

# **A new specimen of the Early Cretaceous bird *Hongshanornis longicresta*: Insights into the aerodynamics and diet of a basal ornithuromorph**

The discovery of *Hongshanornis longicresta*, a small ornithuromorph bird with unusually long hindlimb proportions, was followed by the discovery of two closely related species, *Longicrusavis houi* and *Parahongshanornis chaoyangensis*. Together forming the Hongshanornithidae, these species reveal important information about the early diversity and morphological specialization of ornithuromorphs, the clade that contains all living birds. Here we report on a new specimen (DNHM D2945/6) referable to *Hongshanornis longicresta* that contributes significant information to better understand the morphology, trophic ecology, and aerodynamics of this species, as well as the taxonomy of the Hongshanornithidae. Most notable are the well-preserved wings and feathered tail of DNHM D2945/6, which afford an accurate reconstruction of aerodynamic parameters indicating that as early as 125 million year ago, basal ornithuromorphs had evolved aerodynamic surfaces comparable in size and design to those of many modern birds, and flight modes alike to those of some small living birds.

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## 18 Introduction

19           Until the recent discoveries from the Jehol Group (Zhou & Zhang, 2007; Chiappe, 2007;  
20 O'Connor, Chiappe & Bell, 2011; Zhou, Zhou & O'Connor, 2012) and other Early Cretaceous  
21 sites (You et al., 2006) in northern China, the morphological and taxonomical diversity of the  
22 basal Ornithuromorpha—which advanced members include all living birds—remained one of the  
23 most poorly understood chapters of avian evolutionary history. The global record of these  
24 Cretaceous birds was sparse and limited to either incompletely known taxa such as *Ambiortus*  
25 *dementjevi* (Kurochkin, 1982), *Vorona berivotrensis* (Forster et al., 1996), or *Ichthyornis dispar*  
26 (Marsh, 1880; Clarke, 2004), or highly specialized forms such as the flightless *Patagopteryx*  
27 *deferrariisi* (Alvarenga & Bonaparte, 1992; Chiappe, 2002) and the foot-propelled diving  
28 hesperornithiforms (Marsh, 1880; Martin & Tate, 1976). The abundant discoveries from the  
29 Early Cretaceous Jehol Group of northern China have resulted in the recognition of a diversity of  
30 basal ornithuromorph taxa (e.g., *Yanornis martini*, *Yixianornis grabau*, *Gansus yumenensis*,  
31 *Hongshanornis longicresta*, *Archaeorhynchus spathula*, *Longicrusavis houi*, *Parahongshanornis*  
32 *chaoyangensis*, *Jianchangornis microdonta*, *Schizooura lii*, *Piscivoravis lii*) (Zhou & Zhang,  
33 2001, 2005, 2006; Clarke, Zhou & Zhang, 2006; You et al., 2006; Zhou, Zhang & Li, 2009;  
34 O'Connor, Gao & Chiappe, 2010; Li et al., 2010; Zhou, Zhou & O'Connor, 2012, 2013a), which  
35 are known by nearly complete specimens (albeit for the most part preserved bi-dimensionally)  
36 and in some instances by multiple specimens (e.g., *Yanornis martini*, *Gansus yumenensis*,  
37 *Archaeorhynchus spathula*). These specimens have significantly helped to refine our  
38 understanding of basal ornithuromorph morphology but despite these recent advances,  
39 specimens of these birds remain relatively rare, the vast majority of the Chinese Early  
40 Cretaceous birds belong to more primitive groups such as Enantiornithes and basal pygostylians  
41 (e.g., Confuciusornithidae, Sapeornithidae).

42 Among the newly unearthed avifauna of Chinese basal ornithuromorphs are the  
43 hongshanornithids, which are particularly noticeable because of their small size (Table 1) and  
44 because they are the only lineage of basal ornithuromorphs known from both the Yixian and  
45 Jiufotang formations of the Jehol Group. Originally recognized by the discovery of the holotype  
46 of *Hongshanornis longicresta* (Zhou & Zhang, 2005), subsequent discoveries have added the  
47 closely related species *Longicrusavis houi* (O'Connor, Gao & Chiappe, 2010) and  
48 *Parahongshanornis chaoyangensis* (Li, Wang & Hou, 2011). To date, while two additional  
49 specimens of *Hongshanornis longicresta* have been recognized in the literature (Li, Zhou &  
50 Clarke, 2011; Zheng et al., 2011), the published anatomical information on this taxon is still  
51 limited to the preliminary description of the holotype, which skeleton is entirely preserved as  
52 voids on two slabs (Zhou & Zhang, 2005). Here we provide a detailed description of the  
53 anatomy of another specimen of *Hongshanornis longicresta*, DNHM D2945/6 (Figs. 1-4), which  
54 preservation provides critical evidence for understanding better the morphology and function of  
55 these birds. Furthermore, despite the new discoveries of basal ornithuromorphs, the integument  
56 of these birds has remained poorly known in comparison to other basal avians from the Jehol  
57 Biota, in particular what refers to the rectricial morphology (Zhou, Zhou & O'Connor, 2012).  
58 The complete wing and tail surfaces of DNHM D2945/6, which arguably boasts one of the best-  
59 preserved fan-shaped tail from the Mesozoic, reveals important new information about the  
60 integumentary evolution and flight capabilities of basal ornithuromorphs.

## 61 **Materials and Methods**

### 62 Taphonomy and Preservation

63 DNHM D2945/6 is contained in a slab (DNHM D2945) (Figs., 1, 2) and counterslab  
64 (DNHM D2946) (Figs., 3, 4), its bones preserved in a semi-three dimensional state and partially

65 split between the two slabs. Such preservation differs from that of the holotypes of  
66 *Hongshanornis longicresta* (IVPP V14533) and *Longicrusavis houi* (PKUP 1069), which are  
67 preserved as voids (even if in a slab and counterslab). Such difference in preservation permits to  
68 elucidate morphologies that were obscured in the void-preserved IVPP V14533 and PKUP 1069.  
69 DNHM D2945/6 was mechanically prepared by the staff of the Natural History Museum of Los  
70 Angeles County, who can verify that the specimen is entirely original.

### 71 Locality and Stratigraphy

72 DNHM D2945/6 was collected from the lacustrine deposits of the Yixian Formation at  
73 the Dawangzhangzi locality near Lingyuan (Liaoning Province, China), the same locality that  
74 yielded the holotype (PKUP 1069) of the closely related *Longicrusavis houi* (O'Connor, Gao &  
75 Chiappe, 2010). The holotype of *Hongshanornis longicresta* (IVPP V14533) comes from the  
76 Shifo locality near Ningcheng (Inner Mongolia, China) and also from the Yixian Formation  
77 (Zhou & Zhang, 2005), and is separated from the Dawangzhangzi locality by a distance of  
78 approximately 60 km. The stratigraphic and geographic location of other specimens reported as  
79 belonging to *Hongshanornis longicresta* has not been provided in the publications that make  
80 reference to these specimens (Li, Zhou & Clarke, 2011; Zheng et al., 2011). The holotype of  
81 *Parahongshanornis chaoyangensis* (PMOL-AB00161) is from the younger Jiufotang Formation  
82 in Yuanjiawa Town, Chaoyang City (Liaoning Province, China) (Li, Wang & Hou, 2011), thus  
83 this specimen is 3 to 5 million years younger (see Swisher et al., 2002; Yang, Li & Jiang, 2007;  
84 Chang et al. 2009) than the Yixian hongshanornithids and separated by approximately 100 km  
85 from either Dawangzhangzi or Shifo.

### 86 Aerodynamic Parameters

87 The aerodynamic parameters and definitions used here follow Pennycuik (2008).  
88 Accordingly, wingspan (**B**) is defined as the distance from one wing tip to the other, with the  
89 wings fully stretch out to the sides. Wing area (**S**<sub>wing</sub>) is the area of both wings as they are laid  
90 on a flat surface, and including the part of the body between the wings. Aspect ratio is the ratio  
91 of the wingspan to the mean chord (i.e., the distance from the leading edge to the trailing edge,  
92 measured along the direction of the air flow).

93 Body mass estimates for DNHM D2945/6, based on femoral length, vary substantially  
94 according to the different equations provided by Maloiy et al. (1979), Alexander [1983; as listed  
95 by Hone et al. (2008)], and Peters & Peters (2009). Maloiy et al.'s (1979) equation results in an  
96 unrealistically low body mass, approximately 12 g, comparable to that of many warblers  
97 (Dunning, 2008). The equations of Alexander (1983) and Peters & Peters (2009) result in more  
98 likely estimates, 50 g and 64 g, respectively, more comparable to the body mass of some  
99 cowbirds (e.g., *Molothrus bonariensis*, *Molothrus rufoaxillaris*) and orioles (e.g., *Icterus*  
100 *chrysater*, *Icterus gularis*) (Dunning, 2008). The mean value of these three estimates is 42 g.

## 101 Institutional Abbreviations

102 DNHM, Dalian Natural History Museum, Dalian, China; PKUP, Peking University,  
103 Beijing, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing,  
104 China; STM, Tianyu Museum of Nature, Tianyu, China.

## 105 Results

### 106 Description

107 In this description we primarily highlight morphological information from the new  
108 specimen (DNHM D2945/6) that either supplements or contradicts the description of the

109 holotype (Zhou & Zhang, 2005). Anatomical nomenclature mainly follows Baumel & Witmer  
110 (1993); certain structures not cited therein follow Howard (1929). While the Latin terminology  
111 used by Baumel & Witmer (1993) is retained for muscles and ligaments, osteological structures  
112 are described using the English equivalents of the Latin terms.

113         The entire skeleton of DNHM D2945/6 is preserved and visible in two slabs; the bones  
114 are broken between the two leaving clear voids. DNHM D2945 preserves the bones of the skull,  
115 most of the axial skeleton, right radius, major digit and tibiotarsus, and both feet (Figs. 1, 2).  
116 DNHM D2946 preserves most of the bones of the wings and thoracic girdle, both femora, the  
117 left tibiotarsus, and the distal ends of the pubes (Figs. 3, 4).

118         **Skull.** The skull is rather poorly preserved, embedded in a well-indurated rusty  
119 concretion; the shape of the skull is well preserved, but few anatomical details can be discerned  
120 (Fig. 5). As in the holotype, the skull constricts abruptly into a low and pointed rostrum, different  
121 from the more robust rostrum of *Longicrusavis houi* (O'Connor, Gao & Chiappe, 2010).  
122 Impressions of five teeth can be clearly identified in the maxilla (Fig. 5), contradicting the  
123 previous description of *Hongshanornis longicresta* as edentulous (Zhou & Zhang, 2005; Zheng  
124 et al., 2011). Teeth were suggested for hongshanornithids on the basis of structures that appeared  
125 to be alveoli preserved in the upper jaw of *Longicrusavis houi* (O'Connor, Gao & Chiappe,  
126 2010). The presence of teeth in the premaxilla, however, cannot be determined in DNHM  
127 D2945. There are no obvious pits or scarring on the maxilla or premaxilla to indicate that a beak  
128 was present, as in the edentulous *Archaeorhynchus spathula* (Zhou & Zhang, 2006; Zhou, Zhou  
129 & O'Connor, 2013b).

130         The mandibular symphyseal ossification (prementary bone of Zhou & Martin, 2011) is  
131 visible as a void in DNHM D2945. The fragmentary remains of two to four teeth are preserved  
132 set in the dentary. This confirms the presence of teeth in the dentary of hongshanornithids, which

133 was hypothesized by O'Connor, Gao & Chiappe (2010). Crowns cannot be discerned, but the  
134 dentary teeth appear to be smaller than those preserved in the maxilla. The dentary is caudally  
135 unforked and unfused to the surangular, as in other basal ornithuromorphs.

136 **Axial Skeleton.** The cervical vertebrae are poorly preserved, revealing little more than  
137 the remnants of low neural spines. The anterior dorsal vertebrae (visible in ventral view in  
138 DNHM D2945) bear compressed centra lacking ventral processes; the posterior dorsals have  
139 thicker centra. The articulations are amphiplatan or amphicoelic and the elements are not fused  
140 in a notarium. The lateral surfaces of the dorsal vertebrae are excavated by a broad fossa, as in  
141 other basal ornithuromorphs (e.g., *Yanornis martini*, *Longicrusavis houi*).

142 The synsacrum is incomplete and broken between the two slabs (dorsally exposed in  
143 DNHM D2946 and ventrally exposed in DNHM D2945) (Figs. 1-4). A number of well-  
144 differentiated costal processes project from the side of the synsacrum—these processes have  
145 expanded distal ends for their attachment to the ilium. Judging by the number of costal processes  
146 articulated to the ilium, the synsacrum was composed of no less than nine vertebrae (the  
147 synsacral count cannot be determined in either the holotype of *Hongshanornis longicresta* or  
148 *Longicrusavis houi*), which is comparable to other basal ornithuromorphs and more than is  
149 typical of the more primitive enantiornithines (Chiappe, 1996). The ventral surface of the  
150 synsacrum (anterior half preserved in DNHM D2945) is smooth, lacking a distinct groove (e.g.,  
151 *Archaeorhynchus spathula*, *Patagopteryx deferrariisi*). Dorsally, the portion of synsacrum  
152 preserved in slab DNHM D2946—corresponding largely to the postacetabular portion—is  
153 longitudinally scarred by a pair of shallow grooves.

154 At least four uncinat processes can be discerned, including one that is completely  
155 preserved (DNHM D2946). These ossifications are long (extending across two ribs) with broad  
156 bases and tapered outlines (Fig. 6). The uncinat processes appear not to be fused to the ribs, as

157 in the holotype. Several ventral ribs are preserved in articulation with the sternum (DNHM  
158 D2946). The proximal ends of the thoracic ribs are very robust, the expanded proximal portion  
159 abruptly narrows towards the much thinner shaft (Fig. 6).

160         **Appendicular Skeleton.** The furcula is delicate and U-shaped as in many other basal  
161 ornithuromorpha (e.g., Clarke, Zhou & Zhang, 2006; You et al., 2006; Zhou, Zhang & Li, 2009;  
162 Zhou, Zhou & O'Connor, 2013b). The interclavicular angle is estimated to be between 45° (Fig.  
163 6). The rami are transversely compressed proximally, becoming more dorsoventrally compressed  
164 and wider towards the symphysis. The caudal surface of the bone exhibits a distinct trough  
165 running along the distal half of the rami and converging towards the symphyseal region. The  
166 proximal compression and caudal groove of the furcula of DNHM D2946 are comparable to that  
167 reported by Li, Wang & Hou (2011) as a diagnostic characters of *Parahongshanornis*  
168 *chaoyangensis*. The presence of these conditions in DNHM D2946 indicates that such characters  
169 are unlikely to be diagnostic of the latter taxon. A cross section of the furcula in slab DNHM  
170 D2945 indicates the bone may have been hollow. No long hypocleidium like that reported in the  
171 holotype of *Hongshanornis longicresta* (IVPP V14533) is visible but the symphyseal region of  
172 DNHM D2945/46 is covered by the distal portion of the left coracoid, thus making it unclear if a  
173 hypocleidium was present or not. The similarity between the furcula of DNHM D2945/46 and  
174 that of *Longicrusavis houi* and *Parahongshanornis chaoyangensis*, taxa lacking a long  
175 hypocleidium and possessing only a small tubercle at the symphysis (O'Connor, Gao & Chiappe,  
176 2010; Li, Wang & Hou, 2011), suggests that the furcula of hongshanornithids possibly lacked a  
177 well-developed hypocleidium.

178         The sternum, primarily preserved in DNHM D2946 in dorsal view, has a slightly rounded  
179 cranial margin (Fig. 6). Distally on the left side of the sternum, a bony bar with a terminal  
180 expansion is preserved. Damage makes it difficult to interpret this region of the sternum. One

181 alternative is that this bar corresponds to a slightly displaced, lateral trabecula with an expanded  
182 distal end; the lateral trabecula of the sternum of various basal ornithuromorphs (e.g.,  
183 *Archaeorhynchus spathula*, *Jianchangornis microdonta*, *Yixianornis grabaui*, *Yanornis martini*)  
184 is distally expanded in varying degrees (Zhou, Zhou & O'Connor, 2013b). Alternatively, it may  
185 represent the lateral margin of a sternal fenestra, such as those present in the basal  
186 ornithuromorphs *Songlingornis linghensis*, *Yixianornis grabaui*, and *Yanornis martini* (Clarke,  
187 Zhou & Zhang, 2006; Zhou, Zhou & O'Connor, 2013b), a feature apparently absent in the  
188 sternum of the holotype of *Hongshanornis longicresta*. Zhou & Zhang (2005) described the  
189 sternum of the latter with lateral processes lacking a distal expansion; however the sternum of  
190 this specimen is too poorly preserved to confidently support the absence of such expansion.

191         The strut-like coracoids articulate adjacent to each other on the cranial margin of the  
192 sternum, nearly touching each other if not slightly overlapping (Fig. 6). There is a depression  
193 (possibly corresponding to the impression of the *m. sternocoracoidei* of modern birds) on the  
194 dorsal surface of the sternal half of these bones (also present in Jehol ornithuromorphs such  
195 *Jianchangornis microdonta* and *Yixianornis grabaui*). This feature in ornithuromorphs is not as  
196 pronounced as the dorsal fossa that excavates the coracoids of many Late Cretaceous  
197 enantiornithines (Chiappe & Walker, 2002). The proximal ends of the coracoids are poorly  
198 preserved so that a procoracoid process cannot be identified—the presence of this process in  
199 *Hongshanornis longicresta* is not as clear as was suggested by Zhou & Zhang (2005) and  
200 remains equivocal in this taxon. However, a procoracoid process is known in almost every other  
201 Early Cretaceous ornithuromorph (e.g., *Jianchangornis microdonta*, *Yixianornis grabaui*,  
202 *Yanornis martini*, *Gansus yumenensis*) (Zhou & Zhang, 2001; Clarke, Zhou & Zhang, 2006; You  
203 et al., 2006; Zhou, Zhou & O'Connor, 2012). The body of the coracoid exhibits no evidence of  
204 either a supracoracoid nerve foramen or medial notch (*incisura n. supracoracoidei*). Both the

205 lateral and medial borders of this bone are clearly concave, indicating that the convex lateral  
206 margin described by Zhou & Zhang (2005) for the poorly preserved holotype is incorrect. A  
207 lateral process is present; its squared off morphology is consistent with that of other Early  
208 Cretaceous ornithuromorphs (e.g., *Ambiortus dementjevi*, *Yixianornis grabau*, *Gansus*  
209 *yumenensis*) (Clarke, Zhou & Zhang, 2006; Kurochkin, 1982; You et al., 2006).

210 Both humeri are exposed in caudal view in DNHM D2946 (Fig. 6). The head is prominent  
211 —largely projected caudally—and proximally flat. Such design is more reminiscent to that of the  
212 humeral head of *Patagopteryx deferrariisi* and other basal ornithuromorphs (i.e.,  
213 *Archaeorhynchus spathula*, *Jianchangornis microdonta*) and it differs from the domed-head of  
214 modern birds (Chiappe, 2002). The proximal third of the humerus appears to be very broad,  
215 expanded as in the holotype of *Hongshanornis longicresta*, *Ichthyornis dispar* and *Ambiortus*  
216 *dementjevi* (Kurochkin, 1985; Clarke, 2004) (Fig. 6). The caudal surface is not perforated by a  
217 pneumotricipital foramen and the pneumotricipital fossa is minimally developed. A distinct  
218 furrow—presumably the capital incisure—separates the ventral margin of the head from the  
219 ventral tubercle. Ventral to the latter, on the ventroproximal corner (and the bicipital area) of the  
220 bone, there is a shallow circular depression also present in *Ichthyornis dispar*, possibly  
221 corresponding to the attachment site of the *m. pectoralis superficialis* (Clarke, 2004). The  
222 deltopectoral crest is large—extending longitudinally for more than 1/3 the length of the bone  
223 (Fig. 6)—and rounded, lacking the cranial deflection of more advanced ornithuromorphs  
224 (neornithines). Distally, the margin of the crest gradually diminishes along the dorsal border of  
225 the shaft, typical of Cretaceous ornithuromorphs (e.g., *Jianchangornis microdonta*, *Yixianornis*  
226 *grabau*, *Archaeorhynchus spathula*), as opposed to the rapid step-like constriction of this crest  
227 in most basal birds (e.g., *Confuciusornis sanctus*, *Sapeornis chaoyangensis*, *Rapaxavis pani*) and  
228 some basal ornithuromorphs (e.g., *Schizooura lii*, *Zhongjianornis yangi*).

229 In caudal view (DNHM D2946) the distal humeri bear no evidence of  
230 humerotricipital or scapulotricipital grooves (Fig. 6). The olecranon fossa is present but poorly  
231 developed. A well-developed dorsal supracondylar process is present, clearest on the right  
232 humerus (DNHM D2946) as in *Longicrusavis houi* (O'Connor, Gao & Chiappe, 2010) and  
233 *Ichthyornis dispar* (Clarke, 2004). The flexor process is small and poorly developed; the  
234 transversal distal margin is roughly perpendicular from the longitudinal axis of the shaft as in  
235 other ornithuromorphs, not angled as in many enantiornithines (Chiappe & Walker, 2002). The  
236 cranial surfaces of the humeri are not visible, planted in the matrix.

237 The radius is straight and roughly half the width of the ulna. The ulna, comparable in  
238 length to that of the humerus (Table1), is exposed in caudal-dorsal view. Remige papillae are  
239 absent. The olecranon process is weakly developed. Distally, the ulna's dorsal condyle is  
240 rounded in caudal view. Near its articulation with the radius, it exhibits a small circular  
241 depression that may correspond to the radial depression of living birds (Baumel & Witmer,  
242 1993).

243 The radius and ulna are in articulation with the proximal carpals and the carpometacarpus  
244 (Fig. 7). The radiale is in articulation with the radius. The left carpometacarpus, exposed dorsally  
245 in DNHM D2946, is completely fused, proximally and distally. Close to the contact between the  
246 major (II) and alular (I) metacarpals there is a raised area. Both the major (II) and minor (III)  
247 metacarpals are straight (Fig. 7). Proximally, there is a small depression on the minor metacarpal.  
248 The proximal end of the intermetacarpal space extends proximal to the level of the distal end of  
249 the alular metacarpal (Fig. 7). The alular (I) metacarpal is subrectangular. An extensor process is  
250 not absent, only minimally developed in such a way that the proximal end of the alular  
251 metacarpal is slightly more expanded than its distal end (Fig. 7), as in some other Cretaceous  
252 ornithuromorphs (e.g., *Jianchangornis microdonta*, *Gansus yumenensis*, *Yixianornis grabaui*).

253 The alular digit bears two phalanges. The second phalanx, a claw, extends slightly past  
254 the distal end of the major metacarpal, as described by Zhou & Zhang (2005) for the holotype.  
255 The major digit has three phalanges; the proximal phalanx is broad bearing a well-developed,  
256 sinusoidal lateral flange (Fig. 7). As in the holotype, the intermediate phalanx is S-shaped (Zhou  
257 & Zhang, 2005). The claw of the major digit is much smaller than that of the alular digit. The  
258 minor digit bears a single, wedge-shaped phalanx that tapers distally; *Longicrusavis houi* and the  
259 *Hongshanornis longicresta* holotype bear two phalanges on this digit, the second being  
260 extremely reduced (and not an ungual) suggesting that this small phalanx is simply not preserved  
261 in DNHM D2945/6.

262 The ilia are poorly preserved and broken between the two slabs; the left is visible in  
263 medial view in DNHM D2945, while portions of the right are preserved in DNHM D2946 in  
264 dorsal view. The preacetabular wing has a straight dorsal margin that tapers cranially. The  
265 caudal half of the ventral margin of the preacetabular wing defines a broad notch, a condition  
266 observed in other Jehol ornithuromorphs (e.g., *Archaeorhynchus spathula*, *Schizooura lii*) (Zhou,  
267 Zhou & O'Connor, 2012, 2013b).

268 A fragment of the pubis is preserved near the midshaft of the right tibiotarsus in DNHM  
269 D2946 (Figs, 1-4, 8). The distal ends of both pubes are in contact and only slightly disarticulated.  
270 They are not fused but their flat medial surfaces form a short, expanded symphysis, although a  
271 distinct 'boot', with a prominent caudal projection, like that of some enantiornithines is absent  
272 (Chiappe & Walker, 2002) (Fig. 8). The presence of this distal pubic expansion, identical to that  
273 present in *Parahongshanornis chaoyangensis*, indicates that unlike what was claimed by Li,  
274 Wang & Hou (2011), this feature is not diagnostic of the latter species. The cross-section of the  
275 shaft of the distal portion of the pubis is oval, with the main axis oriented craniocaudally. No  
276 pygostyle or caudal vertebrae are preserved in DNHM D2945/6.

277 The elongate hindlimbs are completely preserved in both slabs as partly bone and partly  
278 void (Figs. 1-4). The left femur is preserved in articulation with the left ilium in DNHM D2945  
279 —its rounded head is visible through the acetabulum, which is exposed medially. The femoral  
280 shaft is only slightly bowed craniocaudally. Its laterodistal end is exposed in DNHM D2946;  
281 similar to other Jehol ornithuromorphs (e.g., *Yixianornis grabau*), there is minimal development  
282 of the fibular trochlea and tibiofibular crest, which are developed in *Patagopteryx deferrariisi*  
283 and ornithurines (Chiappe, 2002; Clarke, 2004).

284 The tibiotarsus is more than 150% the length of the femur (tibiotarsus: femur = 1.6)  
285 (Table 1). The right element is in articulation with the fibula, which is exposed caudally in  
286 DNHM D2946. Proximally, the tibiotarsus exhibits a large, well-developed cnemial crest (Fig.  
287 9). This crest, exposed laterally in DNHM D2946, is limited proximally, and projects proximally  
288 beyond the proximal articular surface of the tibiotarsus. Its cranial edge develops into an inflated  
289 quadrangular prominence that projects laterally (Fig. 9). The morphology of this crest is  
290 comparable to that of other Early Cretaceous ornithuromorphs (e.g., *Schizooura lii*, *Yixianornis*  
291 *grabau*) (Clarke, Zhou & Zhang, 2006; Zhou, Zhou & O'Connor, 2012). This cranial  
292 prominence is separated by a lateral trough from the proximal articular surface of the tibiotarsus.  
293 It is not possible to determine whether the tibiotarsus had one or two cnemial crests; if a cranial  
294 cnemial crest were present, it would be embedded in sediment and obstructed by the lateral  
295 cnemial crest. In caudal view, the proximal fourth of the tibiotarsus is marked by a robust ridge  
296 that slants towards the proximomedial corner of the bone—this feature is not present in  
297 *Longicrusavis houi*, further distinguishing this taxon from *Hongshanornis longicresta*.

298 Distally, the tibia is largely fused to the distal tarsals, however the suture of an ample  
299 ascending process of the astragalus remains visible on both the left (DNHM D2946) and right  
300 (DNHM D2945) tibiotarsi. The distal condyles are preserved in cranial view in DNHM D2945.

301 The lateral condyle is larger than the medial condyle, as in other basal ornithuromorphs  
302 (Chiappe, 1996; Zhou & Zhang, 2006), and separated by a wide intercondylar groove (*incisura*  
303 *intercondylaris*). The cranial surface of the distal end is scarred by a deep extensor sulcus, which  
304 ends near a raised area just proximal to the intercondylar groove—a supratendinal bridge like  
305 that of more advanced ornithurines is not developed. The lateral epicondyle is minimally  
306 developed and there is only a slightly-developed, crescent-like lateral epicondylar depression.  
307 Caudally, neither the lateral or medial crests of the cartilaginous trochlea of the tibia (*trochlea*  
308 *cartilaginosa tibialis*) are developed. These crests are slightly developed in *Yixianornis grabaui*  
309 and well developed in *Apsaravis ukhaana* (Norell & Clarke, 2001; Clarke, Zhou & Zhang,  
310 2006). The fibula is very slender (Figs., 8, 9)—its distal end does not seem to extend beyond the  
311 midpoint of the tibiotarsus.

312 Both tarsometatarsi are well-exposed in cranial view in DNHM D2945. As reported in  
313 the holotype of *Hongshanornis longicresta* (Zhou & Zhang, 2005), metatarsals II-IV are  
314 completely fused to one another. The intercotylar prominence is at best minimally developed.  
315 The proximal cotyla are slightly concave—the lateral one is slightly more distally placed than  
316 the medial one. Metatarsal III is plantarly displaced so that proximally, metatarsal II and  
317 metatarsal IV form ridges defining a recess excavating the central portion of the tarsometatarsus.  
318 Such morphology is consistent with that of other basal ornithuromorphs (e.g., *Yanornis martini*,  
319 *Yixianornis grabaui*, *Gansus yumenensis*, *Ichthyornis dispar*). Inside this proximocentral recess  
320 there is a foramen located between metatarsals III and IV, and medial to it, a tubercle on  
321 metatarsal II (possibly corresponding to the *m. tibialis cranialis* tuberosity of modern birds).  
322 Metatarsal III is the longest; metatarsal IV is slightly shorter, followed by the even shorter  
323 metatarsal II (Fig. 10). Metatarsal I is robust and fairly straight, with a concave medial margin. A  
324 distal vascular foramen is located between metatarsals III and IV as in *Longicrusavis houi*; the

325 distal margin of the foramen is raised. The foramen seems to penetrate the bone at an oblique  
326 angle—from cranial to plantar surfaces. All trochleae appear to be ginglymous.

327 Digit III is the longest (Table 1); digit II is substantially shorter than IV (Fig. 10). Digit I  
328 is short and slender. All the pedal phalanges are long and slender and decrease in length distally.  
329 The phalanges of the second and third digits are approximately 2/3 the length of the preceding  
330 phalanx. The phalanges of digit IV are subequal, but still slightly decrease in length distally. The  
331 ungual phalanges bear distinct flexor tubercles. The morphology of the distal tarsometatarsus  
332 and the proportions of the pedal phalanges are consistent with cursorial function (Hopson, 2001),  
333 as in other Early Cretaceous ornithuromorphs.

334 **Plumage.** DNHM D2945/6 preserves significant portions of the plumage of the wing,  
335 tail, and around the skull and neck. The feathers preserved over the skull question the  
336 assumption that this species was characterized by the presence of a feathery crest projecting from  
337 the head (Zhou & Zhang, 2005). DNHM D2945/6 shows nothing of that sort. The relatively  
338 short feathers of the head become gradually shorter until the plumage ends at the junction of the  
339 rostrum and the orbit, thus indicating that the culmen was devoid of feathers (whether it was  
340 covered by skin or a corneous beak is unknown). Furthermore, contrary to what was suggested  
341 by Zheng et al. (2011) for another specimen putatively identified as *Hongshanornis longicresta*  
342 (STM 35-3), DNHM D2945/6 indicates that these birds had relatively broad, but long and  
343 tapered, wings (Figs. 1-4, 11).

344 The most distal primaries are clearly much shorter than the remaining primaries. Based  
345 on the well-preserved outline of the wing, our estimation of the wingspan of DNHM D2945/6 is  
346 approximately 0.32 m and the wing area is 0.016 m<sup>2</sup> (Fig. 11). There is exquisite evidence of  
347 rectrices forming a fan-like tail preserved in natural orientation, about the extended feet.

348 Although visualization of individual feathers is difficult to due overlap, the tail appears to be

349 composed of at least 10 vaned rectrices. The precise degree of asymmetry of these feathers  
350 cannot be ascertained but it is clear that none of them were strongly asymmetric (Fig. 10). The  
351 caudal margin of the feathered tail is rounded and the pair of central rectrices projects distally  
352 more than the feathers on either side, thus suggesting a gently graded tail (comparable to the one  
353 described for *Piscivoravis lii*; see Zhou, Zhou & O'Connor, 2013a). The holotype of  
354 *Hongshanornis longicresta* also shows evidence of an extensive feathered tail as a series of  
355 partially preserved vaned feathers between the feet (IVPP V14533A); these are very faint and  
356 were not described in the original description (see O'Connor, Gao & Chiappe, 2010). In the  
357 holotype of *Hongshanornis longicresta*, the tail is clearly incomplete and only four feathers can  
358 be discerned; the tail in DNHM D2945/6 appears complete. The number of preserved feathers is  
359 thus greater than the one described in the younger ornithuromorphs *Yixianornis grabaui*  
360 (minimum of eight described) and *Piscivoravis lii* (at least six described) from the Jiufotang  
361 Formation (Clarke, Zhou & Zhang, 2006; Zhou, Zhou & O'Connor, 2013a).

362 **Gastroliths.** At least 11 small geo-gastroliths are clustered in the visceral and pelvic  
363 region of DNHM D2945/6. Some of these 'stomach stones' are still in place while others are  
364 represented by the voids left on the slabs (Figs. 1-4, 8). The smallest of the stones is nearly half  
365 the size the largest (1.71 mm to 3.08 mm) with the mean being 2.2 mm (Table 2). They range in  
366 shape from subspherical to oblong. It is unclear whether gastroliths were preserved with the  
367 holotype (IVPP V14533A) although more than 50 small (~1 mm) geo-gastroliths were reported  
368 in the poorly preserved STM 35-3, a specimen identified as of *Hongshanornis longicresta* by  
369 Zheng et al. (2011). Despite the fact that Zheng et al. (2011) did not provide any anatomical  
370 evidence supporting the identification of STM 35-5 as *Hongshanornis longicresta*, the discovery  
371 of DNHM D2945/6 provides unquestionable evidence of the behavior of ingesting grit by this  
372 basal ornithuromorph species.

373 **Discussion**

374 The specimen described here, DNHM D2945/6, is indistinguishable from the holotype of  
375 *Hongshanornis longicresta* and is thus referred to this taxon. DNHM D2945/6 is from the same  
376 locality and formation (Yixian) that yielded the closely related *Longicrusavis houi* (PKVP 1069;  
377 O'Connor, Gao & Chiappe, 2010). The coexistence of these two closely related taxa in a single  
378 fauna suggests that Hongshanornithidae was a diverse component of the avifauna of the Yixian  
379 Formation.

380 DNHM D2945/6 reveals important new information regarding the morphology, diet, and  
381 ecology of *Hongshanornis longicresta* and other Early Cretaceous ornithuromorphs. The new  
382 specimen of *Hongshanornis longicresta* preserves actual fossilized bone rather than voids of  
383 bone, as in the holotype (IVPP V 14533), and as such this new specimen helps clarify the  
384 osteology of the taxon. DNHM D2945/6 documents the presence of two different skull  
385 morphologies within Hongshanornithidae. It also confirms that the upper and lower jaws of these  
386 birds were toothed, a conclusion previously suggested by morphologies preserved in the  
387 holotype of *Longicrusavis houi* (O'Connor, Gao & Chiappe, 2010). Additionally, DNHM  
388 D2945/6 shows that the lateral margin of the coracoid of hongshanornithids was concave, as is  
389 typical of other basal ornithuromorphs, and not convex as reported by Zhou & Zhang (2005).  
390 DNHM D2945/6 also preserves a dorsal supracondylar process, a feature present in  
391 *Longicrusavis houi* and many extant shorebirds.

392 The presence of a hypocleidium in *Hongshanornis longicresta* is still controversial. This  
393 process does not appear present in DNHM D2945/6, however preservation prevents us from  
394 making an unequivocal statement. While most known Early Cretaceous ornithuromorphs do not  
395 possess even the smallest hypocleidium, basal ornithuromorphs with furculae bearing a distinct

396 hypocleidium have been recently reported (Zhou, Zhou & O'Connor, 2012). Such discoveries  
397 lend credibility to Zhou & Zhang's (2005) claim that the furcula of *Hongshanornis longicresta*  
398 possessed a hypocleidium, although well-preserved specimens are necessary to corroborate such  
399 a claim.

400 Furthermore, the anatomy of DNHM D2945/6 partially undermines the anatomical basis  
401 used by Li, Wang & Hou (2011) to diagnose the hongshanornithid *Parahongshanornis*  
402 *chaoyangensis*. The compression of the proximal portion of the furcula and caudal groove of this  
403 bone in DNHM D2945/6 indicate that these characters cannot be considered as diagnostic of  
404 *Parahongshanornis chaoyangensis*. This is the same for the distal expansion of the pubes, a  
405 condition that is identical in DNHM D2945/6 and the holotype of *Parahongshanornis*  
406 *chaoyangensis*.

#### 407 Diet

408 The presence of teeth on both the maxilla and the dentary, and the reinterpretation of the  
409 hongshanornithids as toothed birds, impact earlier ecological inferences for the clade, suggesting  
410 they were less specialized trophically than previously imagined. The presence of at least two  
411 distinct skull morphologies within Hongshanornithidae indicates intraclade trophic diversity, and  
412 niche partitioning within the specialized wading ecology inferred to have been occupied by this  
413 clade.

414 The geo-gastroliths preserved associated with the visceral region of DNHM D2945/6  
415 offer a glimpse into the digestive system and dietary preferences of hongshanornithids. A variety  
416 of aquatic and terrestrial organisms regularly ingest sand, fine gravel, or coarse sand. These  
417 'stomach stones' or grit are assumed to perform a variety of functions ranging from acting like  
418 ballast in aquatic animals to parasite control and hunger placation (Wings, 2007). Most typically,

419 however, geo-gastroliths are interpreted as grinding devices assisting the digestion of hard food  
420 items. Geo-gastroliths are not only common among living crocodiles (Taylor, 1993; Henderson,  
421 2003) and birds (Gionfriddo & Best, 1999) but they also have been documented in a variety of  
422 extinct archosaurian clades, including pterosaurs (Codorniu, Chiappe & Cid, 2013) and every  
423 major group of dinosaurs (Osborn, 1924; Ji et al., 1998; Weems, Culp & Wings, 2007; Wings &  
424 Sander, 2007). Geo-gastroliths have also been discovered in association with the skeletons of a  
425 number of Early Cretaceous ornithuromorphs from China (e.g., *Yanornis martini*, *Gansus*  
426 *yumenensis*, *Archaeorhynchus spathula*) (Zhou et al., 2004; You et al., 2006; Zhou, Zhou &  
427 O'Connor, 2013b). The presence of geo-gastroliths in fossil dinosaurs (including birds) is  
428 generally regarded as indicative of herbivory (Ji et al., 1998; Gionfriddo & Best, 1999;  
429 Kobayashi et al., 1999; Wings, 2007; Xu et al., 2009; Zanno & Makovicky, 2011; Brusatte,  
430 2012), however such a correlation is not as consistent as often assumed. In the case of DNHM  
431 D2945/6, the closely associated cluster of fairly evenly sized stones located in the abdominal  
432 cavity distal to the sternum but proximal to the pelvic girdle, is consistent with the interpretation  
433 of these geo-gastroliths as gizzard stones. Furthermore, the report by Zheng et al. (2011) of a  
434 specimen (STM 35-3, identified as of *Hongshanornis longicresta*) containing seeds in a crop  
435 provides evidence that these birds were granivorous. Such evidence is consistent with both the  
436 preservation of geo-gastroliths in DNHM D2945/6 and STM 35-3, and the functional  
437 interpretation that highlights the role these stones play in processing hard foods.

### 438 Caudal Plumage

439 Very little is known about the rectrices of basal ornithuromorphs and DNHM D2945/6  
440 represents what is possibly the most informative example for understanding the morphology of  
441 the tail of these birds. Only two types of feathered tails—fan-shaped and forked—have been

442 reported for basal ornithuromorphs (Zhou & Zhang, 2001; Clarke, Zhou & Zhang, 2006; Zhou,  
443 Zhou & O'Connor, 2012, 2013a). Such limited diversity contrasts with what is known for their  
444 sister-group, the Enantiornithes, in which a larger number of tail morphologies (including one  
445 inferred to be aerodynamic; O'Connor et al., 2009) are known (Zhang & Zhou, 2000; Zheng,  
446 Zhang & Hou, 2007; O'Connor, Gao & Chiappe, 2010; O'Connor et al., 2012).

447         DNHM D2945/6 provides evidence that as early as 125 million year ago, basal  
448 ornithuromorphs had evolved a feathered tail comparable in size and design to those of many  
449 modern birds. Such tail had rectrices suitable of fanning and capable of generating aerodynamic  
450 forces much greater than those of more basal birds (Gatesy & Dial, 1996).

451         In living birds, all but the central pair of rectrices of a fan-shaped tail anchor on a  
452 musculo-adipose organ, the rectricial bulb, which controls the fanning of the feathers and as  
453 such, plays a critical role in flight (Gatesy & Dial, 1996). The rectricial bulb is in turn supported  
454 by, and intimately connected to, the pygostyle. Nonetheless, because no direct evidence of a  
455 rectricial bulb has ever been found in any Mesozoic bird, whether the pygostyle is a reliable  
456 osteological correlate of the rectricial bulb has been questioned (Clarke, Zhou & Zhang, 2006).  
457 The morphology of the pygostyle of basal ornithuromorphs (and of their living relatives) differs  
458 from that typical of more basal birds, which commonly possess a long, robust, and club-shaped  
459 pygostyle (e.g., Confuciusornithidae, Enantiornithes). In contrast, the pygostyle of  
460 ornithuromorphs is relatively small, more delicate, and plough-shaped—even if the pygostyle of  
461 hongshanornithids is poorly known (and missing in DNHM 2945/6), its morphology seems to  
462 agree with that of other basal ornithuromorphs (Zhou & Zhang, 2005). The morphological  
463 difference between the pygostyle of ornithuromorphs and that of more basal birds led Clarke,  
464 Zhou & Zhang (2006) to hypothesize that the rectricial bulb evolved in concert with both the  
465 modern avian pygostyle (plough-shaped) and aerodynamic tail morphologies such as those

466 known for basal ornithuromorph taxa. This hypothesis, however, has been somewhat challenged  
467 by the recent report of a tail formed by long, shafted rectrices in the enantiornithine *Shanweinia*  
468 *cooperorum* (O'Connor et al., 2009). In the holotype and only known specimen of this taxon, the  
469 impressions of four vaned feathers can be seen projecting from the end of the caudal vertebral  
470 series. Such evidence suggests that the presence of a large and club-shaped pygostyle, like the  
471 one characteristic of enantiornithines, might not have excluded the development of a fan-shaped  
472 feather tail among non-ornithuromorph birds from such tail feather morphologies (O'Connor et  
473 al., 2009), and therefore that a rectricial bulb might have evolved either prior to the origin of the  
474 Ornithuromorpha or independently in more than one clade of birds (e.g., Ornithuromorpha and  
475 Enantiornithes). The derived phylogenetic position of *Shanweinia cooperorum*, nested among  
476 advanced enantiornithines (O'Connor & Zhou, 2012), and the widespread presence of pintail  
477 morphologies lacking vaned rectrices capable of fanning among other enantiornithines  
478 (O'Connor et al., 2012) favor interpretations of the aerodynamic tail of *Shanweinia* (and  
479 presumably the rectricial bulb that operated the fanning of its rectrices) as an independent  
480 evolutionary event. Likewise, the presence of fan-shaped feathered tails and modern-like  
481 pygostyles in a variety of basal ornithuromorphs (e.g., *Hongshanornis longicresta*, *Yixianornis*  
482 *grabau*, *Yanornis martini*, *Piscivoravis lii*) supports the argument that such morphologies are  
483 ancestral for Ornithuromorpha (Clarke, Zhou & Zhang, 2006).

#### 484 Aerodynamics

485 DNHM D2945/6 possesses relatively broad, but tapered wings. Compared to a general  
486 regression of mass against wing area for birds (data taken from Greenewalt, 1964), the relative  
487 wing area for DNHM D2945/6 is somewhat larger than average, when using the mean body  
488 mass estimate (42 g; residual of -0.37) (see Materials and Methods). However, using the

489 heaviest mass estimate for DNHM D2945/6 (65 g) (see Materials and Methods) yields an  
490 average wing area, and therefore a typical wing loading compared to a modern bird of similar  
491 size (residual of -0.04).

492         The overall size of DNHM D2945/6, along with its wing shape, is qualitatively similar to  
493 that of some living passerines with flexible diets (e.g., *Monticola solitarius*, *Sturnus vulgaris*,  
494 *Turdus naumanni*). These same living birds also tend to have somewhat tapering wings without  
495 extensive wing tip slotting. As a result, we tentatively suggest that DNHM D2945/6 may have  
496 lacked extensive wingtip slotting, even if direct evidence of this is not available in the specimen.  
497 Additional specimens will be required to confirm this prediction. Tip slots are most effective at  
498 slow speeds, where they can increase effective aspect ratio in wings with low geometric aspect  
499 ratio (Tucker, 1993). As a result, it is generally expected that birds without tip slots tend to  
500 either have high geometric aspect ratio (which is not relevant to DNHM D2945/6), or else tend  
501 to fly at relatively high speeds. Based on its intermediate size and moderate aspect ratio, DNHM  
502 D2945/6 would be expected to flap continuously at low speeds, but may have switched to flap-  
503 bounding (a cycle of flapping and bounding with the wings flexed) at higher rates of travel, since  
504 this type of gait transition is seen among modern birds with similar wing shape and body size to  
505 DNHM D2945/6. We note that such gait transitions are related to flight speed and cost of  
506 transport, both of which relate to total body size and wing loading (Tobalske, Peacock & Dial,  
507 1999; Tobalske, 2001). Since we have reliable measurements of the specimen dimensions,  
508 conservative predictions of gait are possible for DNHM D2945/6, even though the wings of the  
509 specimen lack feather details. For the same reasons, we do not expect that these gait transitions  
510 would be particularly sensitive to specifics of osteology (i.e. differences in skeletal structure  
511 between basal ornithuromorphs and modern birds). So long as DNHM D2945/6 was able to fly

512 continuously for significant distances, the same basic patterns of cost of transport relative to size  
513 and flight speed should apply to both living neornithines and DNHM D2945/6.

514 Tail positioning and effective functional area are more difficult to estimate in fossil taxa  
515 than the same variables for the wings, because avian tails can be used at extremely fanned or  
516 collapsed states (or any number of positions in between). While the degree of asymmetry of the  
517 rectrices is unclear, the lateral feathers of the tail in DNHM D2945/6 appear to be less  
518 asymmetrical than it would be expected if these feathers were regularly oriented with their long axis  
519 fully transverse to the air flow (as would be the case for primary feathers on the wings or the  
520 lateral rectrices in a fully fanned tail). This suggests that the tail was typically deployed as a  
521 partially fanned "wedge", rather than a full fan. This is not uncommon among modern birds with  
522 long tails, such as flycatchers, accipiters, and sunbitterns (MH, pers. observation).

523 The preserved plumage of DNHM D2945/6 indicates that hongshanornithids had wing  
524 and tail surfaces comparable to those of living birds of similar sizes. In general, the morphology  
525 of the wing and feathered tail of DNHM D2945/6, combined with estimates of its weight, is  
526 indicative of a flight mode comparable to the intermittent flight of many medium-sized  
527 passerines and congruent with the conclusions reached by Close & Rayfield (2012), whose  
528 geometric morphometric analysis of furculae interpreted *Hongshanornis longicresta* as a  
529 continuous flapper.

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### 536 **Author Contributions**

537 LMC designed and supervised the project, studied the anatomy of the new specimen, and co-  
538 wrote the manuscript, JEO study the anatomy of the new specimen and co-wrote the manuscript,  
539 JML provided the wing and tail parameters, produced size estimates, and gastrolith  
540 measurements, MH, analyzed the aerodynamic parameters and co-wrote the manuscript, CG,  
541 ZB, WR, MQ, and CX supervised the curation of the specimen and provided general support and  
542 logistics in China. All authors contributed to the general discussion of the manuscript

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- 706

# Figure 1

Figure 1.

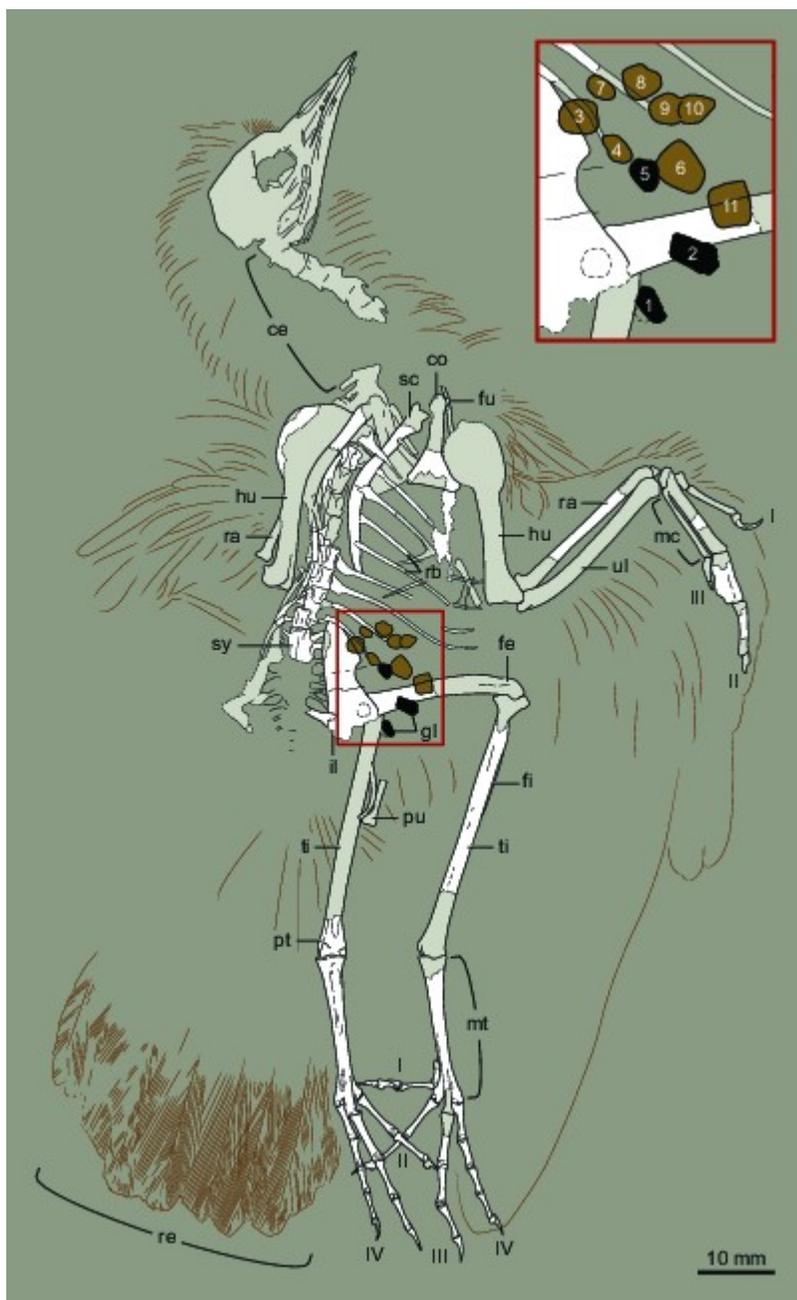
Figure 1: Photograph of DNHM D2945. Red and white arrows point at the maximum extent of the primary and secondary feathers of the wing.



# Figure 2

Figure 2.

Figure 2: Interpretive drawing of DNHM D2945. Abbreviations: ce, cervical vertebrae; co, coracoid; fe, femur; fi, fibula; fu, furcula; gl, gastroliths; hu, humerus; il, ilium; mc, metacarpals; mt, metatarsals; pt, proximal tarsals; pu, pubis; ra, radius; rb, ribs; re, rectrices; sc, scapula; sy, synsacrum; ti, tibia; ul, ulna; I-IV, digits (manual or pedal) I-IV. Numbers in inset (close up of gastrolith cluster) refer to those in Table 2.



# Figure 3

Figure 3.

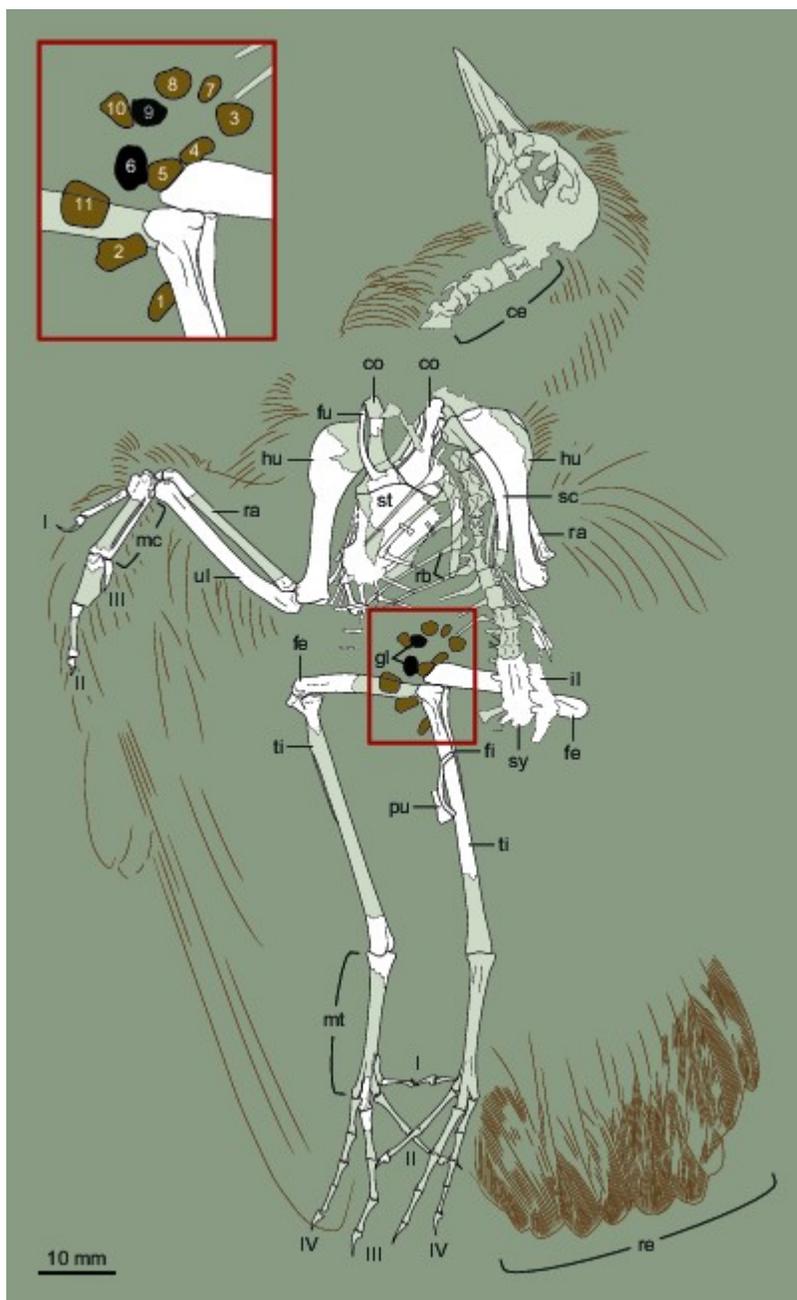
Figure 3: Photograph of DNHM D2946. Red and white arrows point at the maximum extent of the primary and secondary feathers of the wing.



# Figure 4

Figure 4.

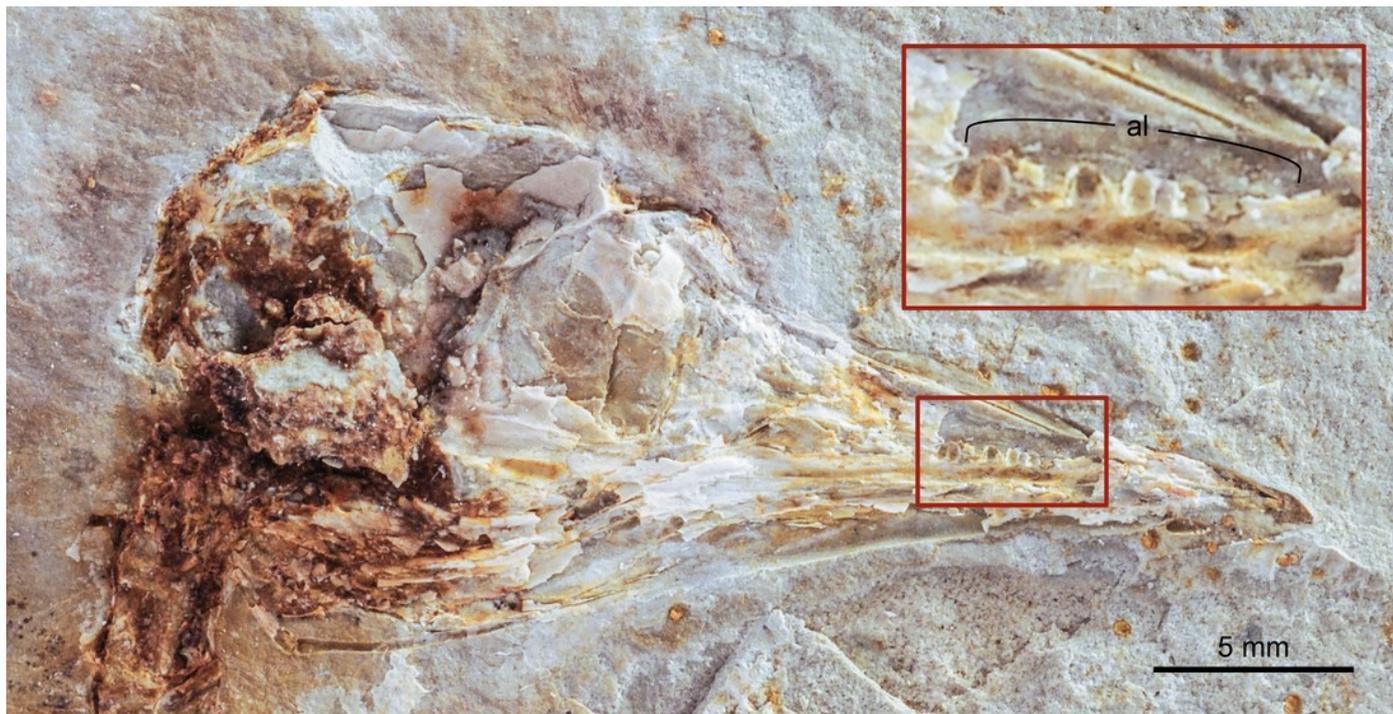
Figure 4: Interpretive drawing of DNHM D2946. Abbreviations: ce, cervical vertebrae; co, coracoid; fe, femur; fi, fibula; fu, furcula; gl, gastroliths; hu, humerus; il, ilium; mc, metacarpals; mt, metatarsals; pu, pubis; ra, radius; rb, ribs; re, rectrices; sc, scapula; st, sternum; sy, synsacrum; ti, tibia; ul, ulna; I-IV, digits (manual or pedal) I-IV. Numbers in inset (close up of gastrolith cluster) refer to those in Table 2.



# Figure 5

Figure 5.

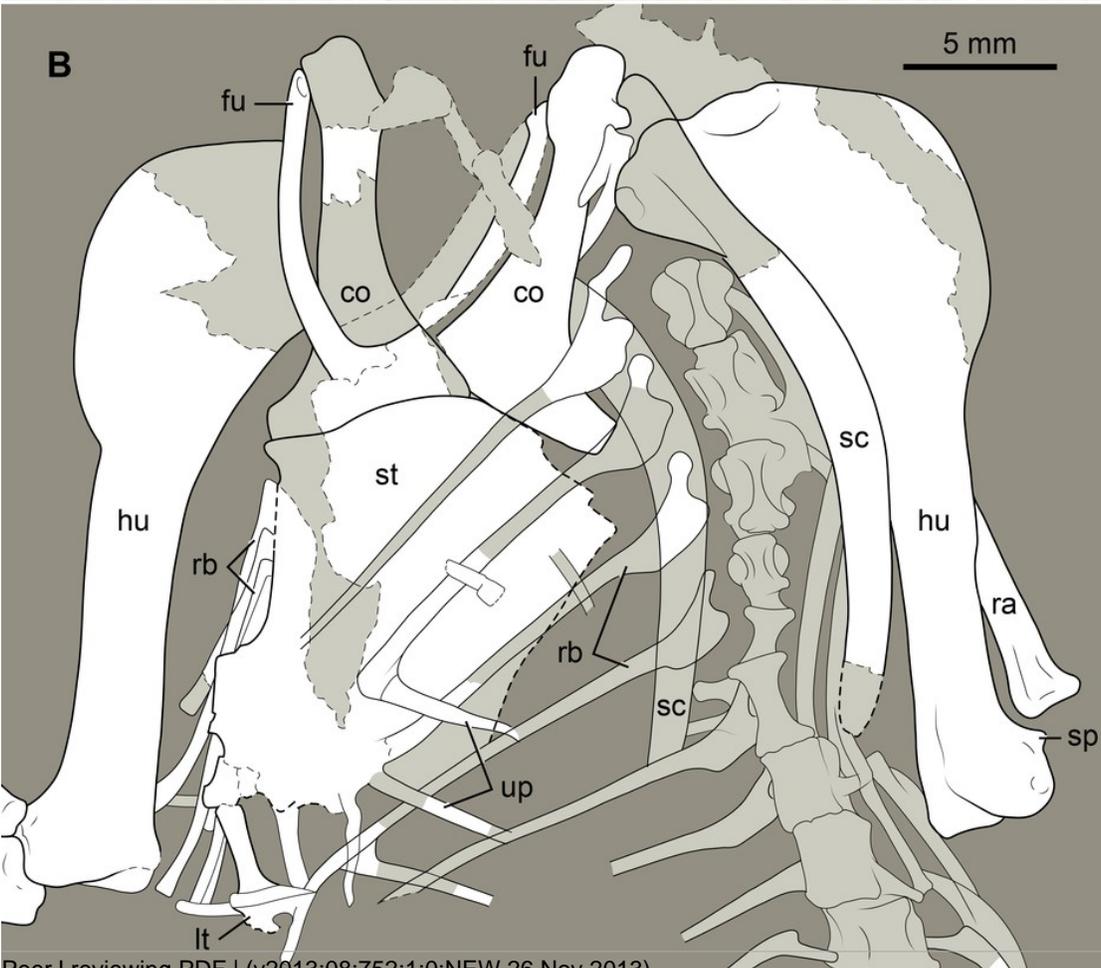
Figure 5: Close up photograph of the skull of DNHM D2945 in right lateral view and detail (inset) of the central portion of its maxilla. Abbreviations: al, alveoli.



# Figure 6

Figure 6.

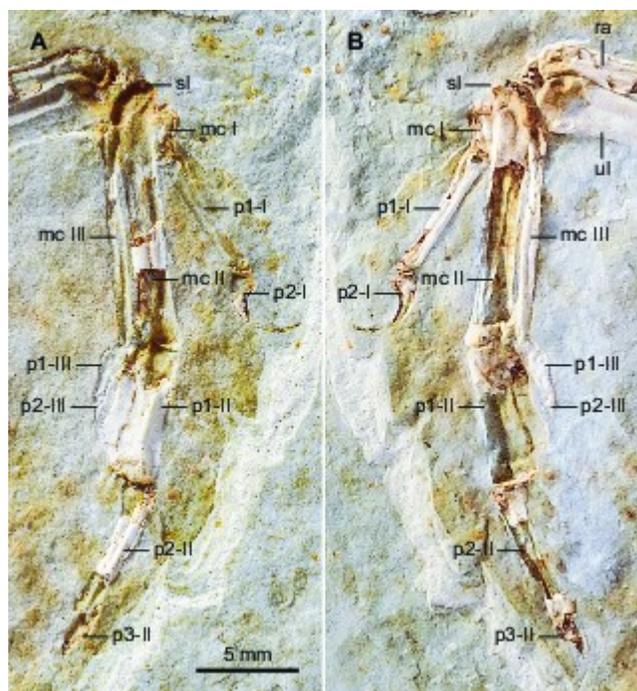
Figure 6: Photograph (A) and interpretive drawing (B) of the thoracic girdle and vertebral series, rib cage, and humeri of DNHM D2946. Abbreviations: co, coracoid; fu, furcula; hu, humerus; lt, lateral trabecular; ra, radius; rb, ribs; sc, scapula; sp, supracondylar process; st, sternum; up, uncinat process.



# Figure 7

Figure 7.

Figure 7: Photograph of the left manus of DNHM D2945/6 in ventral (A; DNHM D2945) and dorsal (B; DNHM D2946) views. Abbreviations: mc I-III, metacarpals I-III; p1-I, phalanx 1 (proximal) of digit I (alular digit); p2-I, phalanx 2 (ungual) of digit I (alular digit); p1-II, phalanx 1 (proximal) of digit II (major digit); p2-II, phalanx 2 (intermediate) of digit II (major digit); p3-II, phalanx 3 (ungual) of digit II (major digit); p1-III, phalanx 1 (proximal) of digit III (minor digit); p2-III, phalanx 2 of digit III (minor digit); ra, radius; sl, semilunate carpal; ul, ulna.



# Figure 8

Figure 8.

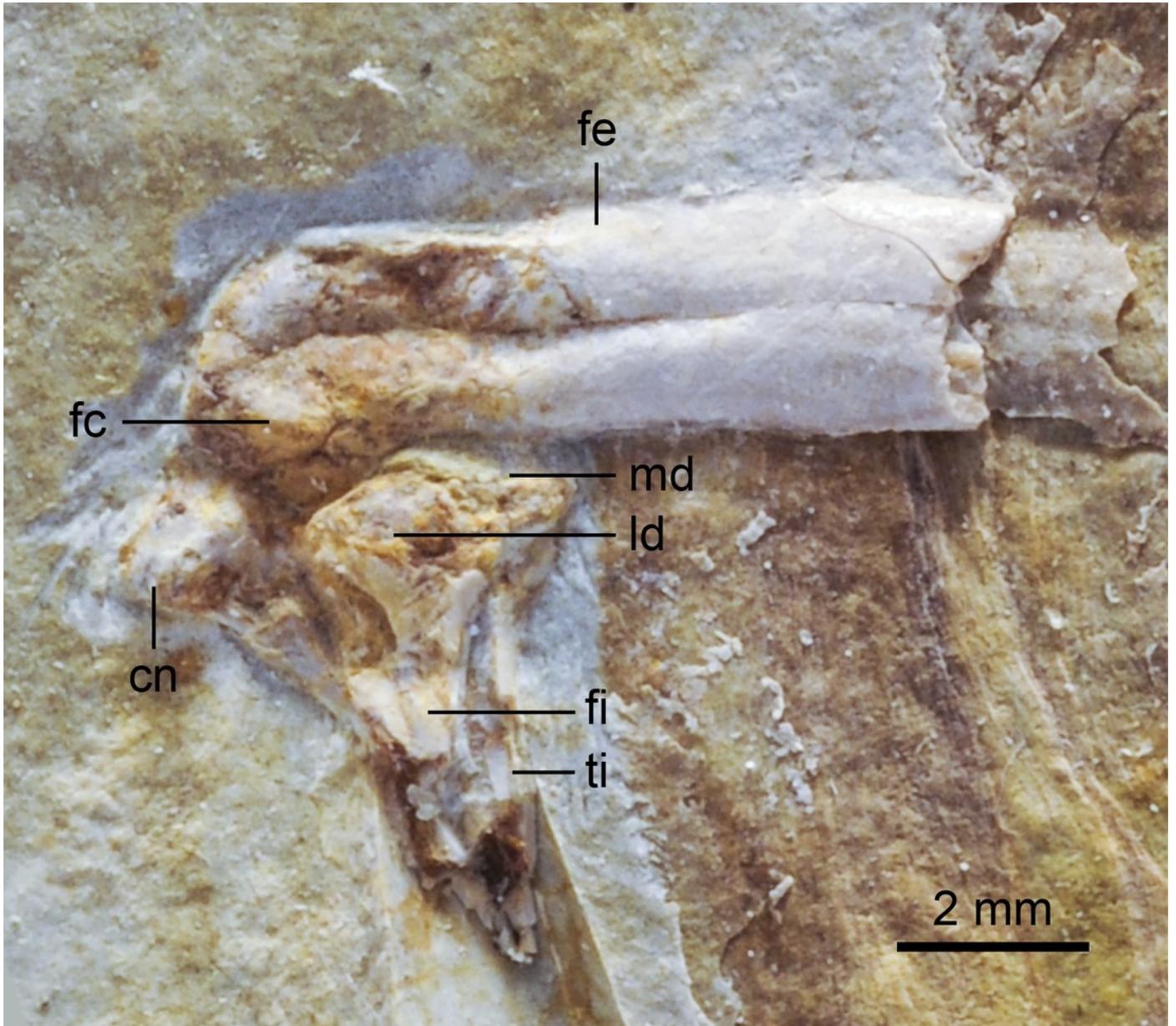
Figure 8: Close up photograph of the right knee (medial view) and pubic symphysis (left laterocaudal view) of DNHM D2946. Note the detail of the gastroliths. Abbreviations: fe, femur; fi, fibula; gl, gastroliths, pu, pubis; ti, tibia. (l) and (r) refer to the left and right pubis, respectively.



# Figure 9

Figure 9.

Figure 9: Close up photograph of the left knee (lateral view) of DNHM D2946. Abbreviations: cn, cnemial crest; fc, fibular condyle; fe, femur; fi, fibula; ld, lateral articular facet of tibia; md, medial articular facet of tibia; ti, tibia.



# Figure 10

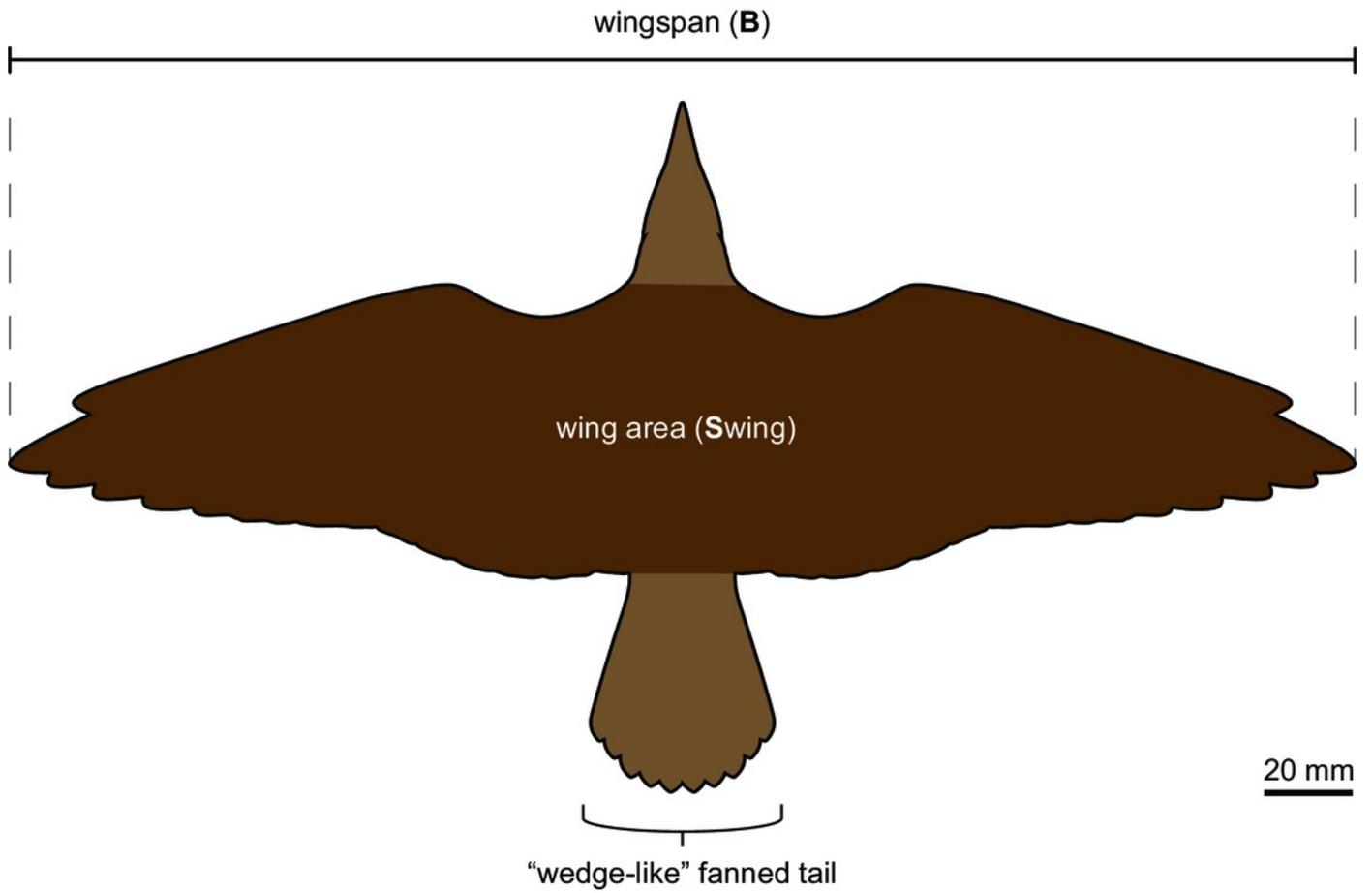
Figure 10.

Figure 10: Close up photograph of the feet and rectrices of DNHM D2945. Abbreviations: mt, metatarsals; re, rectrices; I-IV, digits I-IV.



# Figure 11

Figure 11



**Table 1** (on next page)

Table 1.

Table 1: Comparisons of selective measurements in hongshanornithids. The values highlight the similar sizes and proportions of the three named species of hongshanornithids:

*Hongshanornis longicresta* (DNHM D2945/6 and IVPP V14533), *Parahongshanornis chaoyangensis* (PMOL-AB00161), and *Longicrusavis houi* (PKUP 1069).

Element	DNHM D2945/6	IVPP V14533	PMOL-AB00161	PKUP 1069
Skull	30.5	---	---	30.7
Humerus	24.6	26.0	29.0	26.0
Ulna	24.5	24.0	27.0	25.0
Carpometacarpus	13.0	13.0	12.3	13.1
Manual digit II		---	18.1	17.7
Femur	22.0	22.0	24.0	24.3
Tibiotarsus	35.5	38.0	38.0	37.6
Tarsometatarsus	20.6	22.0	22.0	21.5
Pedal digit III	20.0	---	---	---

## Table 2 (on next page)

Table 2.

Table 2: Measurements (mm) of the gastroliths of DNHM D2945/6. Left column numbers correspond to numbers on figures 2 and 4.

		D2945	D2946	Mean value
2				
3				
4	1	2.21	2.27	2.24
5	2	3.06	3.09	3.08
6	3	2.31	2.07	2.19
7	4	2.05	2.15	2.10
8	5	2.15	2.11	2.13
9	6	2.90	2.59	2.75
10	7	1.84	1.76	1.80
11	8	1.76	1.79	1.78
12	9	1.74	2.08	1.91
13	10	1.84	1.56	1.70
14	11	2.51	3.13	2.82
15				