O’Connor and Clark *Discover Ecology* (2026) 2:12
https://doi.org/10.1007/s44396-026-00026-z

Discover Ecology

REVIEW **Open Access**

The ecology of *Archaeopteryx*

Jingmai K. O’Connor[1*] and Alexander D. Clark[1,2]

*Correspondence:
Jingmai K. O’Connor
joconnor@fieldmuseum.org
[1]Negaunee Integrative Research Center, Field Museum of Natural History, Chicago, IL 60605, USA
[2]Committee on Evolutionary Biology, University of Chicago, Chicago, IL 60637, USA

Abstract

As the oldest known dinosaur to use aerodynamic surfaces comprised of asymmetrical feathers for flight, *Archaeopteryx* undoubtedly occupied a unique ecological niche unlike that utilized by closely related fully terrestrial non-avian theropods, more derived Mesozoic birds, and extant taxa. New specimens together with computed tomography data elucidate how the ecology of *Archaeopteryx* is shaped both by its position as a basal avian close to the terrestrial-volant transition and its environment. The size of the feathered wings, primary vane asymmetry, and the large tertial tract all indicate *Archaeopteryx* was capable of volant locomotion. The reversed hallux, absent in closely related non-avian terrestrial dinosaurs, indicates incipient perching abilities, whereas the proportions of the footpads and morphology of the scales indicate the soft tissue of the foot was predominantly adapted for terrestrial locomotion. Curved manual claws, well developed articular surfaces on the minor digit phalanges, separate major and minor digits, and manual proportions all indicate ancestral grasping abilities were retained and possibly exapted for climbing. All known specimens fit a growth curve suggesting somatic maturity was achieved over a protracted period although even the smallest known individuals preserve wing feathers indicating aerial capabilities. Diet is unknown but avian features of the rostrum indicate increased rostral sensitivity and oral dexterity, which suggests a diet targeting small, energy rich foods. Together these morphologies reveal a generalist bird that foraged on the ground and utilized a diverse set of locomotor behaviors including incipient powered flight.

1 Introduction

Archaeopteryx from the 150 Ma Solnhofen plattenkalk in Southern Germany is the oldest known bird and the oldest known dinosaur to use airfoils formed by feathers for volant locomotion [1, 2]. Although now closely matched by the slightly younger *Baminornis* (149 – 148 Ma) from Fujian Province, China, the pectoral girdle in this taxon is much more advanced and thus *Archaeopteryx* remains the most phylogenetically basal taxon relevant for understanding the terrestrial to volant transition [3]. Although some authors have hypothesized that *Anchiornis* is a bird older than *Archaeopteryx*, and indeed, Anchiornithinae is typically resolved as the sister taxon to all birds (Aves) together forming a clade referred to as Avialae, as more data have come to light, it is increasingly clear from the morphology of the skeleton, forelimb feathers, molt pattern, and ontogenetic changes in proportions that this taxon was non-volant [2, 4–6] and thus here considered a non-avian avialan. These two taxa are indeed similar and likely very closely related, together providing the best available evidence for understanding the evolution of flight in birds from a non-volant terrestrial ancestor [2]. However, these two taxa occupied very different environments, which in turn affects their morphology such that ecology should be considered when interpreting morphological differences in taxa that bracket this important evolutionary transition. *Archaeopteryx* lived in a semi-arid, seasonally wet environment most likely dominated by bushy conifers, whereas the Yanliao environment, occupied by *Anchiornis*, consisted of diverse habitats dominated by hot and humid forests [1, 7]. To fully understand the 'dinosaur-bird' transition from available fossils, the morphology of *Archaeopteryx* must be evaluated in the context of its ecology to separate the influence of its environment from phylogeny. To understand how *Archaeopteryx* interacted with its environment, it is critical to summarize and evaluate hypotheses regarding its locomotor abilities.

The ecology of *Archaeopteryx* has been the subject of interest for over a century, e.g. [8–11]. However, it has been 25 years since the last summary of its paleobiology and the recent descriptions of five additional specimens of *Archaeopteryx*, including the arguably best preserved specimen to date, together with morphological data gleaned from computed tomographic scans have revealed new clues regarding the ecology and lifestyle of this iconic early bird [2, 12–16]. Here we summarize currently available information and hypotheses supported by available fossils and discuss the implications of *Archaeopteryx* ecology with regards to understanding the 'dinosaur-bird' transition and the ecological roles utilized by one of the earliest dinosaurs to fly using feathered airfoils.

2 Results

2.1 Flight capabilities

The feathered surfaces on the elongate forelimb of *Archaeopteryx* are proportionately larger than in closely related non-avian taxa (e.g., *Anchiornis*, *Zhenyuanlong*, *Caudipteryx*) [17–19] and the primary feathers exhibit a degree of vane asymmetry that is within the range of extant volant birds, whereas these feathers are nearly symmetrical in non-avian pennaraptorans with the exception of the volant *Microraptor*[5, 20] (Fig. 1). Furthermore, large tracts of tertial feathers are present which serve to close the gap between the body and the distal wing feathers created by the elongate proportions of the humerus [2]. These feathers are also observed in some Early Cretaceous fossil birds (e.g., *Confuciusornis*) but are noticeably absent in taxa like *Anchiornis*, *Zhenyuanlong*, and *Caudipteryx* indicating the presence of a gap between the feathered airfoil and the body in these non-avian pennaraptorans, which would disrupt lift production and preclude flight [2]. The overall shape of the feathered wing is short and broad [21] but the proportions of the body suggest relatively high wing loading. Together, these features suggest an intermittent flight style such as flap-gliding.

The cross-sectional geometry of the humerus and bone density values observed in *Archaeopteryx* are within the values observed in extant volant birds [22]. The reported cross-sectional geometry most closely resembles birds that utilize short-distance flapping flight. This evidence has been used in favor of the interpretation that *Archaeopteryx* was capable of powered flight and utilized a unique craniodorsal to caudoventral flight stroke more similar to non-avian paravian grasping, based on the presence of an elongate tail, short coracoids, and the potential absence of furcular contact with the sternum

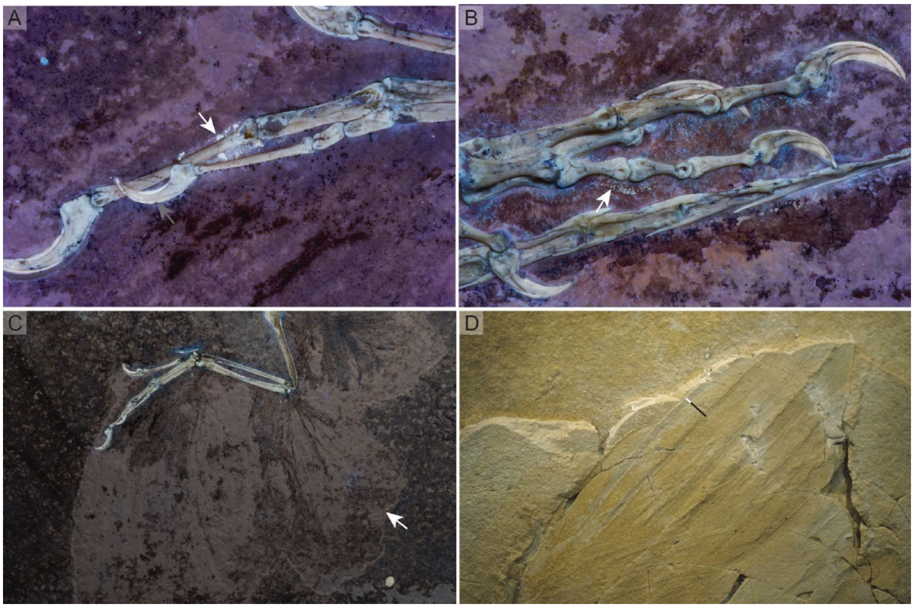

Fig. 1 Indicators of *Archaeopteryx* locomotor habits. **A**, soft tissue of the manus (white arrow) revealing a separate major digit and recurved and laterally compressed unguals (grey arrow) possibly supporting interpretations regarding scansoriality preserved in the Chicago specimen FMNH PA 830; **B**, reversed hallux and preserved foot pads (white arrow) indicating terrestriality preserved in the Chicago specimen FMNH PA 830; **C**, tertials (white arrow) closing the wing body gap preserved in the Chicago specimen FMNH PA 830; **D**, vane asymmetry in the primaries preserved in the Berlin specimen (white, leading edge vane; black, trailing edge vane)

[22]. Although the flight stroke of *Archaeopteryx* would undoubtedly differ from those of modern birds, based on the associations between humeral morphology and flight strategies observed in neornithines, the long yet shallow deltopectoral crest of the humerus in *Archaeopteryx* suggests a flight style with low frequency wingbeats, similar to neornithine flap-gliding [23]. In contrast, neornithines with a deltopectoral crest that is short and deep use high-frequency, rapid wingbeats during flight [23, 24].

Proportions of the semicircular canals and cochlear length gleaned from CT scans of the London specimen are reportedly close to or within the range of modern birds indicating spatial sensory perception nearing that of living birds [16]. The optic lobes are large, but smaller than in crown avians, and laterally positioned, intermediate between the dorsal position in non-avian theropods and caudally rotated position in birds, features interpreted as being consistent with a brain capable of flight [16]. Compared to basal theropods the cerebellum is proportionately larger, although still much smaller than living birds [16]. However, a study that included more paravian taxa concluded that some other non-avian dinosaurs had endocranial and cerebral volumes that exceeded that of *Archaeopteryx* indicating that some cerebral expansion preceded the appearance of flight and further increases in volume in closely related lineages were not necessarily related to volant locomotion [25].

Consistent with its basal position, there is ample evidence from the morphology of the pectoral girdle, including the absence of an ossified sternum, that indicates flight abilities were limited. The pectoral girdle is characterized by a wide boomerang shaped furcula and a fused and axe-shaped scapulocoracoid with a laterally oriented glenoid [26, 27]. Recent research indicates that even in more derived birds in which the scapula and coracoid are separate they articulate through an immobile joint, such that the significance of the morphological transformation from scapulocoracoid to separate elements is unclear [28]. However, the lateral orientation of the glenoid indicates a more restricted range of motion compared to more derived birds limiting the thrust generated by the flight stroke. Compared to the dorsally-oriented glenoid in ornithuromorphs, which allows the wing to be fully elevated above the body for a long and powerful downward phase of the flight stroke, dorsal movement of the forelimb in *Archaeopteryx* would have been relatively limited, potentially indicating an emphasis on gliding after short bouts of relatively dorsally-restricted wingbeats [26].

No specimen preserves an ossified sternum or sternal plates, which are notably also absent in all known troodontids, anchiornithines, and the basal pygostylian bird *Sapeornis*[29]. A previous report of an ossified sternum in the Munich *Archaeopteryx* was later correctly reinterpreted as the coracoid [30, 31]. With regards to anchiornithines and *Sapeornis*, taxa known from hundreds of specimens, the absence of ossified sternal plates can be considered genuine and not preservational [29].

The absence of an ossified sternum in *Archaeopteryx* (and *Sapeornis*) is at odds with the interpretation that flapping flight would induce cyclical tensile stress on cartilaginous sternal plates, resulting in their calcification [32]. As such, it has been proposed that sternal plates were also completely absent in *Archaeopteryx* and alternative hypotheses for the attachment surface of the main flight muscles, the mm. *pectoralis* and *supracoracoideus* have been proposed (such as the coracoid and gastralia) [29, 33]. Alternatively, cartilaginous sternal plates were present but did not serve as the main attachment surface for the m. *pectoralis* as it does in neornithines and thus stress induced ossification did not occur. This is consistent with the expanded distal ends of the third to eighth thoracic ribs [34] and CT data that reveal a slight protuberance on the furcular symphysis [35], both morphologies suggesting these elements contacted cartilaginous sternal plates. In some neornithines (e.g., *Corvus*, *Guttera*, *Ptilonorhynchus*) the hypocleidium of the furcula (*apophysis furculae*) extends dorsally (instead of caudally) to contact the sternum [36], resembling the swelling present in *Archaeopteryx*. It is also possible the sternum ossified very late in ontogeny, in a growth stage not captured by the fossil record of this taxon, which consists entirely of actively growing, presumably immature, individuals [37].

If a cartilaginous sternum was present, it would be craniocaudally short, limited by the cranial extent of the large gastral basket (Fig. 2). Its position would indicate a m. *pectoralis* attaching to this element would have relatively short muscle fibers, consistent with the limited excursion of the forelimb inferred from the glenoid orientation [26]. However, it has been suggested the m. *pectoralis* attached to a coracoclavicular membrane primarily originating on the furcula (also present in living birds), and that the upstroke, rather than being primarily initiated by the m. *supracoracoideus* as in neornithines, may have been engaged by the mm. *deltoideus* complex (mm. *deltoideous pars major*, *deltoideous pars minor*, *deltoideus pars propatagialis cranialis*) (Fig. 2). These muscles primarily originate on the craniodorsal surface of the scapula and are capable of lifting the wing in the absence of the m. *supracoracoideus* [38]. These inferences are consistent with the role of the m. *deltoideus* complex in raising the forelimb in all vertebrates, the well-developed furcula in *Archaeopteryx*, and the morphology of the m. *pectoralis* and coracoclavicular membrane in neornithines [38]. However, as in neornithines in which the m. *supracoracoideus* has been experimentally severed, *Archaeopteryx* would most likely

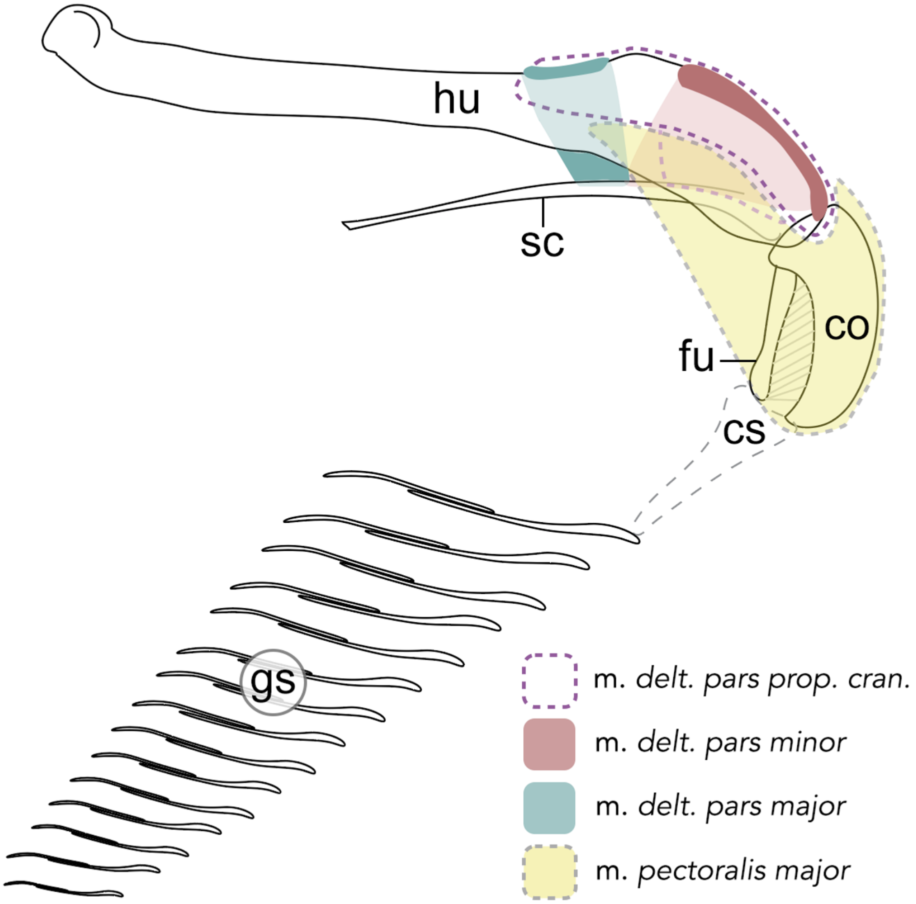

Fig. 2 Reconstruction of the *Archaeopteryx* pectoral girdle in right lateral view depicting a cartilaginous sternum (dashed dark grey) and the hypothetical position of the mm. *pectoralis* and *deltoideus* complex. Muscles are varying levels of transparency to reflect those that are deep and superficial to one another with the exception of the m. *delt pars prop. cran*. which lies superficial to both heads of the m. *deltoides major/minor*. Muscles of the deltoides complex originate from the proximal region of the scapula. The *pectoralis* muscle is shown inserting along the craniolateral surface of the humerus. The coracoclavicular membrane is filled by light grey lines. Skeletal abbreviations: co, coracoid; cs, cartilaginous sternum (predicted); fu, furcula; gs, gastralia; hu, humerus; sc, scapula. Abbreviated muscles: m. delt pars prop. cran., *deltoides par propatagialis cranialis*; m. delt., *deltoides*

be unable to take off from the ground from a standstill, utilizing either a running start [39] or elevation to launch [40].

Adaptations of the wrist necessary for wing folding evolved outside of Aves in order to protect the elongate forelimb feathers [41, 42]. However, compared to crown birds, the structure of the wrist and humerus indicate limited wrist folding and wing pronation, which suggest *Archaeopteryx* would have generally had difficulty flying at low speeds [40, 43]. Potentially aiding in this period of incipient flight, *Archaeopteryx*'s coastal context may have provided consistent head-winds that *Archaeopteryx* may have utilized to launch from the ground [40, 44–46]. Many extant birds utilize headwinds for both take-offs and energy-reduced flight [47, 48]. Bounding flight, an intermittent flight style potentially similar to that utilized by *Archaeopteryx*, is considered only energetically efficient when flying into a headwind [45, 49]. However, the structure of the flight apparatus in *Archaeopteryx* may have lacked the control and thus maneuverability to handle strong winds effectively [40]. *Archaeopteryx* lacked an alula (bastard wing) and a fan-shaped tail controlled by rectricial bulbs, two features neornithines utilize during slow flight [50].

However, the unique flight apparatus of *Archaeopteryx*, including the elongate tail, may have provided novel solutions that served functions similar to features that evolved later in more derived birds, albeit less efficiently or effectively. For example, the elongate tail in *Jeholornis* is hypothesized to have functioned as a stabilizer [51]. The suggestion that *Archaeopteryx* was only capable of "sprawled crash landings" [52] is unlikely due to the risk of injury given that, with its incipient flight abilities, it would have been limited to short bursts of flight and frequent landings.

Morphometric analysis of *Archaeopteryx* skeletal measurements, compared to *Anchiornis*, also supports flight ability in *Archaeopteryx*, and conversely, its absence in *Anchiornis*. In larger specimens of *Archaeopteryx* (e.g., Solnhofen, London), the forelimb becomes proportionately longer, a trend also observed in *Confuciusornis*, whereas in *Anchiornis* the hindlimb is longer in larger individuals [6, 53]. *Archaeopteryx* skeletal measurements also fit a tight regression [54, 55], as observed in *Confuciusornis*, whereas *Anchiornis* specimens do not plot close to the regression line indicating greater variation in proportions [6, 56]. This lower variation observed in flying birds may be related to aerodynamic constraints for the optimal proportions required for flight [6].

2.2 Hindlimb function

The general structure of the hindlimb is very similar to other maniraptoran theropods [57, 58]. It retains the nearly vertical orientation of the elongate femur indicative of hip-driven locomotion, as opposed to the knee driven locomotion present in derived ornithuromorph birds [8, 59, 60]. The major difference lies in the reversed first pedal digit (hallux), which is also present in most other early-diverging (non-ornithuromorph) birds (e.g., *Jeholornis*, *Confuciusornis*, *Sapeornis*, Jinguofortisidae, and Enantiornithes) [61]. Although this morphology was reinterpreted as absent based on the Thermopolis specimen [15], preservation of the 12th and Chicago specimen support earlier interpretations that the first digit is reversed. However, the structure of metatarsal I suggests the orientation of the hallux may be slightly more medial than in most anisodactyl neornithines [2, 13], which is also true of some more derived Cretaceous birds (e.g., *Confuciusornis*) [62]. The reversal of the first pedal digit, opposing digits II-IV allows the foot to grasp more effectively, an advantage for gripping non-flat surfaces (e.g., branches, rocks). This is notably absent in non-volant non-avian theropods including the closely related avialan *Anchiornis* in which the hallux is short, medially oriented, and elevated relative to the metatarsal II-IV trochleae [63]. This suggests the reversed hallux evolved in response to flight as an adaptation for utilizing elevated perches.

Proportions of the hindlimb elements are consistent with terrestrial but not cursorial locomotion, being close to some non-avian theropods and very similar to galliforms, ground birds that typically run only when necessitated by threats [64]. Pedal phalanges are shorter distally within each digit and pedal proportions plot intermediate between arboreal and terrestrial species, close to taxa like extant columbiforms, suggesting broad and generalized locomotive capabilities [65]. The proportions of the footpads and morphology of the scales preserved in the Chicago specimen indicate the soft tissue of the foot was predominantly adapted for terrestrial locomotion [2].

Analyses of pedal claw curvature lack consensus, which may at least partially reflect differences in how curvature is quantified. One study concluded curvature was suggestive of terrestrial foraging consistent with pedal proportions and soft tissues [66], while other studies have concluded that pedal claw curvature is more consistent with arboreal taxa [67, 68]. Yet another study concluded the outer curvature indicated scansoriality whereas the inner curvature indicated terrestriality [69]. These differences may also indicate that the pedal claws served multiple roles.

Contra recent interpretations, pedal digit II lacks features indicative of hyperextension present in troodontids and dromaeosaurids [15, 70]. In these taxa, digit II phalanges are shortened and the proximoventral margin of the penultimate phalanx bears an expanded ‘heel’. Dorsal expansion of the trochlea of the penultimate phalanx in digit II was cited as evidence for hyperextension in *Archaeopteryx*; however, compared to taxa like *Deinonychus*, the trochlea is only weakly dorsally expanded in *Archaeopteryx* and also ventrally expanded [36]. The morphology of digit II is very similar in *Anchiornis*, whereas some anchiornithines, like *Xiaotingia*, possess a greater suite of hyperextension features [71].

2.3 Scansoriality

The proportions of the manual phalanges are consistent with a specialized grasping function present in deinonychosaurs [65]. Manual claw curvature has also been evoked as evidence in favor of a scansorial function for the forelimb [67, 72]. Although this curvature and the presence of well-developed flexor tubercles were likely inherited from the grasping predatory forelimb of non-avian theropods [73], this morphology was likely exapted for scansorial locomotion. This is supported by differences in mediolateral thickness of the manual claws in dorsal view, which are laterally compressed throughout their length consistent with extant climbers [72]. In contrast, in predatory non-avian theropods including most non-avian pennaraptorans the unguals are thicker proximally, tapering distally [72, 74, 75].

Previously, the major and minor digit were thought to be immobile, being bound together ligamentously [8]. However, the Chicago specimen preserves soft tissue traces demarcating the outline of the right major digit around the articulation between the first and second phalanges (Fig. 1A). This suggests that it was not entirely bound to the minor digit by soft tissue, but rather that these digits were separate, further supporting a grasping function for the minor digit [2]. The well preserved articular surfaces of the minor digit visible in the Chicago specimen support interpretations that the minor digit was mobile, whereas the major digit was rigid in support of the flight surface [2].

2.4 Wing-assisted incline running

Observations that many living birds flap their wings when ascending inclines greater than 45°, a behavior referred to as wing-assisted incline running (WAIR), has provided a new hypothesis for the origin of feathered flight in theropods, the ontogenetic transitional wing hypothesis [76–78]. The craniocaudal orientation of the flapping motion during WAIR is consistent with the lateral orientation of the glenoid in *Archaeopteryx*. This behavior is present in a wide range of extant taxa and in immature individuals which lack a fully ossified sternum. This suggests that in addition to other locomotor behaviors, *Archaeopteryx* may have utilized WAIR to scale inclines and flapped its wings to make controlled descents from elevated perches. However, it has been suggested that the shoulder musculature of *Archaeopteryx* was unsuitable for generating the rapid upstroke needed for modern WAIR [79]. Given the differences in shoulder musculature outlined above, if *Archaeopteryx* engaged in WAIR, like its flight style, this behavior likely differed somewhat from the condition in living birds.

2.5 Diet

No direct evidence of *Archaeopteryx* diet exists. Morphological proxies such as size and tooth shape have been previously evoked in favor of an insectivorous diet and skeletal proportions indicate ground foraging (as opposed to catching insects on the wing) consistent with inferences regarding limited aerial capabilities [1, 8, 57]. Larvae are hypothesized to be an important food source for young individuals with larger individuals additionally feeding on larger insects with more durable chitinous exoskeletons [1, 40]. Insectivory is commonly evoked for small theropods with otherwise superficially carnivorous dentition [80]. As in anchiornithines, some troodontids (e.g., *Byronosaurus*) and other Mesozoic birds, the teeth lack serrations [81–83] (Fig. 3). The teeth are basally bulbous rapidly tapering in their apical quarter forming a sharp and slightly recurved tip that closely aligns with the distal margin of the tooth (often located caudal to the distal margin in hypercarnivorous deinonychosaurs) [13]. The number of teeth is reduced from 14 maxillary and 16 dentary teeth in *Anchiornis*, a taxon documented to be at least partially vertivorous [84], to 8–10 maxillary and 11–13 dentary teeth in *Archaeopteryx* [13, 81].

Archaeopteryx preserves three feeding related structures that are not observed in nonvolant theropods and two of which are currently only recognized in birds: a primitive bill-tip organ, oral papillae, and an ossified basihyal [85] (Fig. 3). The latter is only otherwise known in *Microraptor*, a volant dromaeosaurid [86]. The appearance of these features suggests a shift in feeding strategies associated with the greater energetic demands of flight. The bill-tip organ is a sensory structure located at the tip of the rostrum in many living birds that increases sensory discrimination and facilitates adaptation of the rostrum to perform a diversity of complex oral tasks from probing to seed husking [87,

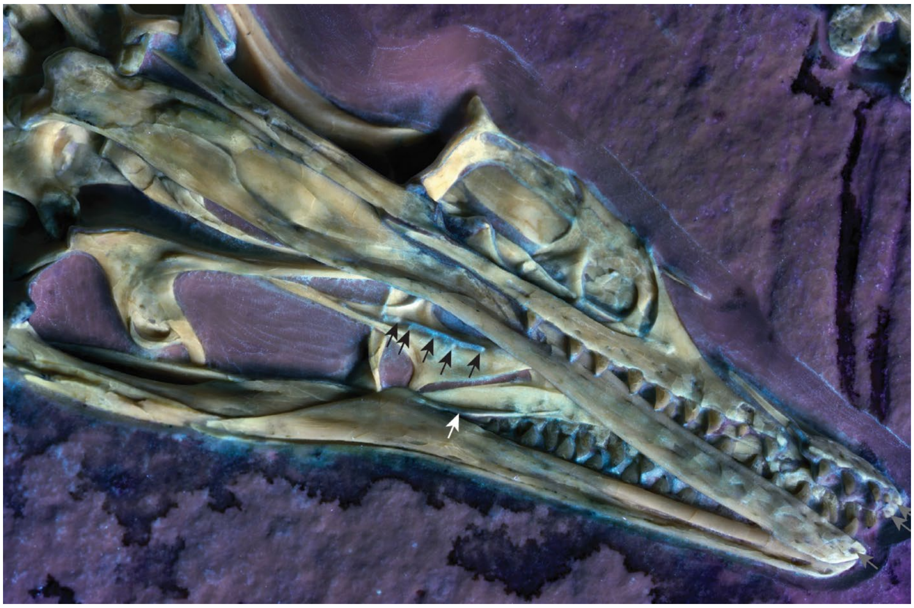

Fig. 3 Cranial features preserved in the Chicago *Archaeopteryx* FMNH PA 830 suggesting an omnivorous diet targeting small, energy rich foods: choanal oral papillae (black arrows); basihyal (white arrow); neurovascular openings suggesting a primitive bill-tip organ (grey arrows)

88]. In crown birds there are two general morphotypes, one in which the sensory cells are located in numerous pits on the rostral bones themselves and another in which they are located within the soft tissue of the rhamphotheca [87]. In Mesozoic toothed birds, a single large neurovascular opening is present on the distal premaxillae and dentaries, continuous with the maxillary and mandibular branches of the trigeminal nerve, respectively. It is hypothesized that these openings, which imply neurovasculature exiting the tip of the bony rostrum, indicate the presence of a sensory organ, protected by a small rhamphotheca [89]. The bill-tip organ in *Archaeopteryx* and other toothed Mesozoic birds differs from that observed in living birds, and is considered an early morphotype representing an intermediate evolutionary step in the evolution of the modern bill-tip organ [85].

The Chicago *Archaeopteryx* also preserves an ossified basihyal, which suggests hyolingual suspension and the presence of complex tongue musculature indicating increased tongue mobility relative to non-volant theropods [86]. This increased tongue mobility improves food manipulation resulting in more efficient ingestion. This specimen also preserves soft tissue traces along the medial margin of the left palatine interpreted as remnants of choanal oral papillae [85] (Fig. 3). In living birds, the mobile tongue is a structure that is interdependent with the oral papillae, soft tissue projections in the oropharyngeal cavity that help to stabilize food items for manipulation by the tongue, similar to early tetrapods with a mobile tongue and palatal teeth [90]. These three oral features are associated with precision feeding, likely targeting small calorie rich foods like some insects, seeds, and grains, and may indicate a shift towards less tooth dependent feeding strategies, consistent with the continued trend towards reduced dentitions observed in crownward birds, with the exception of piscivores [91]. In contrast, most closely related non-avian theropods were carnivorous vertivores and targeted larger food items, which were ingested whole or largely unprocessed [84, 92, 93].

The Solnhofen climate was predominantly warm and dry with the flora being xeromorphic [1]. Fossils indicate the presence of occasional rain (wet season) producing temporary bodies of water [1]. This type of seasonal climate inhabited by *Archaeopteryx* may suggest an omnivorous diet, with variations in food resources throughout the year related to climatic changes. Semi-arid and periodically wet (i.e., rainy season) conditions can significantly impact both seeding plant and insect diversity and abundance [94–98]. The semi-arid climate accompanied by ephemeral bouts of rainfall suggests seasonal bursts of seed germination, leading to intervals of potential seedy and herbaceous food resources, often referred to as periods of “green up” [94, 97, 98]. Similarly, for many terrestrial arthropods, seasonally intense precipitation is a key determining factor of abundance [95, 96]. Odonates and cicadomorphs are found in the Solnhofen, with these taxa’s diversity and emergence success being directly affected by seasonal periods of wet conditions bringing about both ephemeral pools for larval development and favorable moist soil conditions respectively [1, 40, 99, 100]. Taking advantage of this short-lived season, birds and other organisms will target protein and carbohydrate rich food sources. Following the rainy season, vegetative die-back and returning drought conditions may have led to increased detritivorous arthropod communities, yet another seasonally-available food resource [95, 101]. Overall, the climatic context of *Archaeopteryx* suggests periods of shifting primarily-available food resources with seasonal multi-trophic interactions – conditions well suited to an omnivorous generalist diet (Fig. 4).

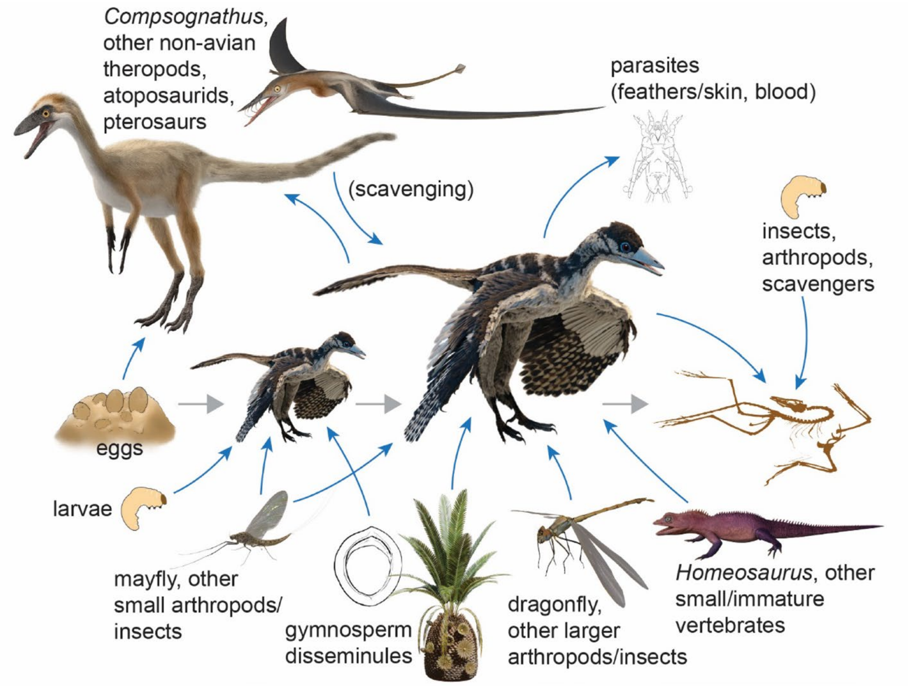

Fig. 4 Preliminary *Archaeopteryx* food web depicting probable omnivorous diet of *Archaeopteryx* at various growth stages (eggs, immature, mature, and carcass) and how *Archaeopteryx* would have provided trophic resources for other organisms as prey at all life stages including parasites and detritus feeders (scavengers). Organisms not to scale although the two *Archaeopteryx* represent the relative size difference between the smallest and largest specimens. (Reconstructions © Field Museum, artwork by NICE PaleoVisLab studio, Institute of Vertebrate Paleontology and Paleoanthropology; eggs, seed, and parasite drawings by Samantha Clark)

2.6 Reproduction

Currently there is no direct preserved evidence regarding reproductive habits. However, comparison with taxa both stemward and crownward of *Archaeopteryx* permit several inferences. Ground nests in non-avian paravians and enantiornithine birds suggest that *Archaeopteryx* also would have utilized ground nests with immobile eggs partially embedded in sediment [102]. Limited flight abilities suggest *Archaeopteryx* nested close to where it foraged [40]. Eggs were most likely unornamented, asymmetrical, and colored [102, 103]. Like almost all known non-avian dinosaurs and as documented in enantiornithine birds, hatchlings were most likely precocial [104, 105].

2.7 Growth and development

The phylogenetic position of *Archaeopteryx* indicates that it was warm-blooded but it can be inferred to have had a lower metabolic rate than crown birds based on the slower deposition of bone tissue in *Archaeopteryx* and other early-diverging Cretaceous birds compared to a subset of ornithuromorphs that includes Neornithes with uninterrupted growth [37, 106]. The Chicago *Archaeopteryx* represents the ontogenetically most immature individual known to date [2]. Although very close in size to the Eichstatt specimen, the better preservation of the Chicago specimen reveals a coracoid and scapula that are completely separated, although still preserved in articulation. These bones are also unfused in the Thermopolis specimen which is 1.4 times larger consistent with the observation that these bones fuse late in ontogeny [15, 107]. The atlas intercentrum and neurapophyses, atlas pleurocentrum, axial, intercentrum and axial pleurocentrum, and sacral vertebrae are all unfused [2]. The preserved fully developed wing feathers indicate that, despite its immaturity, the Chicago specimen was capable of volant locomotion. Specimens of *Archaeopteryx* occupy a considerable size range consistent with a protracted growth strategy like that observed in stemward (e.g., *Anchiornis*) and crownward (e.g., *Confuciusornis*, *Sapeornis*, enantiornithines) taxa [29, 56]. Like non-avian dinosaurs and enantiornithines [108], *Archaeopteryx* most likely reached sexual maturity prior to somatic maturity.

2.8 Plumage

As in volant neornithines (9–11 primaries), the *Archaeopteryx* wing is formed by 11 primaries, although the 11th specimen appears to have 12 [5]. The shape of the wing is broad [21], most closely resembling the elliptical wings of neornithines. The primaries have an asymmetry value of 3.47, within the range of volant neornithines (2.5–6.63) [5, 14]. Two rows of dorsal coverts are present covering approximately half the surface of the remiges [14]. Consistent with the elongate humerus, a tertial tract is present [2] (Fig. 1C). Closed pennaceous feathers are present on the forelimb, hindlimb, and tail [14]. Hindlimb feathers decrease in length significantly at the ankle joint and taper distally not reaching the articulation with the pedal phalanges [14]. Body contour feathers are open pennaceous with a fluffy appearance, as in other non-neornithine pennaraptorans [2]. Contra some reports, there is no strong evidence of molt [109]. However, comparison with volant paravians *Microraptor* and *Confuciusornis* strongly suggests the remiges would have molted sequentially [110, 111] whereas the non-volant *Anchiornis* exhibits an irregular molt [4]. Chemical analyses of the isolated feather (holotype), interpreted as a dorsal wing covert, indicate it was white and black [112, 113]. Given the open environment that *Archaeopteryx* occupied, the entire plumage may have been black and white forming a disruptive color pattern that would hinder predators.

2.9 Other skeletal indicators

The proportions of the scleral ring indicate that *Archaeopteryx* was diurnal, adapted for activity in bright light (photopic) conditions [114].

2.10 Abundance

Archaeopteryx is the most common theropod known from the Solnhofen limestones with all other taxa known from single specimens. This does not necessarily indicate that *Archaeopteryx* was the most abundant theropod in the Solnhofen archipelago, only that the probability of becoming fossilized in the surrounding marine limestones was relatively higher due to its large wings. Of the theropods known from the Solnhofen Limestones, *Archaeopteryx* is the only pennaraptoran with airfoils formed by feathers on the forelimbs. Other recorded theropods, like *Juravenator*, *Compsognathus*, and *Sciurumimus*, would have been covered in a combination of scales and proto-feathers with little to no aerodynamic properties, traces of which are directly documented in *Juravenator* [115] and *Sciurumimus* [116]. The fact all specimens were actively growing at the time of death [37] suggests the *Archaeopteryx* preserved in the marine Solnhofen Limestones likely represent immature and inexperienced individuals caught during storm events and blown out to sea by strong winds acting on their large feathered airfoils [1].

Fig. 5 Reconstruction of *Archaeopteryx* in its habitat utilizing diverse forms of locomotion. **A**, flapping flight to elevated perches; **B**, perching; **C**, gliding flight from elevation and terrestrial lifestyle; **D**, scansorial locomotion (© Field Museum, artwork by NICE PaleoVisLab studio, Institute of Vertebrate Paleontology and Paleoanthropology)

3 Discussion

Despite significant research over a period of more than 150 years, preservational limitations and differences regarding interpretations of the skeleton are such that, although much is known about this important taxon, many aspects of *Archaeopteryx’s* paleobiology remain controversial. As the oldest known dinosaur with flight-capable feathered aerodynamic surfaces, *Archaeopteryx* most certainly occupied a unique ecological niche not captured by the extant diversity of birds. Incipient flight capabilities and clawed forelimbs strongly suggest that *Archaeopteryx* would have relied on a unique combination of locomotor behaviors to interact with its environment distinct from living birds and non-avian dinosaurs (Fig. 5). The recent descriptions of five new specimens of *Archaeopteryx* in the 21 st century has significantly contributed to the data available for this important taxon [2, 12–15]. Four of these specimens are complete or nearly so (Thermopolis, 11th, 12th, Chicago) and two are considered among the best-preserved known specimens (Thermopolis, Chicago). In particular, the Chicago specimen was painstakingly prepared for scientific research leading to the retention of novel soft tissues that provide additional clues (Fig. 1). The application of new methods to known specimens has also resulted in the extraction of significant new data that further contribute to modern interpretations of this bird’s many ecological roles [16, 35, 113].

As the oldest known bird, the most significant question is if and how *Archaeopteryx* could fly. Evidence favors limited powered flight in contrast to obligate gliding volant locomotion, although *Archaeopteryx* almost certainly also utilized gliding flight when energetically favorable, as observed in many living birds (Fig. 5). Earlier hypotheses that *Archaeopteryx* was only capable of gliding flight [38], a locomotor strategy not present in living birds, have lost support and a gliding-only phase for the evolution of avian flight is considered unlikely [2, 22, 78]. The most convincing evidence that *Archaeopteryx* was capable of volant locomotion lies in the soft tissues of the wing, and how it differs from non-volant close relatives (size, feather asymmetry, tertials). Interpretations regarding flight ability are additionally supported by bone density and cross-sectional geometry, and brain morphology [2, 5, 16, 22].

Limitations in the flight apparatus, in particular the range of motion of the forelimb and limited musculature inferred from the pectoral girdle, suggest launching from the ground from a standstill was unlikely. It is more likely that *Archaeopteryx* could only become airborne launching from a run, from an elevated take off point, or possibly utilizing headwinds similar to some extant birds that utilize bounding flight [39, 45, 117]. Grasping abilities in the hand retained from non-volant ancestors suggest elevation was gained through scansorial behaviors [8] (Fig. 5). The hindlimb and forelimb may have been used simultaneously (WAIR) to gain elevation both to evade predation and take flight. Hindlimb proportions and soft tissues indicate *Archaeopteryx* was comfortable both on the ground and in trees. The paleoflora that existed on the Solnhofen archipelagos is poorly understood. Although fossils exist, studies on them are few [1]. Flight abilities and the reversed hallux for perching as well as probable scansorial and WAIR behaviors strongly suggest *Archaeopteryx* spent some time elevated in the foliage, hypothesized to consist of cycads, ferns, and small conifers [1] (Fig. 5).

The morphology of the foot, lacking the hyperextensible second digit present in most non-avian deinonychosaurs except for *Anchiornis*[36], and features of the skull associated with increased dexterity, suggest adaptations for feeding on small food items, as opposed to the hypercarnivory typical of deinonychosaurs [84, 93, 118] (Fig. 4). Compared to *Archaeopteryx*, the closely related *Anchiornis* has a relatively higher tooth count, and proportionately shorter pedal phalanx pads [119]. It also lacks a bill-tip organ, ossified basihyal, and potentially oral papillae [85]. Together, these disparities likely reflect differences in diet, with *Anchiornis* being relatively more predatorial, consistent with the documented remains of a lizard in the esophagus of one specimen pre-egestion [84]. Given limited aerial abilities, *Archaeopteryx* was most likely a terrestrial forager, as indicated by the proportions of the hindlimb. The Solnhofen climate strongly suggests omnivory.

Archaeopteryx growth was protracted, as evident from the considerable size range of recovered specimens [1]. Especially at early ontogenetic stages, *Archaeopteryx* was likely preyed upon by larger theropods like *Compsognathus* and *Juravenator* (Fig. 5). *Compsognathus* is directly documented to have fed on lizards [120] but like other vertivorous theropods it was most likely an opportunistic predator [92]. Inferences regarding ground nesting suggests *Archaeopteryx* eggs would have been a potential resource for predators. However, inferences concerning reproductive habits, and other aspects of ecology such as abundance and distribution remain completely speculative.

Key flight-related differences with *Anchiornis*, the best known non-avian avialan, such as the significant difference in remige surface area and absence of vane asymmetry in *Anchiornis*, cannot be attributed to ecology. The Solnhofen Archipelago would have offered fewer opportunities for perching than the Yanliao forests, yet the hallux is reversed in the volant *Archaeopteryx* and not the terrestrial *Anchiornis*. However, differences in footpad morphology, with the phalanx pads proportionately shorter in *Anchiornis* may reflect ecological differences in diet, which are further supported by the absence of an ossified basihyal and bill tip organ in this non-avian taxon. These differences may reflect the elevated energetic cost associated with the appearance of flight in Aves [85].

4 Conclusions

As a result of its diverse locomotor behaviors *Archaeopteryx* would have interacted with numerous substrates in its environment, spending time on the ground, elevated on medium to large plants, and in the air. Throughout its life history *Archaeopteryx* would have utilized varying food sources spanning the plant and animal kingdoms as well as provided trophic resources to a diversity of organisms from keratinophagous parasites to apex predators. Key differences, explored in an ecological context, reveal how the appearance of flight in birds impacted both skeletal and soft tissue anatomy.

Acknowledgements
We thank the Demkovich family for supporting paleobiological research at the Field Museum and Samantha Clark for the line drawings used in Fig. 4.

Author contributions
J.O'C. and A.C. wrote the main manuscript text and prepared figures. All authors reviewed the manuscript.

Funding
This research was not supported by any funding source.

Data availability
No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate
Not applicable.

Constent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

Received: 18 September 2025 / Accepted: 16 February 2026

References

1. Wellnhofer P. Archaeopteryx, English Edition: The Icon Of Evolution, vol. 208. Verlag Dr. Friedrich Pfeil; 2009.
2. O'Connor JK, et al. Chicago *Archaeopteryx* informs on the early evolution of the avian bauplan. Nature. 2025;641:1201–7.
3. Chen R-S, et al. Earliest short-tailed bird from the Late Jurassic of China. Nature. 2025;638:441–8.
4. Kiat Y, Wang X-L, Zheng X-T, Wang Y, O'Connor JK. Wing morphology of *Anchiornis huxleyi* and the evolution of molt strategies in paravian dinosaurs. Commun Biol. 2025;8:1–9.
5. Kiat Y, K O'Connor J. Functional constraints on the number and shape of flight feathers. Proc Natl Acad Sci U S A. 2024;121:1–11.
6. O'Connor JK. & Marugán-Lobón, J. Evaluating variation in Solnhofen paravians. *Biology Letters* (2026)
7. Hao W-X, et al. Climate-change-enhanced habitat diversification for the Middle Jurassic Yanliao Biota in East Asia. Natl Sci Rev. 2025;12:1–9.
8. Elzanowski A. in *VII International Symposium on Mesozoic Terrestrial Ecosystems* Vol. 7 *Asociación Paleontológica Argentina Publicación Especial* 91–99 (Asociación Paleontológica Argentina, 2001).
9. de Beer G. *Archaeopteryx lithographica*, a study based upon the British Museum specimen. Br Museum Publication. 1954;224:1–68.
10. Heilmann G. The Origin of Birds. D. Appleton and Company; 1926.
11. Dodson P. International *Archaeopteryx* Conference. *Journal of Vertebrate Paleontology* 5, 177–179 (1985).
12. Foth C, et al. A new *Archaeopteryx* from the lower Tithonian Mörnsheim Formation at Mühlheim (Late Jurassic). Foss Rec. 2025;28:17–43.
13. Rauhut OWM, Foth C, Tischlinger H. The oldest *Archaeopteryx* (Theropoda: Avialiae): a new specimen from the Kimmeridgian/Tithonian boundary of Schamhaupten. Bavaria PeerJ. 2018;6:e4191.
14. Foth C, Tischlinger H, Rauhut OWM. New specimen of *Archaeopteryx* provides insights into the evolution of pennaceous feathers. Nature. 2014;511:79–82.
15. Mayr G, Pohl B, Peters DS. A well-preserved *Archaeopteryx* specimen with theropod features. Science. 2005;310:1483–6. https://doi.org/10.1126/science.1120331.
16. Alonso PD, Milner AC, Ketcham RA, Cookson MJ, Rowe TB. The avian nature of the brain and inner ear of *Archaeopteryx*. Nature. 2004;430:666–9. https://doi.org/10.1038/nature02706.
17. Hu D-Y, Hou L-H, Zhang L-J, You H-L. A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus. Nature. 2009;461:640–3.
18. Lü J-C, Brusatte SL. A large, short-armed, winged dromaeosaurid (Dinosauria: Theropoda) from the Early Cretaceous of China and its implications for feather evolution. Sci Rep. 2015;5:1–11. https://doi.org/10.1038/srep11775.

19. Ji Q, Currie PJ, Norell MA, Ji S-A. Two feathered dinosaurs from northeastern China. Nature. 1998;393:753–61.
20. Xu X, Zhou Z, Wang X, Kuang X, Du X. Four-winged dinosaurs from China. Nature. 2003;421:335–40.
21. O'Connor, J. in The Evolution of Feathers (eds C. Foth & O.W.M. Rauhut) 147-172 (Springer, Cham, 2020) Voeten DFAE, et al. Wing bone geometry reveals active flight in Archaeopteryx. Nat Commun. 2018;9:1–9.
22. Voeten DFAE, et al. Wing bone geometry reveals active flight in Archaeopteryx. Nat Commun. 2018;9:1–9.
23. Serrano FJ, Costa-Pérez M, Navalón G, Martín-Serra A. Morphological disparity of the humerus in modern birds. Diversity. 2020;12:1–17.
24. Tobalske BW, Dial KP. Effects of body size on take-off flight performance in Phasianidae (Aves). J Exp Biol. 2000;203:3319–32.
25. Balanoff A, Bever GS, Rowe TB, Norell MA. Evolutionary origins of the avian brain. Nature. 2013;501:93.
26. Jenkins FA. Jr. in *Functional Morphology and Evolution* Vol. 293-A *American Journal of Science* (eds P. Dodson & P. Gingerich) 253–267 (1993).
27. Ostrom JH. *Archaeopteryx* and the origin of birds. Biol J Linn Soc. 1976;8:91–182.
28. Wu Q, O'Connor JK, Wang S-Y, Zhou Z-H. Transformation of the pectoral girdle in pennaraptorans: critical steps in the formation of the modern avian shoulder joint. PeerJ. 2024;12:1–42.
29. Zheng X-T, 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. 2014;111:13900–5.
30. Wellnhofer P, Tischlinger H. Das "Brustbein" von *Archaeopteryx bavarica* Wellnhofer 1993 - eine Revision. Archaeopteryx. 2004;22:3–15.
31. Wellnhofer P. Das siebte exemplar von *Archaeopteryx* aus den Solnhofer Schichten. Archaeopteryx. 1993;11:1–47.
32. Carter DR, Wong M. Modelling cartilage mechanobiology. Philos Trans R Soc Lond B Biol Sci. 2003;358:1461–71.
33. O'Connor JK, Zheng X-T, Wang X-L, Zhang X-M, Zhou Z-H. The gastral basket in basal birds and their close relatives: size and possible function. Vertebr Palasiat. 2015;53:133–52.
34. Foth C. Comment on the absence of ossified sternal elements in basal paravian dinosaurs. Proc Natl Acad Sci U S A. 2014;111:e5334–e5334.
35. Kundrát M, Nudds J, Kear BP, Lü J-C, Ahlberg PE. The first specimen of *Archaeopteryx* from the Upper Jurassic Mörnsheim Formation of Germany. Histol Histopathol. 2019;31:3–63.
36. Nesbitt SJ, Turner AH, Spaulding M, Conrad JL, Norell MA. The theropod furcula. J Morphol. 2009;270:856–79.
37. Erickson GM, et al. Was dinosaurian physiology inherited by birds? Reconciling slow growth in *Archaeopteryx*. PLoS One. 2009;4:e7390.
38. Olson SL, Feduccia A. Flight capability and the pectoral girdle of *Archaeopteryx*. Nature. 1979;278:247–8.
39. Burgers P, Chiappe LM. The wing of *Archaeopteryx* as a primary thrust generator. Nature. 1999;399:60–2.
40. Elzanowski A. In: Chiappe LM, Witmer LM, editors. Mesozoic Birds: Above the Heads of Dinosaurs. University of California Press; 2002. pp. 129–59.
41. Napoli JG, et al. Reorganization of the theropod wrist preceded the origin of avian flight. Nature. 2025. https://doi.org/10.1038/s41586-025-09232-3.
42. Sullivan C, Hone DWE, Xu X, Zhang F-C. The asymmetry of the carpal joint and the evolution of wing folding in maniraptoran theropod dinosaurs. Proc R Soc B Biol Sci. 2010;277:2027–33.
43. Ostrom JH, Poore SO, Goslow GE et al. Jr. in *Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution, Washington, D.C., 4–7 June 1996* Vol. 89 *Smithsonian Contributions to Paleobiology* (eds S.L. Olson 301–309 (1999).
44. Rayner JMV. In: Rayner JMV, Wootton RJ, editors. Biomechanics in Evolution. Cambridge University Press; 1991. pp. 183–212.
45. Sachs G. Wind effects on bounding flight. J Theor Biol. 2013;316:35–41.
46. Taylor GK, Reynolds KV, Thonas ALR. Soaring energetics and glide performance in a moving atmosphere. Philos Trans R Soc Lond B Biol Sci. 2016;371:1–14.
47. Knight K. Shags take advantage of headwind to take off. J Exp Biol. 2016;219:296.
48. Spear LB, Ainley DG. Flight speed of seabirds in relation to wind speed and direction. Ibis. 1997;139:234–51.
49. Tobalske BW. Evolution of avian flight: muscles and constraints on performance. Philos Trans R Soc Lond B Biol Sci. 2016;371:1–10.
50. Gatesy SM, Dial KP. From frond to fan: *Archaeopteryx* and the evolution of short-tailed birds. Evolution. 1996;50:2037–48.
51. O'Connor JK, et al. The unique caudal plumage of Jeholornis and complex tail evolution in early birds. Proc Natl Acad Sci USA. 2013;110:17404–8.
52. Yalden DW. The flying ability of *Archaeopteryx*. Ibis. 1971;113:349–56.
53. Marugán-Lobón J, et al. Quantitative patterns of morphological variation in the appendicular skeleton of the Early Cretaceous bird *Confuciusornis*. J Syst Palaeontol. 2011;9:91–101.
54. Houck MA, Gauthier JA, Strauss RE. Allometric scaling in the earliest fossil bird, *Archaeopteryx lithographica*. Science. 1990;247:195–8.
55. Senter P, Robins JH. Taxonomic status of the specimens of *Archaeopteryx*. J Vertebr Paleontol. 2003;23:961–5.
56. Chiappe LM, Marugán-Lobón J, Ji S, Zhou Z. Life history of a basal bird: morphometrics of the Early Cretaceous *Confuciusornis*. Biol Lett. 2008;4:719–23. https://doi.org/10.1098/rsbl.2008.0409.
57. Ostrom JH. *Archaeopteryx* and the origin of flight. Q Rev Biol. 1974;49:27–47.
58. Gatesy SM. Caudofemoral musculature and the evolution of theropod locomotion. Paleobiology. 1990;16:170–86.
59. Falk AR, Lamsdell JC, Gong E-P. Principal component analysis of avian hind limb and foot morphometrics and the relationship between ecology and phylogeny. Paleobiology. 2021;47:314–36.
60. Gatesy SM. Hind limb scaling in birds and other theropods: implications for terrestrial locomotion. J Morphol. 1991;209:83–96.
61. O'Connor JK, Chiappe LM, Bell A. in *Living Dinosaurs: the Evolutionary History of Birds* (eds G. D. Dyke & G. Kaiser) Ch. 3, 39–114 (J. Wiley & Sons, 2011).
62. Chiappe LM, Ji S, Ji Q, Norell MA. Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the Late Mesozoic of northeastern China. Bull Am Mus Nat Hist. 1999;242:1–89.

63. Xu X, et al. A new feathered maniraptoran dinosaur fossil that fills a morphological gap in avian origin. Chin Sci Bull. 2009;54:430–5.
64. Gatesy SM, Middleton KM. Bipedalism, flight, and the evolution of theropod locomotor diversity. J Vertebr Paleontol. 1997;17:308–29.
65. Hopson JA. in *New Perspectives on the Origin and Early Evolution of Birds* (eds J. Gauthier & L.F. Gall) 211–235Peabody Museum of Natural History, (2001).
66. Glen CL, Bennett MB. Foraging modes of Mesozoic birds and non-avian theropods. Curr Biol. 2007;17:R911–2. https://doi.org/10.1016/j.cub.2007.09.026.
67. Feduccia A. Evidence from claw geometry indicating arboreal habits of *Archaeopteryx*. Science. 1993;259:790–3.
68. Cobb SE, Sellers WI. Inferring lifestyle for Aves and Theropoda: a model based on curvatures of extant avian ungual bones. PLoS One. 2020;15:e0211173.
69. Birn-Jeffery AV, Miller CE, Naish D, Rayfield EJ, Hone DWE. Pedal claw curvature in birds, lizards and Mesozoic dinosaurs - complicated categories and compensating for mass-specific and phylogenetic control. PLoS One. 2012;7:1–11.
70. Feduccia A, Martin LD, Tarsitano S. *Archaeopteryx* 2007: *quo vadis*? *Auk* 124, 373–380 (2007).
71. Xu X, You H-L, Kai D, Han F-L. An archaeopteryx-like theropod from China and the origin of Avialae. Nature. 2011;475:465–75.
72. Yalden DW. in *The Beginnings of Birds* (eds M.K. Hecht, J.H. Ostrom, G. Viohl, & P. Wellnhofer) 91–97 (Freunds des Jura-Museums Eichstatt, 1985).
73. Chiappe LM. Climbing *Archaeopteryx*? A response to Yalden. Archaeopteryx. 1997;15:109–12.
74. Norell MA, Makovicky PJ. Important features of the dromaeosaurid skeleton II: information from newly collected specimens of *Velociraptor mongoliensis*. Am Mus Novit. 1999;3282:1–45.
75. Norell MA, Balanoff AM, Barta DE, Erickson GM. A second specimen of *Citipati osmolskae* associated with a nest of eggs from Ukhaa Tolgod, Omnogov Aimag, Mongolia. Am Mus Novit. 2018;3899:1–45.
76. Dial KP. Wing-assisted incline running and the evolution of flight. Science. 2003;299:402–4. https://doi.org/10.1126/science.1078237.
77. Heers AM, Tobalske BW, Jackson BE, Dial KP. Where is WAIR (and other wing-assisted behaviours)? Essentially everywhere: a response to Kuznetsov and Panyutina (2022). Biol J Linn Soc. 2022;137:157–62.
78. Dial KP, Jackson BE, Segre P. A fundamental avian wing-stroke provides a new perspective on the evolution of flight. Nature. 2008;451:985–9. https://doi.org/10.1038/nature06517.
79. Senter P. Scapular orientation in theropods and basal birds, and the origin of flapping flight. Acta Palaeontol Pol. 2006;51:305–13.
80. Qin Z-C, et al. Growth and miniaturization among alvarezsauroid dinosaurs. Curr Biol. 2021;31:3687–93.
81. Pei R, Li Q-G, Meng Q-J, Norell MA, Gao K-Q. New specimens of *Anchiornis huxleyi* (Theropoda: Paraves) from the Late Jurassic of Northeastern China. Bull Am Mus Nat Hist. 2017;411:1–66.
82. Makovicky PJ, Norell MA, Clark JM, Rowe T. Osteology and relationships of *Byronosaurus jaffei* (Theropoda: Troodontidae). Am Mus Novit. 2003;3402:1–32.
83. O'Connor JK. The trophic habits of early birds. Palaeogeogr Palaeoclimatol Palaeoecol. 2019;513:178–95. https://doi.org/10.1016/j.palaeo.2018.03.006.
84. Zheng X-T, et al. Exceptional dinosaur fossils reveal early origin of avian-style digestion. Sci Rep. 2018;8:1–8.
85. O'Connor JK et al. Avian features of *Archaeopteryx* feeding apparatus reflect elevated demands of flight. *The Innovation* (2025).
86. Li Z-H, Zhou Z-H, Clarke JA. Convergent evolution of a mobile bony tongue in flighted dinosaurs and pterosaurs. PLoS One. 2018;13:e0198078. https://doi.org/10.1371/journal.pone.0198078.
87. du Toit CJ, Chinsamy A, Cunningham SJ. Cretaceous origins of the vibrotactile bill-tip organ in birds. Proc R Soc B Biol Sci. 2020;287:1–10.
88. Krulis V. Struktur und Verteilung von Tastrezeptoren im Schnabel-Zungenbereich von Sing-vogeln im besonderen der Fringillidae. Rev Suisse Zool. 1978;85:385–447.
89. Bailleul AM, Li Z-H, O'Connor JK, Zhou Z-H. Origin of the avian predentary and evidence of a unique form of cranial kinesis in Cretaceous ornithuromorphs. Proc Natl Acad Sci U S A. 2019;116:24696–706. https://doi.org/10.1073/pnas.1911820116.
90. Matsumoto R, Evans SE. The palatal dentition of tetrapods and its functional significance. J Anat. 2016;230:47–65.
91. Zheng X-T, et al. New specimens of *Yanornis* indicate a piscivorous diet and modern alimentary canal. PLoS One. 2014;9:e95036. https://doi.org/10.1371/journal.pone.0095036.
92. O'Connor JK, Xu X, Zhou Z-H. Additional specimen of *Microraptor* provides unique evidence of dinosaurs preying on birds. Proc Natl Acad Sci U S A. 2011;108:19662–5. https://doi.org/10.1073/pnas.1117727108.
93. O'Connor J, et al. *Microraptor* with ingested lizard suggests non-specialized digestive function. Curr Biol. 2019;29:1–7. https://doi.org/10.1016/j.cub.2019.06.020.
94. Céspedes B, Torres I, Urbieta IR, Moreno JM. Effects of changes in the timing and duration of the wet season on the germination of the soil seed bank of a seeder-dominated Mediterranean shrubland. Plant Ecol. 2012;213:919–31.
95. Fischer C, Gerstmeier R, Wagner TC. Seasonal and temporal patterns of rainfall shape arthropod community composition and multi-trophic interactions in an arid environment. Sci Rep. 2022;12:1–9.
96. Tang K, et al. Climatic seasonality shapes insect community composition on the Mongolian Plateau. Ecol Ind. 2025;275:1–10.
97. Martins AA, Opedal ØH, Armbruster WS, Pélabon C. Rainfall seasonality predicts the germination behavior of a tropical dry-forest vine. Ecol Evol. 2019;9:5196–205.
98. Zheng S, et al. Effects of rainfall patterns in dry and rainy seasons on the biomass, ecostoichiometric characteristics, and NSC content of *Fraxinus malacophylla* seedlings. Front Plant Sci. 2024;15:1–24.
99. Wang B, Zhang H, Wappler T, Rust J. Palaeontinidae (Insecta: Hemiptera: Cicadomorpha) from the upper Jurassic Solnhofen Limestone of Germany and their phylogenetic significance. Geol Mag. 2010;147:570–80.
100. Nel A, Bechly G, Martínez-Delclòs X. A new genus and species of Aeschnidiidae (Insecta: Odonata: Anisoptera) from the Solnhofen Limestone, upper Jurassic, Germany. Senckenb Lethaea. 1996;76:175–9.
101. New TR. Beetles and conservation. Wiley-Blackwell; 2010.

102. Varricchio DJ, Jackson FD. Reproduction in Mesozoic birds and evolution of the modern avian reproductive mode. Auk. 2016;133:654–84.
103. Wiemann J, Yang T-R, Norell MA. Dinosaur egg colour had a single evolutionary origin. Nature. 2018;563:555–8.
104. Chiappe LM, Ji S, Ji Q. Juvenile birds from the Early Cretaceous of China: implications for enantiornithine ontogeny. Am Mus Novit. 2007;3594:1–46. https://doi.org/10.1206/0003-0082(2007)3594[1:JBFTEC]2.0.CO;2.
105. O'Connor JK, et al. Description and osteohistology of two early immature enantiornithines (Aves: Ornithothoraces) from the Early Cretaceous Jehol Biota. Geobios. 2025;90:103–22.
106. Wiemann J, et al. Fossil biomolecules reveal an avian metabolism in the ancestral dinosaur. Nature. 2022;606:522–6.
107. Wu Q, Bailleul AM, Li Z-H, O'Connor JK, Zhou Z-H. Osteohistology of the scapulocoracoid of *Confuciusornis* and preliminary analysis of the shoulder joint in Aves. Front Earth Sci. 2021;9:1–16.
108. O'Connor J, et al. Medullary bone in an Early Cretaceous enantiornithine bird and discussion regarding its identification in fossils. Nat Commun. 2018;9:1–8.
109. Kiat Y, Pyle P, Balaban A, O'Connor JK. Reinterpretation of purported molting evidence in the Thermopolis <Emphasis Type="Italic">Archaeopteryx</Emphasis>. Commun Biol. 2021. https://doi.org/10.1038/s42003-021-02349-x.
110. Wang X-L, O'Connor JK, Zheng X-T, Wang Y, Kiat Y. Earliest evidence of avian primary feather moult. Biol Lett. 2024;20:1–6.
111. Kiat Y, et al. Sequential moult in a feathered dinosaur and implications for early paravian locomotion and ecology. Curr Biol. 2020;30:3633–8.
112. Carney RM, Vinther J, Shawkey MD, D'Alba L, Ackermann J. New evidence on the colour and nature of the isolated *Archaeopteryx* feather. Nat Commun. 2012;3:1–8. https://doi.org/10.1038/ncomms1642.
113. Manning PL, et al. Synchrotron-based chemical imaging reveals plumage patterns in a 150 million year old early bird. J Anal At Spectrom. 2013;28:1024–30.
114. Schmitz L, Motani R. Nocturnality in dinosaurs inferred from scleral ring and orbit morphology. Science. 2011;332:705–8.
115. Bell PR, Hendrickx C. Epidermal complexity in the theropod dinosaur *Juravenator* from the Upper Jurassic of Germany. Palaeontology. 2020;64:203–23.
116. Rauhut OWM, Foth C, Tischlinger H, Norell MA. Exceptionally preserved juvenile megalosauroid theropod dinosaur with filamentous integument from the Late Jurassic of Germany. Proc Natl Acad Sci U S A. 2012;109:11746–51.
117. Pennycuick CJ. Modelling the flying bird, vol. 4. Academic Press; 2008.
118. Kielan-Jaworowska Z, Barsbold R. Narrative of the Polish-Mongolian palaeontological expeditions 1967–1971. Palaeontol Pol. 1972;27:5–13.
119. Pittman M, et al. Exceptional preservation and foot structure reveal ecological transitions and lifestyles of early theropod flyers. Nat Commun. 2022;13:1–14.
120. Conrad JL. A new lizard (Squamata) was the last meal of *Compsognathus* (Theropoda: Dinosauria) and is a holotype in a holotype. Zool J Linn Soc. 2017;183:584–634.

Publisher's note