Whence the birds: 200 years of dinosaurs, avian antecedents

Daniel J. Field[1,2], M. Grace Burton[1], Juan Benito[1], Olivia Plateau[1], Guillermo Navalón[1]

[1]Department of Earth Sciences, University of Cambridge, Cambridge, UK

[2]Museum of Zoology, University of Cambridge, Cambridge, UK

Keywords: skeletal pneumaticity, flight apparatus, brain evolution, palate, bird evolution, dinosaur evolution

Abstract

Among the most revolutionary insights emerging from 200 years of research on dinosaurs is that the clade Dinosauria is represented by approximately 11,000 living species of birds. Although the origin of birds among dinosaurs has been reviewed extensively, recent years have witnessed tremendous progress in our understanding of the deep evolutionary origins of numerous distinctive avian anatomical systems. These advances have been enabled by exciting new fossil discoveries, leading to an ever-expanding phylogenetic framework with which to pinpoint the origins of characteristic avian features. The present review focuses on four notable avian systems whose Mesozoic evolutionary history has been greatly clarified by recent discoveries: the brain, the kinetic palate, the pectoral girdle, and postcranial skeletal pneumaticity.

Introduction

2024 marks the 200th anniversary of *Megalosaurus*, the first non-avian dinosaur to be validly named [1]. Though not initially recognised as such, that discovery can be viewed as the genesis of humanity's enduring fascination with the clade Dinosauria, a term first coined in 1842 [2]. While 200 years of research on dinosaurs has revealed a huge amount about the extinct diversity of the Mesozoic Era, arguably the most important single insight arising from the vast body of dinosaur research is the revelation that Dinosauria includes all birds, living and extinct. This insight arose gradually [e.g., 3, 4-12], yet today the emergence of birds among dinosaurs stands as one of the best understood macroevolutionary transformations in the entire history of life. The sheer diversity and ubiquity of extant birds—roughly 11,000 extant species—challenges the view of the Cenozoic Era as 'The Age of Mammals', and nullifies the notion that dinosaurs are long extinct. Nonetheless, despite the fact that

birds *are* dinosaurs, birds are strikingly divergent from other dinosaurs in many aspects of their morphology and biology, and the evolutionary origins of the distinctive 'avian' characteristics that set them apart from other reptiles remains a vibrant area of palaeontological research.

A rush of discoveries beginning in the early 1990's led to fundamental new insights regarding the evolutionary origins of many aspects of avian biology, which have been summarised in numerous well cited reviews published between the late 1990's and 2010's [e.g., 13, 14-17]. This extraordinary pace of discovery continues unabated, and the years since have seen a wealth of new data emerge that further clarify the evolutionary origins of quintessentially 'avian' features.

Crown group birds arose towards the end of the Cretaceous Period [18-21]. The earliest crown birds would have lived alongside representatives of all three major dinosaurian subclades (Ornithischia, Sauropodomorpha, and Theropoda) as well as many lineages of non-neornithine avialans until the end-Cretaceous mass extinction event left crown birds as the only surviving representatives of Dinosauria [22-25]. The rich Mesozoic fossil record of stem-group birds (including pterosaurs, non-avian dinosaurs, and non-neornithine avialans) is the place to turn for insights into the evolutionary origins of crown bird characteristics. In the present review, we aim to summarise recent advances clarifying the origins of several specialised aspects of crown bird anatomy underpinning distinctive avian functional capabilities. We focus on discoveries emerging in recent years (i.e. since 2018) regarding the evolution of the following key traits: (i) an enlarged and anatomically modern brain (enabling advanced cognition and behavioural complexity), (ii) a kinetic palate (facilitating cranial kinesis), (iii) a geometrically modern pectoral girdle (underpinning sophisticated powered flight), and (iv) postcranial skeletal pneumaticity (related to lightening the skeleton). Feathers, one of the hallmarks of bird morphology and a textbook example of a 'crown bird feature' observable in Mesozoic dinosaurs [26-29], are treated in a separate review in this volume. We also identify enduring knowledge gaps that limit a comprehensive understanding of these transitions in the hope that these will be filled in the coming years. We use the term Neornithes as synonymous with crown birds, and Avialae to refer to the clade bracketed by Neornithes and *Archaeopteryx*.

Brain evolution: thinking like a bird

Among living vertebrates, only birds rival mammals in terms of relative brain size and behavioural complexity, and the exceptional problem-solving capabilities and flamboyant displays of many extant

61 birds are well studied [30]. Relatedly, the morphology of the avian central nervous system is highly
62 divergent with respect to all other known reptiles, including non-avian dinosaurs. For instance, the brain
63 of crown birds is larger and more globular than that of other reptiles due to the volumetric expansion of
64 key brain regions, particularly the telencephalon (cerebrum) and the cerebellum [31-34]. In many crown
65 birds the caudal portion of the brain flexes ventrally, which re-orients the spatial relationships of its main
66 anatomical subdivisions (e.g., the telencephalon sits dorsal to the optic lobes) and redirects the
67 connection with the spinal column ventrally, rather than caudally as in most non-avian reptiles [35] (Fig.
68 1A). This derived neuroanatomy co-occurs with similarly derived morphologies of the inner ear (e.g., an
69 enlarged and sinusoidal anterior semicircular canal [36, 37]). These morphological transformations of
70 the brain and associated sensory structures have traditionally been linked to the origin of avian flight
71 [e.g., 34, 35] and other adaptations at least partially underpinning avian evolutionary success (e.g.,
72 survivorship through the K–Pg mass extinction [38]).
73 Tight anatomical correspondence between the bony endocranial cavities and the underlying
74 central nervous system enable reconstructions of endocranial morphology in Mesozoic fossils
75 illuminating the evolutionary history of distinctly ‘avian’ neuroanatomical specialisations [39, 40]. This
76 has enabled the reconstruction of brain morphology in *Archaeopteryx* [41], which is similar overall to
77 that of closely related non-avian maniraptorans in exhibiting limited expansion of the telencephalon,
78 cerebellum, and optic lobes, as well as a similarly unflexed brain connecting to the spinal cord caudally
79 [31, 41].
80 Nonetheless, the rarity of complete, three-dimensionally preserved fossils from the Mesozoic
81 Era has long obfuscated the evolutionary transition from the plesiomorphic central nervous system of
82 the earliest avialans like *Archaeopteryx* to the derived neuroanatomy of crown birds (Fig. 1A). This
83 leaves a gap of more than 70 million years in which our understanding of the evolution of the modern
84 avian central nervous system is practically non-existent (Fig. 1A), an interval that witnessed the
85 origination of all major groups of Mesozoic avialans, as well as the earliest phylogenetic divergences
86 among crown birds.
87 Among non-neornithine avialans, the clade Enantiornithes occupies a phylogenetically pivotal
88 position as the sister group to Euornithes, which includes crown birds (Fig. 3). Enantiornithes dominated
89 Mesozoic avifaunas globally and represents the first great radiation of bird-like animals [42], yet despite
90 their abundance and diversity, the first detailed insights into enantiornithine endocranial morphology

have only recently emerged [43, 44, in press]. The recently described enantiornithine *Navaornis hestiae* is represented by unusually immaculate, three-dimensionally preserved remains, enabling a nearly complete reconstruction of its skull and endocranial morphology [44, in press]. Although its skull geometry is remarkably like that of crown birds, its endocranial morphology retains numerous plesiomorphic features, such that it is roughly intermediate between *Archaeopteryx* and crown birds (Fig. 1A), suggesting a notable degree of independence with respect to evolutionary changes in the skull and brain. These plesiomorphies include a small cerebellum relative to the rest of the brain, and a telencephalon with a mediolateral expansion exceeding the degree observed in *Archaeopteryx* [31, 41] and known non-avian pennaraptoran dinosaurs [45, 46] (Fig. 1A), but less than that observed in most crown birds and crownward avialans in which the telencephalic hemispheres envelop the dorsal surface of the optic lobes [40, 47] (Fig. 1A). Despite these plesiomorphic attributes, *Navaornis* also exhibits several neuroanatomical features only previously known from crown birds and the crownward-most stem birds such as large optic lobes positioned ventral to the telencephalon, and a bony inner ear labyrinth comparable in shape, but much larger, than that of many crown birds. Although the flight apparatus of enantiornithines may have been broadly functionally comparable to that of crown birds (see below), the lack of a full suite of crown-like neuroanatomical features in the brain of *Navaornis* casts doubt on predictions of a tight association between the origin of powered flight and the origin of modern avian neuroanatomy.

Recent work provides the clearest insights yet into the neuroanatomy of the ancestral crown bird [48], illustrating that ‘modern type’ avian brains were present among the earliest known stem palaeognaths. However, phylogenetically pinpointing the evolutionary origin of the modern-type avian brain remains challenging. The earliest apparent evidence of modern-type avian brain morphology comes from a single, isolated 100-million-year-old fossil braincase [47, 49]. Unfortunately, the phylogenetic affinities of this fossil (*Cerebavis cenomanica*) remain enigmatic due to the absence of associated skeletal remains. Moreover, taphonomic deformation (e.g., [38, 50]) and fossil incompleteness (e.g., [51]) continue to hamper our understanding of brain morphology among the crownward-most representatives of the avian stem group. Interrogating the neuroanatomical features of early euornitheans therefore constitutes a top priority for future work; such efforts, and the continued discovery of exceptionally preserved, three-dimensional cranial remains of Mesozoic avialans, will be needed to clarify the phylogenetic and temporal origins of a morphologically modern avian brain.

Palate morphology: origin of a kinetic beak

Most crown birds exhibit cranial kinesis [52], the capacity to move parts of the rostrum independently from the braincase. This specialisation enhances dexterity and precision of the bill—faculties that became all the more important as the ancestors of birds sacrificed hands capable of fine manipulation in favour of wings as avian flight arose [50, 53]. While the kinetic capabilities of extant bird skulls continue to be documented in greater detail [54], these capabilities are facilitated in part by specialised joints within the palate, with recent discoveries clarifying the pattern and timing by which this increased capacity for palatal mobility arose. In the oldest and most stemward avialan known, *Archaeopteryx*, the palate would have remained plesiomorphically rigid, with the organisation of the palate's components (paired vomers, palatines, pterygoids and ectopterygoids) resembling that of non-avian theropod dinosaurs (Fig. 1B) [55-57]. The vomers of *Archaeopteryx* are narrow and elongate, and contact the caudally positioned pterygoids via posteriorly directed rami [55, 58, 59]. The pterygoids are extremely long rostrocaudally, spanning almost the entire length of the palate, and contact the quadrates caudally [55, 58, 59]. Lateral to the rostral portion of the pterygoids, the palatines are slender and rostrocaudally elongate, contacting the pterygoids posteriorly [55, 58, 59]. Tongue-shaped wings of the ectopterygoids [59] extend laterally from the pterygoid, acting as a bridge to the jugal [60]. Although palate preservation is rare among stemward avialans other than *Archaeopteryx*, recent insight from *Jeholornis* [61] suggests other early avialans likely retained a generally similar palatal arrangement.

This plesiomorphic palatal arrangement did not undergo substantial modification among early pygostylians, as revealed by insights from *Sapeornis* [60, 62]. It is currently unclear whether this was also the case among confuciusornithids, whose edentulous beaks are convergent with those of crown birds [e.g., 63, 64, 65]. Despite an abundant Early Cretaceous fossil record, the confuciusornithid palate remains poorly known as a result of a dearth of complete, three-dimensionally preserved cranial remains [63, 66]. Among Enantiornithes, only a few taxa spanning the Early to Late Cretaceous (e.g., *Chiappeavis* [67], *Gobipteryx* [68], *Yuornis* [69], *Yuanchuavis* [70], *Navaornis* [44, in press]), preserve adequate palate material to inform discussions of broad patterns of avialan palate evolution. While isolated enantiornithine remains exhibit broadly similar palatal architecture to *Archaeopteryx*, most remains are too scanty to confirm whether the enantiornithine palate as a whole retained such a plesiomorphic condition.

Among the greatest outstanding questions surrounding enantiornithine palate morphology regards the uncertain presence of ectopterygoids. These large, rounded elements buttress the palate against the lateral wall of the skull in non-avian theropods and early avialans such as *Archaeopteryx* and *Sapeornis* [60], preventing motion of the palate, but their presence in Enantiornithes is controversial. While ectopterygoids were originally interpreted as present in *Gobipteryx* [71], this identification has been disputed [72], and subsequent descriptions have not unequivocally identified enantiornithine ectopterygoids despite the vast number of specimens discovered to date [73]. *Falcatakely*, a possible enantiornithine known only from a bizarre, isolated skull from the latest Cretaceous of Madagascar, exhibits unmistakeable large ectopterygoids [74], yet the referral of *Falcatakely* to Enantiornithes is not foregone [75], and certain phylogenetic analyses have recovered it outside Ornithothoraces altogether [76]. The sheer diversity and cranial disparity of enantiornithines may drive a tendency for isolated cranial remains—even those of non-avialan fossil vertebrates—to be drawn towards Enantiornithes in phylogenetic analyses [77], suggesting that uncertainty regarding both the phylogenetic position of *Falcatakely* and the presence of ectopterygoids in Enantiornithes will persist until discoveries of more complete fossil material emerge. Among early representatives of Euornithes, palates of specimens from the Early Cretaceous are also largely unknown. For several key taxa the quality of preservation is often poor, with palate elements sometimes present but usually not fully described [78-80].

Important palatal innovations appear within the crownward euornithine subclade Ornithurae, as illustrated by representatives of the clades Ichthyornithes and Hesperornithes [38, 81-83]. Unlike stemward Mesozoic avialans, these taxa show no evidence of ectopterygoids, yet they exhibit palatal elements unknown in comparatively stemward taxa: paired hemipterygoids [38, 81, 82]. These articulate with the palatines rostrally and the pterygoids caudally [38, 82], potentially providing an additional degree of freedom for kinesis within the palate. Although the palate of Hesperornithes is considered to be highly autapomorphic [38], that of Ichthyornithes may more closely resemble the plesiomorphic condition for crown birds, and documents changes in the articular relationships among the elements of the palate [81].

The distinction between the two major extant neornithine subclades (Palaeognathae and Neognathae; Fig. 1B) has long been supported by differences in their palatal morphology [72, 84, 85]. While neognaths exhibit a mobile joint between pterygoid and palatine enhancing the capacity for cranial kinesis, the palates of palaeognaths are more robust, with a rigid, often fused connection

between the pterygoid and the palatine [84-86]. Long thought to represent a neognath synapomorphy, the embryonic pterygoid generally undergoes a process of division, termed ‘segmentation’, in early ontogeny [87, 88], resulting in the generation of a transient independent hemipterygoid positioned between the palatine and pterygoid in immature specimens close to hatching [82, 87, 89-97]. Unlike the condition in Ichthyornithes and Hesperornithes, in adult neognaths the hemipterygoid fuses with the caudal end of the palatine such that it ceases to be identifiable as an independent element [38, 94, 97].

In contrast to neognaths, the pterygoids of palaeognaths do not undergo segmentation, resulting in a palate conformation broadly similar to that of non-avian theropod dinosaurs and stemward Mesozoic avialans. As such, the palate morphology of palaeognaths was long assumed to retain the plesiomorphic condition inherited from the last common ancestor of crown birds [98-101]. However, the discovery of a well preserved pterygoid in the ichthyornithine *Janavis* [81], coupled with the well preserved palatines and hemipterygoids recently described from *Ichthyornis* [38], suggest that Ichthyornithes exhibited palates morphologically, and presumably functionally, similar to those of extant chickens (Galliformes) and ducks (Anseriformes), which have kinetic palates. These findings suggest that crownward stem birds, and presumably the earliest crown birds themselves, possessed mobile, neognath-like palates, unlike those of extant palaeognaths.

Deeper insight into avialan palatal evolution is essential for understanding the origin and refinement of avian cranial kinesis [60]. The loss of a solid jugal-postorbital bar and ectopterygoids were necessary for freeing the upper jaw to move relative to the braincase, although poor fossil preservation continues to obscure the precise timing of these transitions in Mesozoic avialan evolutionary history [60, 88]. Indeed, the propensity for many Mesozoic avialan fossils to be preserved flattened [42, 72, 102] ensures that numerous questions regarding the Mesozoic evolutionary history of the avialan palate currently remain unanswered [38, 60, 81].

Pectoral girdle: a shoulder ready for take-off

The evolution of powered flight drove numerous transformations of the avian skeleton [16, 103-110]. This is illustrated most clearly by the flight apparatus, which includes the pectoral girdle and the forelimbs. Although much remains unknown regarding how and when maniraptoran dinosaurs first took to the air [11, 111, 112], recent work has helped clarify our understanding of the origin of a morphologically modern avian flight apparatus. Forelimb morphology was substantially transformed as

211 the dexterous arms of ancestral maniraptorans became the highly specialised wings of avialans [76,
212 113-115], and the pectoral girdle simultaneously underwent dramatic transformations linked to the
213 evolution and refinement of powered flight [11, 115-120].

214 The pectoral girdle consists of the sternum, paired coracoids and scapulae, and the furcula or
215 wishbone. This morphological unit connects the forelimbs to the trunk, provides the primary attachment
216 surfaces for flight muscles, and guides the tendons connecting the flight muscles to the wings. The
217 pectoral morphology of stemward avialans such as *Archaeopteryx* does not differ much from that of
218 non-avialan paravian dinosaurs, exhibiting simple, roughly quadrangular coracoids fused to the
219 scapulae, a short and robust boomerang-shaped furcula, and no evidence of an ossified sternum (Fig.
220 2A) [59, 116, 121-127]. Sternal remains are also unknown from the comparatively crownward avialan
221 *Sapeornis*, suggesting that this element was either absent or largely cartilaginous in certain early
222 avialans, hindering its fossilisation potential [116, 128, 129]. Among stemward avialans, Jeho-
223 lornithiformes and non-ornithothoracine pygostylians exhibit proportionally larger and more elongate
224 coracoids, elongate scapulae, and ossified sterna composed of two incompletely fused sternal plates
225 [116, 122, 127, 130]. Notably, the pygostylian subclades Confuciusornithiformes and Jinguofortisidae
226 convergently evolved fused scapulocoracoids (Fig. 2A), similar to the condition in many non-avialan
227 theropods and extant flightless palaeognaths, despite otherwise exhibiting clear flight adaptations [63,
228 131, 132]. It is unclear to what degree the comparatively plesiomorphic morphology of the pectoral
229 girdle of non-ornithothoracine avialans impacted their flight capabilities, but it has been suggested that
230 sustained flapping and highly manoeuvrable flight would have been impossible [115, 120, 133].

231 The evolution of more advanced flight specialisations within Ornithothoraces was accompanied
232 by the evolutionary acquisition of more complex pectoral morphologies in Enantiornithes and Euornithes
233 [115, 116, 127, 134, 135]. These major clades share elongate coracoids, a complex coracoid-scapula
234 articulation [116], a robust acromion process of the scapula [136], more acutely angled furculae [137],
235 and fully fused sterna, in most cases exhibiting a sternal keel serving as the attachment point for the
236 main flight muscles; these muscles were likely anchored to the coracoid and furcula in non-
237 ornithothoracine avialans instead [115, 116, 127, 128, 134, 138]. However, the pectoral morphologies
238 of Enantiornithes and Euornithes differ in important ways, including divergent mechanisms for linking
239 the coracoid and scapula: in Enantiornithes, the coracoid exhibits a convex protrusion inserting into a
240 concave facet on the scapula [116, 139-142], whereas the opposite relationship exists in Euornithes

241 (including crown birds), where a cotyle on the coracoid receives a condyle from the scapula (Fig. 2A)
242 [127, 143]. Furthermore, recent work has illustrated that this mechanism represents the only point of
243 articulation between the scapula and coracoid in Enantiornithes, whereas in Euornithes, as in all other
244 avialans, the scapula exhibits an additional elongate point of contact with the coracoid [116]. The
245 coracoids of most Euornithes (and only a few Enantiornithes; [144]) exhibit a procoracoid process
246 directing flight muscle tendons arising on the sternum to the humerus [78, 115, 127, 145, 146]. In most
247 crownward Euornithes and in crown birds the procoracoid process contacts the scapula and the furcula
248 (although variability exists [143, 147]), fully enclosing these tendons in a so-called 'triosseal canal', the
249 origin of which may have accompanied a transition to more active flapping flight and more sophisticated
250 take-off capabilities [11, 76, 115, 148]. The presence of an incomplete or incipient triosseal canal in
251 Enantiornithes and stemward Euornithes is contentious [115, 116, 127, 136, 141, 149], but it is likely
252 that Enantiornithes exhibited a tendon arrangement distinct from that of living birds [115, 116]. Most
253 enantiornithines exhibit broad sterna that are mediolaterally wider than rostrocaudally long; their sternal
254 keels – when present – are short, rounded, and extend only along the caudal portion of the sternum
255 (Fig. 2A) [150, 151]. In most Euornithes, by contrast, the sternum is longer than wide, with a well-
256 developed sternal keel that extends along the entire rostrocaudal axis of the bone and, in crownward
257 ornithurines and many living birds, beyond its rostral margin (Fig. 2A) [76, 135, 152]. This more
258 extensive keel has been suggested to be related to the displacement and expansion of the attachment
259 points for the flight muscles related to take-off from the ground [115]. This inference is of particular
260 importance for non-neornithine Euornithes, which have been interpreted as being predominantly
261 ground-dwelling or semiaquatic [25, 134], contrasting with the primarily arboreal ecologies inferred for
262 Enantiornithes [115, 153]. Notably, Avisauridae, a clade of Late Cretaceous enantiornithines,
263 convergently evolved a similarly well-developed sternal keel, suggesting a similar muscular
264 rearrangement to that of Euornithes [154-156]. The evolution of the caudal end of the sternum is
265 perhaps more complex, and its functional significance poorly understood. While early diverging
266 Enantiornithes like *Protopteryx* and Pengornithidae have simpler caudal sternal margins [157-159]
267 most members of the clade, as well stemward Euornithes, such as *Archaeorhynchus,* often exhibit very
268 complex caudal margins, with long lateral and caudolateral processes and deep incisures that are often
269 taxonomically diagnostic (Fig. 2A) [160-162]. More crownward Euornithes exhibit simpler sternal
270 margins [76, 163-165], and, in some taxa, develop fully enclosed fenestrae [78, 146]. Contrasting

morphologies in Enantiornithes and Euornithes are evident in the furcula as well: in the former, the furcula is V-shaped with a narrow, long and rod-like hypocleideum [166]; in the latter, the furcular symphysis is more rounded and a hypocleideum is generally absent [121].

Beyond osteological evidence for the evolution of powered flight, important insights into the nature of early bird flight can be gleaned from exceptionally preserved remains of fossil avialans. These can preserve soft tissues of the wing and pectoral apparatus, including feathers and propatagia [42, 167-169], with implications for understanding the evolution and integrated function of the flight apparatus. Although the wing plumage of early avialans appears superficially similar to that of crown group birds (with the potential exception of Anchiornithidae, which may exhibit evidence of secondary flight reduction [170]), the feather structure of non-ornithothoracine avialans seems comparatively poorly suited for powered flapping flight [133, 171]. Ornithothoraces, by contrast, possessed advanced crown bird-like flight feathers and alulae, which likely conferred sophisticated flight potential comparable to that of their living relatives [111, 133]. Inferences related to the flight style of several fossil avialans have been made based on skeletal morphology and exceptionally preserved soft tissues, suggesting a wide diversity of flight styles arising early in bird evolutionary history [166, 167, 171-176], including thermal soaring [177] and bounding flight [178, 179]. However, such inferences are limited by a poor understanding of the biomechanics of the flight apparatus in all but the crownward-most known stem birds [116, 180]. This is largely due to the continuing scarcity of complete and articulated three-dimensional avialan remains, complicating the application of modern biomechanical methods to address these questions [111, 181]. Nonetheless, the continued development of approaches for fossil retrodeformation [e.g., 180] and computational biomechanical analysis [e.g., 182] are poised to cast light on these fascinating questions in coming years.

Skeletal pneumaticity: lightening the load

Birds are the only extant tetrapod group to exhibit postcranial skeletal pneumaticity (PSP); that is, the invasion of the respiratory system into elements of the postcranial skeleton, resulting in the replacement of comparatively dense marrow with air-filled cavities lined with epithelia [183-186]. PSP is an important avian specialisation that lightens the skeleton, exhibited by most living birds except some aquatic divers [187], making it one of the most distinctive aspects of avian skeletal morphology.

The evolutionary origins of avian PSP may trace back as far as the Triassic Period (~250-210 Ma), as pneumatic postcranial skeletal elements are evident in pterosaurs [188-191], sauropodomorph dinosaurs [192-199], and both avialan and non-avialan theropod dinosaurs [81, 122, 187, 200, 201]. The potential for skeletal pneumaticity to alter the relationship between body mass and body volume [187] has played a clear role in the evolution of enormous body size in the largest terrestrial and volant animals to have ever lived (sauropods and pterosaurs, respectively). Among crown birds, body mass has only been weakly correlated with the extent of PSP [183, 187, 202, 203]. Rather, the relaxation of constraints on PSP development in crown birds has likely allowed for frequent adaptive decoupling of body mass-volume relationships, resulting in PSP patterns driven by selection for particular ecologies and locomotor strategies [183, 187, 202-206].

Despite the broad phylogenetic distribution of PSP across Ornithodira (Fig. 2B), its absence in all known ornithischian dinosaurs and many early-diverging saurischians supports a hypothesis that an invasive air sac system evolved multiple times—once in the lineage leading to pterosaurs, once in sauropods, and another—most likely homologous with that of birds—in theropods [207]. As such, the current consensus suggests that PSP was absent in the last common ancestor of Ornithodira, and even Saurischia, though the pulmonary tissues underpinning the capacity to evolve an invasive pneumatic system are thought to be homologous across Ornithodira [184, 207, 208]. All three Mesozoic ornithodiran groups exhibiting PSP generally show a pattern where pneumatisation of the cervical and anterior dorsal/thoracic vertebrae precedes the evolution of more extensive skeletal pneumatisation (Fig. 2B) [187-189, 191, 192, 194, 197, 198, 200, 209].

Within Avialae, *Archaeopteryx* shows clear evidence of axial pneumaticity of the cervical and anterior thoracic vertebrae and likely some ribs, but ambiguous evidence of PSP in the appendicular skeleton (Fig. 2B) [200, 210]. This pattern of PSP appears to be no more expansive than the common pattern observed among non-avian theropods [200, 211]. The evolution of PSP is poorly understood among more crownward stem birds, due to the difficulties in unambiguously assessing evidence for PSP in specimens that are taphonomically flattened, crushed, and relatively small compared with most other fossil bird-line archosaurs. However, pneumaticity of portions of the vertebral column (e.g., in Confuciusornithiformes; [63]), as well as expansions into ribs and sterna (e.g., in Ichthyornithes [76, 81]) have occasionally been reported in both early and near-crown avialans.

In contrast to axial pneumaticity, there are currently only two instances of pneumatic forelimb elements (humeri and ulnae) reported in non-crown Avialae, both belonging to Late Cretaceous Enantiornithes from Argentina [141, 156]. The presence of pneumatic foramina in these enantiornithines, coupled with their apparent absence in all other avialans outside crown group birds (seemingly including even highly pneumatised crownward ornithurans [81]), suggests the plesiomorphic pattern of postcranial pneumatisation observed in non-avian theropods may have been retained throughout almost the entirety of non-crown avialan evolutionary history. This scenario hints at the possibility of independent evolutionary acquisitions of expansive PSP in Enantiornithes and crown birds; however, our understanding will be refined as additional non-neornithine avialans are investigated in detail.

Unlike most extinct ornithodirans, extant birds exhibit extremely variable degrees of postcranial pneumaticity, both in terms of the proportion of pneumatised elements across the skeleton [183, 187, 202-204], and in the extent to which individual postcranial skeletal elements are filled with air [205, 212]. When present, the most common pattern of postcranial skeletal pneumatisation among crown birds involves a few vertebrae at the cervicothoracic border [187], reminiscent of the ancestral pattern apparent in their extinct ornithodiran relatives. However, elaboration of this pattern is extremely widespread among crown birds, with pneumatic diverticula often expanding into much of the vertebral column, ribs, sternum, pectoral and pelvic girdle elements, humeri, and femora [183, 187]. Pneumatisation of the distal limb elements is comparatively rare, though this occurs in taxa with especially pneumatic skeletons (e.g., pelicans; [187]). At the other extreme, some taxa exhibit completely apneumatic postcranial skeletons (e.g., penguins and loons), though this pattern of PSP reduction is generally associated with specialised aquatic diving ecologies which impose selective constraints against the buoyancy conferred by PSP [187, 203]. The wide range of variation in PSP among crown birds indicates a relaxation of constraints associated with the development of skeletal pneumaticity with respect to the plesiomorphic theropod condition, in which pneumaticity is generally restricted to the axial skeleton.

Conclusions

In only a few decades the field of avian palaeobiology has progressed dramatically. A rich picture of Mesozoic avialan diversity and interrelationships has emerged, providing the necessary phylogenetic framework for discerning the evolutionary patterns and processes that gave rise to many of the

distinctive characteristics of extant birds. Investigations like those covered in the present review have fundamentally reshaped our understanding of how numerous aspects of avian biology evolved.

While flattened and/or incomplete fossil remains have formed the basis for many of the most exciting Mesozoic avialan discoveries to date, two-dimensional fossils are limited in their ability to answer many questions about avian morphology. Indeed, major recent advances in our understanding of the character systems covered in this review have depended on the discovery of exceptional, though rare, three-dimensionally preserved fossils. As additional undistorted specimens emerge to fill key phylogenetic gaps within Avialae, and advances in three-dimensional fossil imaging continue to progress, our understanding of the origins of the 'modern' avian condition of innumerable morphological and functional features will continue to be refined.

Additionally, although *Archaeopteryx* remains the stratigraphically oldest and phylogenetically most stemward avialan known, as well as the first to be discovered, future progress towards understanding the origin of the crown bird body plan will depend far more on filling as-yet undersampled phylogenetic intervals within Avialae than on interrogations of *Archaeopteryx* alone. Such crucial, yet poorly sampled intervals include the early stages of evolution within Ornithothoraces, the early stem lineages of both Palaeognathae and Neognathae, and the crownward-most portion of the avian stem group (crownward of Hesperornithes). Indeed, when the origin of the crown bird condition across different anatomical systems is depicted phylogenetically (Fig. 3), late-stage refinements in all character systems tackled in the present review are ubiquitous along the crownward-most portion of the avian stem. Important evolutionary transformations must have taken place somewhere along the as-yet unsampled interval crownward of Hesperornithes, prior to the origin of crown birds themselves. New insights into this region of avialan phylogeny are poised to dramatically improve our understanding of how and when the distinctive biological characteristics of the world's most diverse terrestrial vertebrates arose.

Figure captions

Figure 1: Evolution of the avian central nervous system and bony palate. (A) The enantiornithine *Navaornis* (indicated by a star) illustrates avialan brain and inner ear morphology in a taxon phylogenetically intermediate between *Archaeopteryx* and crown birds. However, endocranial morphology of non-neornithine avialans phylogenetically stemward and crownward of Enantiornithes

remains poorly known. **(B)** Left: Paravian skulls in ventral view (modified from [72], [44, in press], [81], [213]) with palate osteology highlighted. Light blue of the ectopterygoid illustrates its uncertain presence in Enantiornithes. Stars next to the skulls of Ichthyornithes and *Burhinus* correspond to the enlarged palates illustrated to the right of the phylogeny. Right: Morphological comparison of the pterygoid-palatine complex in an immature neognath (*Burhinus capensis*; above), and Ichthyornithes (below; composite reconstruction of *Janavis* and *Ichthyornis*, modified from [81] and [38], respectively).

Figure 2: Evolution of the avian pectoral girdle and postcranial skeletal pneumaticity. **(A)** Top: Articulated paravian pectoral girdles in ventral view. Bottom: closeup of the glenoid region of the shoulder joint. Scapula and coracoid are fused into a scapulocoracoid in adult Troodontidae, *Archaeopteryx*, and *Confuciusornis*, and unfused in Ornithothoraces (except ratites). Arrows between coracoid and scapula indicate divergent mechanisms for linking these elements in Enantiornithes and Euornithes. Abbreviations: C, coracoid; F, furcula; S, scapula; SC, scapulocoracoid; SP, sternal plates (unfused); ST, sternum. Illustrations modified from [76, 116, 127, 180]. **(B)** Phylogeny of Ornithodira, with colours indicating approximate frequency of pneumatisation across the skeleton reported within each clade.

Figure 3: Phylogeny of bird-line archosaurs and the hierarchical evolutionary acquisition of a bird-like phenotype. White sectors of pie charts indicate retention of the plesiomorphic, non-neornithine condition. Faintly coloured sectors indicate an intermediate, near-crown-bird-like condition, and saturated colours indicate the condition observed in crown birds. Purple, brain morphology; Yellow, palate morphology; Red, pectoral girdle morphology; Blue, postcranial skeletal pneumaticity.

Acknowledgements

We thank Scott Hartman (skeletaldrawing.com) for permission to use and modify his skeletal diagrams of ornithodirans in Fig. 2B. We also thank two anonymous reviewers for thought-provoking comments that improved this manuscript, and Paul Barrett and Susannah Maidment for the invitation to contribute a review on bird evolution to this special issue celebrating 200 years of dinosaurs. This work was funded by UKRI grant MR/X015130/1. For the purpose of open access, the authors have applied a Creative Commons Attribution (CC BY) licence to any Author Accepted Manuscript version arising.

419

420 **References**

421 [1] Buckland, W. 1824 XXI.—Notice on the Megalosaurus or great Fossil Lizard of Stonesfield.
422 *Transactions of the Geological Society of London* **1**, 390-396.

423 [2] Owen, R. 1842 Report on British fossil reptiles, part 2. *Report of the British Association for the*
424 *Advancement of Science* **11**, 60-204.

425 [3] Heilmann, G. 1926 *The Origin of Birds*. London, H.F. & G. Witherby.

426 [4] Ostrom, J.H. 1969 Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower
427 Cretaceous of Montana. *Bulletin of the Peabody Museum of Natural History* **30**, 1-165.

428 [5] Gauthier, J. 1986 Saurischian monophyly and the origin of birds. *Memoirs of the California*
429 *Academy of Sciences* **8**, 1-55.

430 [6] Ji, Q. & Ji, S. 1996 On the discovery of the earliest fossil bird in China (*Sinosauropteryx* gen. nov.)
431 and the origin of birds. *Chinese Geology* **233**, 1-4.

432 [7] Huxley, T.H. 1870 Further evidence of the affinity between the dinosaurian reptiles and birds.
433 *Quarterly Journal of the Geological Society* **26**, 12-31.

434 [8] Chen, P.-j., Dong, Z.-m. & Zhen, S.-n. 1998 An exceptionally well-preserved theropod dinosaur
435 from the Yixian Formation of China. *Nature* **391**, 147-152. (doi:10.1038/34356).

436 [9] Ostrom, J.H. 1973 The ancestry of birds. *Nature* **242**, 136. (doi:doi.org/10.1038/242136a0).

437 [10] Ostrom, J.H. 1974 *Archaeopteryx* and the origin of flight. *The Quarterly Review of Biology* **49**, 27-
438 47.

439 [11] Ostrom, J.H. 1976 Some hypothetical anatomical stages in the evolution of avian flight.
440 *Smithsonian Contributions to Paleobiology* **27**, 1-21.

441 [12] Ostrom, J.H. 1976 *Archaeopteryx* and the origin of birds. *Biological Journal of the Linnean*
442 *Society* **8**, 91-182. (doi:10.1111/j.1095-8312.1976.tb00244.x).

[13] Dyke, G. & Kaiser, G. 2011 *Living Dinosaurs: The Evolutionary History of Modern Birds*, John Wiley & Sons Ltd.

[14] Padian, K. & Chiappe, L.M. 1998 The origin and early evolution of birds. *Biological Reviews* **73**, 1-42.

[15] Brusatte, S.L., O'Connor, J.K. & Jarvis, E.D. 2015 The origin and diversification of birds. *Current Biology* **25**, R888-R898.

[16] Makovicky, P.J. & Zanno, L.E. 2011 Theropod Diversity and the Refinement of Avian Characteristics. In *Living Dinosaurs: The Evolutionary History of Modern Birds* (eds. G. Dyke & G. Kaiser), pp. 9-29, John Wiley & Sons Ltd.

[17] Chiappe, L.M. 2002 *Mesozoic birds*, Wiley Online Library.

[18] Field, D.J., Berv, J.S., Hsiang, A.Y., Lanfear, R., Landis, M.J. & Dornburg, A. 2020 Timing the extant avian radiation: The rise of modern birds, and the importance of modeling molecular rate variation. In *Pennaraptoran Theropod Dinosaurs: Past Progress and New Frontiers* (eds. M. Pittman & X. Xu), pp. 159-181, 1 ed, Bulletin of the American Museum of Natural History.

[19] Brocklehurst, N. & Field, D.J. 2024 Tip dating and Bayes factors provide insight into the divergences of crown bird clades across the end-Cretaceous mass extinction. *Proceedings of the Royal Society B: Biological Sciences* **291**, 20232618.

[20] Jarvis, E.D., Mirarab, S., Aberer, A.J., Li, B., Houde, P., Li, C., Ho, S.Y., Faircloth, B.C., Nabholz, B. & Howard, J.T. 2014 Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science* **346**, 1320-1331.

[21] Prum, R.O., Berv, J.S., Dornburg, A., Field, D.J., Townsend, J.P., Lemmon, E.M. & Lemmon, A.R. 2015 A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature* **526**, 569-573.

[22] Feduccia, A. 2014 Avian extinction at the end of the Cretaceous: Assessing the magnitude and subsequent explosive radiation. *Cretaceous Research* **50**, 1-15.

[23] Feduccia, A. 1995 Explosive evolution in Tertiary birds and mammals. *Science* **267**, 637-638.

[24] Longrich, N.R., Tokaryk, T. & Field, D.J. 2011 Mass extinction of birds at the Cretaceous–Paleogene (K–Pg) boundary. *Proceedings of the National Academy of Sciences* **108**, 15253-15257.

[25] Field, D.J., Bercovici, A., Berv, J.S., Dunn, R., Fastovsky, D.E., Lyson, T.R., Vajda, V. & Gauthier, J.A. 2018 Early evolution of modern birds structured by global forest collapse at the end-Cretaceous mass extinction. *Current Biology* **28**, 1825-1831. (doi:10.1038/s41586-018-0053-y).

[26] Prum, R.O. & Brush, A.H. 2002 The evolutionary origin and diversification of feathers. *The Quarterly Review of Biology* **77**, 261-295. (doi:10.1086/341993).

[27] Prum, R.O. 1999 Development and evolutionary origin of feathers. *Journal of Experimental Zoology* **285**, 291-306.

[28] Xing, X. & Yu, G. 2009 The origin and early evolution of feathers: insights from recent paleontological and neontological data. *Vertebrata PalAsiatica* **47**, 311.

[29] Benton, M.J., Dhouailly, D., Jiang, B. & McNamara, M. 2019 The early origin of feathers. *Trends in Ecology & Evolution* **34**, 856-869.

[30] Clayton, N.S. & Emery, N.J. 2015 Avian models for human cognitive neuroscience: a proposal. *Neuron* **86**, 1330-1342.

[31] Balanoff, A.M., Bever, G.S., Rowe, T.B. & Norell, M.A. 2013 Evolutionary origins of the avian brain. *Nature* **501**, 93-96. (doi:10.1038/nature12424).

[32] Watanabe, A., Balanoff, A.M., Gignac, P.M., Gold, M.E.L. & Norell, M.A. 2021 Novel neuroanatomical integration and scaling define avian brain shape evolution and development. *eLife* **10**. (doi:10.7554/eLife.68809).

[33] Balanoff, A. & Bever, G. 2020 The role of endocasts in the study of brain evolution. In *Evolutionary Neuroscience* (pp. 29-49, Elsevier.

[34] Jarvis, E.D., Güntürkün, O., Bruce, L., Csillag, A., Karten, H., Kuenzel, W., Medina, L., Paxinos, G., Perkel, D.J. & Shimizu, T. 2005 Avian brains and a new understanding of vertebrate brain evolution. *Nature Reviews Neuroscience* **6**, 151-159.

[35] Northcutt, R.G. 2011 Evolving large and complex brains. *Science* **332**, 926-927.

[36] Bronzati, M., Benson, R.B., Evers, S.W., Ezcurra, M.D., Cabreira, S.F., Choiniere, J., Dollman, K.N., Paulina-Carabajal, A., Radermacher, V.J. & Roberto-da-Silva, L. 2021 Deep evolutionary diversification of semicircular canals in archosaurs. *Current Biology*.

[37] Benson, R.B., Starmer-Jones, E., Close, R.A. & Walsh, S.A. 2017 Comparative analysis of vestibular ecomorphology in birds. *Journal of Anatomy* **231**, 990-1018.

[38] Torres, C.R., Norell, M.A. & Clarke, J.A. 2021 Bird neurocranial and body mass evolution across the end-Cretaceous mass extinction: The avian brain shape left other dinosaurs behind. *Science Advances* **7**, eabg7099.

[39] Watanabe, A., Gignac, P.M., Balanoff, A.M., Green, T.L., Kley, N.J. & Norell, M.A. 2019 Are endocasts good proxies for brain size and shape in archosaurs throughout ontogeny? *Journal of Anatomy* **234**, 291-305.

[40] Early, C.M., Iwaniuk, A.N., Ridgely, R.C. & Witmer, L.M. 2020 Endocast structures are reliable proxies for the sizes of corresponding regions of the brain in extant birds. *Journal of Anatomy* **237**, 1162-1176.

[41] Alonso, P.D., Milner, A.C., Ketcham, R.A., Cookson, M.J. & Rowe, T.B. 2004 The avian nature of the brain and inner ear of *Archaeopteryx*. *Nature* **430**, 666-669. (doi:10.1038/nature02706).

[42] Chiappe, L.M. & Qingjin, M. 2016 *Birds of stone: Chinese avian fossils from the age of dinosaurs*. Baltimore, Maryland, John Hopkins University Press.

[43] Chiappe, L.M., Navalón, G., Martinelli, A.G., Nava, W. & Field, D.J. 2022 Fossil basicranium clarifies the origin of the avian central nervous system and inner ear. *Proceedings of the Royal Society B: Biological Sciences* **289**, 20221398.

516 [44] Chiappe, L.M., Navalón, G., Martinelli, A.G., de Souza Carvalho, I., Santucci, R., Wu, Y.-H. &
517 Field, D.J. Cretaceous bird fills key gap in the evolution of the avian skull and brain. *Nature* **In press**.

518 [45] Balanoff, A.M., Norell, M.A., Hogan, A.V. & Bever, G.S. 2018 The endocranial cavity of
519 oviraptorosaur dinosaurs and the increasingly complex, deep history of the avian brain. *Brain,*
520 *Behavior and Evolution* **91**, 125-135.

521 [46] Yu, C., Watanabe, A., Qin, Z., King, J.L., Witmer, L., Ma, Q. & Xu, X. 2024 Avialan-like brain
522 morphology in *Sinovenator* (Troodontidae, Theropoda). *Communications Biology* **7**, 168.
523 (doi:10.1038/s42003-024-05832-3).

524 [47] Walsh, S.A., Milner, A.C. & Bourdon, E. 2016 A reappraisal of Cerebavis cenomanica (Aves,
525 ornithurae), from Melovatka, Russia. *Journal of Anatomy* **229**, 215-227.

526 [48] Widrig, K.E., Navalón, G. & Field, D.J. 2024 Paleoneurology of stem palaeognaths clarifies the
527 plesiomorphic condition of the crown bird central nervous system. *Journal of Morphology* **285**,
528 e21710.

529 [49] Kurochkin, E., Saveliev, S., Postnov, A., Pervushov, E. & Popov, E. 2006 On the brain of a
530 primitive bird from the Upper Cretaceous of European Russia. *Paleontological Journal* **40**, 655-667.

531 [50] Field, D.J., Hanson, M., Burnham, D., Wilson, L.E., Super, K., Ehret, D., Ebersole, J.A. & Bhullar,
532 B.-A.S. 2018 Complete *Ichthyornis* skull illuminates mosaic assembly of the avian head. *Nature* **557**,
533 96-100.

534 [51] Elżanowski, A. & Galton, P.M. 1991 Braincase of *Enaliornis*, an early Cretaceous bird from
535 England. *Journal of Vertebrate Paleontology* **11**, 90-107.

536 [52] Bock, W.J. 1964 Kinetics of the avian skull. *Journal of Morphology* **114**, 1-42.

537 [53] Bhullar, B.-A.S., Hanson, M., Fabbri, M., Pritchard, A., Bever, G.S. & Hoffman, E. 2016 How to
538 make a bird skull: major transitions in the evolution of the avian cranium, paedomorphosis, and the
539 beak as a surrogate hand. *Integrative and Comparative Biology* **56**, 389-403.

[54] Rico-Guevara, A., Sustaita, D., Hurme, K.J., Hanna, J.E., Jung, S. & Field, D.J. Upper bill bending as an adaptation for nectar feeding in hummingbirds. *Journal of the Royal Society Interface* **In press**.

[55] Elżanowski, A. & Wellnhofer, P. 1996 Cranial morphology of *Archaeopteryx*: evidence from the seventh skeleton. *Journal of Vertebrate Paleontology* **16**, 81-94.

[56] Wellnhofer, P. 1993 Das siebte exemplar von Archaeopteryx aus den Solnhofener Schichten. *Archaeopteryx* **11**, 1-47.

[57] Tsuihiji, T., Barsbold, R., Watabe, M., Tsogtbaatar, K., Chinzorig, T., Fujiyama, Y. & Suzuki, S. 2014 An exquisitely preserved troodontid theropod with new information on the palatal structure from the Upper Cretaceous of Mongolia. *Naturwissenschaften* **101**, 131-142.

[58] Mayr, G., Pohl, B., Hartman, S. & Peters, D.S. 2007 The tenth skeletal specimen of *Archaeopteryx*. *Zoological Journal of the Linnean Society* **149**, 97-116.

[59] Rauhut, O.W., Foth, C. & Tischlinger, H. 2018 The oldest *Archaeopteryx* (Theropoda: Avialiae): a new specimen from the Kimmeridgian/Tithonian boundary of Schamhaupten, Bavaria. *PeerJ* **6**, e4191.

[60] Hu, H., Sansalone, G., Wroe, S., McDonald, P.G., O'Connor, J.K., Li, Z., Xu, X. & Zhou, Z. 2019 Evolution of the vomer and its implications for cranial kinesis in Paraves. *Proceedings of the National Academy of Sciences* **116**, 19571-19578. (doi:10.1073/pnas.1907754116).

[61] Hu, H., Wang, Y., Fabbri, M., O'Connor, J.K., Mcdonald, P.G., Wroe, S., Yin, X., Zheng, X., Zhou, Z. & Benson, R.B. 2023 Cranial osteology and palaeobiology of the Early Cretaceous bird Jeholornis prima (Aves: Jeholornithiformes). *Zoological Journal of the Linnean Society* **198**, 93-112.

[62] Hu, H., O'Connor, J.K., McDonald, P.G. & Wroe, S. 2020 Cranial osteology of the early cretaceous Sapeornis chaoyangensis (Aves: Pygostylia). *Cretaceous Research* **113**, 104496.

[63] Chiappe, L.M., Ji, S.-A., Ji, Q. & Norell, M.A. 1999 Anatomy and systematics of the Confuciusornithidae (Theropoda, Aves) from the late Mesozoic of northeastern China. . *Bulletin of the American Museum of Natural History* **242**, 1-89.

566 [64] Louchart, A. & Viriot, L. 2011 From snout to beak: the loss of teeth in birds. *Trends in Ecology &*
567 *Evolution* **26**, 663-673.

568 [65] Brocklehurst, N. & Field, D.J. 2021 Macroevolutionary dynamics of dentition in Mesozoic birds
569 reveal no long-term selection towards tooth loss. *iScience* **24**. (doi:10.1016/j.isci.2021.102243).

570 [66] Wang, M., O'Connor, J. & Zhou, Z. 2019 A taxonomical revision of the Confuciusornithiformes
571 (Aves: Pygostylia). *Vertebrata Palasiatica* **57**, 1-37.

572 [67] O'Connor, J.K., Zheng, X.-T., Hu, H., Wang, X.-L. & Zhou, Z.-H. 2017 The morphology of
573 *Chiappeavis magnapremaxillo* (Pengornithidae: Enantiornithes) and a comparison of aerodynamic
574 function in Early Cretaceous avian tail fans. *Vertebrata Palasiatica* **55**, 41.

575 [68] Chiappe, L.M., Norell, M. & Clark, J. 2001 A new skull of *Gobipteryx minuta* (Aves:
576 Enantiornithes) from the Cretaceous of the Gobi Desert. *American Museum Novitates* **2001**, 1-15.
577 (doi:10.1206/0003-0082(2001)346<0001:ANSOGM>2.0.CO;2).

578 [69] Xu, L., Buffetaut, E., O'Connor, J., Zhang, X., Jia, S., Zhang, J., Chang, H. & Tong, H. 2021 A
579 new, remarkably preserved, enantiornithine bird from the Upper Cretaceous Qiupa Formation of
580 Henan (central China) and convergent evolution between enantiornithines and modern birds.
581 *Geological Magazine* **158**, 2087-2094.

582 [70] Wang, M., Stidham, T.A., O'Connor, J.K. & Zhou, Z. 2022 Insight into the evolutionary
583 assemblage of cranial kinesis from a Cretaceous bird. *eLife* **11**, e81337.

584 [71] Elżanowski, A. 1995 Cretaceous birds and avian phylogeny. *Courier Forschungsinstitut*
585 *Senckenberg* **181**, 37-53.

586 [72] Mayr, G. 2017 *Avian evolution: the fossil record of birds and its paleobiological significance*.
587 Chichester, UK, John Wiley & Sons.

588 [73] Wang, M., Stidham, T.A., Li, Z., Xu, X. & Zhou, Z. 2021 Cretaceous bird with dinosaur skull sheds
589 light on avian cranial evolution. *Nature Communications* **12**, 3890.

590 [74] O'Connor, P.M., Turner, A.H., Groenke, J.R., Felice, R.N., Rogers, R.R., Krause, D.W. &
591 Rahantarisoa, L.J. 2020 Late Cretaceous bird from Madagascar reveals unique development of
592 beaks. *Nature* **588**, 272-276.

593 [75] Field, D.J. 2020 The changing face of birds from the age of the dinosaurs. *Nature* **588**, 221-222.
594 (doi:10.1038/d41586-020-03260-x).

595 [76] Benito, J., Chen, A., Wilson, L.E., Bhullar, B.-A.S., Burnham, D. & Field, D.J. 2022 Forty new
596 specimens of *Ichthyornis* provide unprecedented insight into the postcranial morphology of crownward
597 stem group birds. *PeerJ* **10**, e13919.

598 [77] Xing, L., O'Connor, J.K., Schmitz, L., Chiappe, L.M., McKellar, R.C., Yi, Q. & Li, G. 2020
599 Hummingbird-sized dinosaur from the Cretaceous period of Myanmar. *Nature* **579**, 245-249.

600 [78] Clarke, J.A., Zhou, Z. & Zhang, F. 2006 Insight into the evolution of avian flight from a new clade
601 of Early Cretaceous ornithurines from China and the morphology of *Yixianornis grabaui*. *Journal of*
602 *Anatomy* **208**, 287-308.

603 [79] Zhou, Z. & Li, F.Z.Z. 2010 A new Lower Cretaceous bird from China and tooth reduction in early
604 avian evolution. *Proceedings of the Royal Society B: Biological Sciences* **277**, 219-227.
605 (doi:10.1098/rspb.2009.0885).

606 [80] Zhou, S., Zhou, Z. & O'Connor, J.K. 2013 Anatomy of the basal ornithuromorph bird
607 Archaeorhynchus spathula from the Early Cretaceous of Liaoning, China. *Journal of Vertebrate*
608 *Paleontology* **33**, 141-152.

609 [81] Benito, J., Kuo, P.-C., Widrig, K.E., Jagt, J.W. & Field, D.J. 2022 Cretaceous ornithurine supports
610 a neognathous crown bird ancestor. *Nature* **612**, 100-105.

611 [82] Elżanowski, A. 1991 New observations of the skull of *Hesperornis* with reconstructions of the
612 bony palate and otic region. *Postilla* **207**, 1-20.

613 [83] Gingerich, P.D. 1973 Skull of *Hesperornis* and early evolution of birds. *Nature* **243**, 70-73.
614 (doi:10.1038/243070a0).

615 [84] Huxley, T.H. 1867 On the classification of birds: and on the taxonomic value of the modifications
616 of certain of the cranial bones observed in that class. *Proceedings of the Zoological Society of*
617 *London*.

618 [85] Zusi, R.L. 1993 Patterns of diversity in the avian skull. In *The Skull* (eds. J. Hanken & B.K. Hall),
619 pp. 391-437. Chicago, The University of Chicago Press.

620 [86] Gussekloo, S.W., Vosselman, M.G. & Bout, R.G. 2001 Three-dimensional kinematics of skeletal
621 elements in avian prokinetic and rhynchokinetic skulls determined by Roentgen
622 stereophotogrammetry. *Journal of Experimental Biology* **204**, 1735-1744.

623 [87] Balouet, J.-C. 1983 Les Paleognathes (Aves) sont-ils primitifs? *Bulletin de la Société Zoologique*
624 *de France* **108**, 648-653.

625 [88] Witmer, L.M. & Martin, L.D. 1987 The primitive features of the avian palate, with special reference
626 to Mesozoic birds. *Travaux et Documents des Laboratoires de Géologie de Lyon* **99**, 21-40.

627 [89] Parker, W.K. 1872 On the Structure and Development of the Crow's Skull. *The Monthly*
628 *Microscopical Journal* **8**, 217-226.

629 [90] Parker, W.K. 1875 I. On the Morphology of the Skull in the Woodpeckers (Picidæ) and Wrynecks
630 (Yungidæ). *Transactions of the Linnean Society of London. 2nd Series: Zoology* **1**, 1-22.

631 [91] Parker, W.K. 1876 VII. On the Structure and Development of the Bird's Skull. *Transactions of the*
632 *Linnean Society of London. 2nd Series. Zoology* **1**, 99-154.

633 [92] Parker, W.K. 1878 On the Skull of the ægithognathous Birds. *The Transactions of the Zoological*
634 *Society of London* **10**, 251-314.

635 [93] Bühler, P., Martin, L.D. & Witmer, L.M. 1988 Cranial kinesis in the Late Cretaceous birds
636 *Hesperornis* and *Parahesperornis*. *The Auk* **105**, 111-122. (doi:10.1093/auk/105.1.111).

637 [94] Pycraft, W.P. 1901 Some points in the morphology of the palate of the Neognathæ. *Zoological*
638 *Journal of the Linnean Society* **28**, 343-357. (doi:10.1111/j.1096-3642.1901.tb01756.x).

639 [95] Pycraft, W.P. 1907 *On some points in the anatomy of the emperor and adelie penguins*, Order of
640 the trustees of the British Museum.

641 [96] Jollie, M. 1958 Comments on the phylogeny and skull of the Passeriformes. *The Auk* **75**, 26-35.

642 [97] Zusi, R.L. & Livezey, B.C. 2006 Variation in the os palatinum and its structural relation to the
643 palatum osseum of birds (Aves). *Annals of Carnegie Museum* **75**, 137-180.

644 [98] Cracraft, J. 1974 Phylogeny and evolution of the ratite birds. *Ibis* **116**, 494-521.

645 [99] Paton, T., Haddrath, O. & Baker, A.J. 2002 Complete mitochondrial DNA genome sequences
646 show that modern birds are not descended from transitional shorebirds. *Proceedings of the Royal*
647 *Society of London. Series B: Biological Sciences* **269**, 839-846. (doi:10.1098/rspb.2002.1961).

648 [100] Gibb, G.C., Kardailsky, O., Kimball, R.T., Braun, E.L. & Penny, D. 2007 Mitochondrial genomes
649 and avian phylogeny: complex characters and resolvability without explosive radiations. *Molecular*
650 *Biology and Evolution* **24**, 269-280.

651 [101] Livezey, B.C. & Zusi, R.L. 2007 Higher-order phylogeny of modern birds (Theropoda, Aves:
652 Neornithes) based on comparative anatomy. II. Analysis and discussion. *Zoological Journal of the*
653 *Linnean Society* **149**, 1-95. (doi:0.1111/j.1096-3642.2006.00293.x).

654 [102] Brocklehurst, N., Upchurch, P., Mannion, P.D. & O'Connor, J. 2012 The completeness of the
655 fossil record of Mesozoic birds: implications for early avian evolution. *PloS one* **7**, e39056.

656 [103] Dudley, R. & Yanoviak, S.P. 2011 Animal aloft: the origins of aerial behavior and flight.
657 *Integrative and Comparative Biology* **51**, 926-936.

658 [104] Padian, K. 1985 The origins and aerodynamics of flight in extinct vertebrates. *Palaeontology* **28**,
659 413-433.

660 [105] Rayner, J.M. 1988 The evolution of vertebrate flight. *Biological Journal of the Linnean Society*
661 **34**, 269-287.

662 [106] Brusatte, S.L., Lloyd, G.T., Wang, S.C. & Norell, M.A. 2014 Gradual assembly of avian body
663 plan culminated in rapid rates of evolution across the dinosaur-bird transition. *Current Biology* **24**,
664 2386-2392.

665 [107] Goslow, G., Dial, K. & Jenkins, F. 1989 The avian shoulder: an experimental approach.
666 *American Zoologist* **29**, 287-301.

667 [108] Goslow, G., Dial, K.P. & Jenkins, F. 1990 Bird flight: insights and complications. *BioScience* **40**,
668 108-115. (doi:10.2307/1311343).

669 [109] Jenkins, F. 1993 The evolution of the avian shoulder joint. *American Journal of Science*.

670 [110] Gatesy, S.M. & Middleton, K.M. 1997 Bipedalism, flight, and the evolution of theropod locomotor
671 diversity. *Journal of Vertebrate Paleontology* **17**, 308-329.

672 [111] Pittman, M., Heers, A.M., Serrano, F.J., Field, D.J., Habib, M.B., Dececchi, T.A., Kaye, T.G. &
673 Larsson, B.C. 2020 Methods of studying early theropod flight. In *Pennaraptoran Theropod Dinosaurs:*
674 *Past Progress and New Frontiers* (eds. M. Pittman & X. Xu), pp. 277-294, Bulletin of the American
675 Museum of Natural History.

676 [112] Dececchi, T.A. & Larsson, H.C. 2011 Assessing arboreal adaptations of bird antecedents:
677 testing the ecological setting of the origin of the avian flight stroke. *PloS one* **6**, e22292.

678 [113] Dececchi, T.A. & Larsson, H.C. 2009 Patristic evolutionary rates suggest a punctuated pattern
679 in forelimb evolution before and after the origin of birds. *Paleobiology* **35**, 1-12.

680 [114] Chiappe, L.M., Zhao, B., O'Connor, J.K., Chunling, G., Wang, X., Habib, M., Marugan-Lobon, J.,
681 Meng, Q. & Cheng, X. 2014 A new specimen of the Early Cretaceous bird *Hongshanornis longicresta*:
682 insights into the aerodynamics and diet of a basal ornithuromorph. *PeerJ* **2**, e234.

683 [115] Mayr, G. 2017 Pectoral girdle morphology of Mesozoic birds and the evolution of the avian
684 supracoracoideus muscle. *Journal of Ornithology* **158**, 859-867.

685 [116] Wang, S., Ma, Y., Wu, Q., Wang, M., Hu, D., Sullivan, C. & Xu, X. 2022 Digital restoration of the
686 pectoral girdles of two Early Cretaceous birds and implications for early-flight evolution. *eLife* **11**.

687 [117] Baier, D.B., Gatesy, S.M. & Jenkins, F.A. 2007 A critical ligamentous mechanism in the
688 evolution of avian flight. *Nature* **445**, 307-310.

689 [118] Bock, W.J. 2013 The furcula and the evolution of avian flight. *Paleontological Journal* **47**, 1236-
690 1244.

691 [119] Novas, F.E., Agnolin, F., Brissón Egli, F. & Lo Coco, G.E. 2020 Pectoral girdle morphology in
692 early-diverging paravians and living ratites: implications for the origin of flight. In *Pennaraptoran*
693 *Theropod Dinosaurs: Past Progress and New Frontiers* (eds. M. Pittman & X. Xu), pp. 345-353,
694 Bulletin of the American Museum of Natural History.

695 [120] Senter, P. 2006 Scapular orientation in theropods and basal birds, and the origin of flapping
696 flight. *Acta Palaeontologica Polonica* **51**, 305-313.

697 [121] Nesbitt, S.J., Turner, A.H., Spaulding, M., Conrad, J.L. & Norell, M.A. 2009 The theropod
698 furcula. *Journal of Morphology* **270**, 856-879.

699 [122] Zhou, Z. & Zhang, F. 2003 Jeholornis compared to Archaeopteryx, with a new understanding of
700 the earliest avian evolution. *Naturwissenschaften* **90**, 220-225.

701 [123] Mayr, G., Pohl, B. & Peters, D.S. 2005 A well-preserved Archaeopteryx specimen with theropod
702 features. *Science* **310**, 1483-1486.

703 [124] Kundrát, M., Nudds, J., Kear, B.P., Lü, J. & Ahlberg, P. 2019 The first specimen of
704 *Archaeopteryx* from the upper Jurassic Mörnsheim Formation of Germany. *Historical Biology* **31**, 3-
705 63.

706 [125] Hu, D., Hou, L., Zhang, L. & Xu, X. 2009 A pre-*Archaeopteryx* troodontid theropod from China
707 with long feathers on the metatarsus. *Nature* **461**, 1-5.

708 [126] Wellnhofer, P. 2009 *Archaeopteryx: the icon of evolution*, Verlag Dr. Friedrich Pfeil.

709 [127] Wu, Q., O'Connor, J.K., Wang, S. & Zhou, Z. 2024 Transformation of the pectoral girdle in
710 pennaraptorans: critical steps in the formation of the modern avian shoulder joint. *PeerJ* **12**, e16960.

711 [128] Zheng, X., O'Connor, J., Wang, X., Wang, M., Zhang, X. & Zhou, Z. 2014 On the absence of
712 sternal elements in *Anchiornis* (Paraves) and *Sapeornis* (Aves) and the complex early evolution of the
713 avian sternum. *Proceedings of the National Academy of Sciences* **111**, 13900-13905.

714 [129] Zhou, Z. & Zhang, F. 2003 Anatomy of the primitive bird *Sapeornis chaoyangensis* from the
715 Early Cretaceous of Liaoning, China. *Canadian Journal of Earth Sciences* **40**, 731-747.
716 (doi:10.1139/e03-011).

717 [130] Wang, X., Huang, J., Kundrát, M., Cau, A., Liu, X., Wang, Y. & Ju, S. 2020 A new
718 jeholornithiform exhibits the earliest appearance of the fused sternum and pelvis in the evolution of
719 avialan dinosaurs. *Journal of Asian Earth Sciences* **199**, 104401.

720 [131] Wang, M., Stidham, T.A. & Zhou, Z. 2018 A new clade of basal Early Cretaceous pygostylian
721 birds and developmental plasticity of the avian shoulder girdle. *Proceedings of the National Academy*
722 *of Sciences* **115**, 10708-10713.

723 [132] Wu, Q., Bailleul, A.M., Li, Z., O'Connor, J. & Zhou, Z. 2021 Osteohistology of the
724 scapulocoracoid of *Confuciusornis* and preliminary analysis of the shoulder joint in Aves. *Frontiers in*
725 *Earth Science* **9**, 617124.

726 [133] Feo, T.J., Field, D.J. & Prum, R.O. 2015 Barb geometry of asymmetrical feathers reveals a
727 transitional morphology in the evolution of avian flight. *Proceedings of the Royal Society B: Biological*
728 *Sciences* **282**, 20142864.

729 [134] O'Connor, J.K., Chiappe, L.M. & Bell, A. 2011 Pre-modern Birds: Avian Divergences in the
730 Mesozoic. In *Living Dinosaurs: The Evolutionary History of Modern Birds* (eds. G. Dyke & G. Kaiser),
731 pp. 39-114, John Wiley & Sons Ltd.

732 [135] O'Connor, J. & Zhou, Z. 2015 Early evolution of the biological bird: perspectives from new fossil
733 discoveries in China. *Journal of Ornithology* **156**, 333-342.

734 [136] Novas, F.E., Motta, M.J., Agnolín, F.L., Rozadilla, S., Lo Coco, G.E. & Brissón Egli, F. 2021
735 Comments on the morphology of basal paravian shoulder girdle: new data based on unenlagiid
736 theropods and paleognath birds. *Frontiers in Earth Science* **9**, 662167.

737 [137] Hu, H., O'Connor, J.K. & Zhou, Z. 2015 A new species of Pengornithidae (Aves: Enantiornithes)
738 from the Lower Cretaceous of China suggests a specialized scansorial habitat previously unknown in
739 early birds. *PLoS One* **10**, e0126791.

740 [138] Olson, S.L. & Feduccia, A. 1979 Flight capability and the pectoral girdle of *Archaeopteryx*.
741 *Nature* **278**, 247-248.

742 [139] Walker, C. 1981 New subclass of birds from the Cretaceous of South America. *Nature* **292**, 51-
743 53.

744 [140] Martin, L. 1995 The Enantiornithes: terrestrial birds of the Cretaceous. *Courier*
745 *Forschungsinstitut Senckenberg* **181**, 23-36.

746 [141] Chiappe, L.M. & Walker, C. 2002 Skeletal morphology and systematics of the Cretaceous
747 Euenantiornithes (Ornithothoraces: Enantiornithes). In *Mesozoic birds: above the heads of dinosaurs*
748 (eds. L.M. Chiappe & L.M. Witmer), pp. 240-267. Berkeley, California, University of California Press.

749 [142] Chiappe, L.M., Suzuki, S., Dyke, G.J., Watabe, M., Tsogtbaatar, K. & Barsbold, R. 2007 A new
750 enantiornithine bird from the Late Cretaceous of the Gobi Desert. *Journal of Systematic*
751 *Palaeontology* **5**, 193-208.

752 [143] Mayr, G. 2021 The coracoscapular joint of neornithine birds—extensive homoplasy in a widely
753 neglected articular surface of the avian pectoral girdle and its possible functional correlates.
754 *Zoomorphology* **140**, 217-228.

755 [144] Zhang, F. & Zhou, Z. 2000 A primitive enantiornithine bird and the origin of feathers. *Science*
756 **290**, 1955-1959.

757 [145] Wang, M., Zhou, Z. & Zhou, S. 2016 A new basal ornithuromorph bird (Aves: Ornithothoraces)
758 from the Early Cretaceous of China with implication for morphology of early Ornithuromorpha.
759 *Zoological Journal of the Linnean Society* **176**, 207-223.

760 [146] Wang, Y.-M., O'Connor, J.K., Li, D.-Q. & You, H.-L. 2016 New information on postcranial
761 skeleton of the Early Cretaceous *Gansus yumenensis* (Aves: Ornithuromorpha). *Historical Biology* **28**,
762 666-679.

763 [147] Livezey, B.C. & Zusi, R.L. 2006 Phylogeny of neornithes. *Bulletin of Carnegie Museum of*
764 *Natural History*, 1-544.

765 [148] Poore, S.O., Sanchez-Haiman, A. & Goslow Jr, G. 1997 Wing upstroke and the evolution of
766 flapping flight. *Nature* **387**, 799-802.

767 [149] Kurochkin, E., Chatterjee, S. & Mikhailov, K. 2013 An embryonic enantiornithine bird and
768 associated eggs from the Cretaceous of Mongolia. *Paleontological Journal* **47**, 1252-1269.

769 [150] Wang, M. & Zhou, Z. 2019 A new enantiornithine (Aves: Ornithothoraces) with completely fused
770 premaxillae from the Early Cretaceous of China. *Journal of Systematic Palaeontology*.

771 [151] Zheng, X., Wang, X., O'connor, J. & Zhou, Z. 2012 Insight into the early evolution of the avian
772 sternum from juvenile enantiornithines. *Nature Communications* **3**, 1-8.

773 [152] Lowi-Merri, T.M., Benson, R.B.J., Claramunt, S. & Evans, D.C. 2021 The relationship between
774 sternum variation and mode of locomotion in birds. *BMC Biology* **19**, 1-23.

775 [153] Benito, J. & Olive, R. 2022 *Birds of the Mesozoic: An Illustrated Field Guide*. Barcelona, Spain,
776 Lynx Edicions.

777 [154] Atterholt, J., Hutchison, J.H. & O'Connor, J.K. 2018 The most complete enantiornithine from
778 North America and a phylogenetic analysis of the Avisauridae. *PeerJ* **6**, e5910.
779 (doi:10.7717/peerj.5910).

780 [155] Chiappe, L.M. & Calvo, J.O. 1994 *Neuquenornis volans*, a new Late Cretaceous bird
781 (Enantiornithes: avisauridae) from Patagonia, Argentina. *Journal of Vertebrate Paleontology* **14**, 230-
782 246.

783 [156] Walker, C.A. & Dyke, G.J. 2009 Euenantiornithine birds from the late Cretaceous of El Brete
784 (Argentina). *Irish Journal of Earth Sciences* **27**, 15-62.

785 [157] Chiappe, L.M., Di, L., Serrano, F.J., Yuguang, Z. & Meng, Q. 2020 Anatomy and flight
786 performance of the early enantiornithine bird Protopteryx fengningensis: information from new

787 specimens of the Early Cretaceous Huajiying Formation of China. *The Anatomical Record* **303**, 716-
788 731.

789 [158] O'Connor, J.K., Zheng, X., Pan, Y., Wang, X., Wang, Y., Zhang, X. & Zhou, Z. 2020 New
790 information on the plumage of *Protopteryx* (Aves: Enantiornithes) from a new specimen. *Cretaceous*
791 *Research* **116**, 104577.

792 [159] Wang, X., O'Connor, J.K., Zheng, X., Wang, M., Hu, H. & Zhou, Z. 2014 Insights into the
793 evolution of rachis dominated tail feathers from a new basal enantiornithine (Aves: Ornithothoraces).
794 *Biological Journal of the Linnean Society* **113**, 805-819.

795 [160] Hou, L., Chiappe, L.M., Zhang, F. & Chuong, C.-M. 2004 New Early Cretaceous fossil from
796 China documents a novel trophic specialization for Mesozoic birds. *Naturwissenschaften* **91**, 22-25.

797 [161] Wang, M. & Liu, D. 2016 Taxonomical reappraisal of Cathayornithidae (Aves: Enantiornithes).
798 *Journal of Systematic Palaeontology* **14**, 29-47.

799 [162] Wang, M. & Zhou, Z. 2017 A new adult specimen of the basalmost ornithuromorph bird
800 *Archaeorhynchus spathula* (Aves: Ornithuromorpha) and its implications for early avian ontogeny.
801 *Journal of Systematic Palaeontology* **15**, 1-18.

802 [163] Li, L., Jing-Qi, W. & Shi-Lin, H. 2011 A new ornithurine bird (Hongshanornithidae) from the
803 Jiufotang Formation of Chaoyang, Liaoning, China. *Vertebrata PalAsiatica* **49**, 195.

804 [164] Zhong-He, Z., Fu-Cheng, Z. & Zhi-Heng, L. 2009 A new basal ornithurine bird (*Jianchangornis*
805 *microdonta* gen. et sp. nov.) from the Lower Cretaceous of China. *Vertebrata PalAsiatica* **47**, 299.

806 [165] Zhou, Z. & Zhang, F. 2005 Discovery of an ornithurine bird and its implication for Early
807 Cretaceous avian radiation. *Proceedings of the National Academy of Sciences* **102**, 18998-19002.
808 (doi:10.1073/pnas.0507106102).

809 [166] Close, R.A. & Rayfield, E.J. 2012 Functional morphometric analysis of the furcula in Mesozoic
810 birds. *PLoS One* **7**, e36664.

811 [167] Wang, X., Pittman, M., Zheng, X., Kaye, T.G., Falk, A.R., Hartman, S.A. & Xu, X. 2017 Basal
812 paravian functional anatomy illuminated by high-detail body outline. *Nature Communications* **8**, 1-6.

813 [168] Serrano, F.J., Pittman, M., Kaye, T.G., Wang, X., Zheng, X. & Chiappe, L.M. 2020 Laser-
814 stimulated fluorescence refines flight modelling of the Early Cretaceous bird *Sapeornis*. In
815 *Pennaraptoran Theropod Dinosaurs: Past Progress and New Frontiers* (eds. M. Pittman & X. Xu), pp.
816 333-344, Bulletin of the American Museum of Natural History.

817 [169] Navalón, G., Marugán-Lobón, J., Chiappe, L.M., Sanz, J.L. & Buscalioni, Á.D. 2015 Soft-tissue
818 and dermal arrangement in the wing of an Early Cretaceous bird: implications for the evolution of
819 avian flight. *Scientific Reports* **5**, 1-7.

820 [170] Longrich, N.R., Vinther, J., Meng, Q., Li, Q. & Russell, A.P. 2012 Primitive wing feather
821 arrangement in *Archaeopteryx lithographica* and *Anchiornis huxleyi*. *Current Biology* **22**, 2262-2267.

822 [171] Nudds, R.L. & Dyke, G.J. 2010 Narrow primary feather rachises in Confuciusornis and
823 Archaeopteryx suggest poor flight ability. *Science* **328**, 887-889.

824 [172] Bell, A. & Chiappe, L.M. 2011 Statistical approach for inferring ecology of Mesozoic birds.
825 *Journal of Systematic Palaeontology* **9**, 119-133.

826 [173] Chiappe, L.M., Qingjin, M., Serrano, F., Sigurdsen, T., Min, W., Bell, A. & Di, L. 2019 New
827 *Bohaiornis*-like bird from the Early Cretaceous of China: enantiornithine interrelationships and flight
828 performance. *PeerJ* **7**, e7846.

829 [174] Wang, X., McGowan, A.J. & Dyke, G.J. 2011 Avian wing proportions and flight styles: first step
830 towards predicting the flight modes of Mesozoic birds. *PLoS One* **6**, e28672.

831 [175] Burgers, P. & Chiappe, L.M. 1999 The wing of Archaeopteryx as a primary thrust generator.
832 *Nature* **399**, 60-62.

833 [176] Lowi-Merri, T.M., Demuth, O.E., Benito, J., Field, D.J., Benson, R.B., Claramunt, S. & Evans,
834 D.C. 2023 Reconstructing locomotor ecology of extinct avialans: a case study of *Ichthyornis*
835 comparing sternum morphology and skeletal proportions. *Proceedings of the Royal Society B:*
836 *Biological Sciences* **290**, 20222020.

837 [177] Serrano, F.J. & Chiappe, L.M. 2017 Aerodynamic modelling of a Cretaceous bird reveals
838 thermal soaring capabilities during early avian evolution. *Journal of the Royal Society Interface* **14**,
839 20170182.

840 [178] Serrano, F.J., Chiappe, L.M., Palmqvist, P., Figueirido, B., Marugán-Lobón, J. & Sanz, J.L. 2018
841 Flight reconstruction of two European enantiornithines (Aves, Pygostylia) and the achievement of
842 bounding flight in Early Cretaceous birds. *Palaeontology* **61**, 359-368.

843 [179] Liu, D., Chiappe, L., Zhang, Y., Serrano, F. & Meng, Q. 2019 Soft tissue preservation in two new
844 enantiornithine specimens (Aves) from the Lower Cretaceous Huajiying Formation of Hebei Province,
845 China. *Cretaceous Research* **95**, 191-207.

846 [180] Demuth, O.E., Benito, J., Tschopp, E., Lautenschlager, S., Mallison, H., Heeb, N. & Field, D.J.
847 2022 Topology-based three-dimensional reconstruction of delicate skeletal fossil remains and the
848 quantification of their taphonomic deformation. *Frontiers in Ecology and Evolution*, 125.

849 [181] Heers, A. & Carney, R. 2017 Building a bird: a musculoskeletal model of the *Archaeopteryx*
850 flight apparatus. *Journal of Vertebrate Paleontology, Program and Abstracts* **2017**, 127.

851 [182] Manafzadeh, A.R., Gatesy, S.M. & Bhullar, B.-A.S. 2024 Articular surface interactions
852 distinguish dinosaurian locomotor joint poses. *Nature Communications* **15**, 854.

853 [183] O'Connor, P.M. 2004 Pulmonary pneumaticity in the postcranial skeleton of extant aves: a case
854 study examining Anseriformes. *J Morphol* **261**, 141-161. (doi:10.1002/jmor.10190).

855 [184] O'Connor, P.M. 2006 Postcranial pneumaticity: An evaluation of soft-tissue influences on the
856 postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. *Journal of*
857 *Morphology* **267**, 1199-1226. (doi:10.1002/jmor.10470).

858 [185] Duncker, H.R. 1971 The lung air sac system of birds-a contribution to the functional anatomy of
859 the respiratory apparatus. Adu. Anat. E'mbryol. *Cell Biol* **45**, l-171.

860 [186] King, A.S. 1966 Structural and functional aspects of the avian lungs and air sacs. In
861 *International review of general and experimental zoology* (pp. 171-267, Elsevier.

862 [187] O'Connor, P.M. 2009 Evolution of archosaurian body plans: skeletal adaptations of an air-sac-
863 based breathing apparatus in birds and other archosaurs. *Journal of Experimental Zoology Part A:*
864 *Ecological Genetics and Physiology* **311**, 629-646.

865 [188] Butler, R.J., Barrett, P.M. & Gower, D.J. 2009 Postcranial skeletal pneumaticity and air-sacs in
866 the earliest pterosaurs. *Biology Letters* **5**, 557-560.

867 [189] Claessens, L.P.A.M., O'Connor, P.M. & Unwin, D.M. 2009 Respiratory evolution facilitated the
868 origin of pterosaur flight and aerial gigantism. *PloS one* **4**, e4497.

869 [190] Martin, E.G. & Palmer, C. 2014 Air space proportion in pterosaur limb bones using computed
870 tomography and its implications for previous estimates of pneumaticity. *PLoS One* **9**, e97159.

871 [191] Elgin, R.A. & Hone, D.W. 2013 Pneumatization of an immature azhdarchoid pterosaur.
872 *Cretaceous Research* **45**, 16-24.

873 [192] Wedel, M.J. 2005 7. Postcranial Skeletal Pneumaticity in Sauropods and Its Implications for
874 Mass Estimates. In *The Sauropods: Evolution and Paleobiology* (eds. R. Kristina Curry & W. Jeffrey),
875 pp. 201-228, University of California Press.

876 [193] Yates, A.M., Wedel, M.J. & Bonnan, M.F. 2012 The early evolution of postcranial skeletal
877 pneumaticity in sauropodomorph dinosaurs. *Acta Palaeontologica Polonica* **57**, 85-100.

878 [194] Taylor, M.P. & Wedel, M.J. 2013 Why sauropods had long necks; and why giraffes have short
879 necks. *PeerJ* **1**, e36.

880 [195] Wedel, M.J. 2003 The evolution of vertebral pneumaticity in sauropod dinosaurs. *Journal of*
881 *Vertebrate Paleontology* **23**, 344-357.

882 [196] Wedel, M.J. 2003 Vertebral pneumaticity, air sacs, and the physiology of sauropod dinosaurs.
883 *Paleobiology* **29**, 243-255.

884 [197] Wedel, M.J. 2007 What pneumaticity tells us about 'prosauropods', and vice versa. *Special*
885 *Papers in Palaeontology* **77**, 207-222.

886 [198] Fronimos, J.A. 2023 Patterns and function of pneumaticity in the vertebrae, ribs, and ilium of a
887 titanosaur (Dinosauria, Sauropoda) from the Upper Cretaceous of Texas. *Journal of Vertebrate*
888 *Paleontology*, e2259444.

889 [199] Zurriaguz, V.L. 2024 Variation in the postcranial pneumaticity in derived titanosaurs (Dinosauria:
890 Sauropoda). *Historical Biology*, 1-15.

891 [200] Benson, R.B., Butler, R.J., Carrano, M.T. & O'Connor, P.M. 2012 Air-filled postcranial bones in
892 theropod dinosaurs: physiological implications and the 'reptile'–bird transition. *Biological Reviews* **87**,
893 168-193.

894 [201] Aureliano, T., Almeida, W., Rasaona, M. & Ghilardi, A.M. 2024 The evolution of the air sac
895 system in theropod dinosaurs: Evidence from the Upper Cretaceous of Madagascar. *Journal of*
896 *Anatomy*.

897 [202] Gutherz, S.B. & O'Connor, P.M. 2021 Postcranial Skeletal Pneumaticity in Cuculidae. *Zoology*
898 *(Jena)* **146**, 125907. (doi:10.1016/j.zool.2021.125907).

899 [203] Smith, N.D. 2012 Body mass and foraging ecology predict evolutionary patterns of skeletal
900 pneumaticity in the diverse "waterbird" clade. *Evolution* **66**, 1059-1078. (doi:10.1111/j.1558-
901 5646.2011.01494.x).

902 [204] Gutherz, S.B. & O'Connor, P.M. 2022 Postcranial skeletal pneumaticity in non-aquatic
903 neoavians: Insights from accipitrimorphae. *Journal of Anatomy* **241**, 1387-1398.

904 [205] Burton, M.G.P., Benson, R.B. & Field, D.J. 2023 Direct quantification of skeletal pneumaticity
905 illuminates ecological drivers of a key avian trait. *Proceedings of the Royal Society B* **290**, 20230160.

906 [206] Schachner, E.R., Moore, A.J., Martinez, A., Diaz Jr, R.E., Echols, M.S., Atterholt, J., WP
907 Kissane, R., Hedrick, B.P. & Bates, K.T. 2024 The respiratory system influences flight mechanics in
908 soaring birds. *Nature*, 1-6.

909 [207] Aureliano, T., Ghilardi, A.M., Müller, R.T., Kerber, L., Pretto, F.A., Fernandes, M.A., Ricardi-
910 Branco, F. & Wedel, M.J. 2022 The absence of an invasive air sac system in the earliest dinosaurs
911 suggests multiple origins of vertebral pneumaticity. *Scientific Reports* **12**, 20844.

912 [208] Butler, R.J., Barrett, P.M. & Gower, D.J. 2012 Reassessment of the evidence for postcranial
913 skeletal pneumaticity in Triassic archosaurs, and the early evolution of the avian respiratory system.
914 *PloS one* **7**, e34094.

915 [209] Cerda, I.A., Salgado, L. & Powell, J.E. 2012 Extreme postcranial pneumaticity in sauropod
916 dinosaurs from South America. *Paläontologische Zeitschrift* **86**, 441-449.

917 [210] Schwarz, D., Kundrát, M., Tischlinger, H., Dyke, G. & Carney, R.M. 2019 Ultraviolet light
918 illuminates the avian nature of the Berlin Archaeopteryx skeleton. *Scientific reports* **9**, 6518.

919 [211] Britt, B.B. 1997 Postcranial pneumaticity. In *Encyclopedia of dinosaurs* (eds. P.J. Currie & K.
920 Padian), pp. 590-593. San Diego, Academic Press.

921 [212] Burton, M.G., Benito, J., Mellor, K., Smith, E., Martin-Silverstone, E., O'Connor, P. & Field, D.J.
922 2024 The influence of soft tissue volume on estimates of skeletal pneumaticity: implications for fossil
923 archosaurs. *bioRxiv*, 2024.2010.2008.617080. (doi:10.1101/2024.10.08.617080).

924 [213] Plateau, O., Green, T.L., Gignac, P.M. & Foth, C. 2024 Comparative digital reconstruction of
925 *Pica pica* and *Struthio camelus* and their cranial suture ontogenies. *The Anatomical Record* **307**, 5-
926 48.

927