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Diversity and evolution of the Confuciusornithidae: Evidence from a new 131-million-year-old specimen from the Huajiying Formation in NE China

Guillermo Navalón[a,b], Qingjin Meng [c], Jesús Marugán-Lobón[b,d], Yuguang Zhang [c], BaopengWang [c], Hai Xing [c], Di Liu [c, *], Luis M. Chiappe[d,*]

a. School of Earth Sciences, University of Bristol, Life Sciences Building, Bristol, UK.

b. Unidad de Paleontología, Departamento de Biología, Universidad Autónoma de Madrid, Madrid, Spain.

c. Beijing Museum of Natural History, 126 Tianqiao South Street, Beijing 100050, PR China.

d. Dinosaur Institute, Natural History Museum of Los Angeles County, Los Angeles, CA, USA.

***Co-corresponding authors. Emails:** lchiappe@nhm.org, liudi0716@qq.com

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Abstract

The Huajiying Formation contains the earliest deposits of the Jehol Biota, representing the world's second oldest avifauna. This avifauna includes the early confuciusornithid *Eoconfuciusornis zhengi*, the oldest occurrence of this clade and one of the earliest

divergences of pygostylian birds. Although *E. zhengi* shows unique traits, the holotype's immature age makes comparisons with the better known *Confuciusornis sanctus* problematic. As a result, the taxonomic validity of *E. zhengi* is controversial. We describe a small, osteologically adult confuciusornithid from the same deposits as *E. zhengi.* The new fossil is most similar to *E. zhengi* but also shares traits with the stratigraphically younger *Confuciusornis*. The humerus of the new fossil is straighter and more slender, and bears a less dorsally-developed deltopectoral crest compared with similarly-sized and smaller specimens of *Confuciusornis*. The morphology of the humerus is intermediate between *E. zhengi* and *Confuciusornis* and its proximal portion is pierced by a small deltopectoral foramen, absent in the holotype of *E. zhengi*. However, this foramen is much smaller than in any other confuciusornithid. Shape analyses (geometric morphometrics) of the humerus of confuciusornithids of different ages and representatives of other basal avians and closely-related non-avian theropods supports our observations and indicate that the humeral differences between the holotype of *E. zhengi* and the new specimen are not easily explained as ontogenetic variation within a single species. However, the limited number of early confuciursornithids does not allow us to confidently interpret such differences as interspecific. Nonetheless, these analyses support the morphological distinctiveness of the early confuciusornithids from the Huajiying Formation and suggest a stepwise acquisition of the unique humeral morphology of Confuciusornithidae.

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1. Introduction

The approximately 131 million-year-old lacustrine deposits of the Huajiying Formation (Sichakou-Shenjitu basin, Fengning County, Hebei Province, northeastern China) (Liu et al. 2003, He et al. 2006) contain the oldest known avian fossils of the Jehol Biota, representing the world's second oldest avifauna (Zhang and Zhou 2000, Pan et al. 2013, Chiappe and Meng 2016). Although the fauna yielded by these early deposits is diverse, fossils of birds are scarce. To date, only a handful of early pygostylians (confuciusornithids, enantiornithines and hongshanornithid ornithuromorphs) have been reported (Zhang and Zhou 2000, Zhang, Zhou, and Benton 2008, Wang et al. 2014, Wang et al. 2015, Wang et al. 2016). Despite its dearth, these avian fossils are central to understanding the initial pygostylian radiation and hence, paramount for deciphering the first steps of the evolution of birds (Chiappe, 2007; Wang et al. 2015, Chiappe and Meng 2016).

Confuciusornithids, the earliest divergence of pygostylian birds (Chiappe, 2002; O'Connor et al. 2016), are represented in the Huajiying Formation by just two specimens: an immature specimen used to erect the species *Eoconfuciusornis zhengi* (Zhang et al. 2008) and another specimen recently identified as belonging to the same taxon (Pan et al. 2016), although no morphological evidence was provided in support of the latter taxonomic identification. Despite the ubiquity of *Confuciusornis sanctus* specimens (Fig. 1), a species known from hundreds of individuals (Chiappe et al., 1999; Chiappeet al. 2008, Marugán-Lobón et al. 2011), the taxonomic diversity of this clade is limited to three valid genera, comprising at most four

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species (see comments on *C. dui* below) that, with the exception of *C. sanctus*, are known from a handful of specimens. Three of these species: *Changchengornis hengdaoziensis* (Ji et al. 1999, Chiappe et al. 1999), *Confuciusornis dui* (Hou et al. 1999) and *Confuciusornis sanctus* (Hou et al. 1995, Chiappe et al. 1999) come from the Yixian Formation (~125 MYa; (Swisher et al. 1999, Yang et al. 2007)) (Fig.1). Two reports of *Confuciusornis sanctus* (Dalsätt et al. 2006, Li et al. 2010) from the younger Jiufotang Formation (~120 MYa,; (He et al. 2004)) are based on specimens whose provenance needs further confirmation (Fig.1); *C. dui* is known from a missing holotype and an incomplete, poorly preserved paratype, which makes comparisons with other taxa difficult, and several additional Yixian species (i.e.: *Confuciusornis chuonzhous, C. suniae, C. feducciai, Jinzhouornis yixianensis* and *J. zhangjiyingia*), erected on the basis of anatomical misinterpretations, have been regarded as junior synonyms of *C. sanctus* (Chiappe et al. 2008, Marugán-Lobón et al. 2011, Chiappe and Meng 2016).

The fourth previously described species and the oldest confuciusornithid is *Eoconfuciusornis zhengi*, found in the Huajiying Formation (Zhang et al. 2008) (Fig. 1). The holotype of *E. zhengi* possesses some unique, and possibly primitive, traits (Zhang et al. 2008), yet its early ontogenetic age complicates taxonomic comparisons with stratigraphically younger confuciusornithids, casting doubt over the validity of *E. zhengi*. In the present study, we report on a new confuciusornithid specimen (BMNHC-PH870) from the Huajiying Formation (Figs. 1, 2 & 3), unearthed from the same general locality and horizon as the holotype of *E. zhengi*.

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BMNHC-PH870 is osteologically mature and is morphologically similar to *E. zhengi*, although it also shares traits with the stratigraphically younger *Confuciusornis*. Quantitative data from traditional morphometrics and from shape analysis (geometric morphometrics) of the humerus was also used to: 1) discriminate shape differences between different confuciusornithid species, while 2) taking into account ontogenetic variation in the shape of humerus, and 3) to compare the shape variation of the humerus within Confuciusornithidae with that of other basal avian and related non-avian lineages. BMNHC-PH870 enhances the meagre avian record of the Huajiying Formation, shedding new light on the diversity of the oldest confuciusornithids and the first radiation of pygostylians.

2. Material & Methods

The new fossil (BMNHC-PH870; Beijing Museum of Natural History, Beijing, China; Figs. 2 & 3) is a fairly complete skeleton, although it is mostly disarticulated and missing some elements (e.g: most of the pelvic girdle, the sternum and both ulnae). It is split into two slabs, A and B (Figs. 2, 3).

Traditional morphometrics were used to aid anatomical comparisons; chord lengths were measured digitally using ImageJ v.1.47 (Rasband 1997) on the preserved elements of the axial and appendicular skeletons of BMNHC-PH870, the holotype of *E. zhengi* (IVPP-V11977), a cast of the holotype of *C. dui* (IVPP-11521), and two specimens of *C. sanctus*, representing

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approximately the largest (BSP 1999 I 15) and smallest (Berlin specimen) sizes exhibited by this species (Marugán-Lobón et al. 2011) (Table 1).

Shape analysis (Geometric Morphometrics; GM) was used to explore the morphological variation of the humerus within Confuciusornithidae and across other major Mesozoic avian lineages and closely related non-avian theropods. GM was also used to investigate the late ontogenetic shape variation the humerus in *C. sanctus*. For that purpose, BMNHC-PH870, the cast of the holotype of *C. dui*, and the holotypes of *C. hengdaoziensis* (GMV-2129) and *E. zhengi* (IVPP-V11977), were included along with 38 specimens of *C. sanctus*, including type specimens, the holotypes of *J. zhangjiyingia* (IVPP-12352) and *C. feducciai* (D-2454) (these two specimens are considered synonyms of *C. sanctus;* see Chiappe et al. 2008, Marugán-Lobón et al. 2011, Chiappe and Meng 2016) (Supplementary Materials. Table 1). Sixteen specimens representing 15 taxa comprising the main lineages of Early Cretaceous avians (i.e.: *Jeholornis*, *Sapeornis*, Enantiornithes and Ornithuromorpha) and some non-avian paravian theropods (i.e: *Anchiornis*, *Microraptor*) were also included (Supplementary Materials. Table 1).

A configuration of 4 landmarks and 3 curves (10 evenly separated semilandmarks each) (Fig. 6B) was digitized using the software tpsDig.2 v.2.17 (Rohlf 2006) on the images of each humerus in cranial or caudal views out of the aforementioned specimens (Supplementary Materials. Table 1). Landmarking of the deltopectoral fenestra was omitted to avoid possible

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uncontrolled error produced by mixed taphonomic and preparation factors. The humeri exhibit some degree of flattening by stratigraphic compression; thus, the landmarks of the left humeri in caudal view and those of the right humeri in cranial view can be mirrored assuming reasonable correspondence in shape between both views. We tested this assumption by means of Discriminant Function Analysis (DFA) in MorphoJ (Klingenberg 2008). DFA was used also to test for sexual shape and/or size dimorphism within *C. sanctus*; the gender of the confuciusornithid specimens was assigned on the basis of the presence/absence of ornamental feathers (Chinsamy et al. 2013).

The sliding of the semilandmarks was performed using tpsRelw v.1.65 (Rohlf 2010) and based on the Minimun Bending Energy Method (Bookstein 1996) as it is more stable than Minimum Procrustes Distance Method when dealing with samples with high morphological variation (Perez et al. 2006). Shape data was extracted using a full Procrustes fit and was thereafter imported into MorphoJ (Klingenberg 2008) together with the corresponding centroid sizes as proxies of humeral size. A Principal Component Analysis (PCA) was carried out to explore the patterns of humeral shape variance. A multivariate regression of shape coordinates on centroid size was used to analyse humeral ontogenetic allometry in a subset of 38 specimens referred to *C. sanctus*.

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The majority of the measurements of Confuciusornithidae were extracted from Chiappe et al. 2008 and Marugán-Lobón et al. 2011 (Table 1). Landmark/semilandmark digitizing of the humeri of most of the confuciusornithid specimens was taken from an extensive photographic database built by LMC and JML, and from published photographs for the remaining specimens included here (Supplementary Materials. Table 1).

3. Results

3.1 Description

The poorly preserved skull of BMNHC-PH870 is exposed in an oblique dorsal view in slab A (Fig. 2), and ventrally in slab B (Fig. 3). Its overall morphology is similar to that of other confuciusornithids: the beak is edentulous, robust and straight, and the postorbital region is rounded (Chiappe et al. 1999) (Fig. 2). A scattered pattern of neurovascular foramina and grooves scars the rostrolateral portion of the premaxillae and dentaries, suggesting the presence of a rhamphotheca (Hieronymus and Witmer 2010, Louchart and Viriot 2011) (Fig. 2).

Poorly preserved vertebral remains are scattered throughout both slabs (Figs. 2 & 3). A large portion of the synsacrum composed of seven vertebrae and well-projected transverse processes is preserved on both slabs (Figs. 2 & 3); its morphology and vertebral number is consistent with that of other confuciusornithids (Chiappe et al. 1999). Similarly, remnants of the pygostyle, slightly greater than half the length of the tibiotarsus, show a morphology consistent

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with that of other confuciusornithids (Chiappe et al. 1999, Hou et al. 1999) (Table 1; Figs. 2,3 & 5C&D).

The furcula is robust, craniocaudally flattened, and boomerang-shaped (Figs. 2 & 3). It lacks either a hypocleidum or the characteristic ventral swelling found in some specimens of *Confuciusornis sanctus* and in *Chanchengornis hengdaoziensis* (Chiappe et al. 1999). Each clavicular ramus tapers distally and both form an interclavicular angle of about 64-68 degrees, clearly lower than in *Eoconfuciusornis zhengi* (~78 degrees) (Zhang et al. 2008) and within the range of *Confuciusornis sanctus* (Chiappe et al. 1999). The scapula and coracoid appear fused to one another (Figs. 3 & 5A&B), with their longitudinal axes at slightly less than 90 degrees. The coracoid appears to be more slender and longer than in *E. zhengi* (Fig. 5A&B) (Zhang et al. 2008). The sternum is missing. Scattered remains of ribs are preserved in the slab; few gastralia preserved in a zigzag pattern are visible below the tibiotarsus in slab B (Fig. 3).

The forelimbs are disarticulated except for the elements of the manus (Figs. 2, 3 & 4). As in other confuciusornithids, the manus is markedly longer than either the humerus or the radius (Chiappe et al. 1999, Hou et al. 1999, Zhang et al. 2008). The humerus shows the general axe-shape morphology characteristic of confuciusornithids, although it is more lightly built than in *Confuciusornis* (Chiappe et al. 1999, Hou et al. 1999) (Figs. 4, 6 & 8). The proximal end is ventrally downturned with respect to the longitudinal axis; a condition similar to that of *E. zhengi*

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(Zhang et al. 2008) but seemingly less pronounced than in geologically younger confuciusornithids (Chiappe et al. 1999, Hou et al. 1999) (Figs. 4, 6 & 8). The subrectangular deltopectoral crest extends for about a third of the length of the humerus, ending in a markedly concave distal surface (Figs. 4, 6 & 8). The deltopectoral crest in BMNHC-PH870 extends distally more than in other confuciusornithids, although its dorsal extent is intermediate between *E. zhengi* and the greater development reached in stratigraphically younger confuciusornithids (Hou et al. 1999, Chiappe et al. 1999, Zhang et al. 2008) (Figs. 6 & 8). The crest is pierced by an oval foramen (Figs. 2, 3, 4 & 8). Nonetheless, the foramen is much smaller than in other confuciusornithids (Hou et al. 1999, Chiappe et al. 1999) (Figs. 2, 3, 4 & 8). Ulnae are not preserved either in the slab or the counterslab. The radius is straight, slender, and substantially shorter than the humerus (Figs. 2 & 3). While lacking surface bone, metacarpals II and III appear fused to the semilunate carpal, similarly to adult *Confuciusornis* (Chiappe et al. 1999, Hou et al. 1999) but unlike in the immature holotype of *E. zhengi* (Zhang et al. 2008) (Fig. 4.). Metacarpal I is subrectangular with a sinusoid distal end (Fig. 4.). Metacarpal II is the longest and thickest of the metacarpals; it is approximately three times the length of metacarpal I and more than twice the width of metacarpal III (Table 1; Fig. 4). Like in all confuciusornithids, the manual phalangeal formula is 2-3-4-0-0 (Chiappe et al. 1999, Hou et al. 1999, Zhang et al. 2008). The proximal phalanx of digit I is a robust and straight bone that projects distally more than the end of metacarpal II (Fig. 4C&D); it articulates with a large claw carrying a curved horny sheath

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(Fig. 4C&D). This bony ungual appears proportionally less curved than in some specimens of *C. sanctus* and it is longer and more robust than the bony ungual of digit III (Table 1; Fig. 4C&D). Like in other confuciusornithids, the proximal phalanx of digit II is subrectangular; it is the most robust phalanx, being craniocaudally wider than its metacarpal (Fig. 4C&D). The intermediate phalanx of this digit is longer than the proximal one and much more slender; it displays a bowed shaft typical of confuciusornithids (Chiappe et al. 1999, Zhang et al. 2008, Hou et al. 1999). As in the latter birds, the claw of digit II is straight and the smallest of the hand (Hou et al. 1999, Chiappe et al. 1999, Zhang et al. 2008) (Table 1; Fig. 4C&D). Digit III also shows the unique morphology of confuciusornithids in which the proximal phalanx is much shorter than the following two intermediate phalanges (Fig. 4C&D) (Chiappe et al. 1999, Hou et al. 1999, Zhang et al. 2008).

The femur is straight and gently curved (Figs. 2 & 3). The tibia is straight and substantially longer than the femur (Table 1; Figs. 2 & 3). The metatarsals are comparatively short, about half the length of the tibia (Table 1; Figs. 2 & 3). The metatarsals are fused proximally and individualized throughout their remaining lengths (Fig. 5C&D). Metatarsal III is the longest, followed by metatarsal IV and II respectively (Table 1, Fig. 5C&D). The short metatarsal I is lateromedially compressed and ends in a ball-like distal articulation (Fig. 5C&D). It appears more slender and straighter than in *C. sanctus* and similar in shape to *E. zhengi* but comparatively bigger (Zhang et al. 2008, Chiappe et al. 1999) (Table 1, Fig. 5C&D). The dorsal

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surface of metatarsals II-IV is convex; about a third down the shaft of metatarsal II there is a partially preserved tubercle for the tibialis cranialis muscle (Chiappe et al. 1999). The anisodactyl foot has phalangeal proportions that fall within the range of confuciusornithids and are most similar to *E. zhengi* (Table 1, Fig. 5). Digit III is the longest followed by digit IV and II (Table 1, Fig. 5C&D). All pedal unguals are subequal in length and bear developed flexor processes (Table 1, Fig. 5C&D).

Few remnants of the plumage are preserved as both blackish-to-brownish carbonized feathers and impressions (Figs. 2 & 3). Plumulaceous cover feathers are preserved scattered and are best preserved near the shoulder region. They reveal a basal-apical differential pigmentation (Figs. 2 & 3) although it is unclear whether this represents the actual color pattern or a taphonomic artefact. Numerous pennaceous flight feathers are also preserved but it is difficult to discriminate either their position or degree of vane asymmetry. A segment of the rachis-dominated portion of the characteristic ornamental feathers of confuciusornithids is also preserved. This suggests that BMNHC-PH870 corresponds to a reproductive male (Chinsamy et al. 2013).

3.2 Shape analysis of the humerus

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DFA showed that there are not important biases (i.e.: non-random error) associated with humeral view (cranial or caudal) (Supplementary Material. Fig. 1) suggesting it is reasonable to assume correspondence in shape between both views in our sample.

The first three principal components (PC1 to PC3) account for approximately 80% of the humeral shape variance in our sample (Fig. 6). PC1 is clearly dominant, accounting for approximately 65% of the total variance and describes shape changes in the robustness of the humerus and the relative dorsal protrusion of the deltopectoral crest. In this dimension the Yixian confuciusornithids are clearly separated from the rest of the taxa, with more robust humeri and more dorsally enlarged deltopectoral crests. Most of the basal lineages of avians and non-avian theropods exhibit more slender humeri with smaller deltopectoral crests (Fig. 6). Remarkably, the confuciusornithids from the Huajiying Formation, BMNHC-PH870 and the holotype of *E. zhengi*, lie at an intermediate position between such clusters; likewise, the humeral morphology of BMNHC-PH870 is intermediate between *E. zhengi* and Yixian confuciusornithids in this axis (Fig. 6). The basal ornithuromorphs *Archaeorhynchus spathula* and *Schizooura lii* are bracketed in this axis by *E. zhengi* in one side and by BMNHC-PH870 in the other, exhibiting an intermediate degree of dorsal protrusion of the deltopectoral crest between both early confuciusornithids. Morphological variance dramatically drops to 10.14 % in PC2, accounting for changes in the distal extent of the deltopectoral crest (Fig. 6). PC3 explains 9.49 % of variance and mainly accounts for changes in the shape of the distal margin of the deltopectoral

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crest (Fig. 6). BMNHC-PH870 clearly diverges from *E. zhengi* in PC2 exhibiting the lowest score within the Confuciusornithidae (Fig. 6), underlining that the deltopectoral crest in BMNHC-PH 870 is more distally extended than in any of other confuciusornithid. The basal ornithuromorph *Schizooura lii* exhibits the highest degree of distal expansion of the deltopectoral crest clearly diverging from BMNHC-PH870 in PC2.

The regression of shape on centroid size is only slightly statistically significant (*P*= 0.0129), and size variation only explains approximately 7% of the total humeral shape variance in the subset of *C. sanctus* specimens (Fig. 7). Therefore, since our dataset encompasses the complete known size range of *C. sanctus* (Chiappe et al. 2008, Marugán-Lobón et al. 2011) and the changes in shape associated with the regression vector do not appear to be biological, but more likely due to taphonomic deformation (Fig. 7), these results likely indicate largely isometric growth of the humerus during the late ontogeny in *C. sanctus.*

We found neither size nor shape sexual dimorphism in the skeletons of subset of *C. sanctus* used in the present study (Supplementary Materials. Figs. 2 & 3).

4. Discussion

BMNHC-PH870 exhibits an overall morphology consistent with that of other confuciusornithids, including the presence of edentulous jaws, a prominent and centrally pierced deltopectoral crest of the humerus, a metacarpal I that is neither fused to the semilunate carpal

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nor to the metacarpal II, an ungual phalanx of digit II that is much smaller than the other ungual phalanges of the manus, and the proximal phalanx of digit III that is much shorter than the remaining non-ungual phalanges (Chiappe et al. 1999). Within Confuciusornithidae, BMNHC-PH870 is morphologically most similar to the coeval *Eoconfuciusornis zhengi*, sharing a slender humerus with a less dorsally developed deltopectoral crest. However, BMNHC-PH870 also shows morphological similarities with stratigraphically younger confuciusornithids. Namely, the coracoid appears to be more slender and longer than in *E. zhengi* (Zhang et al. 2008), and the interclavicular angle of the furcula is narrower in BMNHC-PH870 than in *E. zhengi* and closer to the range exhibited by *Confuciusornis* or *Chanchengornis* (Chiappe et al. 1999, Hou et al. 1999, Zhang et al. 2008). Yet, BMNHC-PH870 is distinguishable from any other confuciusornithid by its humeral morphology: the deltopectoral crest is more subrectangular than subquadrangular, extending distally more than one third of the total length of the humerus (more than in any other confuciusornithid), and while this crest is more dorsally developed than in *E. zhengi*, it is significantly less so than in stratigraphically younger confuciusornithids (Figs. 6 & 8). Additionally, the deltopectoral crest is unambiguously pierced by an oval foramen (Figs. 2,3,4 & 8), absent in *E. zhengi*, that is much smaller than in any other Confuciusornithidae with pierced humeri (Hou et al. 1999, Chiappe et al. 1999) (Figs. 8).

Shape analysis underpins these observations, clearly indicating that the humerus of BMNHC-PH870 is morphologically intermediate between *E. zhengi* and the stratigraphically

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younger confuciusornithids, yet it exhibits a distinct morphology from either of these taxa (Fig. 6). Furthermore, BMNHC-PH870 is substantially different to similarly-sized and smaller specimens of *Confuciusornis* (Figs. 6 & 8). *C. feducciai* and *J. zhangjiyingia* fall within the morphological variability of *C. sanctus* (Fig. 6 & 7), thus sustaining arguments arguing for the synonymy of the former with the latter. Importantly, within the morphospace, confuciusornithids are clearly separated from any other avian and non-avian lineage included in the present study, even though some basal ornithuromorphs exhibit similar, yet distinct, humeral morphologies to the early confuciusornithids BMNHC-PH870 and *E. zhengi* (Fig. 6).

The complete fusion of compound bones—scapulocoracoid, tarsometatarsus, tibiotarsus, and the complex semilunate-metacarpals II-III (Figs. 2, 3, 4 & 5)—indicate that BMNHC-PH870 corresponds to an osteologically mature individual. These bones are not fused in the holotype of *E. zhengi*, which together with the coarse periosteal surfaces of its long bones support the interpretation of this specimen as an immature individual (Zhang et al. 2008). The other morphological differences indicated above between BMNHC-PH870 and *E. zhengi* might be explained as changes within an ontogenetic series, thereby suggesting that BMNHC-PH870 might be an adult individual of *E. zhengi*. However, multivariate regressions of humeral shape on centroid size for the subset of differently sized *C. sanctus* specimens showed that humeral shape in this species did not undergo substantial change during late ontogenetic growth. Also, there is no evidence indicating that juvenile specimens of *C. sanctus* lacked humeral fenestration and our

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data do not show any ontogenetic widening of this structure in this species (Fig. 8). Furthermore, our analysis confirmed previous results (Marugán-Lobón et al. 2011) indicating that long bone growth in *C. sanctus* was largely isometric, not allometric (Fig. 7). Interestingly, however, the morphology of the humerus in BMNHC-PH870 is clearly different from that of *E. zhengi* and from that of smaller or similarly sized, geologically younger confuciusornithids (Figs. 6,7 & 8). Assuming a similar ontogenetic growth trajectory for the humerus of *C. sanctus* and other confuciusornithid species, our results suggest that BMNHC-PH870 is neither an adult *E. zhengi* nor a juvenile *Confuciusornis*. Our findings stress the distinctiveness of BMNHC-PH870 within Confuciusornithidae and open the possibility that this fossil may represent a different taxon from *E. zhengi*. Nonetheless, the limited number of confuciusornithid fossils from the Huajiying Formation does not allow us to clearly discriminate whether the differences between BMNHC-PH870 and the holotype of *E. zhengi* are part of an unrecognized intraspecific ontogenetic disparity.

This uncertainty notwithstanding, the similarities in the humeral anatomy of BMNHC-PH870 and *E. zhengi*—and the differences between these early confuciusornithids and later confuciusornithids—reinforce the view that the confuciusornithids from the Huajiying Formation are anatomically distinct from those of the Yixian Formation (Figs. 6 & 8) (Zhang et al. 2008), and perhaps more diverse than previously recognized. The discovery of BMNHC-PH870 adds to the known early diversity of confuciusornithids, filling a gap in the morphological variation of

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this clade. This new fossil, and our quantitative analyses, suggests that the unique humeral anatomy of confuciusornithids likely evolved in a stepwise fashion, perhaps entailing functional changes related to the mechanics of the wingstroke of this primitive group of short-tailed birds.

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Figure Captions

Figure 1. Stratigraphic (A) and geographic (B & C) context of the main outcrops that have yielded fossils of Confuciusornithidae. While geographically and temporally (~131-120 MYa) restricted, confuciusornithids are represented by hundreds of almost complete and articulated

specimens; these, however, belong primarily to *Confuciusornis sanctus* (Chiappe and Meng 2016, Chiappe, Marugán-Lobón, and Zhou 2008, Marugán-Lobón et al. 2011).

Figure 2. Photograph (A) and interpretative drawing (B) of the slab A of BMNHC-PH870. **Abbreviations: br,** braincase; **f,** femur; **fu**, furcula; **gb**, gastral basket; **hu**, humerus; **ma**, mandible; **mc**, metacarpal; **mt**, metatarsal; **mx,** maxilla; **npm,** nasal process of premaxilla (perforated by a rounded foramen, (Chiappe et al. 1999)); **pyg**, pygostyle; **pmx,** premaxilla; **r**, radius; **ri**, ribs; **rf**, racket-plume remigial feathers; **p?**, pisiform sesamoid carpal; **scc**, scapulocoracoid; **syn**, synsacrum; **ti**, tibia; **v**, vertebrae; **X-pX,** Xth phalanx of digit X, **X-u,** ungual phalanx of digit X.

Figure 3. Photograph (A) and interpretative drawing (B) of the slab B of BMNHC-PH870. **Abbreviations in Figure 2.** The occurrence of a subquadrangular bone next to the wrist articulation of the metacarpal III in both forelimbs suggests it might be the ulnare, re-identified as a *de novo* avian pisiform sesamoid carpal bone by (Botelho et al. 2014).

Figure 4. Anatomical details of the humerus (A, B) and the manus (C, D). . **Abbreviations: dc,** deltopectoral crest; **df,** deltopectoral foramen; **hu**, humerus; **ks,** keratinous sheath, **mc**, metacarpal; **p?**, pisiform sesamoid carpal; **scc**, scapulocoracoid; **v**, vertebrae; **X-pX,** Xth phalanx of digit X, **X-u,** ungual phalanx of digit X.

Figure 5. Anatomical details of the scapulacoracoid (A, B) and the feet (A, B). Abbreviations: mc, metacarpal; **mt**, metatarsal; **pyg**, pygostyle; **p?**, pisiform sesamoid carpal; **scc**, scapulocoracoid; **syn**, synsacrum; **ti**, tibia; **v**, vertebrae; **X-pX,** Xth phalanx of digit X, **X-u,** ungual phalanx of digit X.

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Figure 6. Landmark configuration of the humerus used in the geometric morphometric analyses (B), PC1-3 humeral morphospace (C) and simplified phylogenetic relationships (A). Landmarks definition: 1, Middle point of the head of the humerus; **2,** Distal end of the deltopectoral crest of the humerus; **3,** Middle point of dorsal condyle; **4,** Middle point of ventral condyle. **B.** This morphospace accounts for ~80% of total variance. Shaded areas represent approximate shape space occupancy of confuciusornithids from Huajiying Fm. (bluish) and Yixian Fm. (grey). *Holotype of *C. feducciai*, **holotype of *J. zhangjiyingia*.

Figure 7. Multivariate regression of humeral shape on size (log-centroid size) in the subset of 38 specimens of *C. sanctus.* The sample includes the holotypes of *C. feducciai* and *J.zhangjiyingia*. Significant but weak allometry in the humerus during late-ontogeny growth in *C. sanctus*.

Figure 8. Outline drawings of the humeri of the known diversity of Confuciusornithidae. The humeral anatomy of the confuciusornithids from the Huajiying Formation is clearly different to that of confuciusornithids from the younger Yixian Formation. Noteworthy is the difference in morphology even between similarly-sized specimens. The arrow and the question mark represent the unclear systematic relationship between BMNH-PH870 and *E. zhengi*. The high size variance within *C. sanctus* is highlighted.

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Element	BMNHC-PH870		*E. zhengi* (IVPP V11977)		*C. dui* holotype *	*C. sanctus/small* (Berlin)	*C. sanctus/*big (BSP 1999 I 15)
Chord lengths	**Right**	**Left**	**Right**	**Left**			

Skull	46.520	-	42.430	-	39.310	54.510	64.740
Clavicular blade	16.210	15.580	11.780	12.190	-	16.780	-
Interclavicular angle	64.640	-	78.000	-	-	-	-
Scapula	-	-	-		34.590	40.729	-
Coracoid	14.440	-	-	-	-	-	-
Pygostyle	25.500	-	-	24.850	21.200	23.500	34.213
Humerus	46.650	46.470	39.690	32.44 **	40.972	45.510	68.551
Ulna	-	-		35.210	34.066	41.717	58.037
Radius	36.400	40.410	-	32.770	35.950	-	57.797
Metacarpal I	-	7.360	-	6.290	7.034	-	10.649
Metacarpal II	-	24.150	-	19.120	19.699	-	31.902
Metacarpal III	-	22.770	-	16.220	14.060	-	28.194
I, pI	-	17.870	-	16.230	15.660	14.930	24.091
I, ungual	-	9.410	8.890	-	8.190	10.3	15.530
II, pI	-	17.120	15.360	-	-	17.338	22.951
II, pII	-	18.650	15.810	-	15.879	18.938	25.092
II, ungual	-	4.700	3.580	-	-	4.280	4.610
III, pI	-	-	3.000	3.110	3.198	-	5.771
III, pII	-	-	9.620	9.630	8.730	11.810	14.439
III, pIII	-	12.750	11.040	7.890	11.036	13.060	18.064
III, ungual	-	7.040	5.150	-	8.170	7.270	10.740
Femur	40.970	-	37.330	35.530	35.480	41.714	59.467
Tibia/tibiotarsus	51.840	-	44.340	43.490	40.410	48.884	70.241
Metatarsal I	5.240	5.410	4.090	4.180	-	4.108	6.648
Metatarsal II	21.680	22.210	20.380	18.850	17.161	21.137	26.875
Metatarsal III	24.770	25.680	-	22.280	19.504	23.460	31.820
Metatarsal IV	22.540	23.610	-	20.700	18.196	21.804	30.873
Ratio Metatarsal III/ tibia	0.478	-	-	0.512	0.483	0.480	0.453

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I, pI	3.570	-	3.560	3.960	-	5.036	6.650
I, ungual	-	-	3.780	4.040	3.370	5.190	7.240
II, pI	4.830	-	4.910	5.060	5.067	6.063	7.736
II, pII	6.600	-	6.870	6.150	5.370	6.547	9.811
II, ungual	5.810	-	5.900	6.050	-	6.630	8.570
III, pI	6.270	-	6.230	6.150	4.429	6.633	8.401
III, pII	4.990	6.100	4.590	4.960	4.131	5.419	6.991
III, pIII	5.120	5.900	4.740	5.710	4.969	6.331	7.443
III, ungual	-	6.930	-	4.680	-	6.720	-
IV, pI	4.280	3.910	3.590	3.540	-	4.440	5.695
IV, pII	2.950	4.100	3.030	2.770	-	3.772	4.688
IV, pIII	3.020	-	2.830	2.550	3.250	3.142	4.403
IV, pIV	3.640	-	4.090	4.220	-	4.444	6.038
IV, ungual	5.470	-	-	4.270	-	5.850	9.160
Shaft widths							
Humerus	4.300	4.350	2.98 **	-	4.540	4.770	7.720
Ulna	-	-	-	-	2.190	-	5.350
Radius	1.990	1.890	-	-	1.560	-	2.870
Manus/humerus	**1.391**		**1.35726883**				**1.233464036**

*** cast specimen**

**** broken or damaged element**

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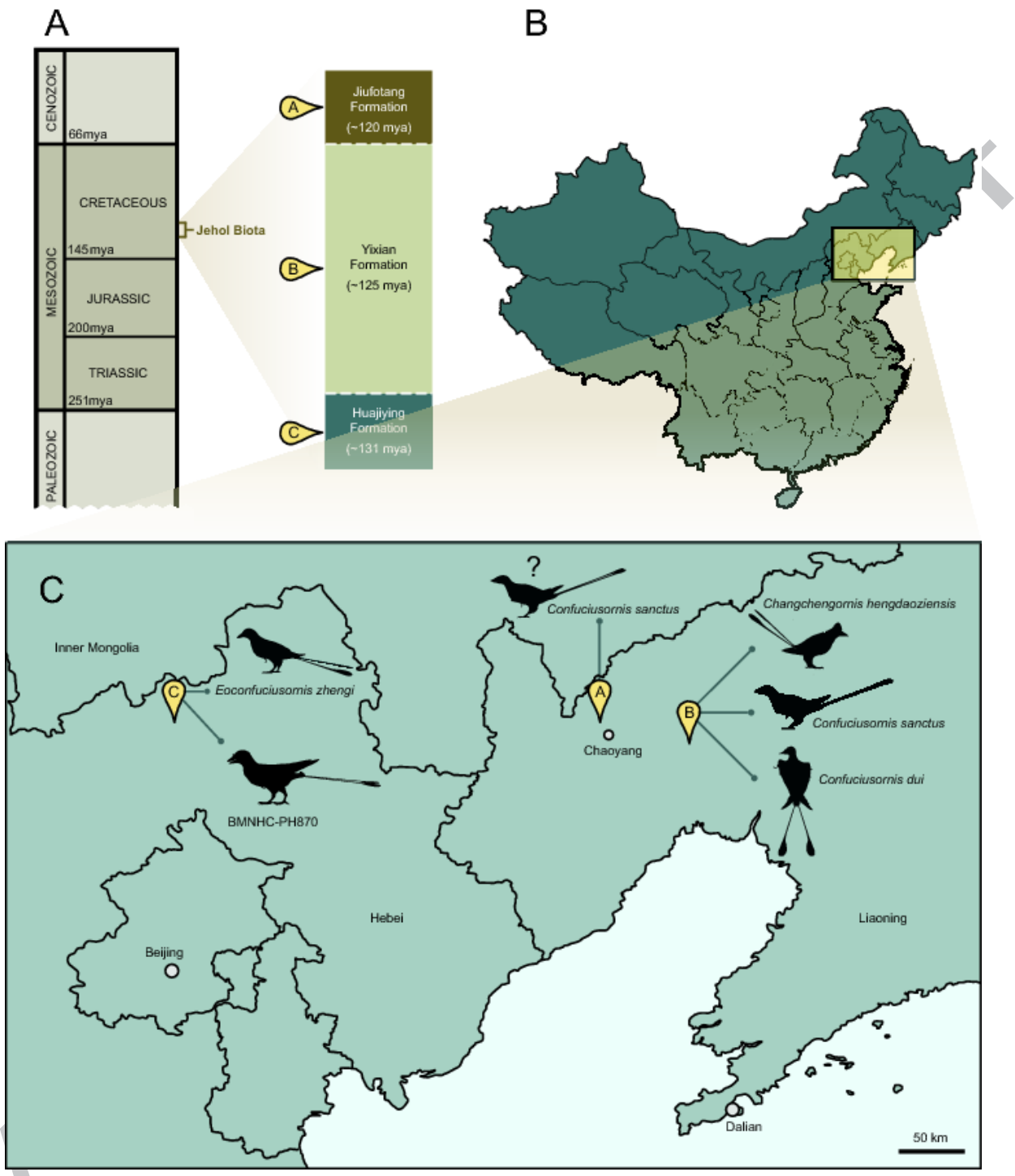
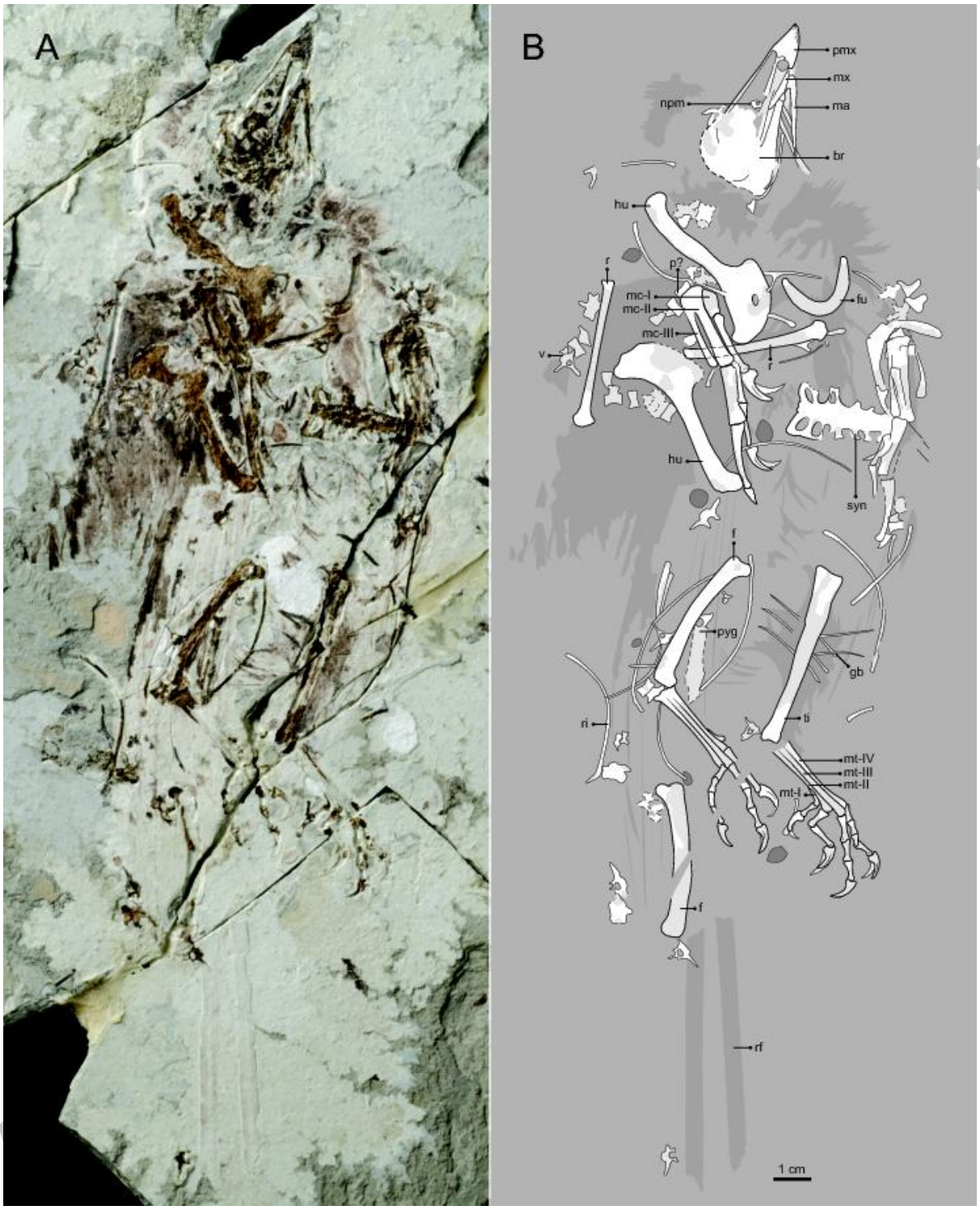
Table 1.

Table of comparative measurements (in mm) of BMNHC-PH870, the holotypes of *E. zhengi* and *C. dui* (cast specimen) and two specimens of *C. sanctus*


A
CENOZOIC
66mya
MESOZOIC
CRETACEOUS
145mya
JURASSIC
200mya
TRIASSIC
251mya
PALEOZOIC
Jehol Biota
A
Jiufotang Formation (~120 mya)
B
Yixian Formation (~125 mya)
C
Huajiying Formation (~131 mya)
B
C
Inner Mongolia
Eoconfuciusornis zhengi
BMNHC-PH870
?
Confuciusornis sanctus
Chaoyang
Changchengornis hengdaoziensis
Confuciusornis sanctus
Confuciusornis dui
Hebei
Beijing
Liaoning
Dalian
50 km


A
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mt-III
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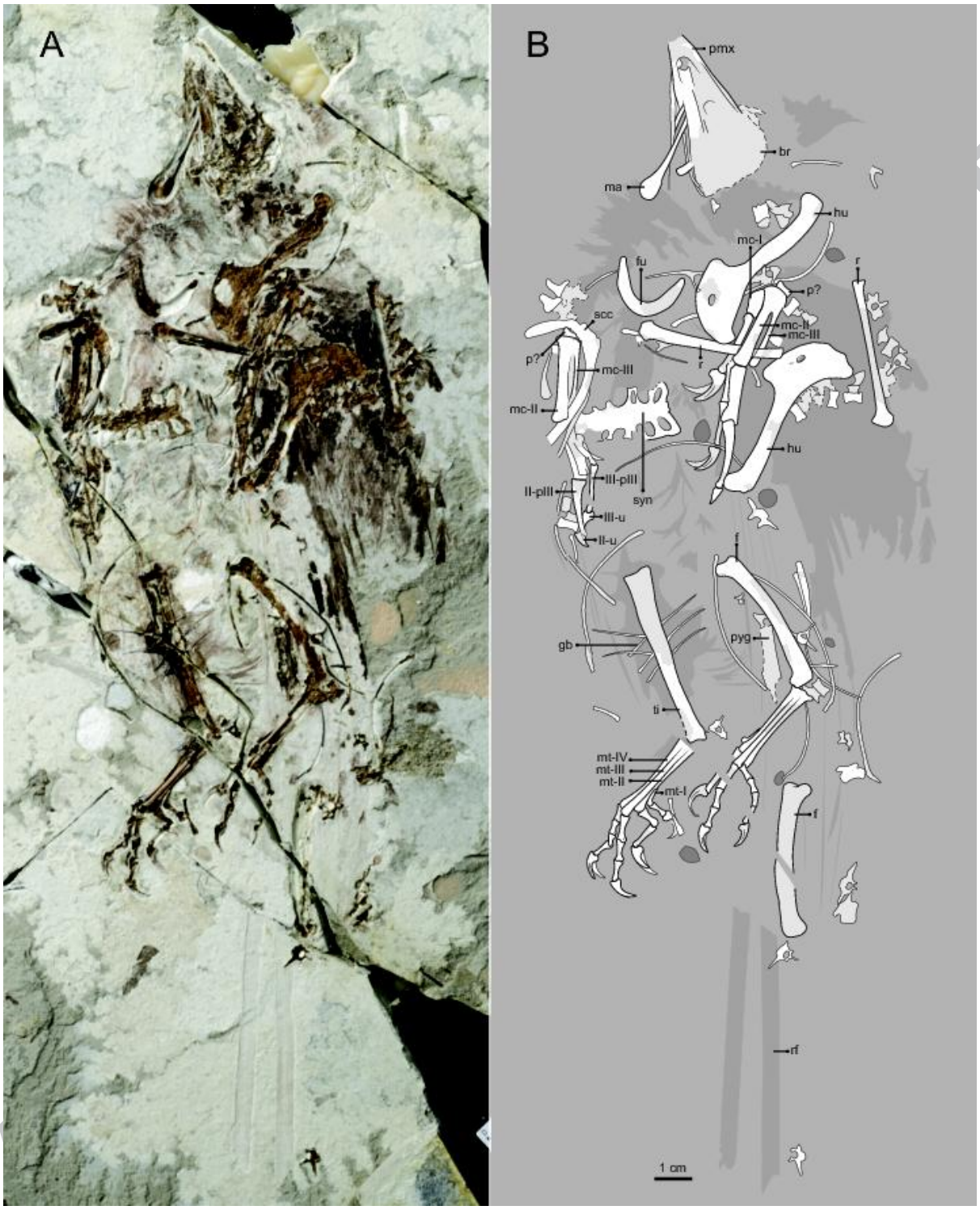
1 cm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p?
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hu
III-pIII
II-pIII
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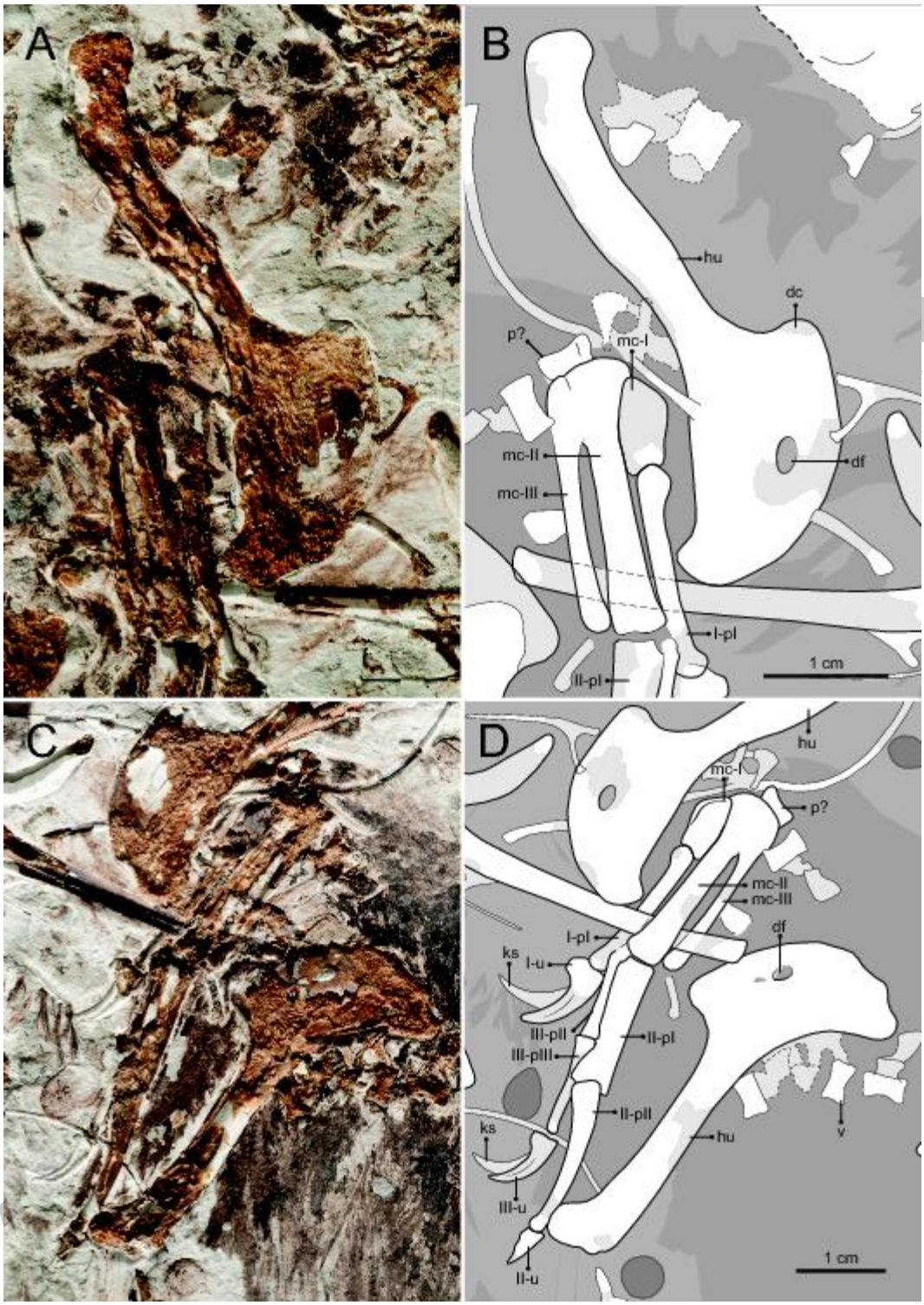
1 cm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1 cm
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mc-III
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II-pI
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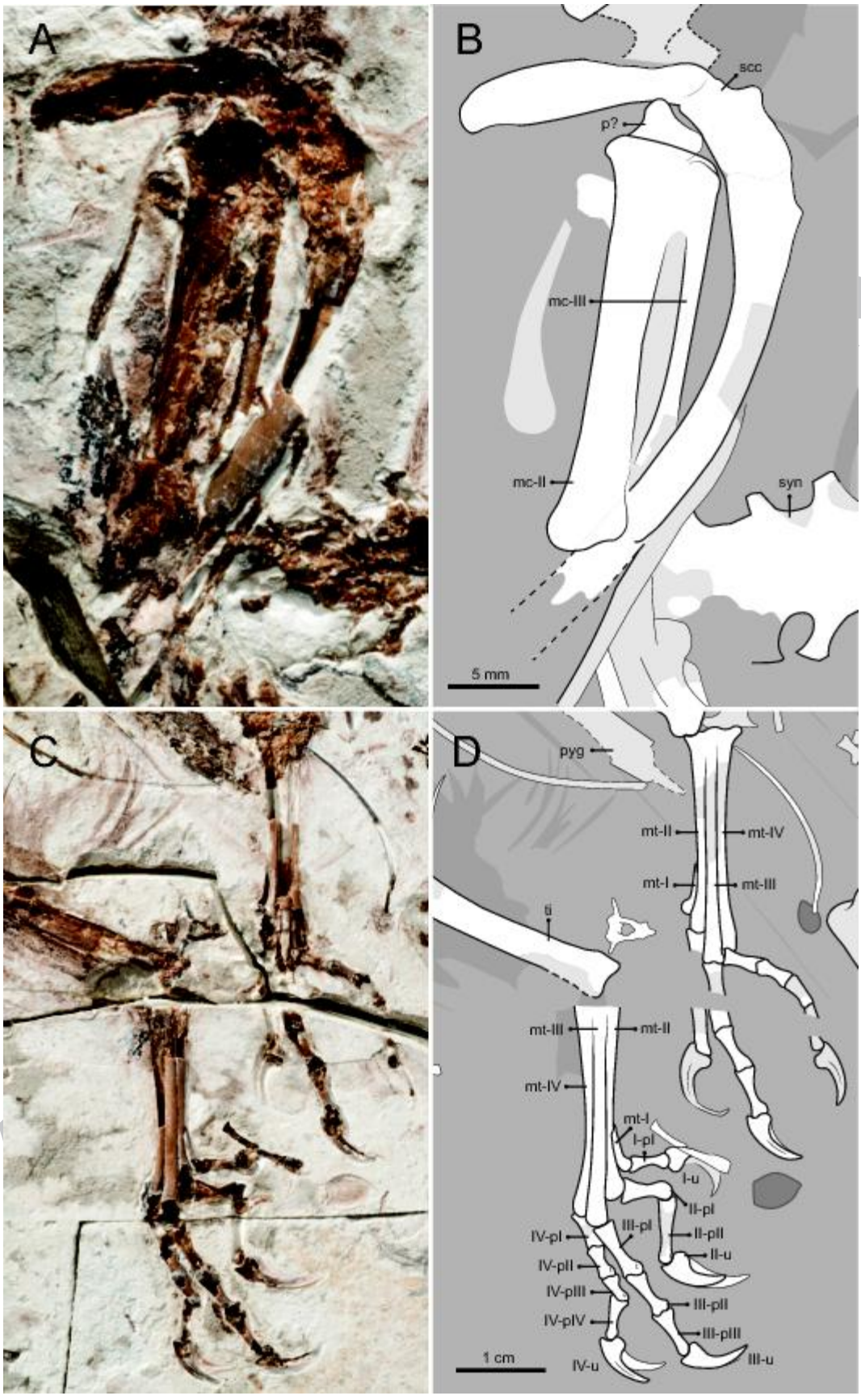
II-u
1 cm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B
scc
p?
mc-III
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syn
5 mm
C
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pyg
mt-II
mt-IV
mt-I
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ti
mt-III
mt-II
mt-IV
mt-I
I-pl
I-u
II-pl
III-pl
IV-pI
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IV-pII
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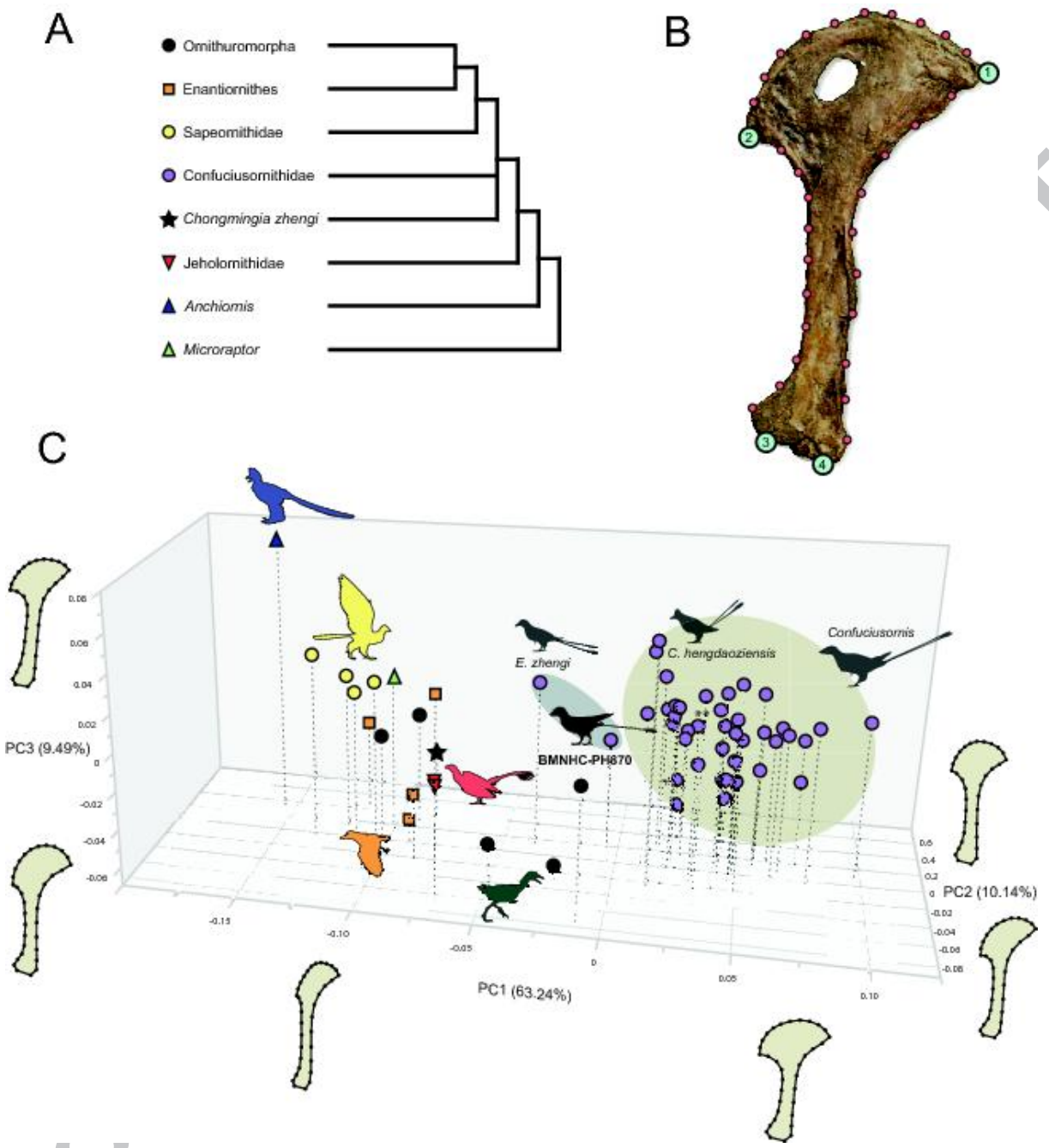
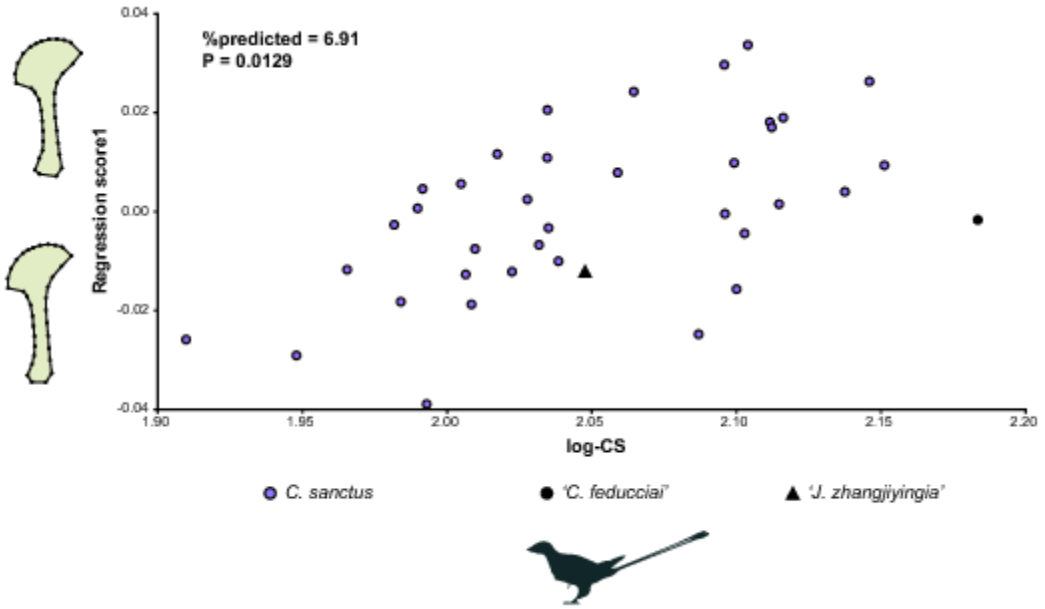
IV-pIV
III-pIII
1 cm
IV-u
III-u


A
Ornithuromorpha
Enantiornithes
Sapeomithidae
Confuciusornithidae
Chongmingia zhengi
Jeholornithidae
Anchiornis
Microraptor
B
1
2
3
4
C
PC3 (9.49%)
PC1 (63.24%)
PC2 (10.14%)
E. zhengi
C. hengdaoziensis
Confuciusornis
BMNHC-PH870



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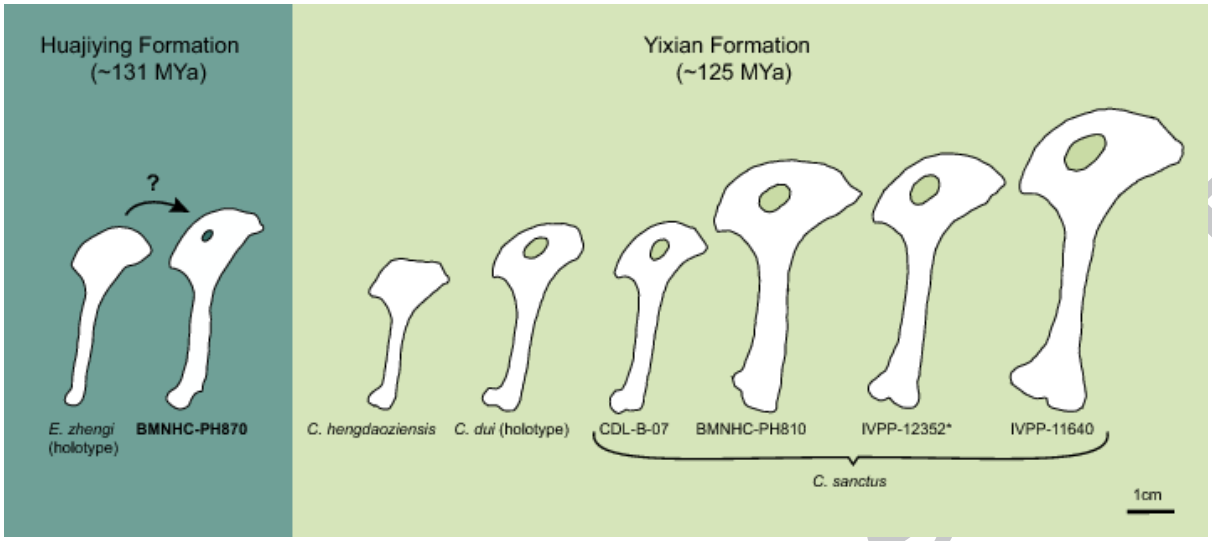

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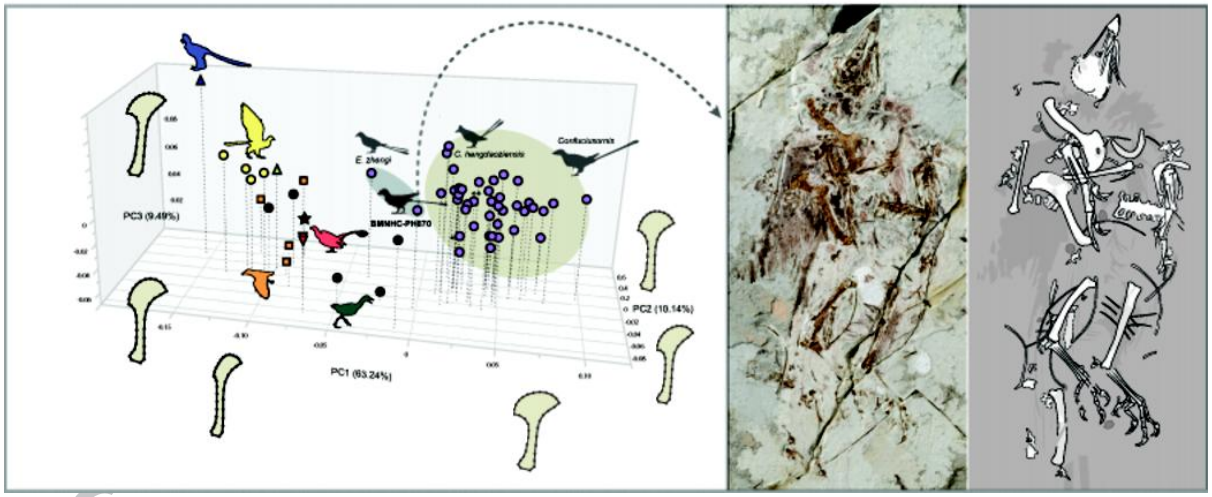
Graphical abstract



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Highlights

- **We describe an adult specimen of a confuciusornithid bird from the Huajiying Formation of the Jehol Biota, which contains the earliest representatives of the clade.**

- **The new fossil is most similar to the synchronic but immature *Eoconfuciusornis zhengi*, supporting the validity of the latter taxon.**

- **The confuciusornithids from the early (Huajiying Formation) and late (Yixian Formation and Jiufotang Formation) Jehol Biota are morphologically distinct from each other.**

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