup>3,4</sup>. The current bird assemblage from Las Hoyas includes three species: *Iberomesornis romerali*, *Concornis lacustris* and *Eoalulavis hoyasi*.

Our knowledge about the avian evolutionary history has dramatically improved during the last two decades. This increase of information about the first steps of bird evolution comes from two sources: our better knowledge of the Mesozoic fossil record, and the phylogenetic systematics (cladistics) approach. Cladistics has allowed more robust and feasible genealogical hypotheses which are the necessary first step for understanding the evolutionary history of every lineage. Twenty years ago a gap in the record existed between the oldest known bird (*Archaeopteryx*, Upper Jurassic) and the Upper Cretaceous toothed birds (Hesperornithiformes and Ichthyornithiformes). During the last few years significant discoveries have been made in the Early Cretaceous of Spain (Las Hoyas) and China (Yixian Formation, Liaoning Province) This new evidences along with other data from Argentina and Madagascar, have radically



**Fig. 1.** Fluorescence-induced ultraviolet photograph of the ornithomimosaur theropod dinosaur *Pelecanimimus polyodon* from the Las Hoyas lithographic limestones. Arrow indicates a soft tissue crest at the posterior side of skull.

changed our ideas about early avian history with respect to important topics as historical diversity, origin and development of flight, feather origin, or life habits of the primitive birds. Nearly half of the present day Mesozoic genera have been described after 1990<sup>5</sup>. Thus, we know that upper Mesozoic avian diversity was much larger than previously supposed, and the present day birds (Neornithes) are a particular lineage coming from a Cretaceous bird lineage. On the other hand, modern avian flight appears during the Early Cretaceous, and feathers are an evolutionary novelty that appeared in the bird ancestors, the non-avian theropod dinosaurs. Early Cretaceous birds were constant components of the terrestrial ecosystems all around the world. This paper deals with the information yielded by the Las Hoyas birds related to some of these aforementioned research topics, especially concerning the development of the modern flight and life habits of the primitive birds

### The Las Hoyas bird Record

The first avian species found at Las Hoyas was *Iberomesornis romerali*, a sparrow-sized small animal (Figure 2) whose mass has been estimated<sup>6</sup> between 15 and 20 g. The specimen is almost complete, lacking the skull and the anterior cervical vertebrae. *Iberomesornis* is characterised by a singular combination of traits, including some primitive ones, present in the non avian theropods, like a sacrum composed of five vertebrae, tarsal not fused to the tibia or to the metatarsals, and lacking any evidence of metatarsal fusion. Along with these symplesiomorphic features, *Iberomesornis* shares with modern



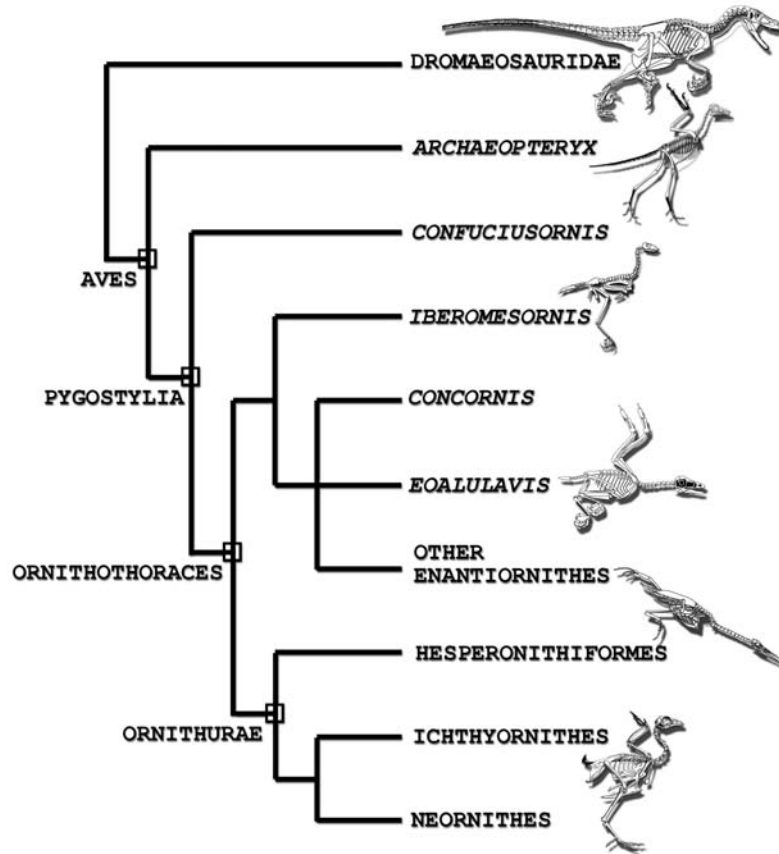
**Fig. 2.** *Iberomesornis romerali*.

birds a number of evolutionary novelties: a derived, modern avian furcula, with a low interclavicular angle, strut-like coracoids, and a series of free caudal vertebrae (eight in number) and a large pygo-style composed by the fusion of 10–15 vertebrae<sup>7–9</sup> (Figure 3). This combination of primitive and derived traits led Sanz *et al.*, 1988 to propose a phylogenetic hypothesis for this Las Hoyas bird, placing it in an intermediate position between *Archaeopteryx* and modern birds. The introduction within the avian ingroup of the Early Cretaceous Chinese genus *Confuciusornis*, along with the reinterpretation of some characters, has recently modified this early phylogenetic hypothesis for *Iberomesornis*. The present proposal is that this primitive Spanish bird is more closely related to the enantiornithine birds than previously supposed<sup>10,11</sup> (see phylogenetic hypothesis of Figure 4).

The Enantiornithes are an extinct group of Cretaceous birds described, for the first time, by Walker in 1981, in the North of Argentina. We now know that this avian lineage have a world-wide distribution, whose remains have been discovered in both Americas, China, Mongolia, Australia and Spain. The Spanish enantiornithine record comes from Las Hoyas and the Montsec<sup>12</sup> (Province of Lleida). Two enantiornithine genera have been described in Las Hoyas: *Concornis* and *Eoalulavis*. The first one (type species *C. lacustris*) is about twice the size of *Iberomesornis*, and it is recognised by an almost complete skeleton lacking the skull and neck with some feathers evidence<sup>6,13</sup>. One of the most singular features of *Concornis* is the sternal morphology (Figure 5). The sternum has a carina developed just in its caudal half, with two crests diverging from its anterior region. The

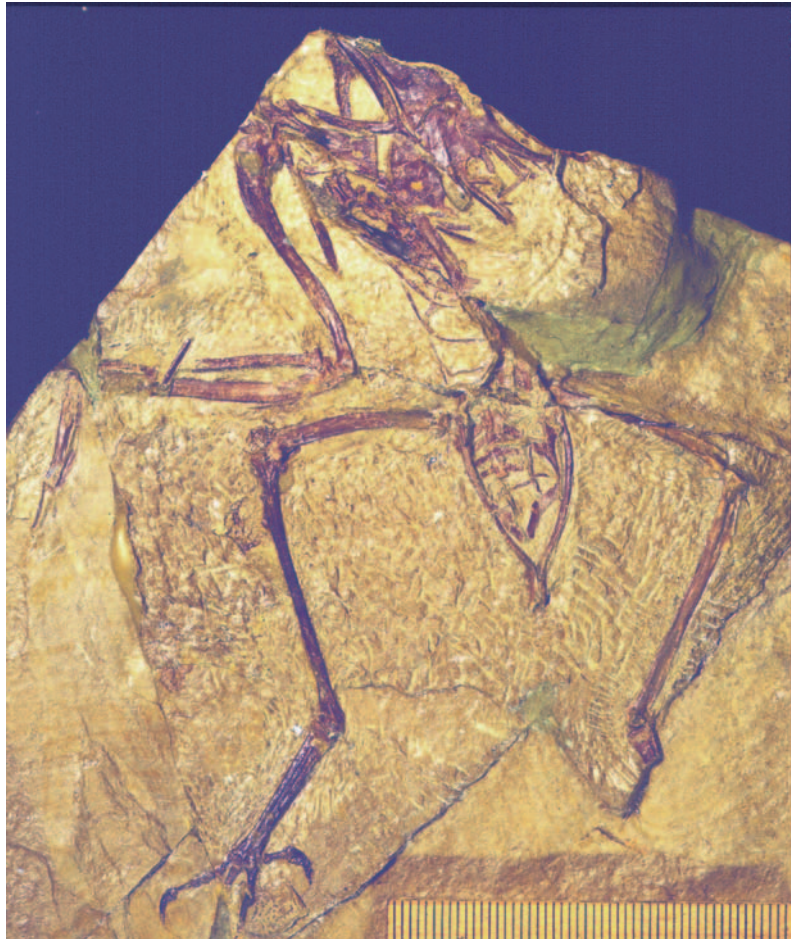


**Fig. 3.** *Iberomesornis romerali*. Fluorescence induced ultraviolet photo.



**Fig. 4.** Cladogram showing a hypothesis of the avian phylogenetic relationships.

sternal caudal zone is deeply notched, in a configuration similar to that of the Chinese genus *Cathayornis*<sup>14</sup>. The furcular morphology is derived with an interclavicular angle of some 60°. The hand is slightly shorter than the forearm and the femur clearly shorter than the tibiotarsus. The fossil remains in which the species *Eoalulavis hoyasi* is based consist of the anterior part of an articulated skeleton lacking the skull and anterior cervical vertebrae (Figure 6). This beautifully preserved specimen includes evidence of wing feathers in position (both primary and secondary ones) and the alula (feathers attached to the first digit of the hand). Some body feathers are visible around the humeri and pectoral girdle. Again, the sternal morphology is characteristic, but very different to that of *Concornis*. The sternum of *Eoalulavis* is lanceolated, with a foot-like caudal expansion, possessing

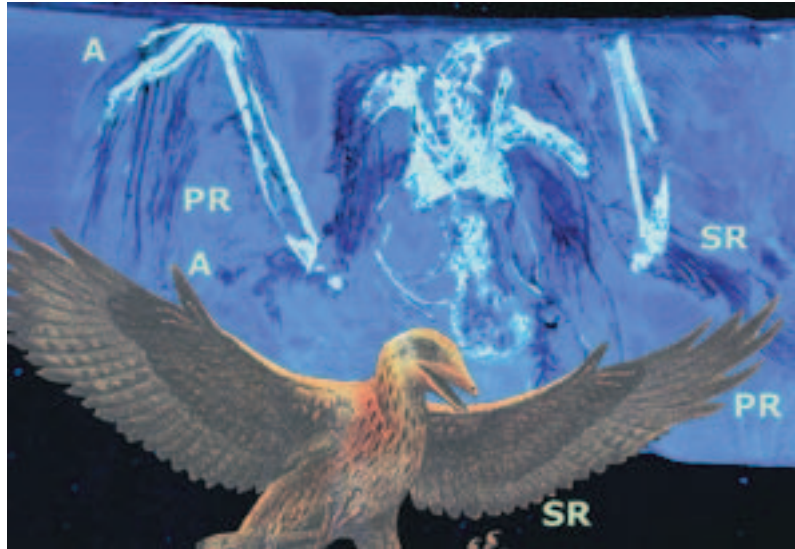


**Fig. 5.** *The enantiornithine bird from Las Hoyas* *Concornis lacustris*.

a faint carina. The anterior sternal third has a narrow cleft, in which the extremely long hypocleidium (posterior process of the furcula) probable fits<sup>15</sup>. Both *Concornis* and *Eoalulavis* present a series of evolutionary novelties, mainly in the coracoid, humeri and metatarsi, typical of enantiornithine birds. The internal relationships within this clade is poorly understood, but most authors agree on its monophyletic status<sup>11,13,16</sup>.

### The avian flight

The evolutionary success of birds is probably related to its skills for flying. From the ancestral groups (cursorial non-avian theropod



**Fig. 6.** *Eoalulavis hoyasi*. Top, fluorescence induced ultraviolet photo of the specimen before preparation. Bottom, reconstruction. A: alula; PR: primary remiges; SR: Secondary remiges.

dinosaurs), descendants with flying capabilities appeared. The known avian fossil record yields general information on the historical morphological changes produced in this process, from non-volant to volant forms. Most of the evolutionary novelties of this sequence of morphological changes are related to the avian flight apparatus, composed of bones, muscles and feathers. The bird fossil record offers information on bones and feathers, but the phylogenetic functional morphology presents information about muscles and associated ligaments. Thus, from the most primitive bird (*Archaeopteryx*) to modern extant birds (Neornithes) a series of evolutionary novelties related to the flight apparatus improved the flight skills of this group of volant theropod dinosaurs<sup>6,8,17,18</sup>.

The morphological change sequence of the flight apparatus has to be analysed in terms of physical forces. Flight requires a combination of lift and thrust. In the avian flight the wings, by means of a set of upstroke and downstroke movements, provide both forces. Weight generated by the pull of gravity has to be balanced by the lift provided by the wings. But lift is not the only aerodynamic effect of the wings: a drag force is also generated, that has to be balanced by the propulsion forces (thrust). Besides the wings, other elements of the avian flight apparatus are significant elements in the volant locomotion. For example, the appearance of a rectricial fan is very important in

order to permit steering and braking. On the other hand, a complex combination of evolutionary novelties is characteristic of the avian respiratory system (lungs and aerial sacs) which are relevant in the conquest of the aerial environment. Thus, after obtaining some information on the flight skills of *Archaeopteryx* we will see that the information provided by the Las Hoyas birds is related to three topics: wing and tail biomechanics, wing evolutionary history, and function of the respiratory system.

### Wing and tail biomechanics

The skeleton and feather systems of *Archaeopteryx* are very similar to those of the most derived non-avian theropods. The retention of a primitive cursorial locomotor module composed by the decoupling of tail and hindlimbs<sup>19</sup>, is combined with the presence of some avian synapomorphies like the relative elongation of the forelimb or the angle between the scapula and coracoid. However, the glenoid cavity (pectoral girdle humeral articulation region) is oriented in a way similar to that of non-avian theropods, implying a smaller efficiency in the wingbeat cycle. The present consensus is that *Archaeopteryx* was not merely a glider, but could probably perform some kind of powered flight, although not as efficiently as extant birds. *Archaeopteryx* was probably capable of taking off from the ground, because of the added thrust provided by its hind limbs<sup>20</sup>. Nevertheless, its capabilities of performing a low speed flight and its manoeuvrability skills were probably limited.

From the forerunner condition present in *Archaeopteryx*, a series of evolutionary novelties appeared in the avian lineage, which implies more efficiency in the volant locomotion. This synapomorphies related with the improved flying skills are present in birds 120 million years old, as the Chinese genus *Confuciusornis* or the Las Hoyas genera *Iberomesornis*, *Concornis* and *Eoalulavis*.

Thus, we will see that the functional interpretation of the three skeletal zones (pectoral girdle, furcula and pygostyle) is modified regarding the conditions present in a primitive flyer as *Archaeopteryx*.

The coracoid of *Archaeopteryx* is short, and subquadrangular in shape. The derived coracoidal morphology (strut-like) is typical of modern birds, but is also present in the primitive birds from Las Hoyas<sup>6,7,8,13,15</sup>. This type of derived coracoid indicates, as in Neornithes, the existence of a complex biomechanical system (triosseum foramen) formed by the scapula, furcula and coracoids. This structure provides the mechanism for the ligament of the supracoracoideus muscle, working as a pulley-like system during the upstroke phase of

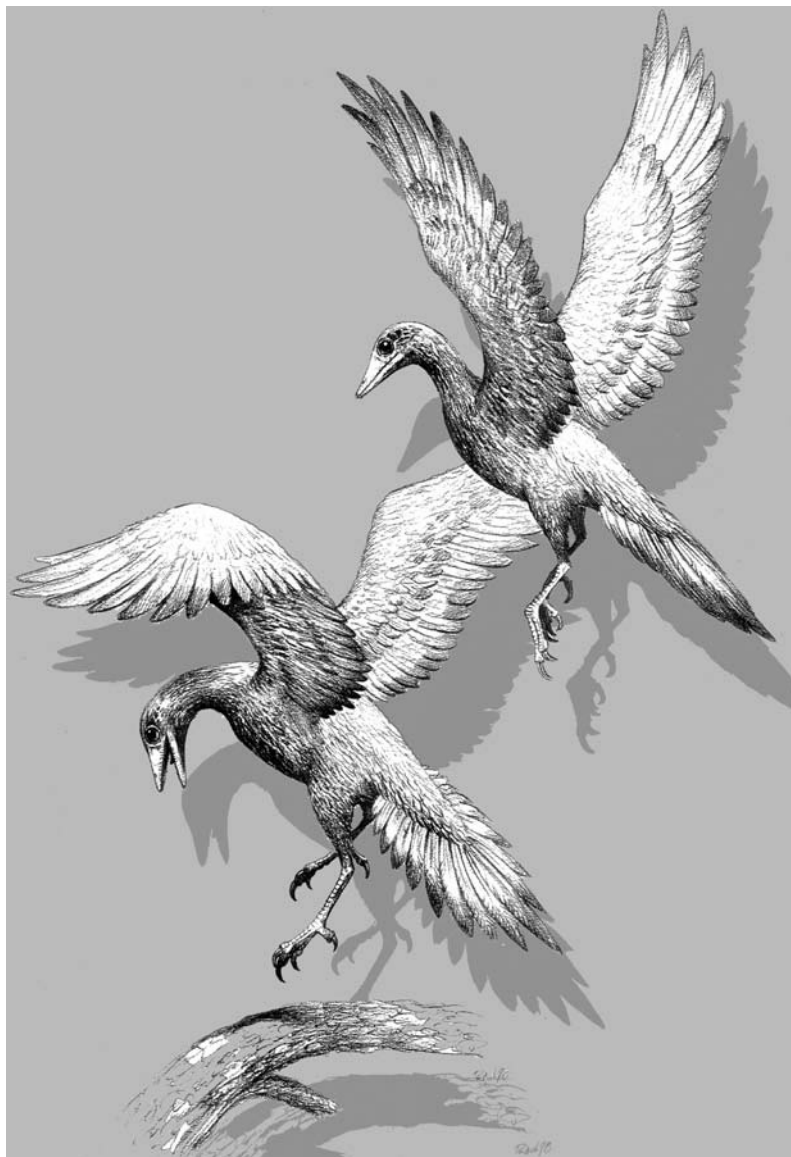


the wingbeat cycle. Recent analysis has concluded that this system not only abduces the wing, but also produces a horizontal rotation of the humerus, to position the wings for the downstroke<sup>21</sup>. The presence of a triosseum foramen in Las Hoyas birds suggest that in these genera, there is a wingbeat cycle mechanism similar to that of extant birds.

The furcular morphology of *Archaeopteryx* is primitive, with interclavicular angle near 90°. This primitive morphology is retained by the basal pygostylian birds, *Confuciusornis* and *Changchengornis* (Confuciusornithidae<sup>22</sup>). *Iberomesornis* presents a derived avian furcula, with a low interclavicular angle and a developed hypocleidium. This type of modern furcula is very important in flight performance, because of the large amount of oxygen needed during the powered flight. The main function of the furcula is contribute to the ventilation of the lungs and air sacs during the active flight<sup>23</sup>. Thus, it is very probable that some primitive birds, like the Las Hoyas genera, had a similar breathing mechanism to that of their extant relatives.

The clade Pygostylia (see Figure 4) is characterised by an evolutionary novelty that dramatically changes the primitive tail morphology present in *Archaeopteryx*. Basal pygostylians, like the Confuciusornithidae, or more derived, like *Iberomesornis*, have fused caudal vertebrae into a single element (pygostyle). In *Archaeopteryx*, the relative long feathered tail could have helped to increase the lift, but the aerodynamic efficiency seems to be low. The presence of a pygostyle implies the existence of a Parson's nose, with rectrice feathers along with a rectricial bulb (that in extant birds facilitates the opening and closing of the fan of caudal feathers). This structure is relevant during the flight since allows a greater manoeuvrability, improves the steering and braking capabilities, and increases the lift<sup>6,9</sup> (Figure 7).

In summary, the flying skills of some Early Cretaceous birds, such as *Iberomesornis*, would be improved with respect to those of *Archaeopteryx*. *Iberomesornis* had better wingbeat cycles and breathing mechanisms, as well as caudal fan functions. Nevertheless, this Las Hoyas bird cannot be considered as a volant form with flying capabilities equivalent to those of its extant relatives. In present day birds, locomotion is characterized by the relationships between three locomotor modules: pectoral, hind limbs and tail<sup>19</sup>. There is a decoupling between the hind limb and tail modules (the tail is no longer involved in cursorial locomotion) and there is a new allegiance between the pectoral and tail ones for performing flight. In *Iberomesornis*, the presence of derived wing proportions, coracoid and furcula, correlated with a large pygostyle, suggest that the allegiance between the pectoral and tail modules began to be formed,



**Fig. 7.** Life reconstruction of a couple of flying *Iberomesornis*.

whereas the decoupling between hind limb and tail modules was not complete. In conclusion, *Iberomesornis* flight skills have to be considered as intermediate between the primitive volant condition represented by *Archaeopteryx* and the sophisticated flight capabilities of the extant birds.

## Wing evolutionary history

During the avian flight locomotion, lift depends on several factors: wing size, air speed, air density, and the angle of attack (angle of the wing with respect to the trajectory)<sup>24,25</sup>. In the evolutionary transition from non-avian dinosaurs to birds an improvement of the flight skills is expected. In fact, the morphological transformations of the skeletal flight apparatus allow us to propose a sequence composed of three stages:

- (1) non-avian dinosaurs showing the cursorial condition;
- (2) primitive fliers, such as *Archaeopteryx*, making up an intermediate stage; and
- (3) derived fliers, such as some primitive birds like *Confuciusornis*, and basal ornithothoracines like *Iberomesornis*.

In the evolutionary transition from cursorial ancestors to derived fliers, one of the locomotory physical requirements is for lift to be increased. The increase of lift in primitive fliers can be evaluated in terms of the wing loading. The wing loading (WL) is the estimation of the lift of a wing by means of the ratio  $W/S$ , in which  $W$ = weight and  $S$ = wing area, the latter is the surface projected by the fully extended wings and the portion of body situated between them<sup>26</sup>. Thus, it is expected that the decrease of the wing loading from members of Stage 1, *i.e.* feathered dinosaurs such as *Protarchaeopteryx* or *Caudipteryx*, to *Archaeopteryx*, and from the latter to the members of Stage 3.

In order to check this hypothesis we need to know or estimate both the weight and the wing area of taxa involved in the origin and development of avian flight.

Weight estimation is based on the equation:  $FL = 0.5659 \times W^{0.3424}$ , resulting from a regression analysis of femur length (FL) on weight in 65 species of extant birds representing 13 different orders<sup>27</sup>. In the same way, wing area is estimated using the equation:  $S = 0.052 + 0.008 \times W$ , for a regression analysis of weight on wing area from a 120 extant birds based on ref. 25.

The results support the formulated hypothesis: wing loading decrease from probable non-flying forms, like *Caudipteryx* and *Protarchaeopteryx*<sup>28</sup>, to primitive fliers, like *Archaeopteryx* and from this to the first derived fliers (*Confuciusornis* and basal ornithothoracine birds). However, an unexpected increase of the wing loading began with the clade Ornithurae. If the hypothesis we propose is correct, then large wing loading values in extant birds are

a reversal of the derived character states of the primitive condition, probably related to different types of flight performance. For example, cruising speed depends on wing loading. The greater the value of this ratio, the faster the bird is able to fly<sup>25</sup>.

Another factor determining the flight performance is the shape of the wing or aspect ratio. This is defined as the ratio between length (span) and width (chord) of the wing. Based on the aspect ratio, there are five basic types of wings<sup>24,29</sup>. The elliptical morphotype is characterised by a slenderness, that is, span dimension is small relative to chord. This morphotype is characteristic of most Passeriformes and doves, which have high manoeuvrability. Long soaring (gliding) wings are morphotypes with a high aspect ratio, and are present in albatrosses and gulls, that is, high-speed soarers<sup>26</sup>. Short soaring wings are morphotypes with intermediate aspect ratios between long soaring and elliptical morphotypes. They are characteristic of vultures, storks, and eagles, that is, low-speed soarers. Swallows and martins have high-speed wings, which are characteristically bowed and acuminate. Finally, there is the hovering morphotype, which is typical of hummingbirds. Hovering flight is characterized by the absence of a thrust component, only a lift component. This type of flight performance requires a large energy input.

The fossil evidence of wing aspect ratio is scarce. Only exceptionally well-preserved specimens, *i.e.* the Berlin *Archaeopteryx*, show its wing aspect ratio. In most fossils, wing aspect ratio is not preserved and a reconstruction exercise is necessary. In these conditions, it is difficult to propose even a general evolutionary pattern of wing aspect ratio. Nevertheless, some conclusions can be made. The elliptical wing morphotype seems to be primitive within Aves. It shares several conditions such as being present in *Archaeopteryx* and probably in basal ornithothoracine birds, and being the least specialized and most frequent type of wing. This primitive wing aspect ratio could be the condition widespread among Enantiornithes. Derived aspect ratio morphotypes (long and short soaring, high-speed, hovering morphotypes) appeared, at least, in the Neornithes, and probably within more inclusive clades. As in the case of wing loading, aspect ratio diversity can be related to different bird life habits associated with different flight requirements.

One of the most important features in the evolutionary history of avian flight is a trend towards reducing drag. When a bird is trying to reduce speed, it extends the alula generating an additional air flux that reduces the eddying that occurs at the posterodorsal zone of the wing, reducing or even eliminating problems of lift maintenance. The most primitive known fossils showing alula evidence are

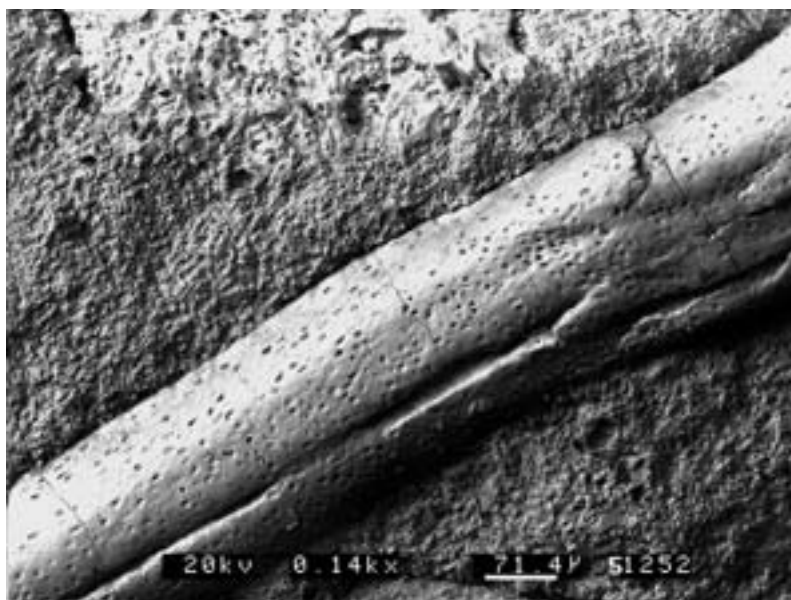
the Early Cretaceous enantiornithine birds *Eoalulavis*<sup>15</sup> and *Eoenantiornis*<sup>30</sup>. The alula feathers of *Eoalulavis* have a derived asymmetric vane, showing no structural differences with the alula feathers of extant birds. However, it is probable that in *Eoalulavis* alula feathers were fewer in number than in extant birds. No alulas are known outside the clade ornithothoraces. Both, *Archaeopteryx* and the well-known *Confuciusornis*, lack the alula<sup>22</sup>. Thus, the most likely hypothesis is that the alula appeared as an evolutionary novelty in ornithothoraces.

### Respiratory system

In order to support the large levels of muscular work involved in flight, birds need a highly efficient respiratory system. The performance



**Fig. 8.** Pellet, probably from a theropod dinosaur, containing fossil remains of, at least, three different species of primitive birds.



**Fig. 9.** SEM photograph of one of the tiny avian long bones of the pellet illustrated in Fig. 8.

of flight at high altitude probably was a problem in the evolutionary history of birds, as there seems to be a decrease of oxygen pressure with height. The respiratory system of the extant bird is made of lungs and air sacs<sup>31, 32</sup> that permit efficient ventilation even in lower oxygen pressure environments. It seems very probable that aerial sacs were present in the avian ancestral groups. It is also probable that some primitive birds like *Iberomesornis*, with a derived flying apparatus, had improved the functional levels of their air sacs. But these primitive birds lacked the pneumatic foramina, present in extant birds in several bones (vertebrae, humerus, sternum, etc). If this absence indicates a lesser efficiency of the respiratory system, then it is possible to formulate a hypothesis about the existence in bird evolutionary history of a trend to produce forms with increasing skills to perform flight at lower atmospheric oxygen pressure. If the oxygen pressure levels of the Mesozoic atmosphere were similar to those of the present day, birds progressively acquired a better capability to fly at elevated altitude. Thus, it seems probable that primitive fliers such as *Archaeopteryx* were able to reach a low ceiling-height, and a long evolutionary trend occurred until the appearance of present day high-altitude soarers.



**Fig. 10.** Life reconstruction of the probable pellet producer of the fossil illustrated in Fig. 8.

### Primitive bird life habits

The presence of birds (both in terms of population density and diversity) in the terrestrial Early Cretaceous ecosystems is clearly more important than previously supposed. Nevertheless, the life habits of these primitive birds are poorly known. The avian fossil record of Las Hoyas has provided some information related to the position of some Early Cretaceous birds in the trophic chains.

The thoracic box of *Eoalulavis* contains organic particles identified as exoskeletal elements of unidentified crustaceans: the oldest known direct evidence of trophic habits for birds<sup>15</sup>. This evidence seems to support some kind of life habit related to aquatic environments.

Another avian material found at the Las Hoyas site yielded evidence about the role of birds in the Mesozoic trophic chains. The fossil is made of a bone assemblage (about 23 cm<sup>2</sup> in surface area) coming

from four tiny juvenile bird individuals (Figure 8). Some morphological differences and size divergences indicate that the fossil bone assemblage comes from at least three different species. The most parsimonious hypothesis to interpret this fossil is that an organic agent was responsible for this bird bone assemblage, resulting from a predator that produced a regurgitated pellet<sup>33</sup>. This hypothesis is supported by the SEM observation of the bones: its surface (periosteum) shows the characteristic pitting of digested bones of birds and mammals (Figure 9). But the identification of the predator is problematic. Based on the actual and putative predator fossil record of Las Hoyas, the most probable producer of this fossil pellet was a large pterosaur or a small-medium sized theropod dinosaurs (Figure 10). This fossil pellet clearly indicates that birds were usual prey in the Early Cretaceous terrestrial ecosystems

## Acknowledgements

We thank all the co-authors of our previous publications and co-workers at the Las Hoyas projects for stimulating the ideas and research discussed here. We want also thank to M. Anton and R. Martín for reconstruction of *Eoalulavis* and *Iberomesornis* and G. F. Kurtz for UV photographs. Work in Las Hoyas fossil site has been supported by funds from Junta de Comunidades de Castilla-La Mancha, Spanish DGICYT and European Union.

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