

An isolated skull from Las Hoyas (Early Cretaceous, Spain) informs the early evolution towards elongated rostra in enantiornithine birds (Aves, Ornithothoraces)

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Abstract

The fossil record of Early Cretaceous enantiornithine birds from the Iberian Peninsula is the most significant in the world outside of China. Despite its historical relevance, taxonomic diversity, and relative abundance, adult cranial remains had not been reported before. In this study, we describe a new enantiornithine species, *Gorgonavis alcyone* gen. et sp. nov. based on a disarticulated skull from the Early Cretaceous locality of Las Hoyas (129–126 Myr; Cuenca, Spain), the first adult cranial remains of a bird from this fossil site. Digital imaging of the μ CT-scanned fossil remains shows that *Gorgonavis* is characterized by a slender and elongated rostrum in which teeth are restricted to the premaxillary corpus, a thin, edentulous maxilla, and a jugal bone with an elongated and strongly angled postorbital process. Despite the fragmentary nature of the holotype, comparative anatomy and phylogenetic analyses suggest the identification of the new species as a longipterygid, a distinct clade of Enantiornithes characterised by an elongated rostrum, a cranial configuration consistent with the new fossil. *Gorgonavis* represents the oldest occurrence of an enantiornithine with relative rostral elongation outside of the Jehol Biota. The new discovery suggests that some specialised early enantiornithine lineages had a broader geographical, and more ecologically diverse distribution than previously thought.

Keywords

Avian evolution, Craniofacial evolution, Early Cretaceous, Enantiornithes, Las Hoyas, Mesozoic birds

Introduction

The Early Cretaceous Konservat-Lagerstätten of the Iberian Peninsula (*i.e.*, Las Hoyas and La Pedrera de Meià) have been crucial for understanding the origin, diversity, evolution, and ontogeny of Enantiornithes, the most speciose

and widespread clade of Mesozoic birds (Chiappe and Walker 2002; O'Connor 2022). Las Hoyas and La Pedrera de Meià collectively form the richest Early Cretaceous bird assemblage outside of China and the second oldest Cretaceous avifauna worldwide after the Jehol Biota's Huajiyi Formation (131–129 Mya; Pan et al. 2013).

The limestones of Las Hoyas (Cuenca, Iberian Range, Spain) preserve a representative wetland ecosystem from a Barremian lacustrine environment (129.4–126.4 million years; Poyato-Ariza and Buscalioni 2016; Fregenal-Martínez et al. 2017; Marugán-Lobón et al. 2023) with relevant avian remains. The publication of the first species from this site, *Iberomesornis romerali* (Sanz et al. 1988; Sanz and Bonaparte 1992), was a significant milestone in our understanding of the evolutionary transition between the few stem bird groups known at the time, *Archaeopteryx lithographica* and some toothed Ornithurae phylogenetically close to the crown group. Two additional species, *Concornis lacustris* (Sanz et al. 1995) and *Eoalulavis hoyasi* (Sanz et al. 1996), also provided crucial information on the anatomical evolution of Enantiornithes, at a time when the record of these birds was globally limited (Chiappe 1995). Several other specimens from this site have been described, including: an association of up to four juvenile individuals of different ontogenetic ages (Sanz et al. 2001), an isolated wing with exceptional preservation of muscles, skin, and feathers (Navalón et al. 2015), a perinate individual (Knoll et al. 2018), and an adult specimen consisting of a disarticulated postcranium (Nebreda et al. 2023). Further studies on these avian remains have also advanced our knowledge of the flight performance, palaeobiology and life history of Enantiornithes (Serrano et al. 2018; Kaye et al. 2019; Cubo et al. 2022; Terol et al. 2025).

The co-eval locality of La Pedrera de Meià, dated as uppermost Hauterivian–Lower Barremian (Martín-Closas and López-Morón 1995; Gil-Delgado et al. 2023), and located in the southern Pyrenees (Montsec Range, Lleida, Catalonia), has yielded two additional specimens of enantiornithine birds: a well-preserved juvenile (Sanz et al. 1997) and the holotype of *Noguerornis gonzalezi*, an incomplete and partially disarticulated postcranial skeleton (Lacasa-Ruiz 1986; Chiappe and Lacasa-Ruiz 2002).

Despite the variety of avian remains, such as feathers, isolated bones, and partial skeletons, adult cranial remains have never been found in neither of these sites. Here, we describe the first non-juvenile cranial remains from Las Hoyas (MUPA-LH-13240), and more broadly, from the entire European Early Cretaceous. Despite the fragmentary nature of the fossil, the uniqueness of this specimen's cranial anatomy justifies the erection of a new enantiornithine species and contributes to our understanding of the evolution of facial elongation in Mesozoic birds.

Geological setting

Las Hoyas is a small basin that forms part of the continental deposits of La Huérguina Formation, located in the southwestern sector of the Iberian Basin (Serranía de Cuenca, Spain; Fregenal-Martínez et al. 2017). The Las Hoyas fossil site consists of finely laminated limestones that were formed in a depositional environment interpreted as part of a freshwater, inland, and seasonal wetland that developed under a subtropical system (Buscalioni and Fregenal-Martínez 2010; Fregenal-Martínez et al. 2017).

The Las Hoyas Basin was dated to 129.4–126.4 My (Fregenal-Martínez et al. 2017).

Materials and methods

Material

The fossil specimen (MUPA-LH-13240) consists of a fragmentary but partially articulated skull mostly preserving rostral and mandibular elements (Fig. 1) exposed in the surface of a single limestone slab, housed at the Museo de Paleontología de Castilla-La Mancha (MUPA; Cuenca, Spain). The specimen was partially acid-prepared and transferred into a polyester resin frame.

CT scanning

MUPA-LH-13240 was μ CT-scanned at the ‘Centro de Instrumentación Científica’ (University of Granada, Spain), using an Xradia 510 VERSA ZEISS micro-Computed Tomographic (μ CT) scanner, comprising 2026 projections and applying the following settings: 80 kV, 7W, 6s, and 18.521 μ m voxel size for all three spatial axes. The scan data were imported to the specialized software Avizo 9.0 to produce three-dimensional volumes for all the preserved cranial bones. To better visualise the small teeth and the premaxillary and maxillary internal anatomy, a second higher resolution scan (i.e., 9986 slices at 6 μ m voxel size) was carried out using a SkyScan 2214 μ CT scanner located at the ‘Servicios Centrales de Apoyo a la Investigación’ at the University of Málaga, applying the following settings: 115 kV; 110 μ A; 10.71W. From this data, we segmented and generated surface models of the four pair of premaxillary teeth recognized in the premaxilla using Avizo v.7.1 software (www.vsg3d.com).

Institutional abbreviations

BMNH, Beijing Museum of Natural History Collections, Beijing, China; **IEI**, Institut d'Estudis Ilerdencs, La Pedrera collection (LP), Lleida, Catalonia, Spain; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MUPA**, Museo de Paleontología de Castilla - La Mancha, Las Hoyas collection (LH), Cuenca, Castilla-La Mancha, Spain.

Phylogenetic analysis

We tested the phylogenetic affinities of MUPA-LH-13240 to other stem birds by incorporating it into two alternative morphological matrices: Benito et al. 2022 (modified from and originally published by Wang et al. 2020) and Chiappe, Navalón et al. 2024 (modified from Chiappe et al. 2019). These matrices included revised scorings for *Iberomesornis romerali*, based on Terol et al. (2025), and

additional modifications (see Suppl. material 1: table S1). Phylogenetic analyses were conducted under maximum parsimony, using TNT 1.5 (Goloboff and Catalan 2016), available with the sponsorship of the Willi Hennig Society. We performed an unconstrained heuristic search with equally weighted characters, 10,000 replicates of random stepwise addition using the tree bisection reconnection (TBR) algorithm. Ten trees were saved per replicate, and all most parsimonious trees (MPTs) were used to calculate a strict consensus tree. Support was obtained by calculating bootstrap values set at 10,000 replicates, using a traditional search, with outputs saved as absolute frequencies. Given the low phylogenetic resolution provided by current character matrices for Mesozoic birds, especially in enantiornithines, which results in large polytomies (e.g., Zhang and Wang 2019), we tested the impact of homoplasy by performing the same phylogenetic analyses on both matrices—using in this case 1,000 replicates and saving ten trees per replicate—applying implied weighting (IW) based on a range of optimized *k-values* according to the number of terminals, as it has been proposed recently (Ezcurra 2024). Following this work, the optimized range for the terminals in Benito et al. (2022) matrix is *k-values* = 4–10 (N = 87), and *k-values* = 3–8 (N = 58) for the Chiappe, Navalón et al. (2024) matrix, using the mean for each range and some additional values.

Morphometric analysis for the elongation of the rostrum

We explored the evolution of the rostrum elongation in Mesozoic birds using phylogenetic comparative methods. For this, we first assembled a phylogenetic tree to account for the evolutionary structure of our data in downstream analyses. We randomly selected one tree from the most parsimonious tree population. This tree was pruned to match the sample of craniofacial measurements (see below) and was time-calibrated, using the first and last fossil occurrences sourced from the Paleobiology Database (www.paleodb.org), Benito and Olivé (2022), and positioning the node separating *Anas* and *Gallus* according to the available fossil record calibration for Neornithes (Brocklehurst and Field 2024). This temporal data was applied to the tree using the “bin_timePaleoPhy” function from the *paleotree* package in R (Bapst 2012), generating 100 trees to account for stratigraphic uncertainty. To avoid zero-length branches, we set a minimum branch length (“mbl” method implemented in the “bin_timePaleoPhy” function) of one million years. From this set of trees, a calibrated consensus tree was constructed using TreeAnnotator (Rambaut and Drummond 2014), applying maximum clade credibility and setting branch length equal to common ancestor node heights.

We estimated the rostro-caudal length of the rostrum and the orbit in lateral view (see Suppl. material 1: table S2). The rostrum length was defined as the distance from the most rostral point of the premaxilla to the most caudal point of the ventral margin of the maxilla at its point of contact with the jugal. While the entire extent of this measurement may

not be fully preserved in MUPA-LH-13240 (Fig. 3A), the rostrum, the jugal, and the rest of the cranium are aligned, suggesting that the caudal portion of the maxilla has not been lost. Furthermore, if this assumption is not entirely correct and part of the caudal end of the maxilla is missing, the elongated condition of the rostrum of MUPA-LH-13240 could only be greater than our estimates. The rostro-caudal extent of the orbit was estimated as the length of the jugal bone (we assume that it is entirely preserved; see Fig. 2A), because this bone typically defines the entire ventral margin of the orbit in Enantiornithes (O’Connor and Chiappe 2011).

We took these two measurements from 27 Mesozoic bird and two crown bird species (Suppl. material 1: table S2), using photographs of the fossils from the literature and the software tpsDig2 to take scaled measurements, and from MUPA-LH-13240, using the 3D skull reconstruction as a reference (Fig. 2A). In order to ensure consistency with avian taxa in which the jugal is reduced and/or fused with the maxilla—which extends caudally to form part of the ventral orbital margin, as seen in hesperornithiforms and Neornithes (Bell and Chiappe 2020)—in these taxa the starting point of the descending ramus of the lacrimal was used as the rostral landmark for orbital length, and the rostral end of the postorbital as the caudal landmark.

These measurements (Suppl. material 1: table S2) were then \log_{10} -transformed and fitted into a Phylogenetic Generalized Least Squares (PGLS) linear model (rostral length ~ orbit length) using the reconstructed phylogenetic tree and Pagel’s correlation, to account for the phylogenetic structure of the data (Symonds and Blomberg 2014). The analysis was performed using the “gls” function from the *nlme* package in R (Heisterkamp et al. 2017). The residuals from this phylogenetic regression are used as a proxy of the degree of rostral elongation relative to orbital length, with positive residuals corresponding to proportionally longer rostra and negative residuals to proportionally shorter ones. Such residuals were thereafter mapped over the phylogeny by estimating ancestral node values using maximum likelihood under the “contMap” and “setMap” functions from the *phytools* package in R (Revell et al. 2012).

Systematic palaeontology

Class Aves Linnaeus, 1758

Ornithothoraces Chiappe, 1995

Enantiornithes Walker, 1981

cf. Longipterygidae Zhang et al. 2000

Genus *Gorgonavis* gen. nov.

<https://zoobank.org/8C3D6F7E-DC77-41A4-BB29-B590EEA22808>

Type species. *Gorgonavis alcyone* sp. nov.

Diagnosis. As for the genus and only species. Enantiornithine showing the following feature: thin postorbital process of the jugal, which is about half the length of the jugal bar and dorsally oriented, defining a ~90° angle with the bar.

Etymology. The generic name alludes to “*Gorgona*”, female protective deities from the Ancient Greek mythology with the ability to turn people into stone with their stare, of which the most famous, Medusa, was beheaded by Theseus, alluding to the isolated cranial remains of the holotype specimen. “*Avis*”, for the Latin word “bird”. The specific name “*alcyone*” alludes to Alcyone, one of the seven Pleiades in Ancient Greek mythology who was transfigured into a kingfisher, a group of crown birds sharing some similarities with enantiornithines that show elongated rostra, such as longipterygids.

Holotype. MUPA-LH-13240, Museo de Paleontología de Castilla-La Mancha, Cuenca, Spain, Las Hoyas collection. An isolated skull preserving the rostrum, mandible, and fragments of the braincase (Fig. 1A), likely belonging to a subadult or adult individual.

Occurrence and age. The Las Hoyas fossil site, Calizas de La Huérguina Formation, southwestern sector of the Iberian Basin (Cuenca, Spain), Barremian, dated to 129–126 million years ago (Mya) (Fregenal-Martínez et al. 2017).

Ontogenetic status. Several cranial bones of MUPA-LH-13240 exhibit a degree of fusion suggesting that this individual was nearing skeletal maturity at the time of death (Hu and O’Connor 2017; Hu et al. 2020; Plateau and Foth 2021). For instance, the premaxillae corpora are fused to one another like in the adult holotype of *Shangyang* (Wang and Zhou 2019), and the postdentary bones of the mandible are extensively fused like in the adult holotype of *Navaornis* (Chiappe et al. 2024).

Description. Anatomical terminology follows Baumel et al. (1993), using English equivalents for the Latin terms.

Premaxilla. The premaxillae of MUPA-LH-13240 (Fig. 1D) are almost complete, exposed in both dorsal and ventral views, but lacking most of the frontal (nasal) process. The right and left portions of the premaxillary corpus are completely fused to one another, as it has been previously reported in other seemingly adult specimens of Early Cretaceous enantiornithines, including taxa such as *Longusunguis* (Wang et al. 2014; Hu et al. 2020), *Bohaiornis* (IVPP V17963; Li et al. 2014), *Linyiornis* (Wang et al. 2016), *Monoenantiornis* (Hu and O’Connor 2017), and *Shangyang* (Wang and Zhou 2019). The rostral end of the premaxillary corpus is relatively pointed and thin. Ventrally, the premaxillae form a deep trough and lack the medial crest visible in some enantiornithines (e.g., Wu et al. 2021) and the palatal processes observed in early-diverging birds (*Archaeopteryx*; O’Connor et al. 2025). The maxillary processes of the premaxillae are slender and long, slightly surpassing the length of the premaxillary corpus; they make up to half of the preserved tomial edge of these bones. While this condition differs from that of many enantiornithines (e.g., *Bohaiornis*), the length of the maxillary processes seems to approach that seen in *Longipteryx* (Zhang et al. 2001; O’Connor and Chiappe 2011; particularly evident in IVPP V12552), *Yuanchuavis* (Wang et al. 2022), *Chiappeavis* (O’Connor et al. 2017), and *Eoenantiornis* (Zhou et al. 2005) in which these processes are approximately 1/2 to 1/3 the

length of the premaxilla. The rostral region of the left maxillary process preserves the anteroventral margin of the external naris, suggesting that it is rostrally elongated and pointed. The maxillary processes are caudally tapered (Fig. 1D). Three to four pairs of premaxillary teeth have been identified in the μ CT images (Fig. 1E, F, Suppl. material 1: fig. S1), as typically occurs in enantiornithines (O’Connor and Chiappe 2011). These teeth are limited to the rostral half of the premaxillae, distributed entirely throughout the premaxillary corpus before the premaxilla diverges into maxillary and frontal processes, as in known longipterygids such as *Longipteryx* or *Rapaxavis* (O’Connor et al. 2011). However, the teeth in MUPA-LH-13240 are not as tightly restricted at the rostral tip as in these species, as in other enantiornithines. Tooth crowns are partially broken or weathered and are barely visible on the surface, and almost completely limited to its alveoli. In cross-section, these teeth are strongly and equally flattened labiolingually (especially the fourth pair)—similar to *Longipteryx*—and caudally progressively increase its mesiodistal length, ranging between 0.4 to 0.7 mm (Fig. 1F). Taking these measurements as reference, the first premaxillary tooth is smaller than the subsequent two teeth (Fig. 1F), a condition shared by many enantiornithines (e.g., *Sulcavis* (O’Connor et al. 2013), *Zhouornis* (Zhang et al. 2014), *Junornis* (Liu et al. 2017)) including longipterygids (e.g., *Longipteryx* (Zhang et al. 2001)). The fourth premaxillary tooth is the largest, contrary to the bohaiornithid BMNHC-Ph1204 (Liu et al. 2022) and similar to other longipterygids (e.g., *Longipteryx* (Zhang et al. 2001)). Relative to rostral size, the teeth are proportionally larger than those of *Rapaxavis*, *Longirostravis* or *Shanweinia* (O’Connor et al. 2009), but smaller than those of *Longipteryx* (Zhang et al. 2001). Caudal to these alveoli, the μ CT scans reveal tight cavities in the rostral-most part of the maxillary processes of the premaxilla. While these cavities resemble alveoli, they are connected to the exterior of the premaxillae and to the fourth alveolus through small canals, thus suggesting that they are more likely remnants of the nutrient canal system.

Maxilla. The maxillae are articulated with the premaxillae, and despite their poor preservation, the transition between both bones is identifiable thanks to the fact that the maxillary processes of the premaxillae are distinctly separated from the maxillae (Fig. 1D). The right maxilla shows some anatomical details such as a short and wide dorsal process. The lateral surface is pierced by nutrient foramina, which are also visible through the μ CT scans as canals communicating labial and medial regions. Ventrally, this bone shows a slightly angled rostral corner that delimits the anterior edge of the antorbital fenestra. The maxillary process of the premaxilla is lateroventrally positioned to the rostral end of the premaxillary process of the maxilla, where both bones are interlocked, and not overlapped (Fig. 1D). Thus, premaxilla forms the lateral rim of the rostrum in this region, in contrast to the normal condition in other enantiornithines. Therefore, we interpret that the preserved

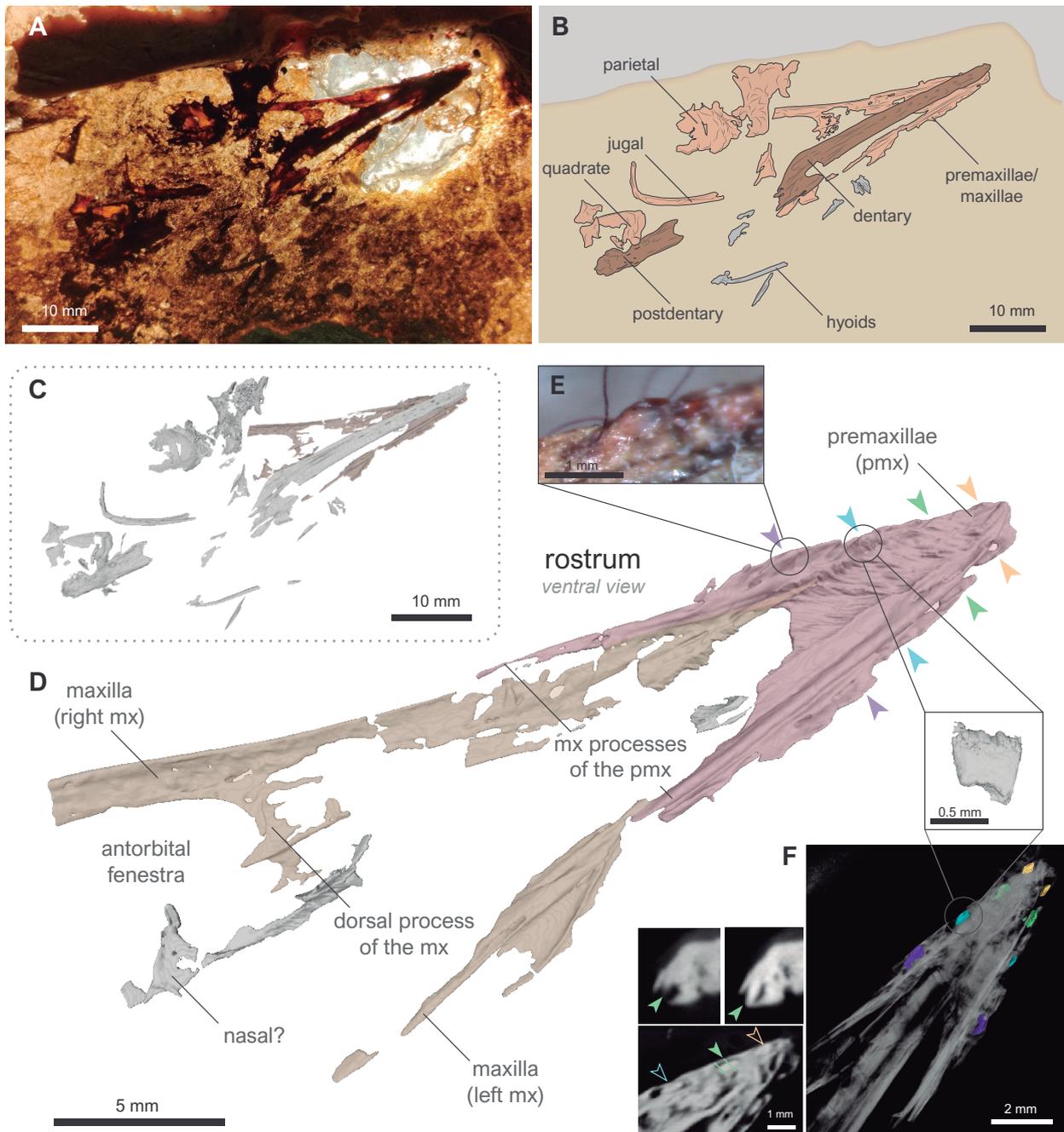


Figure 1. Cranial fossil remains of *Gorgonavis alcyone* (MUPA-LH-13240). **A.** Photograph of the partially transferred fossil of MUPA-LH-13240; **B.** Line drawing and identified bones of MUPA-LH-13240; **C.** Segmented cranial remains from μ CT-scanning; **D.** Close up of the rostral remains of *G. alcyone* in ventral view, showing the separation of the premaxillae (pink pale) and the maxillae (brown); **E.** Close-up photograph of the fourth right premaxillary tooth; **F.** μ CT images and 3D transparent reconstruction of the rostrum indicating the distribution of the teeth (colour code follows coloured arrows in D), showing the morphology of the third right tooth in labial view.

maxillary margin and the premaxilla contribute equally to the margin of the rostrum. Although the total length of the maxilla may not be preserved, the arrangement and length of the remaining cranial elements (i.e., jugal, dentary and postdentary articulated with the quadrate; Figs 1D, 2, 4) suggests that the length of this bone is likely not much greater than what is preserved, supporting the interpretation that the premaxilla and the maxilla contribute subequally to the length of the rostral margin.

The tomial edge of the maxilla is remarkably slender, with no signs of either alveoli or teeth, as in longipterygids (O’Connor and Chiappe 2011). However, one of the aforementioned canals—located in the most rostral part of the right maxilla (at the junction with the base of the maxillary processes of the premaxilla)—is significantly larger, resembling the smaller alveoli of the premaxilla. Although there is no tooth contained within this cavity, and this structure is not observed on the left maxilla, its

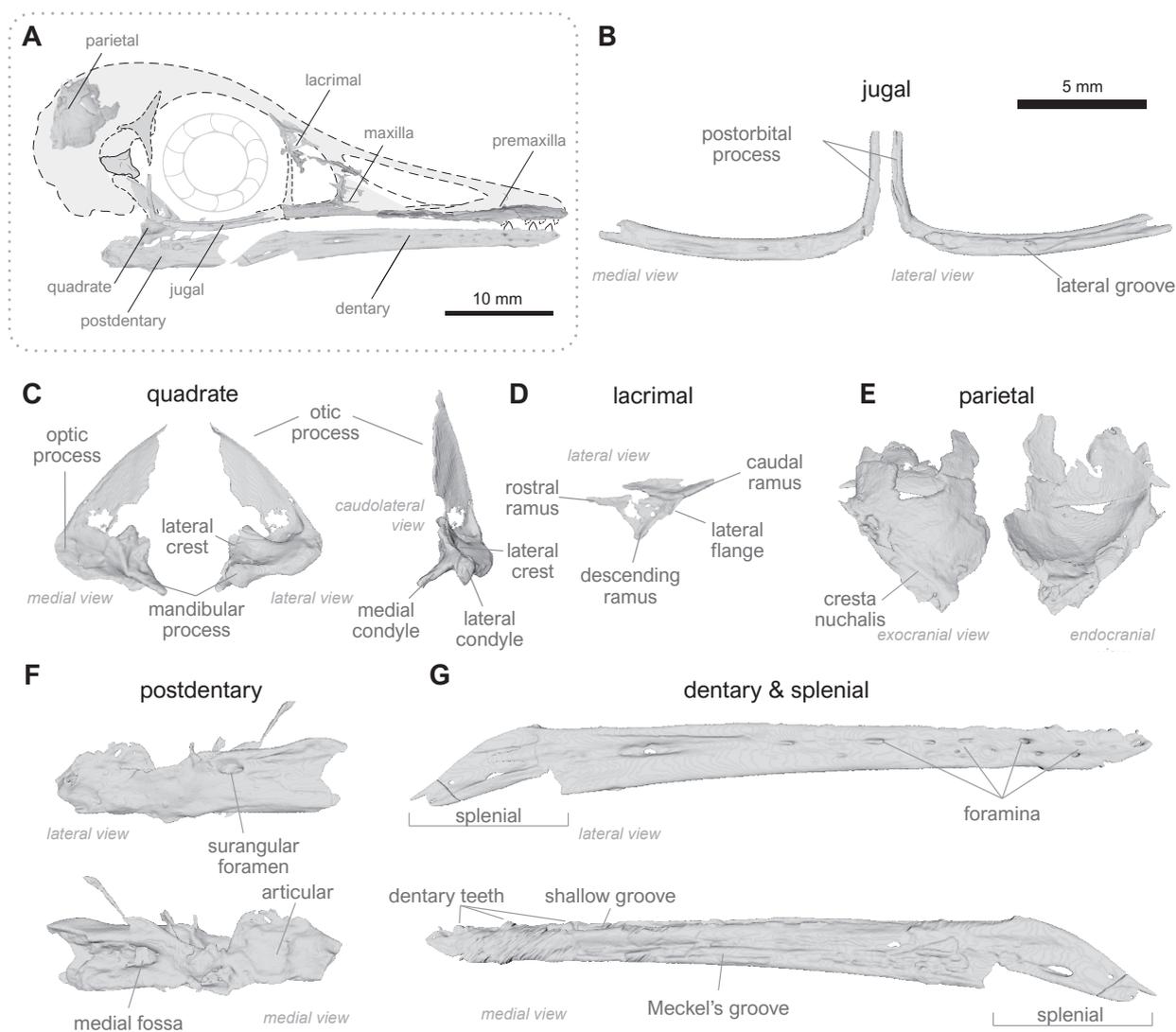


Figure 2. Digital reconstruction of the cranial bones of *Gorgonavis alcyone* (MUPA-LH-13240). **A.** Skull reconstruction based on preserved bones in anatomical position, in lateral view, based on preserved bones; **B.** Jugal; **C.** Quadrate; **D.** Lacrimal; **E.** Parietal; **F.** Postdentary; **G.** Dentary. Scale bar: 5 mm (**B–G**).

presence precludes affirmatively asserting the absence of maxillary teeth in the new taxon. The angle formed by the left and right tomial margins is approximately 26° , remarkably narrower than in other enantiornithines (e.g., $\sim 35^\circ$ in *Navaornis*, $\sim 40^\circ$ in *Gobipteryx*), and than the estimated angle using the whole configuration of the rostrum in most enantiornithines (except longipterygids; O'Connor and Chiappe 2011).

Lacrimal. A disarticulated, triradiate bone caudal to the right maxilla is tentatively identified as the left lacrimal (Fig. 2C). If correctly identified, this bone is missing most of the descending ramus. Its preserved portion is somewhat cranially directed and forming a more acute angle ($\sim 43^\circ$) with the delicate rostral ramus; in contrast, the angle with the caudal ramus is significantly broader ($\sim 160^\circ$). The angular relationship between these rami resembles those of the bohaiornithid BMNHC-Ph 1204 (Liu et al. 2022). The three lacrimal rami bear shallow crests on their lateral

surfaces, coalescing caudodorsally at the junction between the descending and caudal rami, and forming a lateral flange similar to that in *Yuanchuavis* (Wang et al. 2022a).

Jugal. The jugal of MUPA-LH-13240 is rod-like, slender and slightly bowed ventrally (Fig. 2A). Its rostral end slopes rostroventrally, showing what appears to be a notched morphology that differs from that of the enantiornithines *Bohaiornis* (Li et al. 2014), *Longusunguis* (Wang et al. 2014; Hu et al. 2020) and *Enantiornithes* indet. LP-4450-IEI (Sanz et al. 1997) in which the rostral end of the jugal is straight and blunt. Such morphology may alternatively be a taphonomic artefact. However, when we digitally rearticulate the skull, based on the position with respect to the other preserved bones, we interpret that the jugal is completely preserved rostrally, informing about the total length of the rostrum. Caudally, the jugal bears a thin and long postorbital process (assuming the jugal is complete, nearly half the length of the jugal bar,

and proportionally much longer than in other enantiornithines). The postorbital process points directly dorsally, describing a nearly 90° angle with the jugal bar. Such morphology resembles more the L-shaped jugals of other Early Cretaceous enantiornithines (O'Connor and Chiappe 2011) instead of the rod-like appearance of some Late Cretaceous taxa (e.g., *Navaornis*, *Yuornis*; Chiappe et al. 2024; Xu et al. 2021). However, the acute angle between jugal bar and postorbital process of the jugal is distinctive of *Gorgonavis* among enantiornithines. The caudal end of the jugal is unforked (i.e., lacking a quadradojugal process) as in *Pterygornis*, *Cathayornis*, *Bohaiornis* (Wang et al. 2022b), *Yuanchuavis* (Wang et al. 2022a), *Parabohaiornis* (Wang 2023), and most other enantiornithines. As in IVPP V12707 (Wang et al. 2021), a wide and deep longitudinal groove is observed along the entire lateral surface of the jugal; this groove reaches the dorsal end of the postorbital process (Fig. 2A).

Quadrate. The right quadrate, largely exposed in lateral view, is preserved almost in articulation with the mandible (Figs 1A–C, 2B). The orbital process is broad (i.e., flange-like) and lateromedially thin as in other early birds (Chiappe 1996) including enantiornithines (Wang et al. 2015; Chiappe et al. 2024). The otic process is elongated but its dorsal tip and its caudal edge are not preserved. The presence of an incipient caudolateral fossa suggests the presence of a lateral crest, forming much of the lateral margin of the quadrate and ending on the lateral mandibular process. However, this crest is not as developed and is not as clearly visible as in *Longipteryx* (Stidham and O'Connor 2021). Such a difference may reflect a taxonomic distinction between *Longipteryx* and *Gorgonavis*, although in the latter its projection through the otic process is not preserved, so this difference may be due to taphonomic effects. The quadrate of MUPA-LH-13240 has a bicondylar mandibular process, as in other enantiornithines (O'Connor and Chiappe 2011; Wang and Zhou 2020; Wang et al. 2021). The lateral condyle is larger and rounded, similarly to *Longipteryx* and differing from other enantiornithines (Stidham and O'Connor 2021), and the medial condyle is longer and finger-like (similar to that of bohaiornithid BMNHC-Ph 1204; Liu et al. 2022), defining a concave and asymmetric caudal margin for the quadrate. A possible partially broken left quadrate is preserved close to the parietal.

Dentary and splenial. The right dentary, exposed in lateral view, overlaps with the medial region of the upper rostrum (Figs 1A–C, 2G). The dentary is elongated and slender as in longipterygids (e.g., *Shanweinia*, O'Connor et al. 2009; *Longirostravis*, Hou et al. 2004), and clearly different from the much shorter and stouter dentary of most other enantiornithines (O'Connor and Chiappe 2011). It is also generally straight with its ventral and dorsal margins diverging slightly towards the caudal end—this condition resembles more that of *Shanweinia* than the more ventrally curved dentary of *Longipteryx*, *Rapaxavis*, and *Longirostravis*. The caudal end of the dentary slopes caudoventrally as it defines the articulation with the postdentary bones, in a manner typical of

other enantiornithines (e.g., O'Connor and Chiappe 2011; Liu et al. 2022; Chiappe et al. 2024). The μ CT images reveal the presence of at least 3 teeth on the rostral portion of the bone (Fig. 2G). The rostral-most two teeth are closer to each other than to the third tooth (Suppl. material 1: fig. S1). In lateral view, the dentary shows numerous small and oval-shaped nutrient foramina. One of these foramina is placed at the rostradorsal end of the dentary; although speculative, like in other basal avialians, its size and orientation suggest it is possibly the rostralateral foramen (*sensu* Bailleul et al. 2019). The medial view is scarred by a deep Meckel's groove, which is not covered by a triangular-shaped splenial; the splenial is restricted to the caudal portion of the dentary. The splenial bears a small and centrally placed foramen.

Postdentary. The contacts between articular, angular, and surangular (Fig. 2F) cannot be clearly visualized, which suggest that these bones might have been fused to one another (however, the degree to which this is taphonomic cannot be ascertained). The right surangular (Fig. 2F) is preserved in lateral view in contact with the quadrate and displaced caudally with respect to the dentary (Fig. 1A–C). The bone is robust and as preserved, almost three times shorter than the dentary, with subparallel dorsal and ventral margins. As preserved, the rostral end of the surangular is somewhat forked, with both dorsal and ventral rostral ends equally projected, suggesting that the rostradorsal end of this bone could be missing. An oval foramen perforates its lateral surface, near the dorsal margin, in a position comparable to that of the lateral fossa of *Parabohaiornis* (Wang 2023), *Bohaiornis* (Hu et al., 2011), *Fortunguavis* and some juvenile enantiornithines (e.g., IVPP V12707; O'Connor and Chiappe 2011; Wang et al. 2014, 2021). This foramen has been suggested to be homologous to the surangular foramen of non-avian dinosaurs and non-informative of an ontogenetic status (Chiappe et al. 2007; O'Connor and Chiappe 2011; Wang 2023). The position of this foramen, relative to the mandibular articulation with the quadrate, is different to that in the above-mentioned enantiornithines but it coincides with that of a small rostral surangular foramen in *Dapingfangornis* (Wang et al. 2023). This foramen opens internally into a deep and wide fossa, which opens medially at the rostral end of the surangular. Caudally, the postdentary complex is incomplete, and the medial process of the mandible is lacking.

Results

Phylogenetic position

The phylogenetic analyses based on the modified morphological matrix of Benito et al. (2022), returned 264 MPTs with a length of 1,441 steps. *Gorgonavis* is consistently recovered in a nested position within the enantiornithine family Longipterygidae in 100% of the trees (Fig. 3A). A large polytomy for Enantiornithes is recovered in both the strict consensus tree and in the 75% majority rule, with the

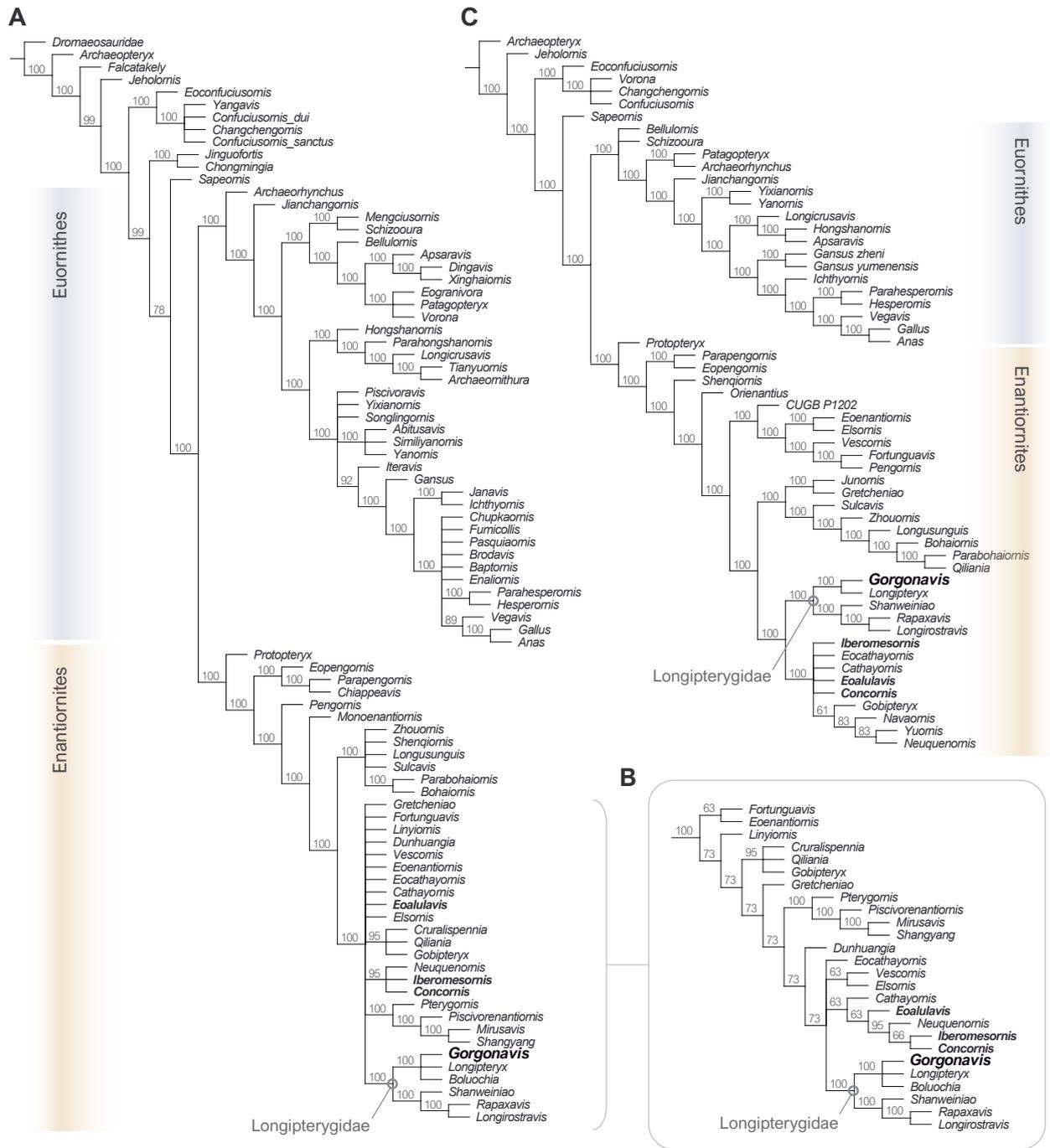


Figure 3. Phylogenetic relationships of *Gorgonavis alcyone* (MUPA-LH-13240). **A.** Strict consensus tree based on modified Benito et al. (2022); **B.** 60% majority rule consensus tree resulting from modified Benito et al. (2022); **C.** 60% majority rule consensus tree resulting from modified Chiappe, Navalón et al. (2024).

Longipterygidae (including *Gorgonavis*), Pengornithidae (excluding *Pengornis*) and Bohaiornithidae being the only robust nodes. Optimisation of character states using this phylogenetic hypothesis shows that all longipterygids share i) premaxillary teeth restricted to the rostral portion, ii) absence of maxillary teeth, and a iii) a preorbital portion that is 60% or more the total length of the skull (this cannot be evaluated in *Gorgonavis*). The consensus trees placed *G. alcyone* as sister taxon of the subfamily Longipteryginae (i.e., *Longipteryx* and *Boluochia*) in

100% of the trees (Fig. 3A). However, *Gorgonavis* differs from longipterygines in that the premaxilla extends for about 1/2 of total length of rostrum (it is shorter than the facial contribution of the maxilla in other taxa, according to the craniofacial reconstruction: Fig. 2A, 4A). Because in the resulting phylogenetic analysis the differences between (Longipteryginae + *Gorgonavis*) and (*Shanweinia* + (*Rapaxavis* + *Longirostravis*)) are postcranial, *Gorgonavis* does not contribute with any new anatomical characters to this differentiation.

The 60% majority rule consensus tree resulting from the modified morphological matrix of Benito et al. (2022) shows a more defined phylogenetic position for the remaining Las Hoyas species (Fig. 3B). *Iberomesornis*, recently proposed as the sister taxon of the entire longipterygid clade (Terol et al. 2025), is instead recovered here as the sister taxon of *Concornis*, in a more inclusive, but poorly supported (63%) clade, together with the enantiornithines *Cathayornis*, *Neuquenornis*, and *Eoalulavis*. The strict consensus tree obtained from the implied weighting using the best optimized k -value ($k = 7$) shows a more resolved tree, classifying *Gorgonavis* again as a longipterygid closer to *Longipteryx* and *Boluochia*, relating *Concornis* and *Eoalulavis* to *Cathayornis* and *Eocathayornis* within a single clade, but including *Iberomesornis* as the sister taxon of *Shanweinia* (see Suppl. material 1).

Based on the analyses using the morphological matrix of Chiappe, Navalón et al. (2024), 17 MPTs of 923 evolutionary steps are obtained. The strict consensus and the majority rule trees place *Gorgonavis* with the longipterygids in 100% of the trees (Fig. 3C). The rest of the Las Hoyas species are placed within a polytomy including the enantiornithines *Gobipteryx*, *Yuornis*, *Navaornis*, *Cathayornis* and *Neuquenornis*. The latter clade is not robustly supported (61%) in the majority rule consensus (Fig. 3C). The strict consensus tree obtained from the implied weighting—using the best optimized k -value for this matrix ($k = 5.5$)—shows again a more resolved tree, finding *Iberomesornis* with the pengornithids, and *Eoalulavis* closer to *Cathayornis* and edentulous enantiornithines. However, this analysis also shows controversial relationships, such as *Gorgonavis* as the sister taxon of all the ornithothoracines, or *Sapeornis* in a more basal position relative to *Jeholornis* (see Suppl. material 1), so this result should be taken with caution, indicating a stronger influence of the homoplasy in this matrix.

Evolutionary tendency towards elongated rostra in early birds

Gorgonavis exhibits a rostrum two and a half times the length of the orbit (as estimated by jugal length, see Methods), placing it within the lower range of other long-snouted enantiornithines, such as longipterygids, similar in size to *Shanweinia* (Fig. 4; O'Connor et al. 2009). Our phylogenetic regression model between the \log_{10} -transformed rostrum and orbit lengths describes an evolutionary continuum that suggests morphological differences between taxa with relatively elongated rostra (positive residuals, above fitted line) from taxa with relatively short to medium rostral length (negative residuals, below fitted line) (Fig. 4B). The most extreme forms in the long-snouted group all belong to the Euornithes, including the Early Cretaceous *Dingavis*, the stem ornithurine *Hesperornis*, and the crown living bird *Anas*. The most extreme short-snouted taxa are represented by several enantiornithines and more stemward taxa,

including *Parabohaiornis* and other bohaiornithids, which display nearly subequal rostrum and orbit lengths. Among Enantiornithes, the only taxa to show positive residuals (i.e., a proportionally elongated rostrum within this evolutionary context) are contained within Longipterygidae. *Gorgonavis* falls within the range of small-sized longipterygids (*Shanweinia* and *Rapaxavis*), differing in size from *Longipteryx*, but exhibiting similar rostrum to orbit proportions. The distribution of the orbit to rostrum residuals along the phylogeny (Fig. 4A) illustrates that longipterygids evolved relatively elongated rostra very early in avian history. This tendency was more widely explored in Euornithes—in some cases reaching more extreme values—but available evidence suggests that *Gorgonavis* and the longipterygids evolved such specialized conditions earlier outside of the clade leading to the crown group.

Discussion

The holotype of *Gorgonavis alcyone* gen. et sp. nov. represents the first non-juvenile cranial remains of a bird from the Early Cretaceous fossil record of Europe. *G. alcyone* gen. et sp. nov. possesses several features typical of the Early Cretaceous enantiornithines, such as a L-shaped, slender jugal with an unforked caudal end lacking a quadratojugal process; a quadrate with a finger-like medial condyle; and a caudoventrally sloping dentary, forming an unforked articulation with the surangular. The configuration of the rostrum, with premaxillae representing between a third and a half of the total rostral length, and a robust and elongated postorbital process of the jugal that is dorsally oriented and strongly angled, support the erection of a new species. Additionally, it shares some features with members of the Longipterygidae, such as the elongated rostral morphology, upper dentition restricted to the premaxillary corpus, elongated maxillary processes of the premaxillae, and a long (e.g., similar to *Longipteryx*, *Longirostravis*) and straight dentary (similar to *Shanweinia*). Most of our phylogenetic analyses, based on the character matrix from Chiappe, Navalón et al. (2024) and Benito et al. (2022), resolve *Gorgonavis* within the Longipterygidae. These phylogenetic results lend support to the anatomical similarities between *Gorgonavis* and longipterygids. However, the specimen is fragmentary, and this makes it difficult to ascertain its placement within Longipterygidae.

Although the absence of postcranial elements complicates the assessment of the ontogenetic status of the holotype of *G. alcyone*, we propose that the extensive fusion of some cranial elements (i.e., medial fusion of premaxillae and fusion of postdentary mandibular elements) supports a skeletally mature or near-mature ontogenetic age. Although these traits are highly variable in known enantiornithines, these fusions are present in adult (e.g., *Shangyang*, *Linyiornis*) or subadult individuals (e.g., *Longusunguis*—IVPPV18693—, *Monoenantiornis*).

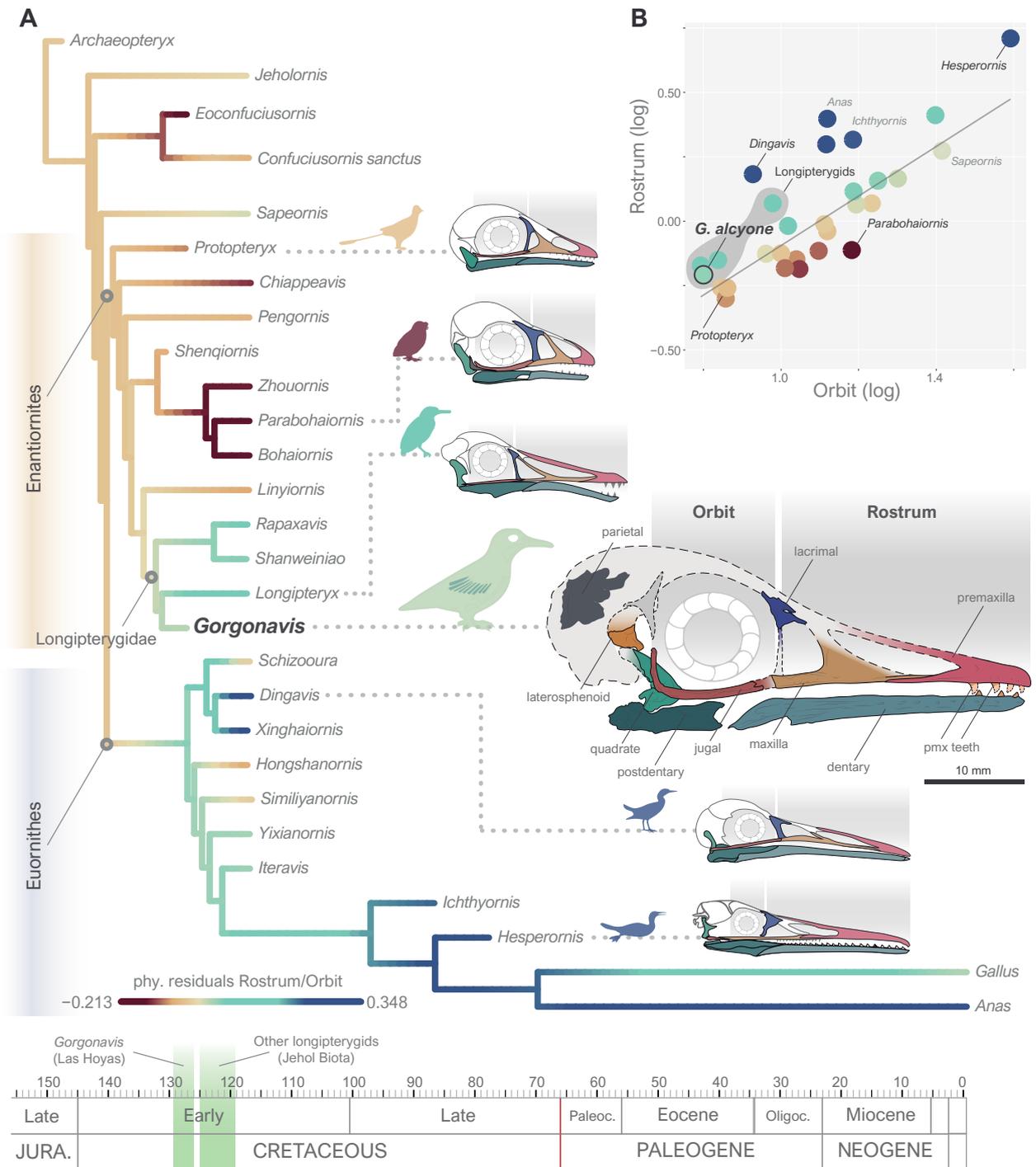


Figure 4. Evolutionary tendency towards elongated rostra in early birds, showing the specialized craniofacial proportions of Longipterygidae (including *Gorgonavis alcyone*), unique among Enantiornithes. **A.** Phylogenetic distribution of the relative elongation of the rostrum, based on phylogenetic residuals from rostrum to orbit length, showing some representatives of the different craniofacial conditions; **B.** Phylogenetic regression model between the \log_{10} -transformed rostrum and orbit lengths.

Furthermore, post-hatchling ontogenetic stages, based on the sequence in which compound bones fuse, indicate that the fusion of the premaxillary corpora occurs after the fusion of vertebral elements (synsacrum and pygostyle) and before the complete formation of compound limb bones (e.g., carpometacarpus) (Hu and O'Connor 2017).

This finding is consistent with our interpretation of the holotype of *G. alcyone* as a subadult or older individual.

The lack of cranial elements in the previously described taxa from Las Hoyas hampers direct comparisons. Therefore, the referral of MUPA-LH13240 to a new species also requires rejecting the hypothesis that this

specimen belongs to other known Las Hoyas enantiornithines (i.e., *Iberomesornis*, *Concornis* and *Eoalulavis*). By virtue of *Gorgonavis* being included within the Longipterygidae, our analyses underscore the fact that none of these Las Hoyas enantiornithines appear to be closely related to either this clade or *Gorgonavis*. While Terol et al. (2025) recently hinted at *Iberomesornis* being the sister taxon of Longipterygidae, our analyses placed *Iberomesornis* as a closer relative to other enantiornithines such as *Concornis*, *Neuquenornis* or *Cathayornis*. In our analyses, *Iberomesornis* (known only by postcranial skeleton) did not share any synapomorphies defining Longipterygidae (most of them are postcranial synapomorphies, see Suppl. material 1). In addition, if we assumed that the holotypes of *G. alcyone* and *I. romerali*, are adults or near adult individuals, the estimated 3-cm-long skull of MUPA-LH-13240 is disproportionately large for the tiny postcranium of the holotype of *I. romerali* (the fully preserved axial skeleton of its holotype measures approximately 5.5 cm). Such a difference in relative size suggests that *Gorgonavis* may have been considerably larger than *Iberomesornis*, and more similar in size to *Shanweinia*. On the other hand, although *Concornis* and *Eoalulavis* are larger in size, better matching MUPA-LH-13240, the absence of postcranial anatomical characters linking these species to Longipterygidae—where most synapomorphies are postcranial—makes it even less likely that this skull belongs to these taxa. Altogether, the above arguments support the erection of *Gorgonavis* as a distinct taxon within the Las Hoyas avifauna.

Until now, the adult skull anatomy of Early Cretaceous enantiornithines is known mainly from fossils in China. The predominant craniofacial configuration of the known Early Cretaceous enantiornithines is relatively short-snouted (i.e., mesorostral; Marugán-Lobón and Buscalioni 2003; O'Connor and Chiappe 2011), with a reduced premaxilla restricted to the anterior-most region of the rostrum and a maxilla that forms much of the lateral margins of the upper jaw (O'Connor and Chiappe 2011). Within the context of early avian evolution, longipterygids are the only non-euornithine taxa characterized by a rostral condition that deviates from this plesiomorphic configuration (Fig. 4), reaching rostrum-to-orbit values more common among euornithines and comparable to taxa close to the origin of the crown group. The discovery of *Gorgonavis* adds diversity to the known cranial morphology of this stem avian lineage, representing the first occurrence of an enantiornithine showing a tendency to elongate the facial skeleton outside the Jehol Biota of Northeastern China.

La Huérguina Lithographic Limestone Formation, where Las Hoyas is located, is dated as Barremian in age (129.4 and 126.4 Mya; Fregenal-Martínez et al. 2017). Thus, *Gorgonavis* represents the earliest record of an enantiornithine with a significant rostral elongation, as all members of Longipterygidae are known from the Yixian Fm (124.6 Mya; *Longirostravis* and *Shanweinia*; Hou et al. 2004; O'Connor et al. 2009) or the Jiufotang

Fm (122–120 Mya; *Rapaxavis*, *Longipteryx*, *Boluochia*; O'Connor et al. 2011) within the Jehol Biota. In those enantiornithine species where the rostrum is elongated, such as *Rapaxavis*, *Longirostravis*, or even the bizarre *Falcatakely* (whose phylogenetic affinities as an enantiornithine are still debated; Benito et al. 2022), the maxillary processes of the premaxillae are frequently short and do not contribute significantly to a maxillary-dominated rostrum, thus retaining the plesiomorphic condition within the evolutionary tendency towards rostrum elongation. Interestingly, *Gorgonavis*, and maybe *Longipteryx* (although this should be confirmed through μ CT imaging), are the only enantiornithines in which these processes appear to form a significant portion (around 50%) of the ventrolateral margin that may be related to rostral elongation. This condition is similar to the construction of the rostrum in Euornithes (O'Connor et al. 2016) and it is shown by many early representatives of the group (e.g., *Yanornis* or *Xinghaiornis*, the latter not included into the analyses but clearly reported as a long-snouted taxon; Wang et al. 2013), and more derived ornithurines (e.g., *Hesperornis*) closer to the crown group (Field et al. 2018; Bell and Chiappe 2022). These findings add another example of convergence between Enantiornithes and Euornithes, clades separated by at least 130 million years of evolution. The new discovery demonstrates how the great lability of craniofacial evolution of birds goes back to the early evolution of the group, and that rostral elongation may have evolved multiple times independently among avians.

The occurrence of a new early bird with an elongated rostrum at Las Hoyas, potentially related to the longipterygids, informs the presence of a specialized craniofacial condition in a well-known subtropical palaeoecosystems. It also suggests a Eurasian distribution for this well-established Early Cretaceous enantiornithine lineage. Beyond its biogeographic implications, if our phylogenetic interpretation of *Gorgonavis* as a longipterygid is correct, this new fossil can clarify intraclade character evolution. On the one hand, *Gorgonavis* shares a caudoventral extension of the maxillary processes of the premaxilla with the longipterygines (e.g., *Longipteryx*); and on the other hand, it exhibits the straight rostrum—particularly the dentary—and smaller teeth of the longirostravines (i.e., *Shanweinia*, *Rapaxavis*, *Longirostravis*). While fragmentary, the fact that *Gorgonavis* combines cranial characters from both longipterygid subgroups (longipterygines and longirostravines) suggests that shared characters might be primitive for the clade. In addition, its age and phylogenetic position substantiate previous assertions (Stidham and O'Connor 2021; O'Connor et al. 2024) that the distinctive characteristics of *Longipteryx* (e.g., a more ventrally curved rostrum, large and recurved premaxillary teeth) may be derived. After decades of excavations at Las Hoyas, the discovery of *Gorgonavis* underscores the continued significance of this site for understanding the early evolution of birds from a global perspective.

Conclusions

Our study reports a new enantiornithine bird species, *Gorgonavis alcyone* gen. et. sp. nov. This species represents the first adult cranial remains of a pygostylian bird from the Early Cretaceous found outside of China, and thus, the first from Las Hoyas (Cuenca, Spain). This discovery reinforces the site's global importance in the context of avian evolution, increasing the diversity of the avifauna in a Barremian wetland. The anatomical features of these cranial remains suggest affinities with longipterygids, a family previously only described from remains in the Jehol Biota. The discovery of this species, with an elongated rostrum, supports the early existence of a trend towards longirostry in this specialized enantiornithine clade also outside of China, offering valuable information on craniofacial disparity within the most dominant clade of Mesozoic birds. This extends the geographical and temporal distribution of specialized lineages, providing insights into its ecological range, and the faunistic connection between the Jehol Biota and Las Hoyas.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Conceptualization Sergio M Nebreda (SMN), Luis M Chiappe (LMC), Guillermo Navalón (GN), Jesús Marugán-Lobón (JML); Data Curation, Formal Analysis SMN, GN, Javier C Terol (JCT); Funding Acquisition LMC, Francisco J. Serrano (FJS), JML; Investigation, Methodology SMN, LMC, GN, JCT; Project Administration SMN, LMC, Ángela D Buscalioni (ADB), JML; Resources SMN, LMC, GN, FJS, ADB, JML; Software SMN; Supervision SMN, LMC, ADB, JML; Validation SMN, LMC, JML; Visualization SMN; Writing – Original Draft Preparation SMN; Writing – Review and Editing SMN, LMC, GN, JCT, FJS, ADB, JML.

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Data availability

The 3D models generated during the current study are available on Morphosource, repository project “The digital world of the birds from Las Hoyas (Early Cretaceous, Spain)” (<https://www.morphosource.org/projects/000502754>).

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Supplementary material 1

Additional information

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