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1 **Complete *Ichthyornis* skull illuminates mosaic assembly of the avian head**

2

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### 3D *Ichthyornis* skull

19 The skull of crown birds is profoundly modified from the ancestral dinosaurian condition,  
20 featuring an enlarged, toothless premaxillary beak and an intricate kinetic system including a  
21 re-engineered palate, reduced temporal arcade, and mobile quadrates. The greatly expanded  
22 avian neurocranium protects an enlarged brain and is flanked by reduced jaw adductor  
23 muscles. Among fossil taxa recording the transition to the skull of crown birds, the Late  
24 Cretaceous toothed bird *Ichthyornis dispar* sits in a pivotal phylogenetic position between  
25 stemward early ornithuromorphs and birds of a more crown-like aspect<sup>1-3</sup>. Despite continued  
26 work affirming its evolutionary significance<sup>3-8</sup>, no substantial new cranial material of *I.*  
27 *dispar* has been described beyond the incomplete and fragmentary remains first recovered in  
28 the 1870s. Jurassic and Cretaceous lagerstätten that have yielded important avialan fossils  
29 typically preserve crushed and distorted skulls<sup>9</sup>. Moreover, with the exception of  
30 *Archaeopteryx*, substantially complete skulls have not been three-dimensionally imaged,  
31 severely limiting reconstructions of avialan cranial morphology. Here we report four new  
32 specimens of *I. dispar* bearing three-dimensional cranial remains, including a new,  
33 extraordinarily complete skull and, unexpectedly, two previously overlooked elements from  
34 the well-studied holotype. We used these specimens to generate a near-complete 3D  
35 reconstruction of the *I. dispar* skull using high-resolution computed tomography. Our study  
36 reveals that *I. dispar* had a transitional beak—small, lacking a palatal shelf, and restricted to  
37 the tip of the jaws—coupled with a crown-like kinetic system, demonstrating an earlier origin  
38 of the feeding apparatus of crown birds than previously understood and supporting  
39 developmentally coordinated transformation of components of this key avian innovation. The  
40 brain was relatively modern, but the temporal region was strikingly and unexpectedly  
41 deinonychosaur-like, bearing a large adductor chamber bounded dorsally by substantial bony  
42 remnants of the upper temporal fenestra. This previously unobserved combination of features

43 illuminates the transitional states of several diagnostic avian cranial innovations, providing  
44 new insight into the assembly of the crown bird skull.

45 **Main Text**

46 The extreme adaptability of the modern bird skull has resulted in spectacular functional  
47 disparity across living birds, the largest major terrestrial vertebrate clade<sup>10</sup>. However, the  
48 earliest appearances of several modern avian cranial innovations—and their sequence of  
49 acquisition—are incompletely known owing to uneven and largely two-dimensional  
50 preservation of early ornithuran cranial material<sup>1,3,11,12</sup>. Toward ameliorating this deficiency,  
51 we report a newly discovered, nearly complete skull of the iconic early ornithuran  
52 *Ichthyornis dispar* housed at the Sternberg Museum of Natural History (FHSM) in Fort Hays,  
53 Kansas, USA. One of us (K.S.) discovered the specimen (FHSM VP-18702) in 2014 near  
54 Castle Rock in Gove County, Kansas, deriving from the base of MU 10 in the Smoky Hill  
55 Member of the Niobrara Formation (Middle Santonian stage, Late Cretaceous).

56 Using FHSM VP-18702 supplemented by elements from three other undescribed  
57 specimens (ALMNH [Alabama Museum of Natural History] 3316, KUVP [University of  
58 Kansas Biodiversity Institute] 119673, BHI [Black Hills Institute of Geological Research]  
59 6421) and the holotype YPM 1450, we have assembled a three-dimensional skull  
60 reconstruction (**Figure 1, Supplementary Information and Plates**) lacking only the vomers,  
61 pterygoids, anterior processes of the nasals, stapes, and (presumed) predentary<sup>13</sup>. Referral of  
62 all newly described specimens to *I. dispar* is supported by a combination of autapomorphies  
63 from across the skeleton (**Supplementary Figure XI**). Surprisingly, we identified two  
64 previously unreported cranial elements from the holotype at the Yale Peabody Museum of  
65 Natural History (YPM 1450): the first and only known lacrimal from *I. dispar*, and the most  
66 complete nasal<sup>3</sup>. Skull material described from *I. dispar* was previously limited to partial

67 braincases, mandibles, partial quadrates, and small fragments of the maxilla and premaxillary  
68 frontal process.

69

## 70 **Results and discussion**

71 Given the distorted preservation of most Mesozoic Avialae<sup>9</sup>, the reconstructed *I. dispar*  
72 skull (**Figure 1**) exceeds in its combination of three-dimensionality and completeness nearly  
73 all Mesozoic avialan cranial material other than that of *Archaeopteryx lithographica*<sup>14</sup> and  
74 *Hesperornis regalis*<sup>15,16</sup>. In particular, almost uniquely among Mesozoic avialans, the FHSM  
75 specimen preserves a complete and relatively undistorted upper temporal and suspensorial  
76 region<sup>9</sup>. The reconstructed skull of *I. dispar* illustrates a transitional point in the evolutionary  
77 history of the ornithuran skull stemward of Hesperornithiformes, a phylogenetic position  
78 recovered by the majority of recent analyses including comprehensive new analyses we have  
79 undertaken, bolstered by new characters and character states described here (**Figure 2A**; See  
80 **Supplementary Information** and **Supplementary Trees** for our suite of phylogenetic  
81 analyses and information concerning the placement of *I. dispar* within Avialae)<sup>11,17</sup>.

82 While the avian stem lineage records numerous transitions towards toothlessness  
83 throughout the Mesozoic, the newly observable bill of *I. dispar* records the most stemward  
84 three-dimensional information on the origin of the toothless bill of crown birds. Dorsal to the  
85 external naris, the upper bill has a concave lateral profile, a derived condition similar to that  
86 of many crown birds and Hesperornithiformes but not stemward ornithurans<sup>11</sup> (**Figure 2B**,  
87 **Supplementary Plates VI, VIII, and IX, Supplementary Movies 01 and 05**). The  
88 previously undescribed premaxillae are considerably shorter than inferred in previous  
89 reconstructions, restricted to the anteriormost quarter of the rostrum. The premaxillae are  
90 medially fused, anteriorly pointed, and toothless, unlike those of more stemward ornithurans  
91 (*e.g.* the posteriorly unfused, posteriorly toothed premaxillae of *Yanornis martini*). In their

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92 relative length they resemble those of the stemward ornithuromorph *Gansus zheni*<sup>18</sup>, which is  
93 known from flattened specimens. Because it is more crownward than *Gansus* and relatives,  
94 *Ichthyornis* therefore provides polarity to the direction of beak transformation and  
95 demonstrates that short premaxillae restricted to the tip of the snout were the plesiomorphic  
96 form of the avian beak. In contrast, the more derived toothless tomial margins of the beak in  
97 the clade consisting of crown Aves and Hesperornithiformes form the greater part of the  
98 lateral margins of the rostral upper jaw<sup>1</sup> (**Figure 2B**). However, *Ichthyornis* shares with this  
99 clade, to the exclusion of more stemward ornithurans including *G. zheni*, a decurvature of the  
100 premaxilla along the tomial margin. The premaxillae are covered in neurovascular foramina  
101 that in living birds often correspond to a highly keratinised region of the rhamphotheca called  
102 the premaxillary nail<sup>19</sup>. There is no discernible nasolabial groove running from the naris to  
103 the tomial margin; in crown birds, this is an osteological correlate for the rhamphothecal  
104 plates posterior to the premaxillary nail<sup>19</sup>. This suggests that the evolutionary origin of the  
105 nail preceded the acquisition of other rhamphothecal segments. The ventral surface of the  
106 premaxillae<sup>20</sup>, observable here for the first time in an ornithuran stemward of  
107 Hesperornithiformes, is vaulted dorsally (**Figure 1, 2B, Supplementary Plates VI and VIII,**  
108 **Supplementary Movies 01 and 05**), a plesiomorphic dinosaurian condition unlike that of  
109 Hesperornithiformes<sup>16</sup> or crown Aves<sup>21</sup> in which a flat palatal shelf is covered by keratinous  
110 rhamphotheca (the *palatum corneum*)<sup>22</sup>. The posterior half of the medial tomial margin is  
111 dimpled by three conspicuous fossae on each side (**Figure 3B**), which correspond to the  
112 occlusal position of the anteriormost dentary teeth. Rostral to these fossae the premaxillae  
113 would likely have interacted with a prementary bone, whose presence we infer based on the  
114 form of the anterior dentary, the relative length of the lower jaw to the upper, and its presence  
115 in other ornithuromorphs<sup>13</sup>. Plesiomorphically and unlike in crown-clade birds, a soft-tissue  
116 internarial septum may have been supported by a median ridge extending caudad from the

117 ventral surface of the premaxillary body onto the ventral surface of the anterior half of the  
118 premaxillary frontal process (**Figure 1, Supplementary Movie 05**)<sup>20,23,24</sup>. Novel observations  
119 about avian evolution from the premaxillae include unambiguous polarization of the short,  
120 anteriorly restricted condition as ancestral along the avian stem, the plesiomorphic nature of  
121 the palatal surface and extent of the rhamphotheca including early presence of the nail.

122 The new fossil data from the FHSM and ALMNH specimens enable a reconstruction of  
123 the only complete, undistorted ornithuran maxilla known from a taxon stemward of  
124 Hesperornithiformes (**Figures 1-2**). Previously only known from a small fragment mistakenly  
125 thought to be part of the tooth row (see **Supplement**), the bone was presumed to be  
126 considerably shorter than its actual length but is in fact plesiomorphically long. The dentition  
127 is extensive in both the upper and lower jaws, occupying nearly the entire length of the  
128 dentaries and maxillae, and shows no indication of reduction relative to stemward Avialae; in  
129 comparison, the teeth of hesperornithiforms are reduced in size and extent (**Figure 2B**).  
130 Distinct sockets are formed by interdental ossifications which develop through ontogeny<sup>25</sup>—a  
131 plesiomorphic condition lost in Hesperornithiformes, where the teeth are set in a continuous  
132 sulcus<sup>16,26</sup> (and crown Aves, where the teeth are lost entirely). To accommodate dental  
133 implantation, the maxillae are robust in lateral view compared to those of crown Aves, in  
134 which these bones are reduced to thin, dorsoventrally flattened, predominantly palatal  
135 elements<sup>23,24</sup>. However, *I. dispar* shares with more crownward avialans maxillary palatal  
136 shelves that are transversely wider than the maxilla is dorsoventrally tall and compose an  
137 extensive portion of the bony palate<sup>16</sup> (**Figure 1, Supplementary Movie 01**). Thus, the  
138 maxilla is in some ways plesiomorphic and in others rather crown-bird-like. The ventral  
139 surface of each maxillary palatal shelf unexpectedly exhibits a series of occlusal fossae for  
140 the lower teeth along the entire caudorostral length of the bone medial to the upper tooth row,  
141 a state previously unrecorded in Avialae (**Figure 1, Supplement**). The new material offers

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142 the first clear evidence of the extent of the palatal shelf at an early node within  
143 Ornithuromorpha, and the surprising presence of extensive occlusal pits along the length of  
144 the palate. The mandibles of *Ichthyornis*, both of which are complete and undistorted in the  
145 FHSM skull and at least partly preserved in all of the other new specimens, have already been  
146 extensively described based on YPM material (see **Figure 1, Supplementary Plates, and**  
147 **Supplementary Movie 06**)<sup>3,27</sup>.

148 Unexpectedly, we discovered a substantially complete lacrimal — never before described  
149 in *Ichthyornis* — and nasal in material composing the *Ichthyornis dispar* holotype YPM 1450,  
150 which had remained undescribed and undocumented despite their presence in the YPM  
151 collection since 1872<sup>3</sup> (**Figure 1, Supplementary Plate X, Supplementary Movie 04**). The  
152 lacrimal is mostly complete, with only the supraorbital and nasofrontal articular region  
153 lacking. It is the only known three-dimensional lacrimal from an ornithuran stemward of  
154 Hesperornithiformes, and shows that at this stemward node the bone was already similar to  
155 that of crown-clade birds<sup>1,9</sup> in being robust, curved caudally, and perforated by a capacious  
156 lacrimal foramen. The caudal half of the nasal including the frontal articular region represents  
157 a previously unknown portion of the bone anterior to the frontals that helps define the shape  
158 of the naris and antorbital fenestra. The frontals, nasals, and premaxillae interdigitated with  
159 one another at their articulation on the dorsal surface of the skull such that, like crown  
160 Palaeognathae and unlike crown Neognathae, *I. dispar* lacked any indication of a transverse  
161 craniofacial hinge between the frontals and nasals<sup>15,21,28,29</sup>. The maxillary process of the nasal  
162 remains unknown for *I. dispar*, but the rostral half of the maxilla exhibits a pair of broad  
163 articular sulci running along the dorsal surface (**Figure 1, Supplementary Plate VI**): one is  
164 located laterally to receive the maxillary process of the premaxillae, and one is positioned  
165 medial to the aforementioned sulcus to receive the maxillary process of the nasal. The size of  
166 the latter sulcus indicates a broad nasal-maxillary contact and correspondingly broad



167 postnarial bar<sup>15</sup>. This condition corresponds to that seen in Neognathae, suggesting that the  
168 narrow or absent contact and bar of Palaeognathae<sup>21,24,30</sup> is derived within crown birds.

169 The previously undiscovered palatine, an element rarely preserved in Mesozoic avialans<sup>28</sup>,  
170 is narrow and elongate (**Figure 1, Supplementary Plate VI, Supplementary Movie 01**), and  
171 is similar to that of crown birds: a strong sutural connection to the maxilla as in all known  
172 stemward dinosaurs is lost<sup>16</sup>. The next-most-crownward examples of interpretable palatines  
173 are from the enantiornithine *Gobipteryx minuta*<sup>28</sup>, which has broad, flat palatines with  
174 extensive maxillary sutural contact similar to those of *Archaeopteryx lithographica* and non-  
175 avialan theropods<sup>14,17</sup>. Thus, the new material reveals that *Ichthyornis* presents the most  
176 stemward manifestation of a crown-like avian palatine yet recorded.

177 The crown-bird-like palatine was linked by the unpreserved pterygoid to a quadrate  
178 essentially indistinguishable from that of crown birds (**Figure 1, Supplementary Plates V-**  
179 **VII, X, Supplementary Movie 06**). The FHSM element, unlike all previously described  
180 material, is complete and undistorted. Similar to certain Neognathae like Anseriformes,  
181 Columbiformes, and the Maastrichtian fossil *Vegavis*, it exhibits two rounded capitular  
182 condyles that fit into cotyles on the proötic and squamosal bones to form a mobile joint with  
183 the cranium<sup>3,17,21,23</sup>; this raises the possibility that a bicondylar morphology is plesiomorphic  
184 for Neornithes. We also identified for the first time the quadratojugal (BHI) and jugals (KU  
185 and FHSM) of *Ichthyornis* (**Figure 1, Supplementary Plates V-VI, Supplementary Movie**  
186 **3**). The quadratojugal is incomplete, but the articular surface for the quadrate is preserved and  
187 would have formed a mobile joint as in crownward taxa. The jugal (FHSM, KU), is deep in  
188 lateral view and transversely compressed. The posterior end is forked and would have  
189 articulated with the quadratojugal, while the anterior end is pointed and would have laid flat  
190 on the dorsal surface of the jugal process of the maxilla. In its depth, the jugal differs from  
191 that of most crown birds, where the jugal is more or less rod-shaped. Nevertheless, we can

192 now conclude for the first time from the tandem arrangement of the  
193 rostrum/jugal/quadratojugal bar, the mobile suspensorium, and the narrow, linear palatine,  
194 that *I. dispar* possessed a fully functional avian cranial kinetic system, the most stemward  
195 known appearance of this key evolutionary innovation<sup>21,23,24</sup>.

196 The virtually complete postorbital cranium of the FHSM skull (**Figure 1, Figure 3,**  
197 **Supplementary Plate VI, Supplementary Movies 2-3**) includes many regions previously  
198 undocumented in *I. dispar*, and poorly known in Mesozoic avialans. These include a  
199 complete interorbital septum, and postorbital and zygomatic processes. The mesethmoid and  
200 parasphenoid rostrum of the FHSM specimen are among the best preserved in any Mesozoic  
201 ornithuran<sup>9,15</sup>. The mesethmoid indicates the acquisition of a morphology virtually  
202 indistinguishable from that of many crown birds: it is pierced with large fonticuli in the  
203 orbital region and does not extend rostral to the frontals, a condition seen in  
204 Hesperornithiformes and Neognathae, but not Palaeognathae. With the polarization permitted  
205 by the phylogenetic position of *Ichthyornis*, we can now hypothesize that the palaeognath  
206 condition, whereby the mesethmoid extends anteriorly to form part of the internarial septum,  
207 is autapomorphic<sup>20,24,29</sup>.

208 The endocranial cavity, observable in relatively undistorted sagittal outline for the first  
209 time in the FHSM specimen, is essentially crown-like (**Figure 3A**). The forebrain is enlarged  
210 and posteroventrally rotated, and the optic lobes are inflated and laterally shifted. Despite  
211 mediolateral compression, the overall structure appears more similar to crown birds and the  
212 enantiornithine *Cerebavis cenomanica*<sup>31</sup> than to *Archaeopteryx lithographica*<sup>32,33</sup>; to date,  
213 these two fossil taxa constitute the only Mesozoic avialans whose endocranial morphology  
214 has been characterised.

215 The FHSM specimen reveals detailed anatomical structure of the temporal and  
216 suspensorial region, which is observable for the first time in a Mesozoic avialan stemward of

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217 *Hesperornis*, The upper temporal fenestra is strikingly expanded (**Figure 1, Figure 3B**), a  
218 superficially plesiomorphic feature similar to that of deinonychosaurs and entirely  
219 unexpected in an avialan crownward of Enantiornithes. The anterior margin of the fenestra is  
220 bounded by a substantial postorbital ossification extending laterally from the skull. This  
221 postorbital process resembles the separate postorbital bone of early avialans and non-avialan  
222 dinosaurs in extending laterally and then posteriorly (**Figure 3B**), unlike the postorbital  
223 process of crown-clade birds, whose apex, even when enlarged (as in multiple modern bird  
224 clades including ducks, Anatidae)<sup>24</sup>, is directed ventrally<sup>9,15,16,21,34</sup>. Since the postorbital  
225 region of the skull is poorly preserved in stemward Avialae, including the three-dimensional  
226 yet incomplete cranial remains of *Patagopteryx deferrariisi*<sup>35</sup>, it is unclear whether the  
227 postorbital ossification in *Ichthyornis* is secondarily enlarged — though, if so, it is enlarged  
228 in a way unseen in crown-clade birds and strikingly convergent on non-avialan theropods  
229 such as deinonychosaurs (**Figure 3**) — or represents the surprisingly late retention of an  
230 ancestral dinosaurian condition. The latter hypothesis would imply the fusion of the  
231 postorbital bone to the cranial roof during the course of avialan evolution or its gradual  
232 replacement by extensions from the calvarial bones while retaining an ancestral shape. In  
233 crown Aves, the postorbital process derives from the combined ossification of the dermal  
234 skull roof (as with the ancestral lost or fused postorbital bone), a cartilaginous process on the  
235 laterosphenoid, and ossified ligaments and tendons. *I. dispar* shows a crown-bird-like  
236 contribution of the laterosphenoid, suggesting that the postorbital ligament and associated  
237 temporal musculature exhibited a crown-like configuration as well<sup>20,21,34</sup>. The temporal  
238 region is deeply embayed, like that of Hesperornithiformes and non-avialan dinosaurs and  
239 unlike that of most extant birds (**Figure 3B**), which generally exhibit reduced adductor  
240 chambers, although hypertrophy of the adductor musculature is also seen in some extant  
241 aquatic, piscivorous birds such as penguins (Spheniscidae)<sup>16,29,36</sup>.

242 The squamosal — which is preserved in only a handful of Mesozoic avialans such as  
243 *Patagopteryx deferrariisi*<sup>35</sup>, and among those is heavily damaged or highly derived in all but  
244 the relatively crownward and crown-like Hesperornithiformes (see Supplementary  
245 Information) — exhibits a plesiomorphic, deinonychosaur-like morphology unseen in  
246 crownward taxa including *Hesperornis*: the zygomatic process widely encircles the posterior  
247 half of the upper temporal fossa, first projecting laterally and then curving anteriorly such  
248 that the process is hooked and directed rostrally (**Figure 3B**). In lateral view, it is deep and  
249 triangular. As in non-avialan dinosaurs and unlike in crownward taxa, the nuchal crest along  
250 the suture between the parietal and supra- and exoccipitals extends from the midline of the  
251 skull onto the squamosal, forming the upper edge of that bone. The majority of the element is  
252 plesiomorphically more peripheral to the braincase than in modern birds, where it is highly  
253 integrated into the neurocranium<sup>36,37</sup> (**Figure 1**). The morphology of the squamosal in its  
254 encirclement of the adductor chamber recalls that of much more stemward, non-ornithuran  
255 theropods, such as *Zanabazar junior* (**Figure 3**), where a complete upper temporal arch is  
256 still present in retention of the ancestral diapsid condition<sup>17</sup>. Whether or not the enlarged  
257 postorbital process is secondary, the nearly complete upper temporal bar may reflect a  
258 relatively recent loss of the postorbital and anterior portion of the squamosal or their  
259 membranous precursors<sup>38</sup>. Its plesiomorphic appearance suggests that the architecture and  
260 topology of the muscles attaching to the posterior part of the upper temporal fossa, which  
261 includes the majority of the adductor externus complex<sup>39</sup>, likewise exhibited a more  
262 plesiomorphic architecture and topology whereas those attaching to the anterior part of the  
263 upper temporal fossa, which incorporates the laterosphenoid as in living birds, were more  
264 crown-like in their configuration.

265 In sum, the new and newly identified material represents the most complete, best  
266 preserved cranial remains of a Mesozoic ornithuran filling the long phylogenetic gap between

### 3D *Ichthyornis* skull

267 *Archaeopteryx* and Hesperornithiformes, revealing a stage of avian evolution for which near-  
268 complete three-dimensional cranial remains have hitherto been unavailable. Other three-  
269 dimensionally preserved skulls populating this portion of the avian stem, such as those of  
270 *Patagopteryx deferrariisi* and *Gobipteryx minuta*, are highly incomplete (the former poorly  
271 preserved and lacking the rostral portion of the skull, and the latter missing the caudal portion  
272 of the skull). Notable novel observations regarding the probable nature of the most recent  
273 common ancestor of *Ichthyornis* and crown birds are distributed across the skull. These  
274 include the transitional nature of the beak—a cranial module exhibiting especially high  
275 evolutionary rates across crown birds<sup>10,40</sup>—permitting us to conclude that the first form of  
276 this key avian innovation was that of a plesiomorphically short premaxillary rostrum bearing  
277 some transitional features including incomplete rhamphothecal coverage. Also notable are the  
278 correspondingly long maxillae exhibiting a plesiomorphically robust structure yet crown-like  
279 extensive palatal shelves; the crown-like lacrimal and neognath-like nasal; the essentially  
280 modern kinetic apparatus including a crown-like palatine, quadrate, and jugal/quadratojugal  
281 bar; the neognath-like ethmoid ossification; and the crown-like endocranial cavity. Certain  
282 morphologies revealed by the new specimens are entirely unanticipated, including a temporal  
283 region strikingly plesiomorphic in its appearance, characterised by a robust and nearly  
284 complete upper temporal bar unlike any in the avian crown. If the enclosure of the temporal  
285 region does not represent retained plesiomorphy (strictly, it optimizes as such even assuming  
286 *Patagopteryx* is undamaged), this configuration at least represents an example of surprising  
287 convergence on non-avian deinonychosaurian dinosaurs, further emphasizing the  
288 conspicuous degree of homoplasy and character reversal that characterizes the Mesozoic  
289 phylogenetic history of Avialae<sup>41</sup>. The extensive adductor chamber bounded by a nearly  
290 complete upper temporal fenestra coupled with a derived, crown-like brain further challenges  
291 a previous suggestion that brain enlargement along the stem of birds drove adductor

292 reduction owing to spatial restriction during embryonic development<sup>17</sup>. The bill, toothless  
293 only in the premaxillary region at its tip, provides the first three-dimensional look at the early  
294 stages of this most characteristic and adaptively important of crown avian cranial structures<sup>40</sup>.  
295 The pincer-like action of a sharp-tipped, toothless bill would probably have facilitated fine  
296 manipulation and preening—essentially performing the role of a surrogate hand as the hands  
297 themselves became bound up into wings<sup>17</sup>. Holding and perforation of prey was still likely  
298 performed in large part by the large, reptilian tooth row retained and highly developed in *I.*  
299 *dispar*<sup>26</sup>. The concurrent appearance of a crown-grade avian kinetic apparatus would have  
300 enabled further precision in grasping as well as expanded gape dimensions. Simultaneous  
301 appearance of a modern beak and modern palate is consistent with recently published  
302 evidence for a deep molecular developmental linkage between the appearance of the fused  
303 premaxillae of the beak and the slimming and detachment of the palatine in the roof of the  
304 mouth<sup>42</sup>. Finally, the modernity of the brain of *I. dispar* is consistent with its relatively  
305 modern postcranium—locomotion and neural form seem to be tightly linked in birds<sup>33</sup>.

306 Both within the head and between head and body of *I. dispar*, this historically important  
307 and phylogenetically pivotal taxon demonstrates the complex and regionalised ways in which  
308 evolution acted to form the skull of crown group birds. The data support some previous  
309 hypotheses and falsify others in addition to providing some entirely unexpected insights.  
310 These new observations help fill a gap in our knowledge of avian cranial evolution spanning  
311 over 60 million years and virtually the entirety of avialan phylogenetic history.

312

313

### Methods

314

315

*Ichthyornis dispar* specimens housed at ALMNH, BHI, FHSM, KUVF, and YPM, were scanned at the University of Texas High-Resolution CT Facility (UTCT), and the Center for

316 Nanoscale Systems at Harvard (CNS). Scan parameters and specimen details are presented in  
317 the **Supplementary Information**.

318 Scanned cranial material was digitally segmented using VGStudio MAX 3.0, and 3D  
319 surface meshes were extracted and imported to MeshLab 2016 for optimisation. Optimised  
320 meshes were then assembled into 3D reconstructions using Autodesk Maya 2017.

### 321 **Supplementary Information**

322 **Supplementary Information** is linked to the online version of the paper at  
323 [www.nature.com/nature](http://www.nature.com/nature).

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338 **Author Contributions**

339 D.J.F. and B.-A.S.B. conceived and directed the study and arranged logistics of  
340 specimen preparation and CT scanning. K.S. discovered the FHSM specimen and donated it  
341 to the museum. D.J.F., M.H., and B.-A.S.B. performed CT scans and processed CT data.  
342 M.H., D.J.F., and B.-A.S.B. scored characters and performed phylogenetic analyses. B.-  
343 A.S.B. and M.H. planned the main text figures and M.H. assembled the skull reconstruction.  
344 M.H. and D.J.F. prepared figures. D.J.F. wrote the supplementary anatomical descriptions  
345 and rendered the supplementary videos. D.B., L.E.W., K.S., D.E., and J.E. collected and  
346 prepared specimens for study, analysed morphology, and edited the paper. B.-A.S.B., D.J.F.,  
347 and M.H. wrote the paper. D.J.F. and B.-A.S.B. acquired funding.

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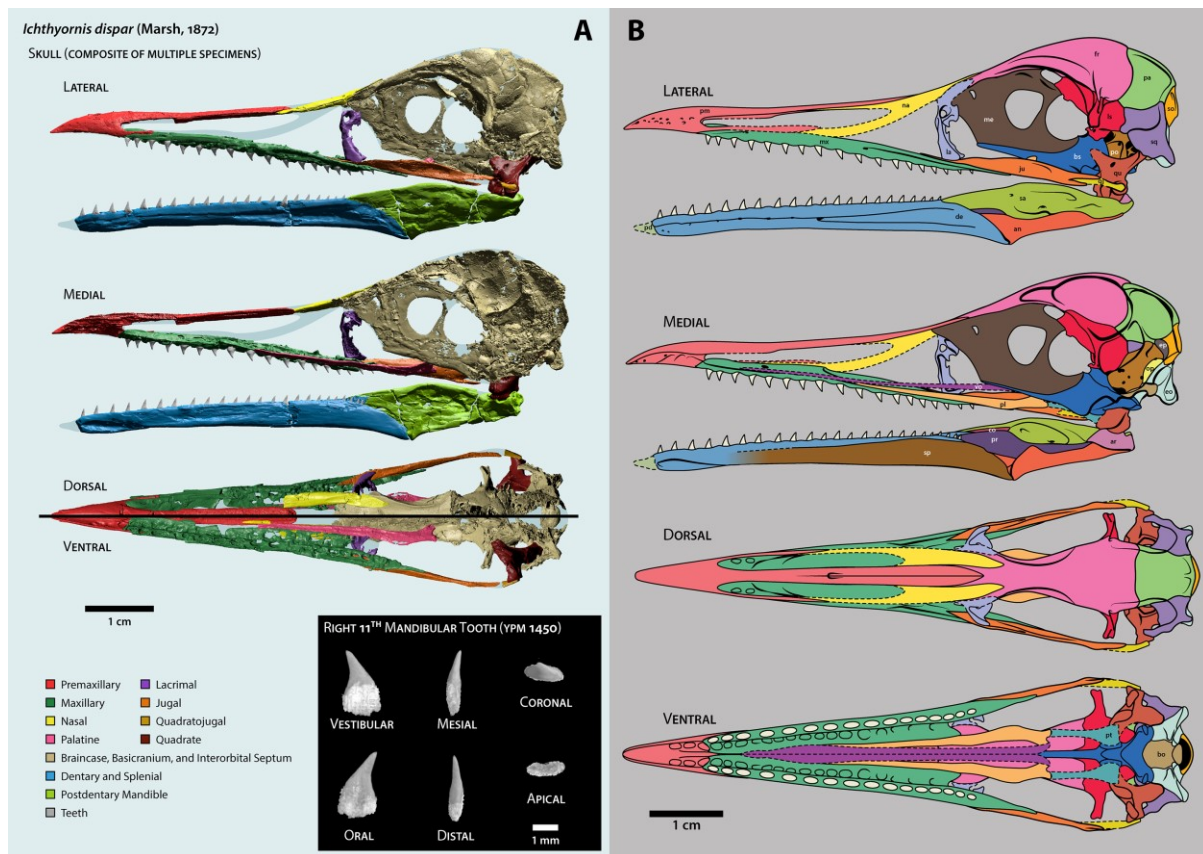
354 [d.j.field@bath.ac.uk](mailto:d.j.field@bath.ac.uk) and [michael.hanson@yale.edu](mailto:michael.hanson@yale.edu).

355



356

## Figures



357

358 **Figure 1. A:** Full 3D reconstruction of the skull of *Ichthyornis dispar*. Details in

359 **Supplementary Information.**

360 **B:** Line drawing of the skull of *I. dispar*, solid lines indicate areas known from fossil

361 specimens, dashed lines indicate unknown areas reconstructed from other ornithuran birds.

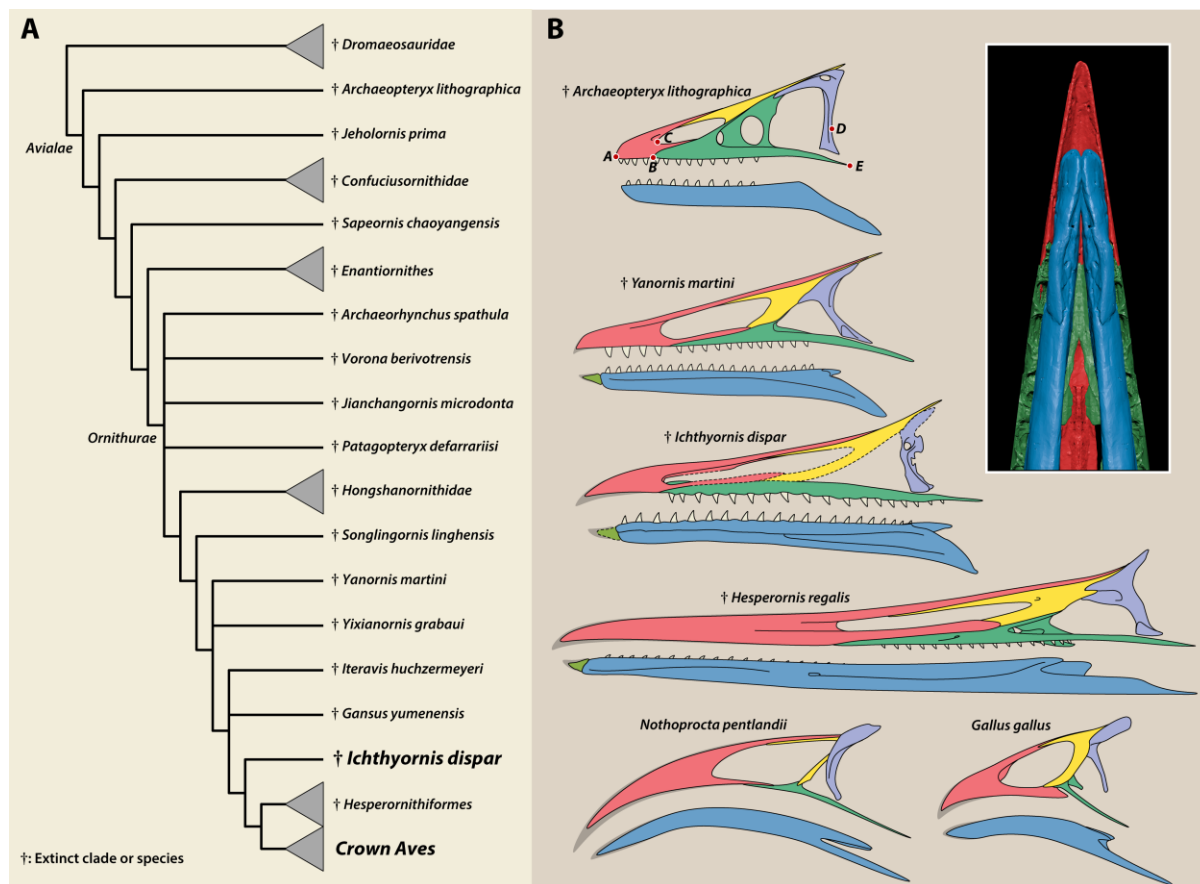
362 Anatomical Abbreviations. an: angular; ar: articular; bo: basioccipital; bs: basisphenoid; co:

363 coronoid; de: dentary; eo: exoccipital; ep: epiotic; ju: jugal; la: lacrimal; ls: laterosphenoid; fr:

364 frontal; me: mesethmoid; mx: maxilla; na: nasal; op: opisthotic; pa: parietal; pl: palatine; pm:

365 premaxillae; po: proötic; pt: pterygoid; qj: quadratojugal; qu: quadrate; sa: supraangular; sp:

366 splenial; sq: squamosal; vo: vomer.



367

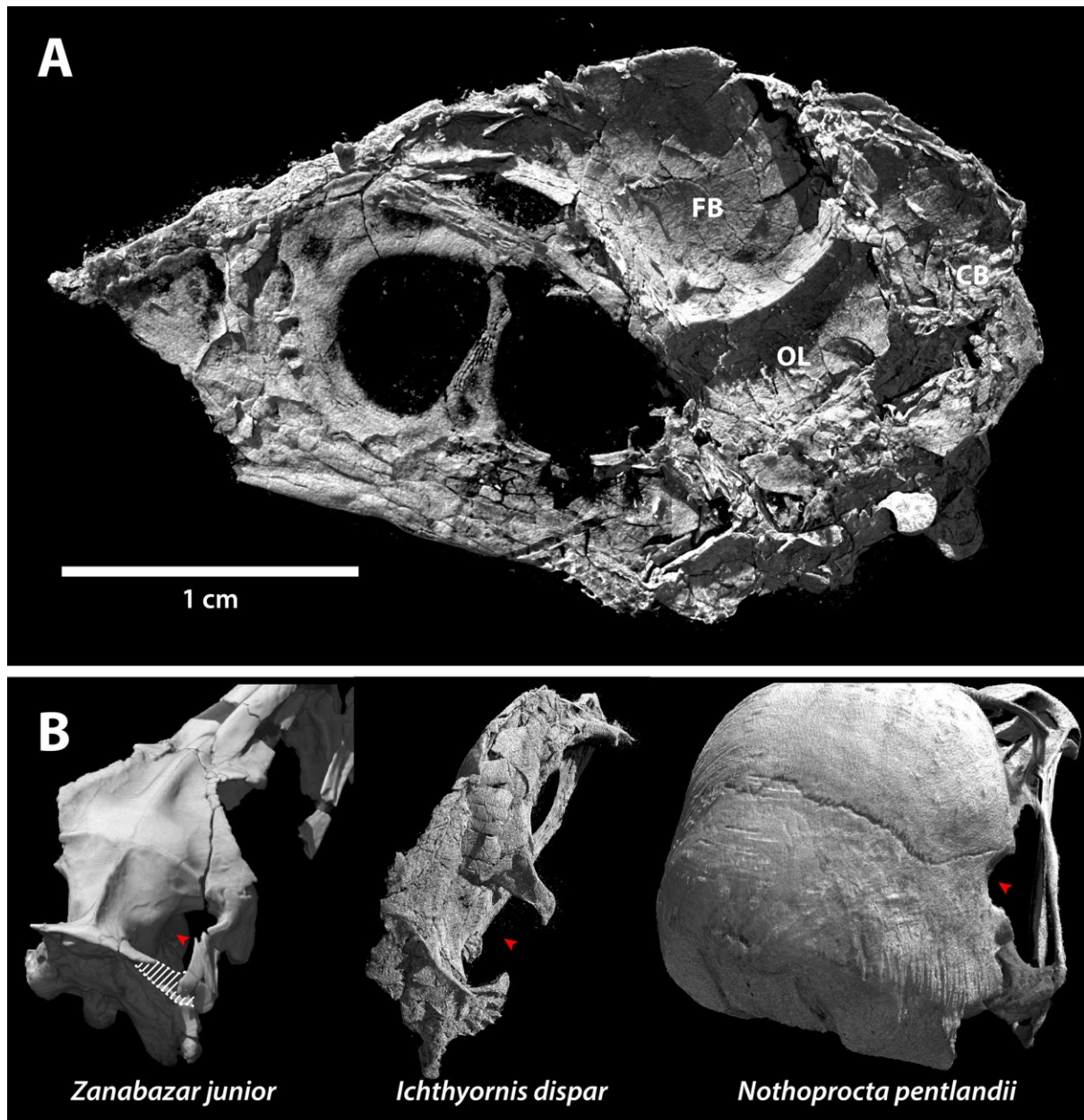
368 **Figure 2. A:** Cladogram showing the phylogenetic position of *Ichthyornis dispar* inferred  
 369 based on novel analyses (abridged and based in part on new codings in multiple datasets; see  
 370 **Supplementary Information** for full phylogenetic results).

371 **B:** Origin of the avian bill. Line drawings of the rostrum of key Mesozoic avialans and crown  
 372 birds (see **Figure 2A** for phylogenetic position). Hypothesised extent of rhamphotheca is  
 373 indicated in grey. Points on the rostrum of *A. lithographica* denote landmarks used for  
 374 comparative measurements presented in the **Supplementary Information**. Inset shows the  
 375 occlusal gap between the tips of the premaxillae (red) and dentaries (blue) in ventral view  
 376 that may have been occupied by a predentary.

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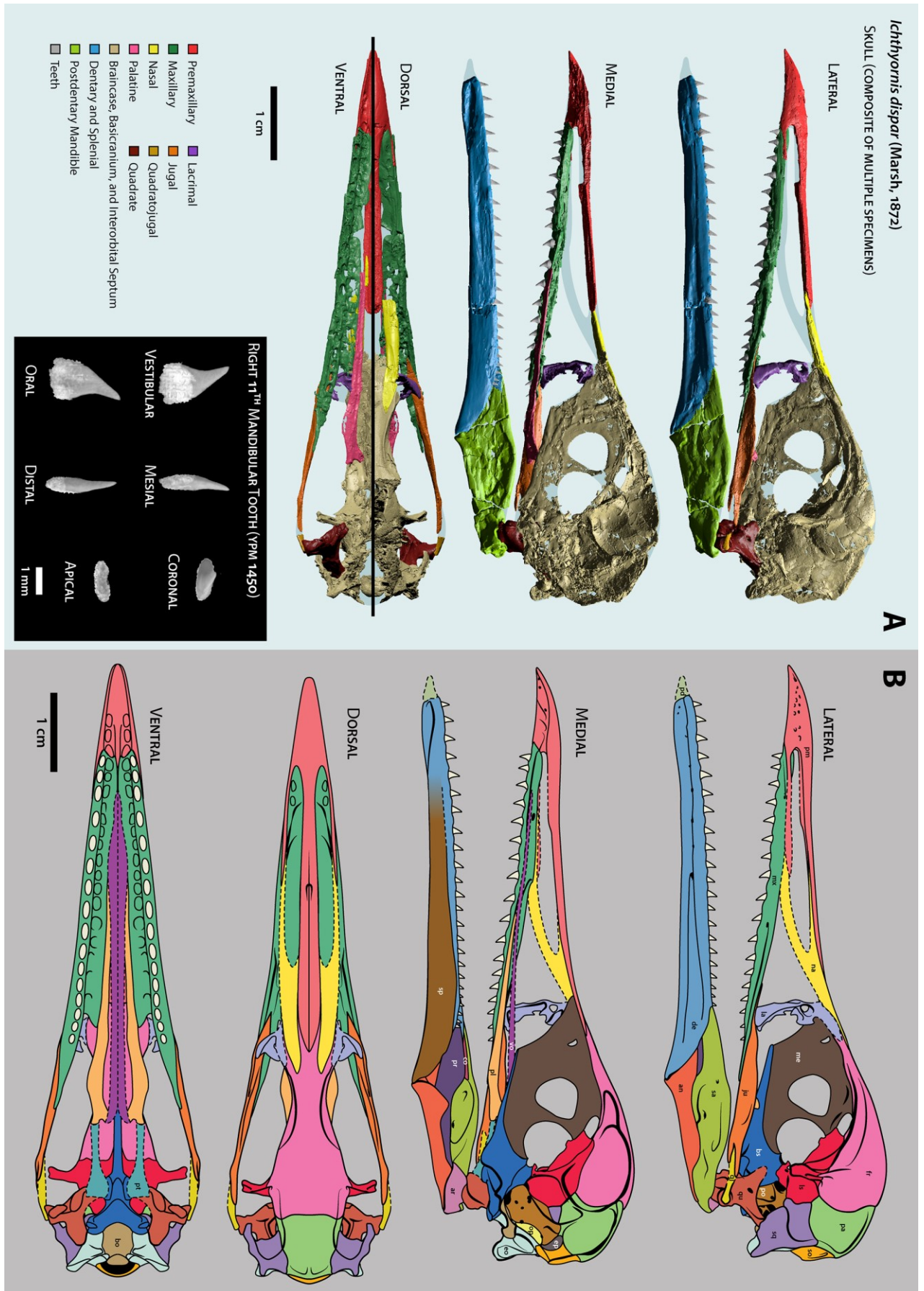


380

381 **Figure 3. A:** Sagittal cutaway of the braincase of *Ichthyornis dispar* revealing the endocranial  
382 space. Cavities labelled for brain divisions as follows — FB: Forebrain, OL: Optic lobe, CB:  
383 Cerebellum.

384 **B:** Comparative views of the temporal region of a nonavian dinosaur (*Zanabazar junior*),  
385 *Ichthyornis dispar*, and a crown bird (Andean Tinamou, *Nothoprocta pentlandii*). Red arrows  
386 denote position of the upper temporal fenestra.

387



388 *Figure 1 enlarged*

389 **References**

390

- 391 1 Huang, J. *et al.* A new ornithurine from the Early Cretaceous of China sheds light on  
 392 the evolution of early ecological and cranial diversity in birds. *PeerJ*, 4:e1765,  
 393 doi:https://doi.org/10.7717/peerj.1765 (2016).
- 394 2 Marsh, O. C. Notice of a new and remarkable fossil bird. *Am J Sci* **4** (1872).
- 395 3 Clarke, J. A. Morphology, phylogenetic taxonomy, and systematics of *Ichthyornis* and  
 396 *Apatornis* (Avialae: Ornithurae). *Bulletin of the American Museum of Natural History*  
 397 **286**, 1-179 (2004).
- 398 4 Olson, S. L. *Ichthyornis* in the Cretaceous of Alabama. *The Wilson Bulletin* **87**, 103-  
 399 105 (1975).
- 400 5 Lucas, S. G. & Sullivan, R. M. *Ichthyornis* in the Late Cretaceous Mancos Shale  
 401 (Juana Lopez Member), northwestern New Mexico. *Journal of Paleontology*, 545-547  
 402 (1982).
- 403 6 Parris, D. & Echols, J. The fossil bird *Ichthyornis* in the Cretaceous of Texas. *Texas*  
 404 *Journal of Science* **44**, 201-212 (1992).
- 405 7 Shimada, T. R. & Wilson, L. E. A new specimen of the Late Cretaceous bird, cf.  
 406 *Ichthyornis* sp., from the Cenomanian of central Kansas, with comments on the size  
 407 distribution of *Ichthyornis* in North America. *Transactions of the Kansas Academy of*  
 408 *Science* **119**, 231-237 (2016).
- 409 8 Gingerich, P. D. A new partial mandible of *Ichthyornis*. *Condor* **74**, 73-88 (1972).
- 410 9 Chiappe, L. M. & Qingjin, M. *Birds of Stone: Chinese Avian Fossils from the Age of*  
 411 *Dinosaurs*. (JHU Press, 2016).
- 412 10 Felice, R. N. & Goswami, A. Developmental origins of mosaic evolution in the avian  
 413 cranium. *Proceedings of the National Academy of Sciences*,  
 414 doi:10.1073/pnas.1716437115 (2017).
- 415 11 Mayr, G. (John Wiley & Sons, 2016).
- 416 12 Gauthier, J. Saurischian monophyly and the origin of birds. *Memoirs of the California*  
 417 *Academy of Sciences* **8** (1986).
- 418 13 Zhou, Z. & Martin, L. D. Distribution of the predentary bone in Mesozoic ornithurine  
 419 birds. *Journal of Systematic Palaeontology* **9**, 25-31,  
 420 doi:10.1080/14772019.2010.504080 (2011).
- 421 14 Rauhut, O. W. New observations on the skull of *Archaeopteryx*. *Paläontologische*  
 422 *Zeitschrift* **88**, 211-221 (2014).
- 423 15 Bühler, P., Martin, L. D. & Witmer, L. M. Cranial kinesis in the Late Cretaceous  
 424 birds *Hesperornis* and *Paraesperornis*. *The Auk*, 111-122 (1988).
- 425 16 Elzanowski, A. New observations on the skull of *Hesperornis* with reconstructions of  
 426 the bony palate and otic region. *Postilla* **207**, 1-20 (1991).
- 427 17 Bhullar, B.-A. S. *et al.* How to Make a Bird Skull: Major Transitions in the Evolution  
 428 of the Avian Cranium, Paedomorphosis, and the Beak as a Surrogate Hand.  
 429 *Integrative and Comparative Biology*, doi:10.1093/icb/icw069 (2016).
- 430 18 Liu, D. *et al.* An advanced, new long-legged bird from the Early Cretaceous of the  
 431 Jehol Group (northeastern China): Insights into the temporal divergence of modern  
 432 birds. *Zootaxa* **3884**, 253-266, doi:10.11646/zootaxa.3884.3.4 (2014).
- 433 19 Hieronymus, T. L. & Witmer, L. M. Homology and evolution of avian compound  
 434 rhamphothecae. *The Auk* **127**, 590-604 (2010).
- 435 20 Baumel, J. J. *et al.* Handbook of Avian Anatomy: Nomina Anatomica Avium Second  
 436 Edition. *Publications of the Nuttall Ornithological Club, No. 23*, 1-401 (1993).
- 437 21 Bock, W. J. Kinetics of the avian skull. *J. Morphol.* **114**, 1-42 (1964).

### 3D *Ichthyornis* skull

- 438 22 Homberger, D. G. in *The biology of the avian respiratory system* 27-97 (Springer,  
439 2017).
- 440 23 Jollie, M. T. The head skeleton of the chicken and remarks on the anatomy of this  
441 region in other birds. *Journal of Morphology* **100**, 389-436 (1957).
- 442 24 Zusi, R. L. Patterns of diversity in the avian skull. *The Skull* **2**, 391-437 (1993).
- 443 25 Martin, L. D. & Stewart, J. Teeth in *Ichthyornis* (Class: Aves). *Science* **195**, 1331-  
444 1332 (1977).
- 445 26 Dumont, M. *et al.* Synchrotron imaging of dentition provides insights into the biology  
446 of *Hesperornis* and *Ichthyornis*, the “last” toothed birds. *BMC evolutionary biology* **16**,  
447 178 (2016).
- 448 27 Marsh, O. C. *Odontornithes: a monograph on the extinct toothed birds of North*  
449 *America. US Government Printing Office* **18** (1880).
- 450 28 Chiappe, L. M., Norell, M. & Clark, J. A new skull of *Gobipteryx minuta* (Aves:  
451 Enantiornithes) from the Cretaceous of the Gobi Desert. *American Museum Novitates*  
452 **3346**, 1-15 (2001).
- 453 29 Zusi, R. L. A functional and evolutionary analysis of rynchokinesis in birds.  
454 *Smithsonian Contributions to Zoology* **395**, 1-40 (1984).
- 455 30 Gussekloo, S. W. & Bout, R. G. Cranial kinesis in palaeognathous birds. *Journal of*  
456 *Experimental Biology* **208**, 3409-3419 (2005).
- 457 31 Walsh, S. A., Milner, A. C. & Bourdon, E. A reappraisal of *Cerebavis cenomanica*  
458 (Aves, Ornithurae), from Melovatka, Russia. *Journal of anatomy* **229**, 215-227 (2016).
- 459 32 Domínguez Alonzo, P., Milner, A. C., Ketcham, R. A., Cookson, M. J. & Rowe, T. B.  
460 The avian nature of the brain and inner ear of *Archaeopteryx*. *Nature* **430**, 666-669,  
461 doi:10.1038/nature02706 (2004).
- 462 33 Balanoff, A. M., Bever, G. S., Rowe, T. B. & Norell, M. A. Evolutionary origins of  
463 the avian brain. *Nature* **501**, 93-96 (2013).
- 464 34 Müller, H. J. Die Morphologie und Entwicklung des Craniums von *Rhea americana*  
465 Linné. II. Viszeralskelett, Mittelohr und Osteocranium. *Zeitschrift für*  
466 *Wissenschaftliche Zoologie* **168**, 35-118 (1963).
- 467 35 Chiappe, L. M. Osteology of the flightless *Patagopteryx deferrariisi* from the Late  
468 Cretaceous of Patagonia (Argentina). *Mesozoic Birds: Above the Heads of Dinosaurs*,  
469 281-316 (2002).
- 470 36 Elzanowski, A. & Galton, P. M. Braincase of *Enaliornis*, an early cretaceous bird  
471 from England. *Journal of Vertebrate Paleontology* **11**, 90-107,  
472 doi:10.1080/02724634.1991.10011377 (1991).
- 473 37 Cracraft, J. The origin and early diversification of birds. *Paleobiology* **12**, 383-399  
474 (1986).
- 475 38 Vickaryous, M. K. & Hall, B. K. Development of the dermal skeleton in *Alligator*  
476 *mississippiensis* (Archosauria, Crocodylia) with comments on the homology of  
477 osteoderms. *Journal of morphology* **269**, 398-422 (2008).
- 478 39 Holliday, C. M. & Witmer, L. M. Archosaur adductor chamber evolution: integration  
479 of musculoskeletal and topological criteria in jaw muscle homology. *Journal of*  
480 *Morphology* **268**, 457-484 (2007).
- 481 40 Cooney, C. R. *et al.* Mega-evolutionary dynamics of the adaptive radiation of birds.  
482 *Nature advance online publication*, doi:10.1038/nature21074  
483 [http://www.nature.com/nature/journal/vaop/ncurrent/abs/nature21074.html#supplementary-](http://www.nature.com/nature/journal/vaop/ncurrent/abs/nature21074.html#supplementary-information)  
484 [information](http://www.nature.com/nature/journal/vaop/ncurrent/abs/nature21074.html#supplementary-information) (2017).
- 485 41 Xu, X., You, H., Du, K. & Han, F. An *Archaeopteryx*-like theropod from China and  
486 the origin of Avialae. *Nature* **475**, 465-470, doi:10.1038/nature10288 (2011).

- 487 42 Bhullar, B. A. S. *et al.* A molecular mechanism for the origin of a key evolutionary  
488 innovation, the bird beak and palate, revealed by an integrative approach to major  
489 transitions in vertebrate history. *Evolution* **69**, 1665-1677 (2015).
- 490 1 Huang, J. *et al.* A new ornithurine from the Early Cretaceous of China sheds light on  
491 the evolution of early ecological and cranial diversity in birds. *PeerJ*, 4:e1765,  
492 doi:<https://doi.org/10.7717/peerj.1765> (2016).
- 493 2 Marsh, O. C. Notice of a new and remarkable fossil bird. *Am J Sci* **4** (1872).
- 494 3 Clarke, J. A. Morphology, phylogenetic taxonomy, and systematics of *Ichthyornis* and  
495 *Apatornis* (Avialae: Ornithurae). *Bulletin of the American Museum of Natural History*  
496 **286**, 1-179 (2004).
- 497 4 Olson, S. L. *Ichthyornis* in the Cretaceous of Alabama. *The Wilson Bulletin* **87**, 103-  
498 105 (1975).
- 499 5 Lucas, S. G. & Sullivan, R. M. *Ichthyornis* in the Late Cretaceous Mancos Shale  
500 (Juana Lopez Member), northwestern New Mexico. *Journal of Paleontology*, 545-547  
501 (1982).
- 502 6 Parris, D. & Echols, J. The fossil bird *Ichthyornis* in the Cretaceous of Texas. *Texas*  
503 *Journal of Science* **44**, 201-212 (1992).
- 504 7 Shimada, T. R. & Wilson, L. E. A new specimen of the Late Cretaceous bird, cf.  
505 *Ichthyornis* sp., from the Cenomanian of central Kansas, with comments on the size  
506 distribution of *Ichthyornis* in North America. *Transactions of the Kansas Academy of*  
507 *Science* **119**, 231-237 (2016).
- 508 8 Gingerich, P. D. A new partial mandible of *Ichthyornis*. *Condor* **74**, 73-88 (1972).
- 509 9 Chiappe, L. M. & Qingjin, M. *Birds of Stone: Chinese Avian Fossils from the Age of*  
510 *Dinosaurs*. (JHU Press, 2016).
- 511 10 Felice, R. N. & Goswami, A. Developmental origins of mosaic evolution in the avian  
512 cranium. *Proceedings of the National Academy of Sciences*,  
513 doi:10.1073/pnas.1716437115 (2017).
- 514 11 Mayr, G. (John Wiley & Sons, 2016).
- 515 12 Gauthier, J. Saurischian monophyly and the origin of birds. *Memoirs of the California*  
516 *Academy of Sciences* **8** (1986).
- 517 13 Zhou, Z. & Martin, L. D. Distribution of the predentary bone in Mesozoic ornithurine  
518 birds. *Journal of Systematic Palaeontology* **9**, 25-31,  
519 doi:10.1080/14772019.2010.504080 (2011).
- 520 14 Rauhut, O. W. New observations on the skull of Archaeopteryx. *Paläontologische*  
521 *Zeitschrift* **88**, 211-221 (2014).
- 522 15 Bühler, P., Martin, L. D. & Witmer, L. M. Cranial kinesis in the Late Cretaceous  
523 birds *Hesperornis* and *Paraheperornis*. *The Auk*, 111-122 (1988).
- 524 16 Elzanowski, A. New observations on the skull of *Hesperornis* with reconstructions of  
525 the bony palate and otic region. *Postilla* **207**, 1-20 (1991).
- 526 17 Bhullar, B.-A. S. *et al.* How to Make a Bird Skull: Major Transitions in the Evolution  
527 of the Avian Cranium, Paedomorphosis, and the Beak as a Surrogate Hand.  
528 *Integrative and Comparative Biology*, doi:10.1093/icb/icw069 (2016).
- 529 18 Liu, D. *et al.* An advanced, new long-legged bird from the Early Cretaceous of the  
530 Jehol Group (northeastern China): Insights into the temporal divergence of modern  
531 birds. *Zootaxa* **3884**, 253-266, doi:10.11646/zootaxa.3884.3.4 (2014).
- 532 19 Zhou, S., O'Connor, J. K. & Wang, M. A new species from an ornithuromorph (Aves:  
533 Ornithothoraces) dominated locality of the Jehol Biota. *Chinese Science Bulletin* **59**,  
534 5366-5378, doi:10.1007/s11434-014-0669-8 (2014).
- 535 20 Hieronymus, T. L. & Witmer, L. M. Homology and evolution of avian compound  
536 rhamphothecae. *The Auk* **127**, 590-604 (2010).

- 537 21 Baumel, J. J. *et al.* Handbook of Avian Anatomy: Nomina Anatomica Avium Second  
538 Edition. *Publications of the Nuttall Ornithological Club, No. 23*, 1-401 (1993).
- 539 22 Bock, W. J. Kinetics of the avian skull. *J. Morphol.* **114**, 1-42 (1964).
- 540 23 Homberger, D. G. in *The biology of the avian respiratory system* 27-97 (Springer,  
541 2017).
- 542 24 Jollie, M. T. The head skeleton of the chicken and remarks on the anatomy of this  
543 region in other birds. *Journal of Morphology* **100**, 389-436 (1957).
- 544 25 Zusi, R. L. Patterns of diversity in the avian skull. *The Skull* **2**, 391-437 (1993).
- 545 26 Martin, L. D. & Stewart, J. Teeth in *Ichthyornis* (Class: Aves). *Science* **195**, 1331-  
546 1332 (1977).
- 547 27 Dumont, M. *et al.* Synchrotron imaging of dentition provides insights into the biology  
548 of *Hesperornis* and *Ichthyornis*, the “last” toothed birds. *BMC evolutionary biology* **16**,  
549 178 (2016).
- 550 28 Marsh, O. C. *Odontornithes: a monograph on the extinct toothed birds of North*  
551 *America. US Government Printing Office* **18** (1880).
- 552 29 Chiappe, L. M., Norell, M. & Clark, J. A new skull of *Gobipteryx minuta* (Aves:  
553 *Enantiornithes*) from the Cretaceous of the Gobi Desert. *American Museum Novitates*  
554 **3346**, 1-15 (2001).
- 555 30 Zusi, R. L. A functional and evolutionary analysis of rynchokinesis in birds.  
556 *Smithsonian Contributions to Zoology* **395**, 1-40 (1984).
- 557 31 Gussekloo, S. W. & Bout, R. G. Cranial kinesis in palaeognathous birds. *Journal of*  
558 *Experimental Biology* **208**, 3409-3419 (2005).
- 559 32 Walsh, S. A., Milner, A. C. & Bourdon, E. A reappraisal of *Cerebavis cenomanica*  
560 (Aves, *Ornithurae*), from Melovatka, Russia. *Journal of anatomy* **229**, 215-227 (2016).
- 561 33 Domínguez Alonzo, P., Milner, A. C., Ketcham, R. A., Cookson, M. J. & Rowe, T. B.  
562 The avian nature of the brain and inner ear of *Archaeopteryx*. *Nature* **430**, 666-669,  
563 doi:10.1038/nature02706 (2004).
- 564 34 Balanoff, A. M., Bever, G. S., Rowe, T. B. & Norell, M. A. Evolutionary origins of  
565 the avian brain. *Nature* **501**, 93-96 (2013).
- 566 35 Müller, H. J. Die Morphologie und Entwicklung des Craniums von *Rhea americana*  
567 Linné. II. Viszeralskelett, Mittelohr und Osteocranium. *Zeitschrift für*  
568 *Wissenschaftliche Zoologie* **168**, 35-118 (1963).
- 569 36 Chiappe, L. M. Osteology of the flightless *Patagopteryx deferrariisi* from the Late  
570 Cretaceous of Patagonia (Argentina). *Mesozoic Birds: Above the Heads of Dinosaurs*,  
571 281-316 (2002).
- 572 37 Elzanowski, A. & Galton, P. M. Braincase of *Enaliornis*, an early cretaceous bird  
573 from England. *Journal of Vertebrate Paleontology* **11**, 90-107,  
574 doi:10.1080/02724634.1991.10011377 (1991).
- 575 38 Cracraft, J. The origin and early diversification of birds. *Paleobiology* **12**, 383-399  
576 (1986).
- 577 39 Vickaryous, M. K. & Hall, B. K. Development of the dermal skeleton in *Alligator*  
578 *mississippiensis* (Archosauria, *Crocodylia*) with comments on the homology of  
579 osteoderms. *Journal of morphology* **269**, 398-422 (2008).
- 580 40 Holliday, C. M. & Witmer, L. M. Archosaur adductor chamber evolution: integration  
581 of musculoskeletal and topological criteria in jaw muscle homology. *Journal of*  
582 *Morphology* **268**, 457-484 (2007).
- 583 41 Cooney, C. R. *et al.* Mega-evolutionary dynamics of the adaptive radiation of birds.  
584 *Nature advance online publication*, doi:10.1038/nature21074.
- 585 42 Xu, X., You, H., Du, K. & Han, F. An *Archaeopteryx*-like theropod from China and  
586 the origin of *Avialae*. *Nature* **475**, 465-470, doi:10.1038/nature10288 (2011).



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588 innovation, the bird beak and palate, revealed by an integrative approach to major  
589 transitions in vertebrate history. *Evolution* **69**, 1665-1677 (2015).  
590