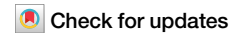


<https://doi.org/10.1038/s42003-025-09019-2>

Wing morphology of *Anchiornis huxleyi* and the evolution of molt strategies in paravian dinosaurs

Yosef Kiat^{1,2}✉, Xiaoli Wang^{3,4,5}, Xiaoting Zheng⁴, Yan Wang^{3,4}✉ & Jingmai O'Connor⁶

As one of the most diverse terrestrial amniote clades, Aves has attracted enormous interest regarding its Jurassic origins and the evolutionary transition from terrestrial to volant in theropod dinosaurs. While abundant research has focused on the skeletal transformations associated with the emergence of flight ability, fewer studies have documented the changes to the soft tissues forming the airfoil itself. Newly emerging information concerning the wing structure in pennaraptorans highlights unexpected complexity in the evolution of wing-like structures in non-volant theropods that complicate efforts to understand the origins of flight. No taxon exemplifies this better than *Anchiornis*, controversial with regards to its flight abilities and phylogenetic position, alternatively regarded as volant or non-volant, and as an avialan or as a troodontid. Here we provide new information concerning the wing structure of this key taxon including temporary changes due to molt based on nine specimens. *Anchiornis* preserves the first evidence of an irregular molt in a non-avian pennaraptoran, which, together with the unique wing structure, indicates flightlessness. The plumage diversity reflected by this new information highlights the significant gaps in our understanding of the evolution of the avian wing and the ability of new discoveries to drastically alter current interpretations.

The relationship between form and function is crucial in evolutionary biology, as morphological adaptations often reflect functional necessities that enhance survival and reproduction. Feathered aerodynamic surfaces on the forelimbs, hindlimbs, and tail of pennaraptoran dinosaurs, including modern birds, not only enable powered flight but also facilitate numerous other biological and ecological functions^{1–3}. While abundant research has focused on skeletal transformations associated with the locomotor transition in pennaraptorans from terrestrial to volant^{4–7}, morphological changes to the airfoils themselves have received relatively less attention⁸. The shape and structure of the feathered surfaces on the limbs and tail are closely linked to their ability to generate aerodynamic forces capable of supporting flight^{9–12}. Understanding these relationships may help elucidate the selective pressures underpinning morphological change and diversification of these feathered surfaces in pennaraptorans^{13,14}.

The aerodynamic properties of feathered surfaces are determined by several variables, including the shape, proportions, thickness, and mechanical strength of the ‘wing’^{2,15}. These are in turn determined by the feathers themselves, including their number, length, and arrangement^{8,16}.

Properties of the individual feathers, such as the structure and thickness of the feather rachis and the presence or absence of interlocking barbs, influence feather morphology and, consequently, the entire flight surface^{17,18}. The shape of feathered surfaces also changes temporarily, slightly over time due to wear, and more considerably and seasonally due to the renewal process¹⁹. Known as molting, this is the process by which new feathers are formed to replace old ones. Unlike other keratin-based structures, full-grown feathers are incapable of growth, and the only way to renew an old and abraded feather is to replace it with a new one²⁰. Despite the structural and functional variation among different types of feathers², this trait is universal, underscoring both the complexity of the full-grown structure and the need for molt as a response to the decrease in functionality resulting from abrasion and other forms of damage. As a result, during the evolution of dinosaurs, molting strategies co-evolved with specific functions of the plumage^{19,21}. Molt is especially critical in volant taxa, in which the renewal of the feathers forming the aerodynamic surfaces of the wings (remiges) and tail (rectrices) significantly changes the shape of these structures, affecting aerodynamic function^{19,22,23}. The impact of molt on flight ability was likely a key factor

¹School of Zoology, Faculty of Life Sciences, Tel Aviv University, Tel Aviv, Israel. ²Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel. ³College of Life Science, Linyi University, Linyi, Shandong, China. ⁴Tianyu Natural History Museum of Shandong, Pingyi, Shandong, China. ⁵College of Earth Science and Engineering, Shandong University of Science and Technology, Qingdao, Shandong, China. ⁶Negaunee Integrative Research Center, Field Museum of Natural History, Chicago, IL, USA. ✉e-mail: yosefkiat@gmail.com; wangyan6696@lyu.edu.cn

leading to the evolution of the diverse remex molting strategies observed among modern birds^{19,21,24}. These strategies minimize the temporary negative impact of the molting process on flight-related functionality, including the ability to escape predators and foraging. Therefore, remex molt strategies reflect – and can be used to predict – aerodynamic function^{21,25}.

Among modern birds, there are three remex molt strategies: (1) a gradual sequential molt, (2) simultaneous molt, and (3) irregular molt, characterized by a non-sequential and unpredictable replacement of remiges^{20,21}. During a gradual sequential molt, aerodynamic capabilities are maintained throughout the molting period^{19,25}. This strategy is present only in volant species and most likely evolved in flight-dependent taxa to maintain this critical locomotor function²¹. A gradual sequential molt is characterized by the staggered sequential molting of one to six primary feathers concurrently, but not the replacement of all remiges simultaneously, with molt symmetry between the two wings^{20,25}. In most taxa, sequential molt starts with the renewal of the innermost primary and proceeds centrifugally toward both the distal and proximal parts of the wing, although alternative patterns occur in some taxa¹⁹. Therefore, this is a slow strategy, resulting in a protracted molt duration, especially in large taxa due to the relatively size-invariant rate of feather growth^{26,27}. For example, simultaneous molt of the remiges lasts ~4 weeks in the Great Crested Grebe (*Podiceps cristatus*), 6 weeks in the Whooper Swan (*Cygnus cygnus*), and 3 weeks in the Razorbill (*Alca torda*), whereas gradual and sequential molt lasts about 22 weeks in the Peregrine Falcon (*Falco peregrinus*), 21 weeks in the Herring Gull (*Larus argentatus*), and 20 weeks in the Raven (*Corvus corax*)²⁰. Consequently, this strategy is costly with regard to the prolonged duration during which wing shape is impacted and demands for resources are elevated to fuel feather growth.

However, simultaneous molt of all flight feathers evolved in some volant clades—this more rapid molt strategy is only viable in taxa whose habitat protects them from predation while they are temporarily flightless, for example, waterfowl or birds that reside in dense habitats, such as marshes and wetlands (e.g., Anatidae and Rallidae)^{19–21}. Notably, although simultaneous molt has evolved among flying taxa, birds with this strategy are more likely to evolve flightlessness²⁸. A third strategy, which includes non-sequential and unpredictable irregular molt of remiges, occurs only among flightless taxa^{19,21}. Among most flightless taxa, the remiges have undergone significant morphological changes and size reduction (e.g., Sphenisciformes and *Casuarius*) or have been nearly or completely lost (e.g., Apterygiformes and *Dromaius*)⁸. Consequently, species with irregular remex molt are extremely rare, with only three extant taxa documenting this pattern: ostriches (Struthionidae), Flightless Cormorant (*Nannopterum harrisi*) and Kākāpō (*Strigops habroptilus*)^{21,29}.

Due to the link between molt strategy and flight ability, understanding molt strategy can elucidate the evolution of aerodynamic ability in pennaraptoran dinosaurs, one of the most significant evolutionary transitions among vertebrates. It is currently debated whether flight evolved once or multiple times during pennaraptoran evolution and whether through a direct appearance of the powered flight stroke or through an intermediate gliding stage^{7,8,30}. Due to these unknowns, both gliding flight and powered flight are referred to together as volant locomotion. The appearance—and secondary loss—of feather-dependent locomotion in pennaraptorans had a direct influence on the evolution of molting since molt characteristics, such as molt rate and sequence, have evolved to minimize the impact of molt on flight performance^{25,31,32}. Identifying these characteristics in non-avian pennaraptoran fossils may be informative regarding plumage function in these taxa and thus provide information relevant for understanding flight origins³¹.

In this study, we report on the remex molt strategy in *Anchiornis huxleyi*, a Late Jurassic non-avian paravian theropod dinosaur from the ~160 mya Tiaojishan Formation in northeastern China^{33–35}. Previous studies have shown that *Anchiornis* had open-vaned contour feathers³⁶ and narrow, symmetrical remiges^{34,37} that were at least partially open-vaned³⁶. In addition, anchiornithines are characterized by having proportionately long

coverts³⁷ and 20–28 primary feathers, which contrasts with the 9–11 primaries present in volant neornithines and other non-avian (and non-volant) pennaraptorans (e.g., *Caudipteryx*, *Zhenyuanlong*)⁸. An examination of color-imparting melanosomes showed that the body feathers of *Anchiornis* were gray and dark, the face had rufous speckles, the crown was rufous, and the long limb feathers were white with distal black spangles³⁸. Based on plumage morphology, it has been suggested that this taxon was non-volant⁸. Furthermore, the large number of primaries may indicate that this taxon is secondarily flightless, similar to the condition in some crown birds (e.g., Struthioniformes and Sphenisciformes), although the limited fossil record of feathered pennaraptorans constrains the confidence with which the currently available data can be interpreted⁸.

Morphological characteristics of the feathers and of the feathered flight surface can directly or indirectly indicate an active feather molt. These characteristics primarily include an absence of feathers, especially if symmetrical between the two wings, or proportionately short feathers indicating active growth, both of which produce gaps within the wing^{19,20}. The challenge in using these characteristics to identify molt in a fossil specimen lies in the need for a high level of plumage preservation, and especially the ability to distinguish the contours of individual feathers. In this study, we utilized the large collection of the Shandong Tianyu Museum of Nature (STM) to identify specimens with well-preserved plumage. Using the plumage color pattern of *Anchiornis* and its deviations, we were able to investigate wing morphology and molt strategy, even when the contours of each feather were not optimally detectable. Consistent with hypotheses suggesting that *Anchiornis* was non-volant, we predict that this taxon would exhibit an irregular molt characterized by non-sequential and unpredictable replacement of the remiges. In such a case, immature feathers could appear anywhere on the wing rather than following an orderly sequence. This molt pattern, although present in flightless species of modern birds, has not been previously documented in non-avian dinosaurs, and contrasts with the gradual and sequential remex molt observed in the volant *Microraptor*²¹.

Results

Wing morphology

We identified nine *Anchiornis* fossils that preserved a visual indication of the feather color pattern, allowing us to examine the morphology of the primary feathers and their coverts (STM0-3, STM0-65, STM0-106, STM0-115, STM0-136, STM0-143, STM0-166, STM0-188, STM0-214). As described in previous studies, this taxon possesses light-colored wing feathers with darkened tips^{36,38}. Due to the size and structure of the feathers, their overlapping morphology, and the preservation quality of the available fossils, it was challenging to accurately count the primary feathers. However, data from these nine specimens indicate that the number of primary feathers varies among individuals; for most individuals, it ranges from 20 to 25 feathers (e.g., STM0-166 and STM0-214), but STM0-65 preserves 28 primary feathers. *Anchiornis* has three series of primary coverts (PC) with darkened tips that, when fully grown, create three uniform wing bars. A fourth wing bar is formed by the darkened tips of the primary feathers along the trailing edge of the wing (Fig. 1). In most fossils, only two PC series are clearly visible, and based on their relative lengths, they correspond to the second and third series observed in specimens where all three are preserved (e.g., STM0-65). This suggests that the first and shortest series is often difficult to distinguish, primarily due to poor preservation. Therefore, the lengths of the PC series were measured only for STM0-214, which preserves the most complete wing and all three PC series. The third and longest PC series in *Anchiornis* covers over 80% of the wing's length (Fig. 1). In contrast, only two PC series are present in volant neornithines (31 species of different orders, representing 86% of the orders, including flying species; Figs. 2 and 3; Supplementary Table 1). In these volant neornithines, the mean coverage of the longest PC series (the 2nd) is 47.9% of the wing's length (range = 38–62%; standard deviation = 6.0%). Our measurements indicate that the first and second PC series in *Anchiornis* are significantly longer than the corresponding series in flying Neornithes (first PC series: $t = 3.28$, $P = 0.003$, second PC series: $t = 2.76$, $P = 0.010$; phylogenetically-informed

Fig. 1 | *Anchiornis huxleyi* STM0-214. This fossil exhibits nearly complete wings and preservation of feather coloration, allowing for a detailed identification of wing morphology. The wings have four dark bars, formed by dark spots at the tips of the feathers attached to the manus (a). Three wing bars are created by the three series of primary coverts, and an additional bar is formed by the spots at the tips of the primary feathers along the trailing edge of the wing. The third and longest PC series in this specimen covers over 80% of the wing's length. Additionally, this specimen shows several short immature feathers that can be identified by the spots that do not reach the wing bar line of the other feathers (marked with white arrows; b). The scale bar (bottom right) equals 10 cm.

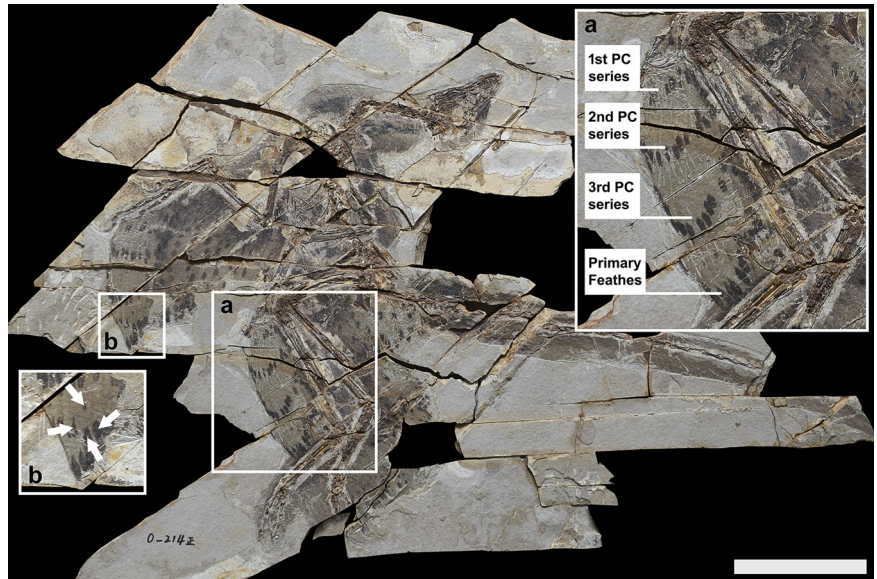
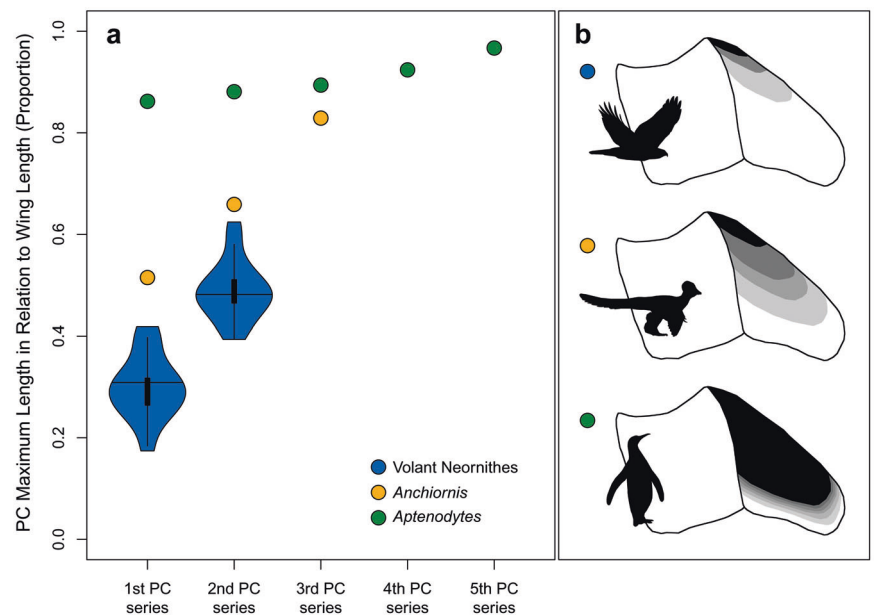


Fig. 2 | Pattern of primary coverts in modern birds and *Anchiornis huxleyi*. The number of primary covert series and their length in relation to wing length among volant modern birds ($n = 31$ species from different orders), *Anchiornis* (STM0-214), and penguins of the genus *Aptenodytes*, numeric display (a) and graphical display (b). The mean maximum PC coverage in modern birds (2nd series) is <50%, whereas penguins have more series of primary coverts covering more than 95% of the wing length, resulting in a thicker wing that functions as a flipper during swimming. In *Anchiornis*, the maximum coverage (3rd series) exceeds 80%, a value we have not found among flying species of modern birds. For the two PC series in Neornithes (a), the width of each blue patch represents sampling frequency, while the vertical bar represents the 95% confidence interval, and the horizontal bar represents the median value. In b, the black area at the base of the primaries represents small coverts that are not part of any distinct series, while the progressively lightening gray areas represent the different PC series.



test). In contrast to other extant species (both volant and non-volant), the penguin *Aptenodytes*, in which the wing is heavily modified into a paddle, possesses five to six distinct series of PCs. Along with the small coverts that are not part of any distinct series, these feathers cover more than 95% of the wing's length (Fig. 2).

Molt

Typically, to identify a growing feather, its contour must be discernible, which requires a high level of preservation. However, deviations in the unique four-wing-bar pattern of *Anchiornis* due to the shorter length of a growing feather permit identification of molt, even with suboptimal preservation. A similar situation occurs in many modern bird species with distinctive wing feather patterns (Fig. 3d, e and Supplementary Fig. 1). Specifically, in shorter feathers in the wing of *Anchiornis*, whether primaries or PCs, the darkened tip of the feather is visibly closer to the postpatagium, deviating from its usual position, and disrupting the uniform wing bar. Note that the parallel arrangement of the preserved feathers provides evidence

against the possibility that the darkened tip of the feathers identified as immature is positioned unnaturally due to poor preservation. Our visual examination indicates that this pattern of shorter feathers is present in all nine exceptionally preserved fossils (Fig. 1). Most fossils show up to five primary feathers, which are incompletely grown to varying degrees, with variable positioning in the wing and asymmetry between the two wings (e.g., STM0-65, STM0-166 and STM0-214). Due to the low molt rate and the small number of growing feathers in each of these specimens, the overall wing morphology nevertheless conforms to the description above. However, specimen STM0-143 exhibits a high degree of inconsistency in feather lengths, indicating a greater proportion of feathers at different stages of growth (Supplementary Fig. 2). The lack of a consistent pattern in wing feather growth in the examined fossils, along with the asymmetry between the wings, is interpreted as evidence of an irregular molt, similar to the pattern documented in some flightless modern birds. Additionally, the high number of specimens preserving molt is unusual compared to the general rarity of molt evidence in dinosaur fossils^{39,40}. However, in a random sample

Fig. 3 | Examples of wing morphology in Neornithes. **a** Volant modern birds have two series of primary coverts (PCs), for example, Marbled Godwit *Limosa fedoa* (in the small figure, bottom right, the 1st PC series is highlighted in yellow and the 2nd PC series in red; photo by S. Cahill, ML547608961, the Cornell Lab of Ornithology | Macaulay Library). **b** However, in many groups, the 1st PC series is short and hidden under the alula feathers and is not visible, for example, most Accipitrids, Falconiformes and Passeriformes (Peregrine Falcon *Falco peregrinus*; photo by S. Uddin, ML585916741). **c** Penguins of the genus *Aptenodytes* have five to six series of primary coverts covering most of the wing length, resulting in a thicker wing that functions as a flipper during swimming (King Penguin *Aptenodytes patagonicus*; photo by J. Porter, ML532366881). **d** The feather coloration pattern may help identify temporary changes in wing morphology due to feather molting. This African Sacred Ibis *Threskiornis aethiopicus* demonstrates how the dark tips of the remiges appear during active molt, where the dark tips of the immature feathers do not reach the wing bar at the trailing edge of the wing (photo by W. Paes, ML511733181; more examples are given in Supplementary Fig. 1). In contrast, **e** when all the feathers are fully grown, the remiges form a uniform black bar (photo by P. Kennerley, ML195762481). **f** Irregular remex molt in the Flightless Cormorant *Nannopterum harrisi* (photo by S. Watson, ML414658191).

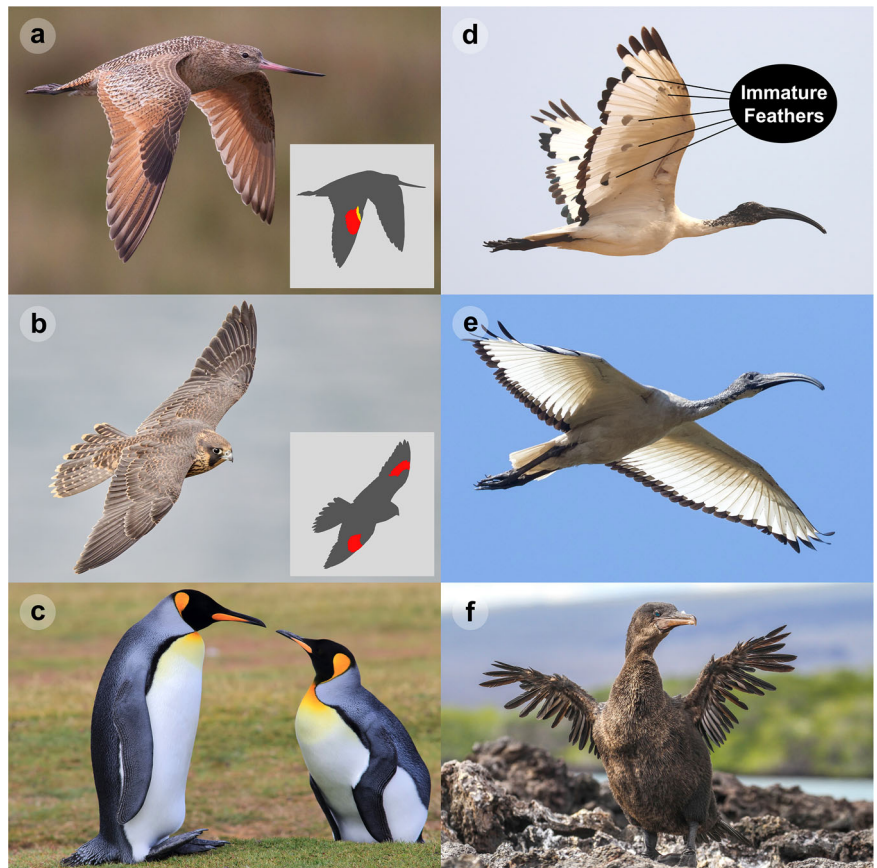


Table 1 | Three continuous-time Markov models used for reconstructing ancestral molt strategies among Paravian dinosaurs (gradual and sequential versus irregular molt), along with their Akaike information criterion (AIC) scores

Model	logLik	AIC	AICc	Δ AICc	Akaike weight
Equal transition rates	-13.72	29.44	29.60	0.00	1.0
Irreversible 0 → 1	-28.11	60.21	60.73	31.13	0.0
Irreversible 1 → 0	-48.83	101.67	102.19	75.59	0.0

of 143 Flightless Cormorants tested in this study, we also found a high proportion of individuals undergoing an active irregular molt (79.0%; Supplementary Fig. 3). Molt asymmetry between the two wings was also frequently observed in these cormorants.

Recent documentation of molt strategies in fossil pennaraptorans^{21,40} permits an ancestral trait reconstruction analysis for a phylogenetic tree that includes the evolutionary reconstruction of dinosaurs spanning 160 million years, from the earliest known Paraves to Neornithes. The equal transition rates model was selected as the best-supported explanation for ancestral trait reconstruction (Δ AICc = 31.13, Akaike weight = 1.00; Table 1). This analysis indicates that the ancestral molt strategy in this monophyletic group was likely gradual and sequential (89.2%), whereas irregular molt evolved independently in flightless neornithines and *Anchiornis* (Fig. 4).

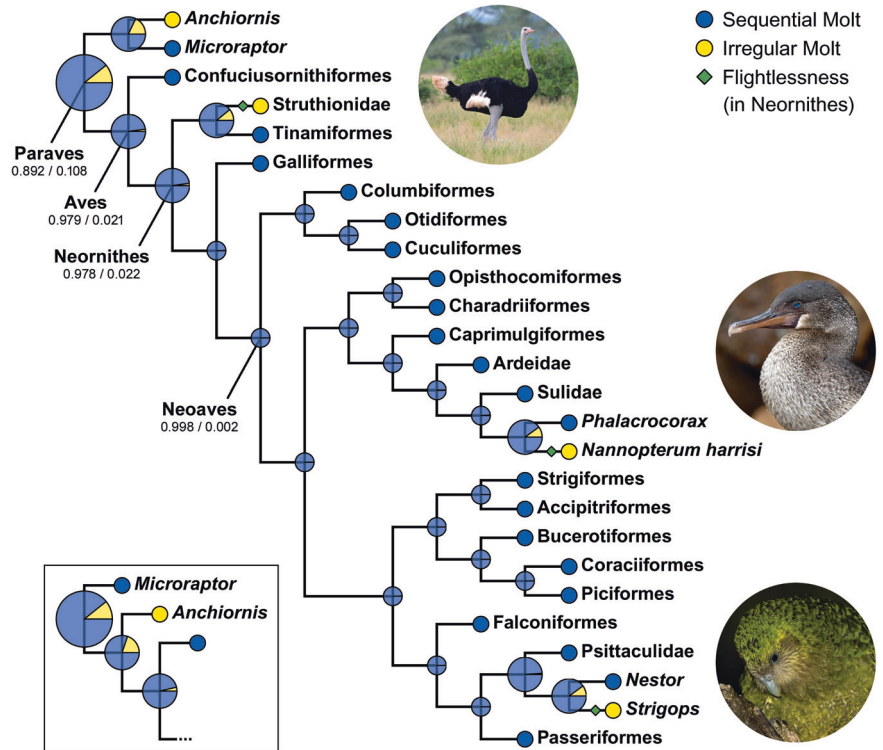
Discussion

As the best-known non-avian paravian, *Anchiornis* is a critical taxon for understanding the evolution of flight in dinosaurs. Even though hundreds of specimens have been recovered, the locomotor function of the feathered limbs in this taxon remains controversial, with flight potential inferred by some authors but not by others^{7,8,38}. Better understanding of the forelimb

plumage in this taxon, and the functional and evolutionary significance of observed morphologies, is critical for elucidating the acquisition of flight in pennaraptorans and the early evolution of the avian wing structure.

Longrich et al.³⁷ described the wing morphology of *Anchiornis* based on BMNHC PH828. This study described the extensive coverage of the remiges by the PCs that characterizes this taxon³⁷, corroborated by observations from the STM fossils. However, examination of feather lengths suggests that many remiges and coverts in BMNHC PH828 are not fully grown, likely indicating an intensive, active wing molt involving a relatively large number of feathers growing within the same time interval, similar to the pattern found in STM0-143 (Supplementary Fig. 2). Therefore, the wing structure in BMNHC PH828 is atypical. Utilizing the larger sample of fossils examined at the STM, including at least one specimen in which most of the wing feathers are fully grown (STM0-214; Fig. 1), we are able to reconstruct the typical wing structure of *Anchiornis*. Longrich et al.³⁷ suggested that the relatively elongated and numerous layers of coverts in the wing of *Anchiornis* may compensate for the slender primary feather shafts, thereby providing the wing with the mechanical strength necessary for flight. However, no biomechanical analyses were conducted to test this hypothesis. We consider this explanation unlikely, given that the evolution of the feathered wing represents a compromise between mechanical strength and low mass due to demands for high aerodynamic efficiency to maximize fitness and reduce the energetic cost of flight. Comparison with extant birds suggests the extensive coverage of the wing by multiple series of coverts is the result of selective pressures not related to flight. Among extant birds, increases in the number of PC rows are only observed in the feathered forelimbs of flightless lineages, in which the forelimb no longer serves an aerodynamic function, that have survived long enough to evolve new forelimb functions and thus have undergone evolutionary changes in their wing structure^{8,41-43}. For example, penguins have similarly evolved multiple layers of coverts (Fig. 2), resulting in a thicker wing that functions as a

Fig. 4 | The evolutionary history of the molt strategy among Paravian dinosaurs, including birds. The results of this analysis show that the ancestral trait among this monophyletic group was likely gradual and sequential, while irregular molt evolved as a response to the secondary loss of flight in modern birds and in *Anchiornis* *huxleyi*. A similar result was obtained in the analysis based on an alternate phylogenetic scenario (small square). The photos were obtained from the Cornell Lab of Ornithology | Macaulay Library: Somali Ostrich *Struthio molybdophanes* (photo by D. Bormann, ML102336971), Flightless Cormorants *Nannopterum harrisi* (photo by D.A. Marques, ML131181371), and Kākāpō *Strigops habroptilus* (photo by O. Thomas, ML424216831).



‘flipper’ during subaqueous locomotion. Yet, penguins, as flightless wing-propelled divers, are not analogous to *Anchiornis*. This unique wing structure highlights how *Anchiornis* was fundamentally different from extant taxa, even flightless ones, and that it has no extant analog. This is consistent with ancestral state analyses that suggest a wing formed by 9–11 primaries is the ancestral pennaraptoran condition, and the increase of primary remiges in Anchiornithinae is autapomorphic to this clade⁸. Furthermore, the extent of wing coverage by the primary coverts affects wing thickness and likely also the cambered profile of the wing, which is necessary for generating lift. This combination of features strongly suggests that the feathered forelimbs of *Anchiornis* served a unique non-aerodynamic function. Future studies involving controlled experiments using biomechanical models may contribute to our understanding of the functional significance of the morphological patterns described in this study.

Systematic comparison of PC lengths between *Anchiornis* and other Mesozoic pennaraptorans is not currently possible due to differences in plumage color patterns between taxa and poor preservation of available material. However, a more general examination of wing structure in *Microraptor* (e.g., IVPP V13352; Xu et al.⁴⁴), *Confuciusornis* (e.g., STM7-21; Wang et al.⁴⁰), *Eoconfuciusornis* (e.g., IVPP V11977⁴⁵), *Protopteryx* (e.g., BMNHC PH1060⁴⁶) and *Sapeornis* (e.g., DNHM D3078⁴⁷) suggests that in these taxa at least half of the primary feather length is exposed beyond the coverts, similar to the common pattern found in modern birds. This suggests that long PCs covering most of the primary feather length, as well as multiple primaries (20–28), may be unique to *Anchiornis*. Although Longrich et al.³⁷ describe elongated PCs as also being present in *Archaeopteryx* based on the Berlin specimen, this finding is not corroborated by observations from other specimens of *Archaeopteryx*^{48–50}, including the newly reported Chicago specimen⁵¹. The function of the unusual forelimb feathers in *Anchiornis* is mysterious. With no analogs among extant birds, only biomechanical modeling has the potential to shed light on the effects of extensive PC coverage over a surface formed by numerous, narrow primaries.

The feather coloration pattern of the forelimb feathers in *Anchiornis*, characterized by light contour and primary feathers with dark tips, is a common pattern among modern birds. The richer concentration of melanin

makes the feathers more durable, where abrasion is greatest^{52,53}. The unique four-bar feather patterning of the *Anchiornis* wing allows for the easy identification of molt. Since feathers develop from the base, the coloration pattern at the feather’s tip emerges first and is pushed outward as the feather grows. Consequently, the feather’s color pattern differs from the mature morphology during early growth stages, especially in an irregular molt, as in *Anchiornis* (Fig. 3d and Supplementary Fig. 1). The uneven color pattern observed in the tested specimens of *Anchiornis* indicate an irregular molt strategy characterized by a gradual replacement of flight feathers without a fixed or predictable sequence and often lacking symmetry between the two wings. This molt pattern is only known among flightless species of modern birds, documented in the ostriches, Flightless Cormorant and Kākāpō^{21,29}. This contrasts with the molt pattern observed in most flying taxa, which follows a consistent and predictable sequence of wing feather replacement (the remaining flying and flightless taxa molt simultaneously^{19,21}). These findings align with previous studies suggesting that *Anchiornis* was non-volant⁸. Supporting evidence includes the presence of a high number of primary feathers (20–28), compared to nine to 11 primaries in flying species, the symmetry of these feathers compared to the asymmetry in flying species, the higher number of secondary feathers relative to ulna length, the proportions of the PCs, the open pennaceous morphology of the remiges, and the absence of a postpatagium for support (contra some reports, wing patagia are clearly absent in *Anchiornis*, as demonstrated by the exceptional preservation in BMNHC PH828)^{8,34,36}. In addition, we suggest that variation in primary feather number among individuals, relative to overall feather count, which is extremely rare in flying modern birds, also reflects a lack of constraint on wing shape, consistent with flightlessness. In contrast, studies in which plumage structure and the morphology and arrangement of the feathers were not considered predicted flight potential in *Anchiornis*⁷.

Unlike *Microraptor*, fossils of *Anchiornis* visibly preserving forelimb feather color pattern reveal a high occurrence of feather molting, although most individuals display only a few feathers in growth. STM0-143, and likely also BMNHC PH828, exhibit more intensive molting, involving a greater number of primary feathers and coverts. Variation in the number of immature feathers is also observed in many extant bird species with irregular or gradual sequential molt^{19,25}. Among species with gradual sequential molt,

this variation may be attributed to differences in age, sex, and the varied effects of habitat conditions⁵⁴. The high occurrence of actively molting individuals of *Anchiornis* is significantly greater compared to species that molt all their feathers simultaneously within a short period, and even exceeds the rate documented for most flying species of modern birds that undergo sequential molt³⁹ (but see Rohwer and Wang⁵⁵). We examined approximately 200 *Microraptor* specimens at the STM and found no further evidence of the sequential molt previously documented in this taxon²¹. This reinforces earlier findings regarding the rarity of molt evidence in most fossil species³⁹. The high occurrence of feather molting among *Anchiornis* suggests an irregular molt occurring over an extended period, similar to the pattern observed in Flightless Cormorants (Fig. 3f and Supplementary Fig. 3). This pattern, which includes ongoing feather replacement, might result from the relatively low energetic cost required by a flightless species during molting or the fact that molt is not constrained to a shorter period of time in order to reduce the period during which flight is impacted, as occurs in volant taxa. While it includes the production of new feathers, it excludes the additional cost needed by a flying species to compensate for the loss in wing surface area during flight. This condition may result in a lack of pressure to complete molt within a limited period when resources are abundant. Such pressure is experienced by many species of modern birds living in regions with seasonal climates^{19,56,57}, but not by species living in tropical regions^{58,59}. However, it should be noted that the unique color pattern of *Anchiornis* allows for easier identification of growing feathers, especially in smaller feathers like coverts, which could bias results such that active molt appears more frequent in *Anchiornis* than in a species without a distinctive pattern (e.g., *Microraptor*). This may also be amplified by the greater number of forelimb feathers in *Anchiornis*, characterized by double the number of primaries found in most other pennaraptorans, and an additional row of primary coverts. Simply having more feathers to replace may prolong even an irregular molt duration.

Numerous lines of evidence indicate *Anchiornis* was non-volant. Ancestral state reconstruction analysis of flight-related feather characteristics further suggests that *Anchiornis* was probably secondarily flightless⁸, as has been suggested for a majority of non-volant pennaraptorans (the so-called 'neoflightless' hypothesis). The findings of Kiat and O'Connor⁸ further indicate that the feather molt strategy is an important trait that changes rapidly in response to the secondary loss of flight. In the current study, ancestral trait analysis of available molt data reconstructed across two competing phylogenetic scenarios (Fig. 4) suggests that the ancestor of Paraves likely had a gradual and sequential molt, similar to that of flying species of modern birds and documented in the extinct flying dinosaur species *Microraptor*²¹ and *Confuciusornis*⁴⁰. However, this is based on extremely limited data (molt recorded in only three Mesozoic taxa) and the strong correlation between molt strategy and aerodynamic ability, which suggests rapid evolutionary changes in molt strategy in response to the loss of flight ability, may also limit our ability to draw broad conclusions from this analysis, especially considering widespread homoplasy in pennaraptorans. Even recently flightless neornithines, which lose the ability to fly independently of the evolution of simultaneous molt, do not replace their feathers using a gradual and sequential replacement²¹. For example, the Flightless Cormorant, which lost its flight ability about five million years ago⁸, replaces its remiges in an irregular sequence, unlike its flying relatives, which have a sequential molt. On the other hand, this information is only relevant to the loss of the sequential molt (e.g., Flightless Cormorant) and not to the evolutionary timescale during which this strategy initially evolved. Therefore, the findings suggesting the presence of sequential molt at the base of Paraves only tentatively support the neoflightless hypothesis and the interpretation that flight was ancestral to Paraves and possibly even to all Pennaraptora.

In contrast to the molt strategy, which differs between flying and flightless species, many modern flightless bird species exhibit a pattern of PCs, including wing coverage by PCs, that resembles the pattern observed in flying species, for example, flightless rails (Rallidae) and the Flightless Cormorant. This may suggest that the PC pattern is a trait that is retained

over a long evolutionary period following the secondary loss of flight ability. Just as the large number of primary remiges suggests the *Anchiornis* lineage lost its flight ability long before the deposition of the Tiaojishan Formation⁸, similarly, the significant changes in PC pattern and wing coverage compared to other known Mesozoic pennaraptorans also suggest significant divergence times. Birds that have lost their flight ability secondarily in recent evolutionary history (e.g., flightless rails and Kākāpō) do not exhibit similar changes to their wing structure. This disparity in wing feather arrangement in *Anchiornis* and *Archaeopteryx*, taxa that are considered to be closely related and indeed are skeletally similar, indicates that the evolution of forelimb plumage in paravians was far more complex than previously acknowledged and further highlights significant gaps in the fossil record of pennaraptoran plumage. Detailed plumage data from a greater number of Mesozoic paravians is required to understand the patterns and evolutionary pressures responsible for this diversity and how this relates to the evolution of flight.

Anchiornis exhibits numerous plumage traits, including the pattern of remex renewal, that do not support interpretations that this taxon was capable of flight. Understanding molt strategy and how it integrates into the life cycle is fundamentally important for comprehending a species' biology, ecology, and evolution⁶⁰. Indeed, the findings of this research emphasize the importance of studying molt strategies in fossil taxa to reconstruct the evolution and ecology of dinosaurs, particularly the evolution of flight, one of the most important vertebrate transitions. Future research that addresses gaps in our understanding of molt strategies or morphological patterns in extant bird species, particularly among flightless ones, is crucial for enhancing our comprehension of the ecology and evolution of these species, as well as extinct taxa from the Mesozoic.

Methods

Study of fossil specimens

We examined a large sample ($n = 226$) of fossilized *Anchiornis* specimens in the collection of the STM (Pingyi, China)⁶¹. All specimens were visually inspected under appropriate lighting conditions and were classified into two groups, (1) those that did not preserve the plumage or plumage coloration at a level sufficient to allow precise observation of wing feather morphology, and (2) those characterized by a high level of plumage preservation, including visual indications of feather color patterns that made it possible to distinguish the wing feathers, as well as their outline, length, and position on the wing. Among the second group, we looked for characteristics indicative of active molt in the primary feathers or primary coverts (PC), such as feathers that were proportionately shorter than adjacent ones or molt-related gaps in the feathered wing surface. The proportionately high occurrence of feather color preservation in this taxon allowed new observations of the wing structure, as described.

Wing length measurement

To describe the morphology of the remiges and covert feathers attached to the manus, we employed a wing measurement method commonly used in ornithology. This method involves measuring the maximum distance between the carpal joint (i.e., the bend of the wing) and the tip of the longest primary feather⁶². Similarly, we measured the length of each series of covert feathers in this part of the wing, from the carpal joint to the tip of the longest feather (Fig. 5). These measurements were taken from representatives from most orders of volant modern birds and *Anchiornis* STM0-214, which exhibits a high level of preservation of wing feathers. The measurements of modern birds were done at the Steinhardt Museum of Natural History (Tel Aviv University, Israel). To assess whether the value observed in *Anchiornis* significantly deviates from expectations among volant neornithines under a Brownian-motion model of evolution, we performed a phylogenetically informed deviation test. A phylogenetic generalized least squares (PGLS) model was fitted using all other taxa (excluding *Anchiornis*) with an intercept-only model, and the residual variation was used to compute a t -statistic comparing the *Anchiornis* value to the predicted mean.

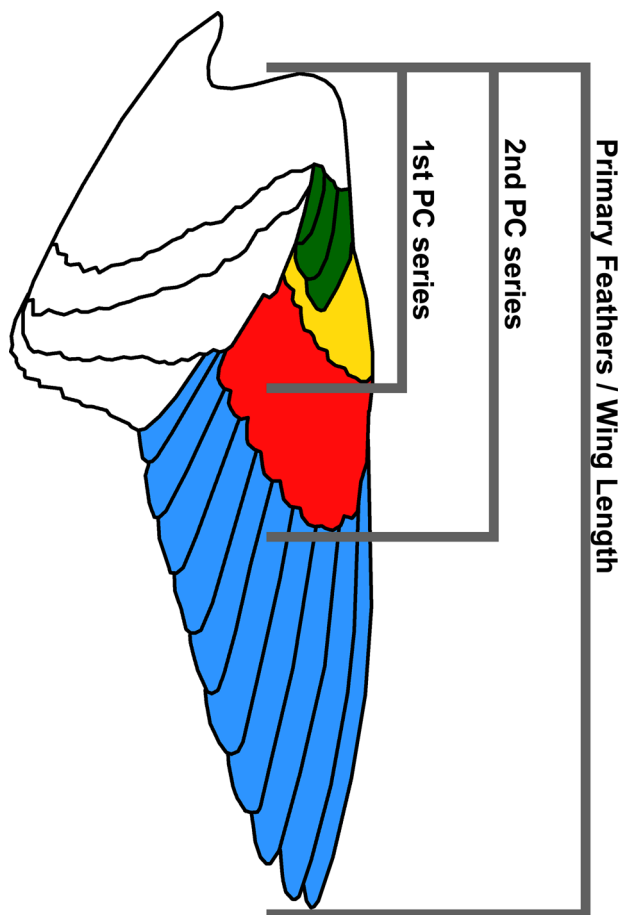


Fig. 5 | The measurements of the wing feathers were performed in the study. This method involves measuring the maximum distance between the carpal joint and the tip of the longest primary feather and the longest feather in each PC series. The figure shows an example of a modern bird's wing. The feathers attached to the are manus colored as follows: alula feathers = dark-green, 1st PC series = yellow, 2nd PC series = red, and primary feathers = blue.

Feather molt data in flightless taxa

Comparison of the relationships observed in modern birds between morphology and function may allow us to infer the function and ecology of extinct species based on their morphology as studied from fossils⁶³. While information regarding molt strategy is not available for all modern bird species^{60,64}, data are available for a significant number of species, permitting statistical comparisons. Specifically, three flightless taxa (*Struthio*, *Nannopterum harrisi*, and *Strigops habroptilus*) retain true remiges (unlike, for example, Sphenisciformes and *Casuaris*) and belong to lineages in which the loss of flight was not related to the evolution of simultaneous remex molt (unlike, for example, Anatidae, Podicipedidae, and Rallidae; *Nannopterum harrisi* and *Strigops habroptilus* have close relatives that exhibit sequential molting, and none of the three taxa inhabits an environment where simultaneous molting would be feasible)²⁵. Although we know that these three flightless taxa exhibit irregular molt^{21,29}, detailed information regarding the sequence, extent, frequency and seasonality of the molt is still missing. This information may be particularly important, as we suggest that these taxa may represent a prevalent condition among early pennaraptorans: non-volant with elongated forelimb feathers—for example, *Caudipteryx*, *Eosinopteryx*, and *Protarchaeopteryx*^{8,65–67}. Therefore, we expanded available information on the Flightless Cormorant to enable comparisons that may provide insights into the ecology and function of extinct species. Wing feather molt in this taxon can be examined using photographs due to its habit of standing with wings outstretched for extended periods. Photos of

this species were examined from the Macaulay Library (Cornell Lab of Ornithology), as previously suggested and conducted in several studies^{68–71}.

Phylogenetic evolutionary analysis

In order to study the evolution of remex molt strategy, as well as to estimate the ancestral state of these traits, we used an ancestral trait reconstruction analysis. We fitted three continuous-time Markov models of binary character evolution using the R package 'phytools' (function 'fitMk'; version 2.4-4; Phylogenetic Tools for Comparative Biology): (1) equal transition rates model, (2) irreversible 0 → 1, and (3) irreversible 1 → 0⁷². For this purpose, we built two cladograms based on the tree used by Kiat and O'Connor (2024) representing the evolutionary relationships of paravians (including Neornithes), encompassing about 160 million years³⁵, including three Mesozoic taxa: *Anchiornis*, *Microraptor* and Confuciusornithiformes. Although findings regarding molt strategy have been published for an additional Mesozoic bird, *Archaeopteryx*⁷³, these findings remain disputed⁷⁴, and therefore, this taxon was not included in our analysis. Two alternative cladograms were required because of the uncertainty regarding the phylogenetic position of *Anchiornis*, as either a non-avian avialan⁷ or a non-avian deinonychosaur⁷⁵. Information regarding the molt strategies of neornithines was based on data published in the scientific literature^{21,29,76–78}. Neornithine evolutionary relationships are based on an analysis of global bird diversity^{79,80} and the BirdTree project⁸¹ and revised based on more recent avian phylogeny⁸². In order to select the most appropriate model, we used the Akaike Information Criterion, modified for small sample sizes (AICc⁸³). A given model was selected only if its Δ AICc exceeded 2.00 compared to alternative models.

Institutional abbreviations

Institutional abbreviations for the paleontological and zoological collections mentioned in this study: BMNHC Beijing Museum of Natural History, Beijing, China; DNHM Dalian Natural History Museum, Dalian, China; IVPP Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; SMNH Steinhardt Museum of Natural History, Tel Aviv University, Israel; STM Shandong Tianyu Museum of Nature, Pingyi, China.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The data that support the findings of this study are available in the Open Science Framework (OSF; <https://osf.io/a2e5c/>)⁸⁴.

Received: 4 February 2025; Accepted: 9 October 2025;

Published online: 21 November 2025

References

- Baumgart, S. L., Sereno, P. C. & Westneat, M. W. Wing shape in waterbirds: morphometric patterns associated with behavior, habitat, migration, and phylogenetic convergence. *Integr. Org. Biol.* **3**, obab011 (2021).
- Terrill, R. S. & Shultz, A. J. Feather function and the evolution of birds. *Biol. Rev.* **98**, 540–566 (2023).
- O'Connor, J. The plumage of basal birds. in *The Evolution of Feathers: from Their Origin to the Present* (ed Foth, C.) 147–172 (Springer, 2020).
- Ossa-Fuentes, L., Soto-Acuña, S., Bona, P., Sallaberry, M. & Vargas, A. O. Developmental evolution of the distal ankle in the dinosaur–bird transition. *J. Exp. Zool. Part B Mol. Dev. Evol.* **338**, 119–128 (2022).
- Brusatte, S. L., Lloyd, G. T., Wang, S. C. & Norell, M. A. Gradual assembly of avian body plan culminated in rapid rates of evolution across the dinosaur–bird transition. *Curr. Biol.* **24**, 2386–2392 (2014).
- Bhullar, B.-A. S. et al. How to make a bird skull: major transitions in the evolution of the avian cranium, paedomorphosis, and the beak as a surrogate hand. *Integr. Comp. Biol.* **56**, 389–403 (2016).

7. Pei, R. et al. Potential for powered flight neared by most close avialan relatives, but few crossed its thresholds. *Curr. Biol.* **30**, 4033–4046 (2020).
8. Kiat, Y. & O'Connor, J. K. Functional constraints on the number and shape of flight feathers. *Proc. Natl Acad. Sci. USA* **121**, e2306639121 (2024).
9. Sheard, C. et al. Ecological drivers of global gradients in avian dispersal inferred from wing morphology. *Nat. Commun.* **11**, 2463 (2020).
10. Dawson, A. The scaling of primary flight feather length and mass in relation to wing shape, function and habitat. *Ibis* **147**, 283–292 (2005).
11. Biewener, A. A. Biomechanics of avian flight. *Curr. Biol.* **32**, R1110–R1114 (2022).
12. Weeks, B. C. et al. Morphological adaptations linked to flight efficiency and aerial lifestyle determine natal dispersal distance in birds. *Funct. Ecol.* **36**, 1681–1689 (2022).
13. Xu, X. & Barrett, P. M. The origin and early evolution of feathers: implications, uncertainties and future prospects. *Biol. Lett.* **21**, 20240517 (2025).
14. Lauder, G. V. Form and function: structural analysis in evolutionary morphology. *Paleobiology* **7**, 430–442 (1981).
15. Videler, J. J. *Avian Flight* (Oxford University Press, 2006).
16. Deeming, D. C., Durkin, M. & Nudds, R. L. Maintaining the avian wing aerofoil: relationships between the number of primary and secondary flight feathers and under-lying skeletal size in birds. *J. Zool.* **322**, 272–280 (2024).
17. Lingham-Soliar, T. Microstructural tissue-engineering in the rachis and barbs of bird feathers. *Sci. Rep.* **7**, 45162 (2017).
18. Laurent, C. M., Palmer, C., Boardman, R. P., Dyke, G. & Cook, R. B. Nanomechanical properties of bird feather rachises: exploring naturally occurring fibre reinforced laminar composites. *J. R. Soc. Interface* **11**, 20140961 (2014).
19. Jenni, L. & Winkler, R. *The Biology of Molt in Birds* (Bloomsbury Publishing, 2020).
20. Ginn, H. B. & Melville, D. S. *Molt in Birds (BTO Guide)* (British Trust for Ornithology, 1983).
21. Kiat, Y. et al. Sequential molt in a feathered dinosaur and implications for early paravian ecology and locomotion. *Curr. Biol.* **30**, 3633–3638 (2020).
22. Hedenström, A. Flying with holey wings. *J. Avian Biol.* **34**, 324–327 (2003).
23. Hedenström, A. & Sunada, S. On the aerodynamics of molt gaps in birds. *J. Exp. Biol.* **202**, 67–76 (1999).
24. Lind, J. Escape flight in moulting tree sparrows (*Passer montanus*). *Funct. Ecol.* **15**, 29–35 (2001).
25. Kiat, Y., Izhaki, I. & Sapir, N. Determinants of wing-feather molt speed in songbirds. *Evol. Ecol.* **30**, 783–795 (2016).
26. de la Hera, I., Díaz, J. A., Pérez-Tris, J. & Tellería, J. L. A comparative study of migratory behaviour and body mass as determinants of molt duration in passerines. *J. Avian Biol.* **40**, 461–465 (2009).
27. Rohwer, S., Ricklefs, R. E., Rohwer, V. G. & Coppole, M. M. Allometry of the duration of flight feather molt in birds. *PLoS Biol.* **7**, 1246 (2009).
28. Terrill, R. S. Simultaneous wing molt as a catalyst for the evolution of flightlessness in Birds. *Am. Nat.* **196**, 775–784 (2020).
29. Brom, T. G. & Dekker, R. W. R. J. Molt of wing and tail-feathers in the Ostrich, *Struthio camelus*. *Beaufortia* **40**, 103–109 (1990).
30. Sullivan, C., Xu, X. & O'Connor, J. K. Complexities and novelties in the early evolution of avian flight, as seen in the Mesozoic Yanliao and Jehol Biotas of Northeast China. *Palaeoworld* **26**, 212–229 (2017).
31. Kiat, Y. & Bloch, I. The relationship of molt timing, duration and sequence to the aerial lifestyle of the Little Swift *Apus affinis*. *Ibis* **165**, 1331–1342 (2023).
32. Kiat, Y. Divergent rectrix molt: the implications and conditions of molt sequence. *J. Avian Biol.* **49**, jav-01609 (2018).
33. Xu, X. et al. A new feathered maniraptoran dinosaur fossil that fills a morphological gap in avian origin. *Chin. Sci. Bull.* **54**, 430–435 (2009).
34. Hu, D., Hou, L., Zhang, L. & Xu, X. A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus. *Nature* **461**, 640 (2009).
35. Xu, X. et al. An integrative approach to understanding bird origins. *Science* **346**, 1253293 (2014).
36. Saitta, E. T., Gelernter, R. & Vinther, J. Additional information on the primitive contour and wing feathering of paravian dinosaurs. *Palaeontology* **61**, 273–288 (2018).
37. Longrich, N. R., Vinther, J., Meng, Q., Li, Q. & Russell, A. P. Primitive wing feather arrangement in *Archaeopteryx lithographica* and *Anchiornis huxleyi*. *Curr. Biol.* **22**, 2262–2267 (2012).
38. Li, Q. et al. Plumage color patterns of an extinct dinosaur. *Science* **327**, 1369–1372 (2010).
39. Kiat, Y. & O'Connor, J. K. Rarity of molt evidence in early pennaraptoran dinosaurs suggests annual molt evolved later among Neornithes. *Commun. Biol.* **6**, 687 (2023).
40. Wang, X., O'Connor, J., Zheng, X., Wang, Y. & Kiat, Y. Earliest evidence of avian primary feather molt. *Biol. Lett.* **20**, 20240106 (2024).
41. Rader, J. A. & Hedrick, T. L. Morphological evolution of bird wings follows a mechanical sensitivity gradient determined by the aerodynamics of flapping flight. *Nat. Commun.* **14**, 7494 (2023).
42. Gaspar, J., Gibb, G. C. & Trewick, S. A. Convergent morphological responses to loss of flight in rails (Aves: Rallidae). *Ecol. Evol.* **10**, 6186–6207 (2020).
43. Beauchamp, G. Is wing morphology across birds associated with life history and sociality?. *Front. Bird Sci.* **2**, 1305453 (2023).
44. Xu, X. et al. Four-winged dinosaurs from China. *Nature* **421**, 335 (2003).
45. Chiappe, L. M. & Meng, Q. *Birds of Stone: Chinese Avian Fossils from the Age of Dinosaurs* (JHU Press, 2016).
46. Chiappe, L. M., Di, L., Serrano, F. J., Yuguang, Z. & Meng, Q. Anatomy and flight performance of the early enantiornithine bird *Protopteryx fengningensis*: information from new specimens of the Early Cretaceous Huajiyang Formation of China. *Anat. Rec.* **303**, 716–731 (2020).
47. Gao, C. et al. A subadult specimen of the Early Cretaceous bird *Sapeornis chaoyangensis* and a taxonomic reassessment of sapeornithids. *J. Vertebr. Paleontol.* **32**, 1103–1112 (2012).
48. De Beer, G. R. *Archaeopteryx lithographica: A Study Based on the British Museum Specimen* (British Museum Natural History, 1954).
49. Foth, C., Tischlinger, H. & Rauhut, O. W. M. New specimen of *Archaeopteryx* provides insights into the evolution of pennaceous feathers. *Nature* **511**, 79–82 (2014).
50. Mayr, G., Pohl, B., Hartman, S. & Peters, D. S. The tenth skeletal specimen of *Archaeopteryx*. *Zool. J. Linn. Soc.* **149**, 97–116 (2007).
51. O'Connor, J. K. et al. Chicago *Archaeopteryx* informs on the early evolution of the avian bauplan. *Nature* **641**, 1201–1207 (2025).
52. Bonser, R. H. C. The mechanical properties of feather keratin. *J. Zool.* **239**, 477–484 (1996).
53. Bonser, R. H. C. Melanin and the abrasion resistance of feathers. *Condor* **97**, 590 (1995).
54. Kiat, Y. & Sapir, N. Sex-dependent elevational effects on bird feather molt. *Evol. Ecol.* **1**, 11 (2021).
55. Rohwer, S. & Wang, L.-K. A quantitative analysis of flight feather replacement in the Moustached Tree Swift *Hemiprocne mystacea*, a tropical aerial forager. *PLoS ONE* **5**, e11586 (2010).
56. Barta, Z. et al. Annual routines of non-migratory birds: optimal molt strategies. *Oikos* **112**, 580–593 (2006).
57. Kiat, Y. & Sapir, N. Age-dependent modulation of songbird summer feather molt by temporal and functional constraints. *Am. Nat.* **189**, 184–195 (2017).

58. Jarrett, C. et al. Differences in phenology across three trophic levels between two Afrotropical sites separated by four degrees latitude. *Ecol. Evol.* **14**, e70274 (2024).
59. Fogden, M. P. L. The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis* **114**, 307–343 (1972).
60. Kiat, Y. Molt terminology: let's make it simpler!. *Ibis* **165**, 697–703 (2023).
61. Zheng, X. et al. On the absence of sternal elements in *Anchiornis* (Paraves) and *Sapeornis* (Aves) and the complex early evolution of the avian sternum. *Proc. Natl Acad. Sci. USA* **111**, 13900–13905 (2014).
62. Svensson, L. *Identification Guide to European Passerines* (Ugga, 1992).
63. Bell, A. et al. Quantitative analysis of morphometric data of pre-modern birds: phylogenetic versus ecological signal. *Front. Earth Sci.* **9**, 663342 (2021).
64. Bridge, E. S. Mind the gaps: what's missing in our understanding of feather molt. *Condor* **113**, 1–4 (2011).
65. Ji, Q. & Ji, S. A. Protarchaeopterygid bird (*Protarchaeopteryx* gen. nov.)—fossil remains of archaeopterygids from China. *Chin. Geol.* **238**, 38–41 (1997).
66. Godefroit, P. et al. Reduced plumage and flight ability of a new Jurassic paravian theropod from China. *Nat. Commun.* **4**, 1394 (2013).
67. Ji, Q., Currie, P. J., Norell, M. A. & Shu-An, J. Two feathered dinosaurs from northeastern China. *Nature* **393**, 753–761 (1998).
68. Rueda-Hernández, R., Guallar, S. & Pyle, P. Preformative molt extent of *Cardellina* warblers increases with breeding latitude and migration distance. *Wilson J. Ornithol.* **135**, 46–55 (2023).
69. Kiat, Y. & Pyle, P. Recent changes in distribution and plumage phenologies of the White-winged Tern (*Chlidonias leucopterus*) in the Middle East. *J. Ornithol.* **166**, 21–28 (2025).
70. Clark, C. J., Areta, J. I. & Quiroga, J. Citizen science data reveal molt into drab nonbreeding plumage in five woodstar species (*Mellisuginae*, Trochilidae). *Wilson J. Ornithol.* **136**, 307–319 (2024).
71. Pyle, P. Examination of Macaulay Library images to determine avian molt strategies: a case study on hummingbirds. *Wilson J. Ornithol.* **134**, 52–65 (2022).
72. Revell, L. J. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**, 217–223 (2012).
73. Kaye, T. G., Pittman, M. & Wahl, W. R. *Archaeopteryx* feather sheaths reveal sequential center-out flight-related molting strategy. *Commun. Biol.* **3**, 1–5 (2020).
74. Kiat, Y., Pyle, P., Balaban, A. & O'Connor, J. K. Reinterpretation of purported molting evidence in the Thermopolis *Archaeopteryx*. *Commun. Biol.* **4**, 1–3 (2021).
75. Gianechini, F. A., Makovicky, P. J. & Apesteguía, S. The cranial osteology of *Buitreraptor gonzalezorum* Makovicky, Apesteguía, and Agnolin, 2005 (Theropoda, Dromaeosauridae), from the Late Cretaceous of Patagonia, Argentina. *J. Vertebr. Paleontol.* **37**, e1255639 (2017).
76. Billerman, S. M., Keeney, B. K., Rodewald, P. G. & Schulenberg, T. S. *Birds of the World* (Cornell Laboratory of Ornithology, 2020).
77. Pyle, P. *Identification Guide to North American Birds: A Compendium of Information on Identifying, Ageing, and Sexing 'Near-Passerines' and Passerines in the Hand* (Slate Creek Press, 1997).
78. Pyle, P. *Identification guide to North American birds: Anatidae to Alcidae* (Slate Creek Press, 2008).
79. Jetz, W. et al. Global distribution and conservation of evolutionary distinctness in birds. *Curr. Biol.* **24**, 919–930 (2014).
80. Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in space and time. *Nature* **491**, 444–448 (2012).
81. Rubolini, D., Liker, A., Garamszegi, L. Z., Møller, A. P. & Saino, N. Using the BirdTree.org website to obtain robust phylogenies for avian comparative studies: a primer. *Curr. Zool.* **61**, 959–965 (2015).
82. Stiller, J. et al. Complexity of avian evolution revealed by family-level genomes. *Nature* **629**, 851–860 (2024).
83. Akaike, H. Factor analysis and AIC. *Psychometrika* **52**, 317–332 (1987).
84. Kiat, Y. *Anchiornis* wing morphology. OSF <https://doi.org/10.17605/osf.io/a2e5c> (2025).

Acknowledgements

This work was supported by grants from NSFC (41402017, 41688103, and 42572027), Shandong Provincial Natural Science Foundation (ZR2020MD026) and Ts20190954. We thank Xiaomei Zhang, Xuwei Yin, and Shiyang Yin for facilitating our visit to the STM.

Author contributions

Y.K. and J.O. designed the study. X.W., X.Z., and Y.W. facilitated access to critical fossil material and supported data collection. Y.K. carried out the statistical and ancestral state reconstruction analyses and prepared the figures. J.O., X.W., and Y.K. acquired funding. Y.K. and J.O. wrote the manuscript. All authors reviewed, proofread, and approved the final manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s42003-025-09019-2>.

Correspondence and requests for materials should be addressed to Yosef Kiat or Yan Wang.

Peer review information *Communications Biology* thanks Corwin Sullivan and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Primary Handling Editors: Katie Davis and Johannes Stortz.

Reprints and permissions information is available at <http://www.nature.com/reprints>

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by-nc-nd/4.0/>.

© The Author(s) 2025