A Novel Hypothesis for the Evolution of Flight in Chiroptera by Comparison to Aves

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Abstract

Powered flight has only ever evolved within four taxa: Insecta (in the mid-Devonian), Pterosauria (an extinct taxon from the late-Triassic), Aves (early Cretaceous), and Chiroptera (Paleocene). While powered flight is rare, it seems to confer a great evolutionary advantage since flying taxa tend to be very speciose. It is estimated that there are over 20,000 extant species of birds (Barrowclough, 2016) and over 1,100 species of bats (which are the second most speciose clade of mammals) (Gunnell and Simmons, 2005). The question of how such a mechanistically complicated form of locomotion evolved is complex. The fossil record leading up to Aves is very rich, with many transition fossils (such as *Archaeopteryx lithographica*) that allow paleontologists to propose well-justified hypotheses on the basis of morphology and presumed lifestyle. The two main hypotheses are evolution from a cursorial ancestor and evolution from an arboreal gliding ancestor, with the former now considered more likely (on the basis of available fossil evidence and extant avian behaviors). In Chiroptera, however, there are no known transitional fossils. The earliest fossils, *Onychonycteris finneyi* and *Icaronycteris index* (from the early Eocene), represent essentially modern morphology and were both fully capable of powered flight. Thus, it is much more difficult to reconstruct the evolution of flight in Chiroptera. The two main hypotheses are evolution through a gliding intermediate, and evolution via direct flapping flight. In this paper, I compare the morphology, lifestyle, and behavior of fossil and extant members of Aves to that of fossil and extant Chiropterans and argue that the evolution of direct flapping flight, co-opted from passive prey detection and gleaning behavior, is most likely for Chiroptera.

Introduction

Powered flight has only evolved four times, in Insecta (in the mid-Devonian), Pterosauria (an extinct taxon from the late-Triassic), Aves (early Cretaceous), and Chiroptera (Paleocene). The evolution of powered flight allowed these taxa to exploit a previously untouched habitat space which unlocked the potential for new modes of feeding (with less competition) and offered an escape from predation. Thus, powered flight is a great evolutionary advantage. This is reflected in the extreme species richness seen in flying insects, birds, and bats. The substantial advantage conferred makes the evolution of powered flight an interesting topic to study.

For all taxa capable of powered flight, the evolution of flight required a complex assembly of new morphological characters, over a long period of time. In Aves, this assembly is laid out nearly stepwise in the fossil record, with many exceptionally preserved transition fossils (like *Archaeopteryx lithographica*). This wealth of information on skeletal and integumentary evolution allows paleontologists to propose well-based hypotheses for the evolutionary pathway to flight in Aves. The two main proposals are evolution from a cursorial, flapping ancestor, and evolution from an arboreal gliding ancestor. On the basis of comparison to extant birds as well as morphological character development, the evolution from a cursorial ancestor is now deemed most likely. In comparison, the fossil record for Chiroptera is incredibly sparse. Bats appear suddenly in the fossil record in the early Eocene, with *Onychonycteris finneyi* and *Icaronycteris index* being the oldest fossils found to date. These two "transition" fossils retain minimal ancestral traits and both have essentially modern chiropteran morphology, so they do not reveal much about the assembly of the morphological features necessary for chiropteran flight. Based on the little information the fossil record does provide, along with kinematic, behavioral, and ontogenetic studies of extant bats, paleontologists propose two theories for the evolution of flight in bats: evolution from an arboreal glider, and evolution from an arboreal ancestor via direct flapping. The former theory is the most widely held, yet I believe the latter is most likely.

In this paper, I propose that bats evolved via direct flapping flight from an arboreal ancestor. My novel hypothesis suggests that bats evolved flight as a means of increasing predatory success, using a combination of reach hunting and rudimentary passive prey detection and gleaning. I strengthen this hypothesis through comparisons to the well-known functional morphology studied in Aves (since birds and bats are ecomorphs). I propose that similar hunting strategies in birds and bats led to the convergent evolution of lifestyle and locomotion, with their discreet morphological adaptations resulting from different ancestral habitats.

Evolution of Powered Flight in Aves[1]

Aves is a successful and diverse clade of vertebrates, with estimates of nearly 20,000 extant species (Barrowclough, 2016). The success of Aves (referred to as birds, from here on) can be contributed, in large part, to the evolution of powered flight, since powered flight allowed

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[1] For the phylogenies referenced, see Appendix A.

birds access to new ecological niches in vertical habitat space. Birds, however, evolved from carnivorous theropod dinosaurs, which lacked any flight capabilities. How, then, did birds come to be? A very rich fossil record for the lineage leading up to modern birds demonstrates the morphological changes over time that led to the general avian body plan as it is known today. The major changes include at least 50 million years of sustained decrease in body size starting from the base of Theropoda (Lee et al., 2014), increasing lightness of the skeleton, reduction of manual digits, fusion and elongation of forelimb elements, reorientation and increasing robustness of the pectoral girdle, fusion of the pelvic girdle, and the evolution of asymmetric flight feathers. These many modifications will be discussed in detail.

Pectoral girdle and forelimbs:

Extant birds have a heavily ossified pectoral girdle to provide ample surface area for flight muscle attachment. The scapula and coracoid are fused into the scapulocoracoid, which contacts the sternum to immobilize the shoulder joint (Ostrom, 1979). The scapulocoracoid is located dorsally, to shift the glenoid fossa laterally rather than posteroventrally (the ancestral condition). The glenoid fossa has a dorsally facing component which allows the wing to extend to a position above the body axis, providing the necessary range of motion for a strong flight stroke. The hemi-sellar glenohumeral joint allows for three degrees of freedom of motion in the wing. The sternum is robust with a large sternal keel for the attachment of the supracoracoideus muscle (for the upstroke) and part of the pectoralis muscle (for the downstroke) (Jenkins, 1993). The clavicles are fused to form the v-shaped furcula, which acts to resist compression of the thoracic cavity during the flight stroke. Birds also have a pulley-like structure that reverses the action of the supracoracoideus muscle to power the recovery stroke, called the triosseal canal (Ostrom, 1979). There is a large deltopectoral crest on the humerus, for more muscle attachment. The humerus has bony tubercules for attachment of the subscapularis, supracoracoideus, and coracobrachialis posterior – the muscles that assist in wing folding (Ostrom, 1974). The humerus is also relatively long. The ulna has a greater diameter than the radius to serve as a surface for flight feather anchoring. The carpals and metacarpals of the wrist and manus fuse to form the carpometacarpus (increasing wing rigidity), and the morphology of the semilunate carpal allows for hyperflexion of the wrist, which is critical for the flight stroke.

During the downstroke, the carpometacarpus, cuneiform, and ulna lock together to prevent hyperpronation and dislocation of the wrist. The wrist is also stabilized during gliding, as extension of the manus locks the carpometacarpus and scapholunar together to prevent supination. During the upstroke, however, air resistance is minimized by releasing this locking mechanism so the manus can rotate perpendicular to the plane of the wing. When the wing retracts, the cuneiform shifts to its most ventrocaudal position along the ulnar ridge, allowing the manus to rotate relative to the radius and ulna. At the end of the upstroke, the wing is extended once again, causing the ulnar carpometacarpal ligament to tighten and rapidly pronate the manus back into the normal plane of the wing. This rapid flicking motion at the end of the upstroke provides both thrust and lift during low-speed locomotion, such as takeoff and landing (Vasquez, 1992). Finally, in modern birds, the hands are reduced to three fused digits (loss of digits IV and V), and the manus is shortened to increase wing rigidity. Digit II has twice the radius of digit I, reflecting its function for anchoring flight feathers. The first digit, called the alula, also has a small number of attached flight feathers (only about two to six individual feathers). It can move freely to help control flight at low speeds by increasing the angle of attack of the wing (Padian and Chiappe, 1998b).

Clearly, the morphology of the avian pectoral girdle and forelimb is highly specialized for flight. This suite of unique morphological characters was assembled slowly over time. The earliest known member of the avian stem lineage, *Teleocrater rhadinus* (a member of Avemetatarsalia, from the mid-Triassic – see Fig. 1), shows the ancestral shoulder orientation, with a posteroventrally oriented glenoid fossa that directs the forelimb into a position for quadrupedal locomotion

Figure 1. Reconstruction of *Teleocrater rhadinus*. Reprinted from Nesbitt, 2017.

(Nesbitt et al., 2017). Further along the avian stem lineage, into Dinosauria, we see more bird-like features evolve. *Coelophysis bauri* (a member of Coelophysidae – see Fig. 2), is a stem Theropod. It has a posteroventrally oriented glenoid fossa (like *Teleocrater*) but was bipedal. It also retains the more ancestral condition of shorter forelimbs compared to the hindlimbs.
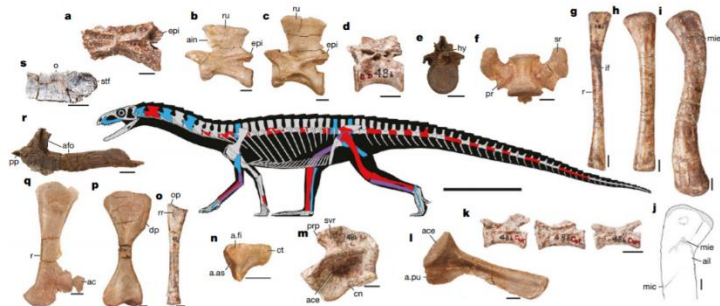
Figure 2. Neotype cast of *Coelophysis bauri*, specimen AMNH FR 7224 from the Redpath Museum in Quebec. Reprinted from Wikipedia.

Features that demonstrate its closer relation to birds than *Teleocrater* include a v-shaped furcula and relatively large scapulocoracoid (Rinehart et al., 2009). However, it lacks large sternal plates, so pectoral musculature likely attached to the anterior gastralia and ribs, as in crocodilians. Its ancestral characters include the retention of four manual digits (the outermost being reduced

and nonfunctional) and the lack of a semilunate carpal. *Allosaurus fragilis* (Fig. 3), which diverged from the avian lineage after *Coelophysis*, accordingly shows slightly more bird-like features. It has a larger scapulocoracoid, a reduction to three manual digits, and a semilunate carpal (Carpenter, 2002).

Figure 3. Skeletal reconstruction of *Allosaurus fragilis.* Reprinted from *Allosaurus*. (2013) Usu.edu.

Deinonychus antirrhopus (Fig. 4), a dromaeosaurid, is more closely related to extant birds than *Coelophysis* and *Allosaurus*. It is a bipedal theropod dinosaur that shows a combination of ancestral archosaurian traits and derived avian traits. Its large body size indicates it was not an arboreal species (Fowler et al., 2011), yet its scapulocoracoid is oriented more horizontally, which causes the glenoid fossa to be oriented somewhat ventrally. This orientation caused the protractive and retractive movements of the forearms to result in humeral elevation and depression, a precursor for the flight stroke (Jenkins, 1993). *Deinonychus* also has an

ossified sternum (like birds) but lacks a sternal keel for flight muscle attachment. Other bird-like features include a furcula (American Museum of Natural History, n.d.), elongated forelimbs, three manual digits, and a semilunate carpal (allowing for rotation of the manus relative to the rest of the arm). In *Deinonychus*, the three manual digits retain a more ancestral state; they are unfused (so they could move independently) and they retain large, recurved claws with flexor tubercles. Thus, the elongation of the arms and morphology of the

Figure 4. *Deinonychus antirrhopus,* specimen AMNH 3015. Reprinted from Wikipedia.

wrist and digits indicate that the forearms were used to seize prey, rather than for flight or an arboreal, climbing lifestyle (Padian and Chiappe, 1998a). Interestingly, a study on the morphological stages in the ontogeny of *Deinonychus* indicates that the shallow, open glenoid fossa, orientation of the olecranon process, and low body mass seen in juveniles might have allowed for powered flight at young ages (Parsons and Parsons, 2015).

 Microraptor is another genus of dromaeosaurids from the early Cretaceous (Fig. 5). Based on the morphology of these species, they were likely capable of gliding flight. Like *Deinonychus,* they have an ossified sternum, but no sternal keel (Zheng et al., 2014). The glenoid fossa is positioned laterally, so the forelimbs had a range of motion that allowed them to be held out perpendicular to the body axis. *Microraptor*, however, lacks uncinate processes on its ribs, indicating that it had less area for muscle attachment and a weaker, less reinforced rib cage, which would

Figure 5. *Microraptor gui*, specimen IVPP V 13352. Reprinted from Wikipedia.

preclude flapping flight (Guo et al., 2018).

Eosinopteryx brevipenna and *Anchiornis huxleyi* are small, paravian maniraptorans of the family Troodontidae. They are likely sister species in a polytomy at the base of Troodontidae (Godefroit et al., 2013), but *Eosinopteryx* might be slightly more basal than *Anchiornis* – the exact relationships are difficult to resolve since the radiation of Avialae in the mid to late Jurassic was very rapid (Guo et al., 2018). These species are more derived than *Deinonychus,* implying that Troodontidae might be more closely related to Avialae than Dromaeosauridae. *Anchiornis huxleyi* (Fig. 6) has a scapula that extends distally, a laterally oriented glenoid fossa, a humerus elongated relative to the femur (even more elongated than in *Deinonychus*), a short deltopectoral crest on the humerus, a straight ulna but curved radius, a reduced semilunate carpal (covering only metacarpal I and half of metacarpal II – whereas in *Deinonychus* it covers the proximal surface of both metacarpal I and II), a relatively longer manus relative to the femur, and deep ligament fossa in the phalanges (which indicate grasping ability) (Guo et al., 2018). The small deltopectoral crest and long, grasping manus show the primitive features retained in *Anchiornis*, while the modifications to the shoulder and wrist show its morphological similarity to birds.

Figure 6. *Anchiornis huxleyi*, specimen BMNHC PH828. Reprinted from Wikipedia.

Eosinopteryx brevipenna shows a similar suite of features (Fig. 7). It has a much shorter scapula and forelimb compared to *Anchiornis*, but it has a reduced manus and an elongated humerus. Its radius and ulna are both straight and closely aligned, indicating that supination and pronation of the manus relative to the arm would have had a limited range of motion (Godefroit et al., 2013). Both *Eosinopteryx* and *Anchiornis* lack an

Figure 7. *Eosinopteryx brevipenna.* Reprinted from Godefroit, 2013.

ossified sternum, which adds support to the assumption that their flight ability would have been quite minimal (Zheng et al., 2014).

Arguably, the most important discovery in the evolution of avian flight was the discovery of *Archaeopteryx lithographica,* an obligate biped whose morphology indicates that it was capable of weakly powered flight (Fig. 8). *Archaeopteryx,* from the late Jurassic (about 150 million years ago) is likely the most basal member of Avialae (Brusatte et al., 2014), and it represents the intermediate between flightless theropods and birds. In *Archaeopteryx*, the scapula lies on the proximal ends of the ribs, shifting the scapula more dorsally. This results in the lateral orientation of the glenoid fossa, allowing for more vertical range of motion in the forelimb than in more basal theropods. However, since there is no dorsally oriented component to the glenoid fossa, *Archaeopteryx* would have had a lesser range of motion in the glenohumeral joint than extant birds (Jenkins, 1993). *Archaeopteryx* also has a robust furcula, but it lacks an ossified, keeled sternum, and has short and thin coracoids that lack prominent coracoid processes (Padian and Chiappe, 1998b). Like extant birds, its forelimbs are longer than its hindlimbs, but the biceps tubercle of the radius is located below the glenoid fossa, so there was no triosseal
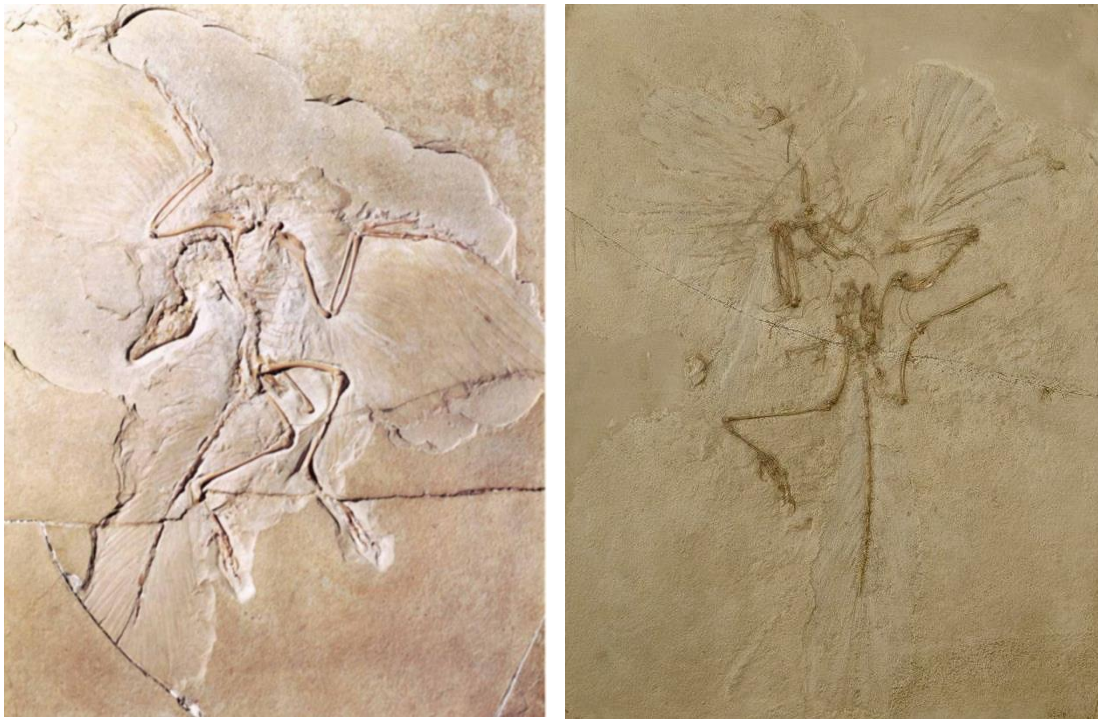

Figure 8. Two specimens of *Archaeopteryx.* Left: Reprinted from Wellnhofer, 1990. Right: Reprinted from Yale Peabody Museum of Natural History, YPM VP 002910.

canal to help automate the upstroke (Ostrom, 1974). The deltopectoral crest of the humerus is fairly large (Ostrom, 1979), but the proximity of the deltopectoral crest to the body midline indicates that the downstroke would have been initiated from a lower forelimb position than in extant birds (Jenkins, 1993). There are no body tubercles on the humerus, so it is unlikely that *Archaeopteryx* could fold its wings in to protect them against the body (Ostrom, 1974). In addition to an only moderately derived shoulder girdle, it has underived, coelurosaurian hands; its fingers could move independently (Wellnhofer, 1990) and retained large claws (Brusatte et al., 2015). Additionally, the small cuneiform and scapholunar lack articular facets, and the ulna has no conspicuous articular ridge, therefore, the mechanism to prevent hyperpronation of the wrist during the flight stroke was not in place in *Archaeopteryx* (Vasquez, 1992). Lastly, *Archaeopteryx* lacks an alula, so it would have had poor low-speed flight control (Padian and Chiappe, 1998b).

Confuciusornis sanctus (Fig. 9 and 10) lies closer to modern birds along the avian stem linage than *Archaeopteryx*, so it demonstrates even more derived features. It has a much more heavily ossified shoulder girdle than seen in *Archaeopteryx* (Padian and Chiappe, 1998a). It has an ossified, flat sternum that directly contacts the coracoids. The coracoids are slender and have large bicipital processes which articulate with the furcula. The coracoids and scapula are fused into a scapulocoracoid (as in extant birds). The humerus is stout with a very large deltopectoral crest. The morphology of its manus is quite similar to that of *Archaeopteryx*, retaining claws on its three, non-fused digits. However, unlike *Archaeopteryx*, older specimens show the fusion of the carpals and metacarpals into the carpometacarpus to make the wing more rigid (Martin et al., 1998).

Figure 9. *Archaeopteryx* (left) compared to *Confuciusornis* (right). Reprinted from Martin et al., 1998.

Figure 10. *Confuciusornis sanctus,* specimen NHMW-Geo 1997z0112/0001. Reprinted from Wikipedia.

Figure 11. *Sinornis santensis* specimen. Reprinted from Wikipedia.

Later fossil birds, *Sinornis santensis* and *Ichthyornis,* increase even further in morphological functionality for flight. *Sinornis santensis* (Fig. 11), a 135-million-year-old bird from the lower Cretaceous, has a flexible manus with the carpus and manus not fused into the carpometacarpus. The manus is also shortened relative to the rest of the forearm, offering greater wing tip control. Only digits I and II articulate independently, and they have very small distal unguals. Digit I is reduced relative to digit II, as digit II supports the primary flight feathers (this is transitional to modern birds). The forearm is preserved with 70 degrees of flexion relative to the manus, indicating that the wing fold mechanism existed to minimize drag during the upstroke (in *Archaeopteryx* and other maniraptorans, this angle is never less than 90 degrees). This hyperflexion is clearly not an effect of preservation, based on the morphology of the ulnare, which is v-shaped with a slot, as in modern birds, to fit the lateral margin of the manus. Additionally, *Sinornis* has a very broad sternum for attachment of large, aerobic flight muscles, with the coracoid tightly abutting it to resist thoracic compression during the powerful flight stroke. *Ichthyornis* (Fig. 12), a gull-like bird, has the same shoulder and forearm morphology as *Sinornis*. It, however, also has a large sternal keel (as in modern birds), for even greater flight muscle

Figure 12. *Ichthyornis.* Reprinted from Wikipedia.

attachment. Thus, most of the prerequisite morphology for powered flight in birds had originated by the early Cretaceous (Sereno and Chenggang, 1992).

<u>Pelvic girdle and hindlimbs:</u>

In extant birds, there are two modes of locomotion: powered flight and digitigrade, bipedal motion. Birds have a heavily fused pelvic girdle (to increase skeletal strength during flight), with a perforated acetabulum and a retroverted pubis. As the center of gravity shifted towards the forelimbs along the evolutionary pathway to modern birds, the pelvic region needed to increase in strength to support the body. Then, as the pubis became retroverted, the sternum evolved to take over the role of supporting the internal organs (Wellnhofer, 1990). In the hindlimbs, the spherical head of the femur is rotated 90 degrees relative to the shaft, and it articulates in the acetabulum to form a ball-and-socket joint with great mobility. The tibia and fibula are longer than the femur, which is very short and horizontally oriented (Brusatte et al., 2015). The fibula is almost fully reduced and shorter than the tibia (Padian and Chiappe 1998b). Birds also have fused metatarsals that are elongated relative to the femur and tibia lengths (this is an adaptation for a cursorial habit) (Nesbitt et al., 2017). The tarsals and metatarsals fuse into the tarsometatarsal, which articulates with the tibia to form the unique mesotarsal ankle joint of birds (Ostrom, 1979). Most birds have four, clawed, pedal digits, with digit I reversed and opposable (called the hallux). This arrangement of digits is well adapted for grasping and perching (Fowler et al., 2011).

In *Teleocrater rhadinus* (the most basal bird-line archosaur from the mid-Triassic), we see the basal archosaurian pelvic girdle and hind limb morphology. It has a closed acetabulum (there is possible evidence of a small perforation). The ratio of femur to tibia to metatarsal length seen in *Teleocrater* is more similar to that seen in early archosaurs than in bird-like dinosaurs. It also has relatively short metatarsals, which are consistent with a non-cursorial, quadrupedal lifestyle. Another ancestral character is seen in the ankle joint. The morphology of the calcaneum and astragalus suggest that it had a crocodile-normal ankle, indicating that the mesotarsal, hinged ankle evolved within Avemetatarsalia (Nesbitt et al., 2017).

Coelophysis and *Allosaurus* also show more ancestral hindlimb proportions. Most obviously, they both have hindlimbs that are longer than their forelimbs. Additionally, they both have somewhat elongated femurs relative to the tibiotarsus (as compared to extant birds), which is less adapted to a cursorial habit (Gatesy, 1991). They do, however, have bird-like features, including a bipedal stance, functionally tridactyl pes, and a mesotarsal ankle joint.

Deinonychus antirrhopus has hindlimb morphology well suited for predation. It has derived, birdlike features, including a fully perforated acetabulum, legs oriented for bipedal running, and a mesotarsal ankle. Its metatarsals are relatively short, so *Deinonychus* would not be as fast of a runner as species with an elongate metatarsus. However, the shorter metatarsals reduce the length of the flexor tendons connected to the flexor tubercles on the claws. This length reduction increases the grip strength of the pedal digits and claws – a benefit for grasping prey. Such a trend is seen when comparing extant bird species. For example, cursorial birds (like emus), have long metatarsals, while predatory raptors have shortened metatarsals. Thus, *Deinonychus* was likely an ambush predator that used its highly recurved claw on digit II to grasp onto and immobilize its prey. Since *Deinonychus* and other non-avian theropods hold their metatarsus at a low angle, the metatarsus serves as the palm of a "fist" that they could clasp for grasping. The grasping foot is stabilized by the ginglymoid phalangeal joints, which restrict the joint to one plane of articulation. These ginglymoid joints are also seen in extant raptors (Fowler et al., 2011). The first pedal digit is held off the ground and not fully reversed, but oriented to point medially, so it is unlikely that *Deinonychus* could perch. The pelvic morphology of *Deinonychus* is shared with other dromaeosaurids. It has a posteroventrally directed pubis with a pubic foot directed posteriorly and lacking an anterior projection. Its ischium is shortened relative to the pubis (Padian and Chiappe, 1998a). This shows a pelvic orientation that is intermediate to that of modern birds.

Eosinopteryx brevipenna and *Anchiornis huxleyi* show the same trunk to hindlimb proportions (Godefroit et al., 2013), both having the femur shorter relative to the humerus (Guo et al., 2018). *Eosinopteryx* has a short ischium and long ilium (with a dorsally curved shaft), and a fully retroverted pubis – as in modern birds (likely an example of convergent evolution, since *Eosinopteryx* is a sister group to Avialae). However, none of these pelvic elements are co-ossified (Godefroit et al., 2013). *Anchiornis* has the same pelvic conformation, but with a very well-developed pubic foot (Guo et al., 2018). They were both obligate bipeds, as their perforated acetabula are laterally oriented to articulate with the femoral heads, which are directed dorsomedially relative to the femoral shaft (Guo et al., 2018). They both show cursorial foot morphology, with the phalanges of digits II, III, and IV decreasing distally and having small, minimally recurved distal unguals (Godefroit et al., 2013). The orientation of digit I differs

between the two; in *Eosinopteryx* it is only partially reversed (oriented medially), and in *Anchiornis* it is positioned at the posterior end of digits II, III, and IV (Godefroit et al., 2013).

Archaeopteryx has similar pelvic morphology as saurischian dinosaurs; it has the three-pronged design to accommodate what would have likely looked like saurischian hindlimb muscle morphology (Wellnhofer, 1990). Furthermore, *Archaeopteryx* lacked the level of pelvic fusion seen in birds (it lacked a fully ossified synsacrum) (Ostrom, 1979). Showing its closer relation to birds, *Archaeopteryx* has a partially reverted pubis, that is directed posteroventrally, with a posteriorly facing pubic foot and a short ischium (Padian and Chiappe, 1998a). It is also clear that *Archaeopteryx* was an obligate biped. It has a tridactyl pes with a reversed hallux, but the hallux is short and higher on the metatarsus than would be helpful for perching (Ostrom, 1979). It has partially fused metatarsals, with the fifth pedal digit reduced to a metatarsal (Sereno and Chenggang, 1992). Its pedal digits have weak flexor tubercles (indicating that the grasping strength of the foot would be minimal), and its claws are smaller with morphology similar to extant cursorial birds (Ostrom, 1979). It has the bird-like mesotarsal ankle joint, but it lacks the posture of extant birds, where the body tips forwards and the femur is situated horizontally; instead, it had a nearly vertical parasagittal stance (Ostrom, 1974), and used its long tail to counterbalance the upper body (Wellnhofer, 1990).

Confuciusornis shows synchronicity in its hindlimb and forelimb modifications. As the fusion of the carpometacarpal elements occurred, so did the evolution of large, recurved claws and an opposable hallux (this reflects the transition to an arboreal lifestyle) (Padian and Chiappe, 1998a). The pelvic morphology shows that *Confuciusornis* had adopted a bird-like posture. The pubis is oriented posteriorly, and the ilium becomes wider anteriorly and abuts the transverse processes on the last three sacral vertebrae to stabilize the pelvis. The acetabulum is completely open, and the spherical head of the femur fits into it to form a mobile ball-and-socket joint, allowing the femur to swing forwards to fold the leg up towards the body while flying. Furthermore, the acetabulum has a broad articular surface anteriorly and posteriorly but lacks a dorsal articular shelf, which indicates that *Confuciusornis* could not adopt a dinosaur-like posture (Martin et al., 1998). These are examples of avian synapomorphies since *Confuciusornis* is a sister group to all other members of Avialae (Brusatte et al., 2014).

<u>Integumentary system:</u>

The flight surface of birds is formed out of feathers. However, it is highly unlikely that feathers evolved for flight. Sauropodomorphs (the outgroup to theropods), lacked feathers. Most basal theropods lacked feathers as well. It is in basal coelurosaurs that we find the first simple, filamentous protofeathers (Lee et al., 2014). *Sinosauropteryx*, a member of Compsognathidae, also had simple protofeathers (Brusatte et al., 2015). Since feathers evolved so much earlier than other flight features, they must have evolved due to a selective pressure unrelated to aerodynamics. By the divergence of Ornithomimosauria and Maniraptora we see a much greater diversity of feather types, as well as complex, asymmetric flight feathers like we see in modern birds (Lee, 2014).

Asymmetric flight feathers are a very derived feather type. The most primitive feather type was down feathers. These fluffy feathers trap a lot of air, which makes them great insulators. Thus, these early feathers would help minimize heat loss and gain, which is important for homeotherms (Ostrom, 1974). Since early feathered dinosaurs did not have feathers confined to their limbs, but rather had primitive down feathers covering their whole bodies, it is likely that feathers originated for insulation and were later co-opted for flight. Additionally, the evolution of feathers for insulation could explain why we see the trend towards smaller body size, even before flight occurs (since insulating a smaller body would be more efficient) (Lee et al., 2014).

A second theory is that feathers evolved via sexual selection. A recent study showed that *Anchiornis huxleyi* had different color patterns on its feathers, caused by melanin pigment deposits (Fig. 13). Earlier on, in Coelurosauria (based on evidence of the coloration pattern in

Sinosauropteryx), the color pattern occurred among individual feathers, whereas in Maniraptora, color patterning occurred within individual feathers (Li et al., 2010). Since color patterning does necessarily confer survival advantage, this might indicate that sexual selection played a role.

Figure 13. Color reconstruction of *Anchiornis huxleyi*. Reprinted from Li et al., 2010.

Furthermore, in a sampling of *Confuciusornis* specimens, only about 5-10% of the specimens had evidence of long tail feathers. This might be evidence of lek display (Martin et al., 1998). Finally, the evolution of large-feathered wings in dromaeosaurids (like *Deinonychus* and *Velociraptor*) could have evolved for display, since these taxa did not fly (Fowler et al., 2011).

One issue regarding the evolution of flight feathers is seen in genera that use their forelimbs for grasping prey, such as *Velociraptor* and *Deinonychus.* Wouldn't long feathers get in the way when catching prey and result in decreased fitness? Unless display benefits outweighed the cost to predation, they must not have been a detriment. Ostrom postulates that increasing the size of forelimb feathers aided in prey capture by forming a net-like snare to corral the prey towards the predator's body (1974).

As feathers continued to elongate (whether they evolved to take on diverse forms due to selective pressures for increased insulation, more elaborate display, and/or prey capture), they would have inherently become more aerodynamic. These small airfoils, while not large enough for powered flight, could then be large enough to aid in stability flapping. Basal paravian species, such as dromaeosaurids, had large, recurved pedal claws that could have been used to slash or immobilize prey. While pinning down prey, the hindlimbs would lose the ability to help balance the body. The wings, freed from use in prey restraint, could then be used, along with feathered tails, to help stabilize the body. This behavior is seen in extant raptors (Fowler et al., 2011). Continuing to increase the surface area of the airfoil would lead to more effective stability flapping, as well as the new ability to jump up to reach flying prey (Ostrom, 1974). This would have been particularly beneficial for insectivorous species, like *Archaeopteryx* (which has the small, sharp teeth characteristic of insectivores) (Ostrom, 1979).

In species less related to extant birds than *Archaeopteryx*, we also see evolution of larger pennaceous, flight feathers. *Microraptor, Anchiornis,* and *Eosinopteryx* all have forelimb, hindlimb, and tail feathers (Dyke et al., 2013). *Microraptor gui* was the only member of *Microraptor* with asymmetric flight feathers and was likely a strong glider. The rest of the species within the genus *Microraptor* had symmetric flight feathers (Brusatte et al., 2015). Yet, studies using models of *Microraptor* with symmetric feathers showed equal gliding ability to *Microraptor gui*, indicating that symmetric feathers could have evolved first, and later evolved to be asymmetric in response to aerodynamic selective pressures (Dyke et al., 2013). Like most

members of *Microraptor*, *Anchiornis* lacked asymmetric flight feathers (Li et al., 2010). Instead, it was covered with simple pennaceous flight and contour feathers (feathers on metatarsus and pes would be useful for insulation) (Godefroit et al., 2013). As the study by Dyke et. al. discovered, even symmetric flight feathers have aerodynamic capabilities (2013). This finding, when combined with the shoulder girdle and forelimb morphology, implies that *Anchiornis* was likely capable of weakly powered flight or gliding. These arial capabilities suggest convergent feather evolution to that seen in Avialae.

Finally, *Archaeopteryx* has beautifully preserved feather impressions, which show that it had asymmetric flight feathers on its fore and hind limbs, and slightly less asymmetric feathers on its tail; this is very similar to the feather morphology seen in modern birds. *Archaeopteryx* lacks the aspect ratio seen in the flight surfaces of gliding tetrapods, so it was likely a weakly powered flapping flier (its shoulder morphology, as discussed, confirms this) (Padian and Chiappe, 1998a). A study by Marden, which scaled flight performance with size, determined that *Archaeopteryx* was likely capable of ground takeoff and weakly powered flight for short distances (1994). Thus, *Archaeopteryx* continues to be a wonderful representative form for the intermediate between flightless basal theropods and extant birds.

Pathway to powered flight:

There are two main hypotheses for the pathway to powered flight in birds: the "ground up" cursorial hypothesis (proposed by Samuel W. Williston in 1879), and the "trees down" arboreal hypothesis (proposed by O.C. Marsh in 1880). I believe that the former hypothesis is the most likely.

The "trees down" hypothesis suggests that bipedal theropods transitioned into an arboreal lifestyle. Large flight surfaces were favored in this habitat, as they granted the ability to jump from branch to branch with more control. This led to an intermediate gliding stage. There was then a selective pressure to improve maneuverability and extend the length of gliding. Eventually, these selective pressures shaped the morphology of extant, powered flying birds. *Archaeopteryx* is frequently referenced in defense of this theory. The claim is that its hand and foot morphology are indicative of an arboreal lifestyle; the reversed hallux was used for grasping

branches, and its manual and pedal claws were used for grasping tree bark while climbing. *Archaeopteryx* also had a relatively weak shoulder girdle (as described in a previous section). It had very modern flight feathers but lacked the musculature and dorsoventral range of motion necessary for a powerful flight stroke. Therefore, it seems logical that *Archaeopteryx* might have been a glider – it even had feathers on its hindlimbs, and large tailfeathers to add more surface area for gliding flight. Recent studies on metabolism and flight kinematics, however, refute this logic in favor of the "ground up" hypothesis. Comparison to extant vertebrate gliders also weakens this hypothesis. All arboreal gliding vertebrates are quadrupedal. Clinging morphology evolved in the forelimbs of gliders that lack powered flight to make an arboreal lifestyle safer. If birds had an intermediate gliding stage, they either would have had much more developed wings before entering the trees (to help prevent uncontrolled falls), or they would have developed clinging forelimbs like extant gliders. The fossil record lacks evidence of either of these traits (Ostrom, 1979).

The "ground up" cursorial hypothesis posits that flight evolved as a result of basal theropods running to chase prey (such as insects and small mammals). To catch flying insects or climbing mammals, the ability to jump high would have been under positive selective pressure. Theropods with larger feathered forearms could flap while running to generate lift that would allow them to reach prey that was higher in the air. As selective pressure led to increasingly larger wings to produce more lift, this ultimately led to powered flight, which allowed the predator to follow the prey into the air to secure it. This explanation requires the least number of transitional stages, since basal theropods were bipedal, cursorial predators (an intermediary arboreal stage before powered flight would be an extra step). *Archaeopteryx* has the hindlimb morphology expected for a runner; it has a tridactyl pes, reversed hallux, fused metatarsus, mesotarsal joint, a parasagittal orientation of the hindlimb (Ostrom, 1974), and very well-developed hind limbs (more developed than the forelimbs) (Ostrom, 1979). The main argument against this hypothesis is that *Archaeopteryx* lacked the shoulder morphology and musculature necessary for powered flight, especially powered flight with a takeoff from the ground. Its forelimbs, while feathered, retain a relatively coelurosaurian morphology, which is well suited for grasping prey (with its clawed manual digits), but lack the morphology required for a powerful flight stroke.

A study by Burgers and Chiappe calculated the ability of *Archaeopteryx* to take off from the ground (1999). They found that during takeoff, the propulsion generated by the hindlimbs was gradually supplemented by thrust from the wings. Flapping helped increase running speed, as the lift from the wings decreased the portion of body weight being propelled by the legs. As the relative weight decreased, running speed would increase, causing lift to increase, creating a positive feedback loop that would allow *Archaeopteryx* to take off from the ground, even with a low amplitude wing beat and reduced pectoral musculature (as compared to extant birds). Thus, the flight stroke could have evolved from initial use for terrestrial thrust production. *Archaeopteryx* would likely have had a metabolism capable of such activity since we see such burst speed capability in extant lizards, which have the ancestral muscle state (Burgers and Chiappe, 1999).

The implications of predatory behavior in the "ground up" hypothesis refute the arboreal theory even further, by showing that hindlimb and forelimb morphology were likely evolved for predatory functionality, rather than climbing and perching behavior. Based on its skull morphology, *Archaeopteryx* preyed on small animals, such as insects, small mammals, and small lizards; it had conical, sharp teeth, raptorial claws on its manus, and a reversed hallux for grasping. Upon developing obligatory bipedalism, theropods freed their forearms for use in prey capture. Elongation of the forelimb, as well as an increase in the size of feathers, would allow the forelimb to be an effective grasping appendage, with the feathers acting as a net to corral small prey towards the feet (Ostrom, 1974). The motion of the forearm for grasping seen in maniraptorans is similar to the flight stroke seen in birds, and the intermediate orientation of *Archaeopteryx*'s shoulder might have produced the doughnut-shaped vortices necessary for forward propulsion during flight (Padian and Chiappe, 1998b). Like the forelimbs, the reversed hallux seen in *Archaeopteryx* likely had a predatory application, rather than a perching function. Firstly, the hallux is shortened and oriented slightly above the plane of the anterior toes. This morphology is less useful for perching and is most commonly seen in extant terrestrial birds (Ostrom, 1974). In *Deinonychus*, which was clearly not arboreal, the reversed hallux was used for grasping, as it could flex in towards the metatarsals to form a closed fist, used to immobilize prey. This same pedal morphology is seen in cursorial troodontids (which have reduced forelimbs that would likely have prohibited climbing) (Fowler et al., 2011), but it is not seen in

bipedal herbivorous ornithopods. Thus, the evolution of the opposable, reversed hallux was most likely evolved for predatory behavior, since its morphology aligns with diet (Ostrom, 1974).

Stability flapping and wing-assisted incline running, behaviors seen in extant birds, both support the cursorial, predatory theory for the evolution of flight in birds as well. While grasping prey with their feet, extant accipitrids flap their wings to maintain balance. Their long tail plumage also helps to enhance balance. *Deinonychus* could have similarly used its feathered arms to help balance itself while immobilizing prey with its hypertrophied second pedal digit. Likewise, *Archaeopteryx* has wings very similar in shape to extant accipitrids, so it might have used its wings for stability flapping. The lift provided by stability flapping, over time, could have been co-opted for flight (Fowler et al., 2011). *Archaeopteryx* might have also employed wing-assisted incline running to chase prey into trees or escape from predators. In juvenile Galliformes and Tinamiformes, the chicks flap their wings to increase traction while walking up vertical surfaces. Mature birds often use wing-assisted incline running to climb up overhangs as sharp as 105 degrees. This allows them to scale up to five meters without a running start. *Archaeopteryx* has an anteroposterior range of motion in its shoulder which would have been well suited to wing-assisted incline running (Dial, 2003). Thus, the evolution of the modern flight stroke likely evolved because of adaptations to improve cursorial predation in early avian ancestors.

Evolution of Powered Flight in Chiroptera[2]

Members of Chiroptera (bats, from here on) are the only mammals capable of powered flight. Like birds, bats took advantage of a new ecological niche and experienced great success as a clade. The over 1,100 species of extant bats represent over 20% of mammalian species. Additionally, bats inhabit every continent but Antarctica (Gunnell and Simmons, 2005). Bats have many unique morphological features that allow them to undertake powered flight: fusion of various vertebrae in all parts of the vertebral column (depending on the species) to increase skeletal rigidity, a bell-shaped rib cage, a well-developed pectoral girdle (with a large, keeled sternum, large clavicles, and an anteroposteriorly elongated scapula), an elongated forelimb

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[2] For phylogenies of Chiroptera referenced, see Appendix B.

(with secondary humeroscapular contact to lock the glenohumeral joint), a weak pelvic girdle (fused to the vertebral column), and well-formed feet with equal length digits for grasping (Walton, D. W. and Walton, G. M., 1970). The wing of bats is quite distinct from that of birds. Instead of reducing and fusing elements in the forelimb, bats retain them and elongate them (extreme elongation is seen in the metacarpals and phalanges). A very thin layer of skin forms the flight surface of bats, called the patagium. The propatagium connects the neck to the first digit, the dactylopatagium (also called the hand wing) stretches over the manual digits, the plagiopatagium stretches from the fifth digit to the ankle (Bishop, 2008), and the uropatagium spreads between the two hindlimbs (supported by the calcar – a cartilaginous or ossified structure that projects medially from the proximal calcaneum) (Anderson and Ruxton, 2020).

Unfortunately, unlike birds, the fossil record for bats is quite scarce. Bats are small, have delicate bones, and likely lived in forested areas with low preservation potential. The oldest fossils that have been presented as bats consist of individual teeth or isolated postcranial elements. Yet, since bats have such similar skull morphology to contemporaneous mammalian insectivores, these bone fragments cannot definitively be identified as bats and will not be described here (Gunnell and Simmons, 2005). The oldest definitive fossil bats are those preserved as fully articulated skeletons. The oldest found to date are *Onychonycteris finneyi* and *Icaronycteris index,* both from the early Eocene (Simmons et al., 2008). These two specimens are nearly identical to extant bats, and they are both fully capable of powered flight. Therefore, the fossil record does not reveal much about the evolution of flight in bats. By the middle Eocene, the extant families of bats begin to radiate, which affirms that *Onychonycteris* and *Icaronycteris* are highly evolved. These fossils indicate that the divergence of bats from non-flying ancestors likely occurred in the early Paleocene (Bishop, 2008). Identification of the morphological changes that occurred between these early bats and modern species might help piece together an image of what the ancestral, non-flying bat might have looked like, as well as the lifestyle and behavior that led to the evolution of powered flight.

Pectoral girdle and forelimbs:

Like birds, bats have very well-developed, robust pectoral girdles and elongated forearms to support the musculature and flight surface area necessary for powered flight. The scapula is

large and anteroposteriorly elongated, with large acromial and coracoid processes to stabilize the shoulder and provide sites for the attachment of flight muscles (Walton, D. W. and Walton, G. M., 1970). Unlike birds, which have a hemi-sellar glenohumeral joint, bats have the typical mammalian ball-and-socket joint, which confers five degrees of freedom for mobility (Anderson and Ruxton, 2020). The glenoid fossa is oriented laterally. The sternum is composed of a manubrium (with two lateral processes and one vertical process) and the sternal body, which has a median ridge/keel for flight muscle attachment (particularly the m. pectoralis, which powers the downstroke). The sternal keel, however, is not nearly as large in bats as it is in birds. The clavicles are long and large, with a smooth, expanded surface for articulation with the lateral processes of the sternal manubrium, and a knoblike terminus that articulates with the scapula. The large clavicle likely serves as a lever for pectoral movement.

Pectoral muscles involved in the flight stroke also connect to the rib laminae. For example, the m. serratus anterior complex (the posterior portion is critical for the downstroke, and the anterior portion helps initiate the upstroke) connects to the rib laminae. The connection of flight muscles to the rib cage causes the wing stroke to ventilate the lungs for more efficient breathing during flight (Simmons and Geisler, 1998). Respiratory modifications for flight are also seen in birds, which have unidirectional airflow.

The forearm articulates with the pectoral girdle via the glenohumeral joint. In bats, the ball-like head of the humerus projects medially from the humeral shaft. The radius is greatly elongated and somewhat arched to increase the horizontal cambering of the wing. It articulates with the humerus to form the elbow joint, which has a locking mechanism to prevent forearm rotation. In this mechanism, the medial epicondylar process of the humerus articulates with the radius to restrict mobility to a single plane for flexion and extension of the forearm. The radius also locks with the scapholunar and cuneiform in a tongue-in-groove socket in the wrist to prevent hyperextension of the limb, using strong tendons in place of heavy musculature to reduce weight towards the wingtip (similar to the mechanism seen in birds). In contrast to the radius, the ulna is rudimentary, with its proximal end joining to the radius at its midpoint. In some species, it is reduced to a small plate or doesn't exist at all. This serves to reduce weight. The presence of a sesamoid bone in the elbow (the ulnar patella) helps protect tendons during

forearm movement. The uniquely large quantity of protective sesamoid bones found in bats is a reflection of the power of the flight stroke.

In bats, the carpus is rotated 90 degrees compared to that of other mammals, so that the carpus lies in the plane of the wing. The metacarpals are extremely elongated and slender, with distal expansion for phalangeal articulation. The first manual digit (the thumb) is the most flexible, while digits II-V have metacarpals that are compressed together at their proximal ends to restrict movement. This restriction is beneficial for the wing stability, as these digits support the dactylopatagium (Walton, D. W. and Walton, G. M., 1970). Bats also have a reduced number of phalanges, which are all controlled by a single ligament. This increases the strength of the manus and decreases weight distally (Simmons and Geisler, 1998). To protect the elongated tendons from slipping, bats have many sesamoid bones in their manus to redirect the tendons and ligaments to be more mechanically efficient and protected (Anderson and Ruxton, 2020). Megabats retain claw-like nails on digits I and II, whereas microbats only have a claw on digit I (Walton, D. W. and Walton, G. M., 1970).[3]

The elongation and thinning of the bones of the forearms would have resulted in a lack of structural integrity if additional modifications to bone chemistry and development did not occur. In general, diameter decreases, medullary cavities become smaller, and the mineral content of bones decreases from the proximal to the distal end of the forearm. The humerus and radius have large diameters and high mineral content to increase rigidity, but they have thin cortical walls to minimize weight. In contrast, the metacarpals and phalanges have very small diameters but low mineral content, so they are light and flexible. This allows them to deform when acted on by forces during flight, instead of breaking (Bishop, 2008). The flexibility of the distal elements of the wing might also have evolved to provide spring-like tensioning of the flight membranes (Hedenström and Johansson, 2015).

As previously mentioned, all known fossil bats are essentially fully derived and capable of powered flight. Thus, only small morphological differences are discernable. *Onychonycteris finneyi* (52.5 million years ago, from the Green River Formation in Wyoming) shows some minor transitional characters (Fig. 14). It has a larger body size than most extant bats and more

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[3] Note that the most recent phylogenies reclassify Chiroptera into Yinpterochiroptera and Yangochiroptera. The older classification (Megabat vs. Microbat) is used here for simplicity of character assignment.

primitive limb proportions. Its radius is elongated but much less so than in extant bats. Thus, it has relatively short wings. The morphology of its pectoral girdle is nearly identical to those in extant bats; it has large clavicles and a sternal manubrium with a keel. The morphology of its rib cage is the same as extant bats, so it has that additional site for flight muscle attachment. It also has the same elongated manus and patagium seen in extant bats. Thus, *Onychonycteris* was capable of powered flight. It was probably a strong climber, as it retains claws on all five manual digits (the claws on digits IV and V are slightly reduced compared to those

Figure 14. *Onychonycteris finneyi.* Reprinted from American Museum of Natural History, 2014.

on digits I-III), which is likely the primitive condition (extant bats only retain claws on one to two digits, depending on the clade) (Simmons et al., 2008).

     Icaronycteris index is another fossil bat from the Green River Formation (Fig. 15). It is slightly younger than *Onychonycteris*. Like *Onychonycteris*, it is highly derived and has almost

Figure 15. *Icaronycteris index,* specimen YPM VPPU 018150. Reprinted from the Yale Peabody Museum of Natural History

all the same features as extant bats. It, however, has slightly more primitive limb proportions and claws on digits I and II, as well as small ossifications on digits III-V (Gunnell and Simmons,

2005). It lacks an ulnar patella (which serves to protect ligaments in the elbow joint), which may be an indication that the flight stroke was somewhat weaker than in extant bats (Walton, D. W. and Walton, G. M., 1970).

Many other fossil bats are found in the Messel Pit in Germany, including *Tachypteron franzeni, Archaeonycteris trigonodon*, *Palaeochiropteryx tupaiodon*, and *Hassianycteris messelensis* (Fig. 16). These bats are all from the middle Eocene, so they are slightly younger than *Icaronycteris*. They all show essentially modern morphology of the pectoral girdle and forelimbs but have less aerodynamically specialized wings than modern bats (which have wing shapes adapted to particular habitat types) (Habersetzer et. al., 1994). These fossil bats show that by the time *Hassianycteris* had diverged, the modern morphology of the shoulder girdle (specifically the glenohumeral locking mechanism with the secondary articulation of the humerus and scapula) and forearm (specifically the reduced number of phalanges and lack of claws) had evolved (Simmons and Geisler, 1998).
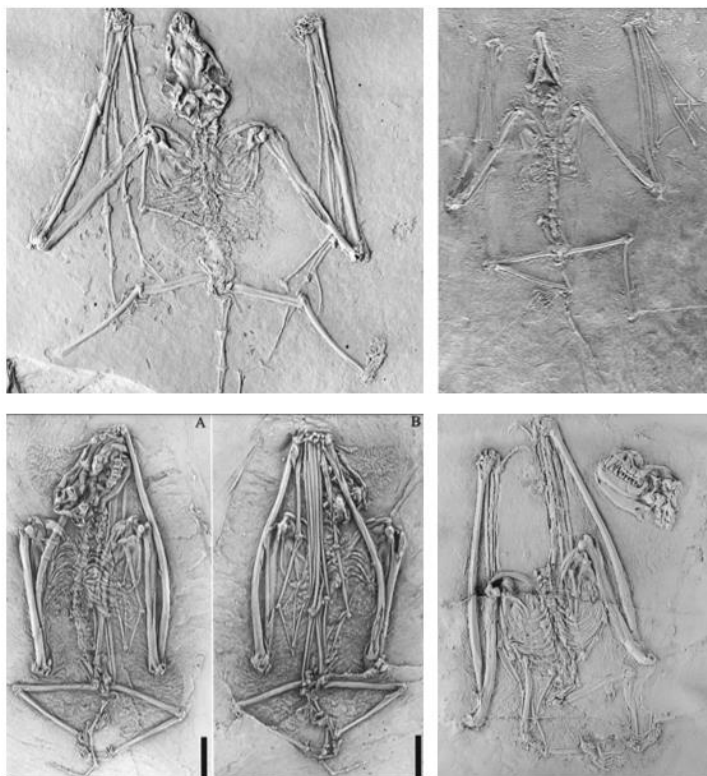

Figure 16. Bottom left: dorsal and ventral views of *Tachypteron franzeni*. Reprinted from Storch et al., 2002. Top left: *Palaeochiropteryx tupaiodon*. Top right: *Archaeonycteris trigonodon*. Bottom right: *Hassianycteris messelensis*. Reprinted from Simmons and Geisler, 1998.

Pelvic girdle and hindlimbs:

Since the primary mode of locomotion for bats is powered flight, well-developed hindlimbs are not necessary. Roosting and flight membrane support are the primary purposes of the hindlimbs in bats. Thus, the pelvis of bats is reduced and oriented differently compared to most other mammals. The ilium fuses with the sacrum to form the sacroiliac joint, which

increases pelvic stability when the hindlimbs and pelvis are subject to flight forces. Additional adaptations in the hindlimb and pelvis for membrane support include the parallel orientation of the pelvis relative to the vertebral column (which contrasts with the angled orientation seen in most other mammals), and the dorsolateral orientation of the acetabulum. This allows bats to hold their hindlimbs laterally and parallel to the plane of the body (Walton, D.W. and Walton, G.M., 1970), with the knee pointing outwards (Thewissen and Babcock, 1992). The femur morphology is similar to that seen in other mammals (Walton, D.W. and Walton, G.M., 1970). The femoral head is angled slightly medially with respect to the shaft, with an extremely reduced/absent neck. There are two trochanters on either side of the head for muscle attachment (Louzada, Nogueira, and Pessôa 2019). The femur shaft is very straight and has ridges for further muscle attachment involved in extending the legs to support the flight membrane. The tibia is about as long as the femur, and it is also quite straight. It lacks groves, however, for muscle attachment (which would be seen in quadrupedal mammals). The fibula, like the ulna, is very reduced (consistent with the evolution of a lighter skeleton for flight). Both the tibia and the fibula articulate loosely with the astragalus, so the foot has greater mobility relative to the leg (the ankle is not a hinge joint, so the pes can rotate caudally to assist in climbing). The legs remain somewhat elongated relative to the body, as they serve to support the patagium.

The tarsus consists of seven bones, organized into two rows (as in most mammals). The calcar (a medially projecting bone) articulates with the calcaneum in the first row of tarsal bones. Unique to bats, the calcar serves to support the uropatagium. In addition to flying, bats spend a lot of time hanging upside-down by their feet to rest and eat. The feet have short metatarsals and five digits of equal length with large claws for grasping (Walton, D.W. and Walton, G.M., 1970). The pedal digits also have a tendon locking mechanism that is activated when the claws are tensioned to assist in roosting (Simmons and Quinn, 1994).

As with the pectoral girdle and forearms, the pelvic girdle and hindlimbs of all known fossil bats are very modern in character. *Onychonycteris* differs from modern bats with its more robust leg morphology. It has long hindlimbs with a complete fibula (in extant bats, the fibula is reduced or nonexistent). It has a calcar and a long tail, which suggests it had a uropatagium. Pedal digit I is shorter than the other four digits, and they all have large claws (in modern bats, the pedal digits are usually the same length). The robustness of the hindlimbs suggests that

Onychonycteris might have utilized some form of quadrupedal locomotion, such as walking or climbing trees. Most fossil bats have more robust hindlimbs than modern bats (with femoral ridges for muscle attachment), which shows that the hindlimbs were involved in locomotion before the evolution of powered flight. *Onychonycteris* has pelvic morphology identical to that of modern bats, with the acetabulum oriented such that the hindlimbs can rotate outwards to support the flight membrane (Simmons et. al., 2008).

Icaronycteris index has similar morphology to *Onychonycteris*, with the head of the femur inclined relative to the axis of the femoral shaft and a robust fibula that is longer than the tibia. It has a long tail, but no calcar (Walton, D.W. and Walton, G.M., 1970).

The middle Eocene bat fossils from the Messel Pit show practically modern morphology. *Tachypteron franzeni* (which is an extinct member of the extant family, Emballonuridae), is well described. Its pelvis is fused to the sacral vertebrae. The femur and tibia both have very straight shafts (well-adapted for flight membrane support), and the fibula is very reduced (but still ossified). It also has a short calcar for support of the uropatagium. Unlike modern bats, it has a shortened pedal digit I relative to the other digits (Storch, et al., 2002). Other mid-Eocene bats, *Palaeochiropteryx* and *Archaeonycteris*, show similarly modern pelvic and hindlimb morphology (Walton, D.W. and Walton, G. M., 1970).

Integumentary system and flight kinematics:

The flight surface of bats is a membrane of very thin skin (Hedenström and Johansson, 2015). This skin on the flight surfaces is much thinner than that of the rest of the body (which is a normal thickness, when compared to similarly sized mammals). Membranes span between different parts of the body. The dactylopatagium (also called the hand wing) extends between the elongated digits of the manus (providing low-speed control by increasing the angle of attack, similar to the alula in birds). The propatagium stretches between the first digit and the neck, and the plagiopatagium stretches between the fifth digit and the ankle (the primary surface for lift and thrust generation). The uropatagium, which is present in some bat species, connects the ankles and the tail, with its trailing edge supported by the calcar (Thewissen and Babcock, 1992). In extant insectivorous bats, the uropatagium is a thicker and more durable membrane; based on

extant aerial hawking behaviors, it likely evolved to capture insects. The flight membrane is also thicker and more durable parallel to the digits and along the trailing edge of the plagiopatagium, possibly to help reduce shearing forces during flight (Hedenström and Johansson, 2015).

Unlike stiff bird wings, the wing membranes of bats make their wings flexible. The retention of a heavily jointed manus with all five digits enclosed in the wing membrane allows bats to manipulate their wing morphology to optimize its shape for the given aerodynamic conditions. This gives them better maneuverability and agility than birds. Like birds, bats reduce resistance during the upstroke by reducing the functional surface area of the wing. While birds rotate the manus, bats take advantage of their heavily jointed wings and reduce surface area by folding the forelimb at the shoulder and elbow joints. To improve aerodynamic efficiency during low-speed flight, bats perform an upwards wing flick to generate thrust and lift (Panyutina et al., 2015). This is analogous to the wing flick seen in birds during takeoff and landing. The main tradeoff that comes along with increased wing flexibility is that forces applied to the wing membrane pull the digits together, causing the wing to collapse and lose surface area. To counteract this, the plagiopatagium has muscles that originate on the body and insert into the membrane. For example, contraction of the m. occipito-pollicalis keeps the leading edge of the propatagium taut. Other intramembranous muscles act similarly and contract to take up the slack from the wing membrane when the digits are drawn together (Hedenström and Johansson, 2015).

The stages of evolution of bat wings can be inferred from developmental studies. During development, the dactylopatagium forms first. This occurs through a simple genetic modification, whereby the gene that leads to the selective apoptosis of interdigital tissue is never expressed. Similar to the theory of feather evolution in birds, the dactylopatagium might have initially been used to help corral prey and was later co-opted for flight. The other membranes then might have evolved in response to selective pressures towards increasing surface area for increased aerodynamic ability (Adams and Pedersen, 2013).

Onychonycteris had a wing with an aspect ratio of 5.0 (which is the smallest aspect ratio seen in the wings of extant bats, similar to that of the genus, *Nycteris*), a wing loading force much higher than that of extant bats (Amador, et al., 2019), and a small wingtip (Simmons et. al., 2008). These rudimentary features, in addition to a relatively large body mass, indicate that

Onychonycteris was probably a weak flyer. Its wing dimensions are similar to mouse-tailed bats, which fly by alternating rapid flapping with gliding, so *Onychonycteris* likely traveled short distances with undulating flight (Simmons, et. al., 2008). *Icaronycteris* and *Archaeonycteris* also have very low aspect ratio wings, and thus were likely perch hunters that flew short distances to compensate for weak sustained flight ability. They also both lack calcars, and thus lacked uropatagia (Speakman, 2001).

Tachypteron franzeni has more derived patagial features; it has nearly the same aspect ratio as extant *Taphozous melanopogon* (the black-bearded tomb bat, a fellow Emballonurid). *Taphozous* flutters its wings rapidly during flight, so *Tachypteron*, with its high aspect ratio wings and high wing loading likely also needed to flap rapidly to sustain flight (Storch, 2002).

Pathway to powered flight:

It is a general consensus that the early ancestors of bats were quadrupedal, arboreal insectivores (extant bats still employ awkward quadrupedal locomotion on occasion, so their morphology implies such ancestral capability). The ancestral condition (represented by *Onychonycteris*) of clawed hands and feet would have been well adapted for grasping trees. Additionally, the sprawling posture of the hindlimbs, now used for flight membrane support, would have increased stability while climbing up a flat surface (such as a thick tree trunk); this same hindlimb orientation allows colugos to effectively cling to flat surfaces (Panyutina et al., 2015). Furthermore, the mammalian fossil record from the Jurassic and Cretaceous is dominated by small, insectivorous taxa (Speakman, 2001). Most fossil bats have dentition indicative of insectivory and many extant bats are insectivores, so an insectivorous ancestor for bats is quite likely. How this quadrupedal, arboreal ancestor evolved to fly is less agreed upon by experts. As with birds, there are two main hypotheses for the evolution of flight in bats: evolution of flapping flight via a gliding intermediate, and direct evolution of flapping flight.

The evolution of flight in bats via a gliding intermediate is the most commonly cited since gliding flight occurs in other groups of extant mammals (Dermoptera, Rodentia, and Marsupialia). Thus, gliding flight in mammals might just be common enough for it to have evolved in bats as well (Gunnell and Simmons, 2005). If, in fact, bats had a gliding intermediate,

it likely looked very similar to modern gliding mammals, which all have a very strict morphological convergence. Extant bats even show a degree of morphological convergence with Dermopterans, which have hand and foot morphology well adapted to under-branch hanging (unlike bats, though, the forelimb elongation in Dermoptera does not occur in the manus, but in the stylopodium and zeugopodium) (Bishop, 2008).

The gliding theory suggests that the ancestors of bats evolved the plagiopatagium first to help stabilize and control their leaps between branches (Anderson and Ruxton, 2020). Since the plagiopatagium conferred the benefit of traveling farther distances more safely and effectively, the selective pressure would have existed to evolve an increasingly larger patagium to increase aerodynamic ability. This would be the least difficult path to powered flight since gliding is more energetically efficient than flapping. Additionally, when compared to the hemi-sellar glenohumeral joint in birds, the ball-and-socket equivalent in bats is much more flexible, so the musculature and motion required to extend the forearm and hold it in the frontal plane could have more easily been modified into the flight stroke from a gliding phase in bats than in birds. We also see extant gliding mammals adjust their forearm positioning to stabilize their glide, which could represent a very rudimentary precursor to the flight stroke (Bishop, 2008). A comparison to extant mouse-tailed bats (which have low aspect ratio wings, like expected in a gliding precursor), shows an intermediate flight style. These bats perform a flight style that alternates rapid flapping with gliding. This could represent the flight style of the transitional gliding-to-powered flapping bat ancestor (Simmons et al., 2008).

There are, however, various issues with this theory. Firstly, none of the mammalian gliders ever evolved a flapping form. This indicates that there might be a morphological restriction preventing this adaptation from occurring. This thought was affirmed with kinematic tests on gliding squirrels, which showed that the transition from a gliding form to a flapping form would actually be quite difficult (Adams and Pedersen, 2013). Additionally, most bats don't glide, so their patagia might not be the correct shape to form an airfoil for gliding. Perhaps the elongation of the manus in addition to the stylopodium and zeugopodium makes bat wings too flexible for gliding. Noting that gliding mammals never flapped and extant bats rarely glide, it seems unlikely that bats evolved from a gliding intermediate (Bishop, 2008).

The direct evolution of flapping flight seems like a larger than possible evolutionary step, but it can be well supported by the ontogenetic stages of extant bats. For gliding flight, it would be expected that the larger flight surface, the plagiopatagia, would evolve first (extant gliding mammals all have fleshy patagia between their fore and hind limbs). Bats, however, have elongated manual digits and a large dactylopatagium. In development, the dactylopatagium forms first (Adams and Pedersen, 2013). Bats also have plagiopatagia that extend from digit V to their ankle, whereas in other gliding mammals it extends from the wrist to the ankle (Anderson and Ruxton, 2020).

The extreme elongation of the manual digits unique to bats indicates that there was a unique selective pressure on bats that wasn't acting on other gliding mammals, so they must have had different lifestyles/behaviors. The direct flapping flight theory suggests that the ancestral bat was arboreal and used long digits with interdigital webbing to catch insects. It would hop and climb in the trees to prey on insects, so a larger forelimb surface area could have provided stability when landing by fluttering in addition to increased prey catching ability. This stability flapping mechanism is seen in the extant bat species, *Carollia perspicillata*, a member of Yangochiroptera. Shortly after birth, juvenile *C. perspicillata* bats undergo a "flop stage," where they reflexively flap their wings rapidly when falling to help control their descent. When they are about 17 days old, they flutter to control their jumps and increase the distance of jumps. Before their pectoral musculature and wings are fully developed, they can fly, but lack agility (this stage of development is very similar to the morphology seen in *Onychonycteris*) (Adams and Pedersen, 2013).

While this theory of evolution via direct flapping flight is doubted by many, it gains newfound support through comparison to the evolution of flight in birds.

A Novel Hypothesis, Supported by Comparison to Aves

Birds and bats are the only vertebrates to have evolved powered, flapping flight. Since birds and bats are also ecomorphs, their evolutionary pathways will likely have similarities. Birds and bats, however, adapted very distinct morphologies to allow for powered flight. Birds have a forearm with elongated stylopodia and zeugopodia but reduced and non-functional

manual digits. In contrast, bats form the skeletal support for their flight surface by greatly elongating manual digits II-V. They even retain functional claws on digits I and II. In birds, the initial driving force for the evolution of wings was predation. I propose that this was the initial driving force in bats as well, and that the different early habitat preferences of the taxa (terrestrial for birds and arboreal for bats) led to the stark anatomical differences seen in the two groups.

One argument against the direct origin of flapping flights in bats is that the flight surface, as in other mammals, should have evolved in response to selective pressures relating to increased aerodynamic ability. For an arboreal lifestyle, it seems as though a gliding intermediate would be highly advantageous for safe navigation amongst branches. Yet extant mammalian gliders all lack the manual modifications seen in bats. I suggest that the evolution of flight surfaces is closely tied to feeding strategy (which differed from ancestral gliding mammals), rather than aerodynamics, and that bats used their elongated manual digits to catch insects via stationary reach hunting and passive prey detection and gleaning. This inferred distinction between the feeding habits of early gliding mammals and early bats is supported by extant behavior. Extant gliding mammals are mostly herbivorous (relying on nectar, sap, and vegetation) (Goldingay, 2021), and they are never seen to catch prey or eat while gliding (Adams and Pedersen, 2013)). Therefore, there was no pressure selecting for large hands in the precursors to extant mammalian gliders, since they weren't grasping predators. In contrast, many bats use their uropatagium to capture insects mid-flight. Thus, it is possible that bats evolved their unique flight surface to assist in prey capture, with the elongated manual digits and dactylopatagia evolving to help corral prey towards the body. Increasing arm length and surface area would have increased the three-dimensional space that early bats could forage in while stationary reach hunting. The retention of large grasping claws on their pedal digits and a digital tendon locking mechanism could allow bats to have remained securely in trees while sweeping their forearms to gather insects. This is not an efficient method of hunting, so early bats probably supplemented stationary reach hunting with passive prey detection and gleaning, where they would perch to search for prey, and then hop down to capture it. The larger surface area of the forelimb patagia would help to control the descent towards the prey and capture the prey once it was within reach. Interestingly, tarsiers (primates), show greatly elongated manual digits. Tarsiers have a lifestyle similar to the proposed ancestral bat; they are quadrupedal, arboreal insectivores, that leap and use their long fingers to catch insects and cling to branches (Bearder, 2008). This could

represent morphological convergence, making tarsiers an extant example of what an ancestral bat might have looked like.

This novel hypothesis is supported through comparison to the evolution of the avian flight surface. The evolution of feathers in birds was clearly not driven by aerodynamics. As described in the sections on the avian integumentary system, feathers likely first evolved for insulation. Sexual selection and predatory strategies were likely selective pressures that led to the elongation of feathers, and the ultimate evolution of asymmetric flight feathers. In terms of predation, long feathers on the forearms of theropod dinosaurs (such as dromaeosaurids) could have been used to sweep insects and mammals towards the feet to be captured and immobilized by the large, retractable pedal claws (behavior that is seen in extant birds of prey). As the feathers elongated to benefit prey sweeping, they would have become inherently more aerodynamic. This allowed ancestral birds to jump and flutter up into the air to capture flying insects from a distance, and eventually run after prey while flapping to take off and follow prey into the air. Early birds jumped up after prey, and I propose that early bats jumped down.

Early maniraptorans and extant birds also employ stability flapping while restraining prey with their feet. When the feet are restraining prey and unable to assist in balancing the upper body, the wings are flapped rapidly to balance and orient it. From stability flapping, birds evolved flapping while running to ultimately take off into powered flight. Bat flight might have evolved similarly, but from the trees down, instead of the ground up. As mentioned, early bats might have hunted by dropping from high branches down to lower ones, catching insects with their patagia as they descended, all while using stability fluttering to reorient their body and achieve a controlled descent and landing. This would be a more rudimentary form of passive prey detection and gleaning, a hunting strategy seen in some extant bats (such as *Rhinolophus formosae* and *Megaderma lyra*), where they wait on a perch until prey is spotted, and then fly down to capture it (Lee et al., 2020). An analog for the proposed rudimentary stability flapping is seen in extant juvenile bats with underdeveloped wings and pectoral musculature (as described in the "Pathway to Powered Flight" section for chiropterans). At these early ontogenetic stages, *C. perspicillata* (a member of Yangochiroptera) had similar morphology to *Onychonycteris* (Adams and Pedersen, 2013), so it isn't unlikely that early bats used similar flapping methods to control their descent through tree branches. This stability flapping is also seen in *Megaderma*

lyra, a member of Yinpterochiroptera, whose juveniles show an undulating fluttering and gliding flight when dropped before the flight muscles and wings are fully developed (Rajan and Marimuthu, 1999). The fact that this behavior is seen in both Yinpterochiroptera and Yangochiroptera lends strong support to the proposed theory of direct flapping flight.

Bats, unlike birds, retained clawed grasping digits on both their hands and feet, and fossil bats show more robust and developed hindlimbs. These are adaptations for climbing. Thus, after controlled descent through branches and prey capture, early bats could have climbed back up to a higher perch to reset and continue hunting. Over time, selective pressures to increase the ancestral bat's ability to control its body during drop hunting would lead to increasingly more aerodynamic wings and a stronger flight stroke. Once powered flight evolved, bats could fly up to a perch to reset, eliminating the need for climbing to regain a perch. This led to the eventual reduction in the number of manual claws that we see in the fossil record.

In sum, based on comparisons with the more well-known evolution of birds, I propose that ancestral bats were initially arboreal insectivores, well adapted to climbing. To increase their ability to capture flying insects, long arms and a greatly elongated manus with interdigital webbing evolved. To increase caloric intake and hunting efficiency, early bats began dropping from branches to capture insects outside of their reach, using stability flapping to reorient their body and control their descent. Their manual claws, robust legs (with a loose ankle joint), and pedal claws were well adapted for climbing, allowing them to ascend trees back to a hunting perch. As stability flapping evolved to powered flapping flight, the manual digits lost their claws since climbing became a less necessary form of locomotion. Thus, the benefit of increased predatory efficiency likely led to the evolution of powered flights in bats, without a gliding intermediate.

Conclusions

The fossil record shows that the origin of flight in Aves is closely tied to predatory behavior. Likely, forearms were originally used to catch and grasp flying insects, and elongated forearm feathers were used to sweep prey towards the feet. The feet were then used to immobilize prey, freeing the forearms for use in stability flapping. When the manus was freed

from use in prey capture, bones co-ossified to make the wing more robust and aerodynamic. As forearms and feathers evolved to be longer, they gained more aerodynamic ability, allowing early birds to take off by flapping and running, as seen in extant birds. I propose that the evolution of flight in bats was equally tied to the predation of flying insects. My hypothesized ancestral bat was an arboreal insectivore, with elongated fingers adapted for grasping branches and catching insects. The dactylopatagium evolved first to help catch insects, and its inherent aerodynamic qualities had the additionally benefit of helping early bats navigate safely between the branches. Ancestral bats likely hunted by perching in branches and reaching their arms out to grab/sweep insects towards them. To supplement this calorically deficient hunting method, passive prey detection and gleaning was employed. After the prey was captured, the early bat would recover its perching spot by climbing. As the flight surface evolved to become larger (for more effective prey capture and controlled descent), it became aerodynamically capable of sustaining powered flight. Thus, the need for climbing decreased, and manual claws were lost. Through extensive research of the evolution of functional morphology for flight in Aves and Chiroptera, I propose that bats, like birds, evolved flight through direct flapping, co-opted from previous insectivorous predatory behaviors, and I resolve the discreet morphological adaptations for flight as a reflection of their initial habitats: from the ground up in birds, and the trees down in bats.

Acknowledgements

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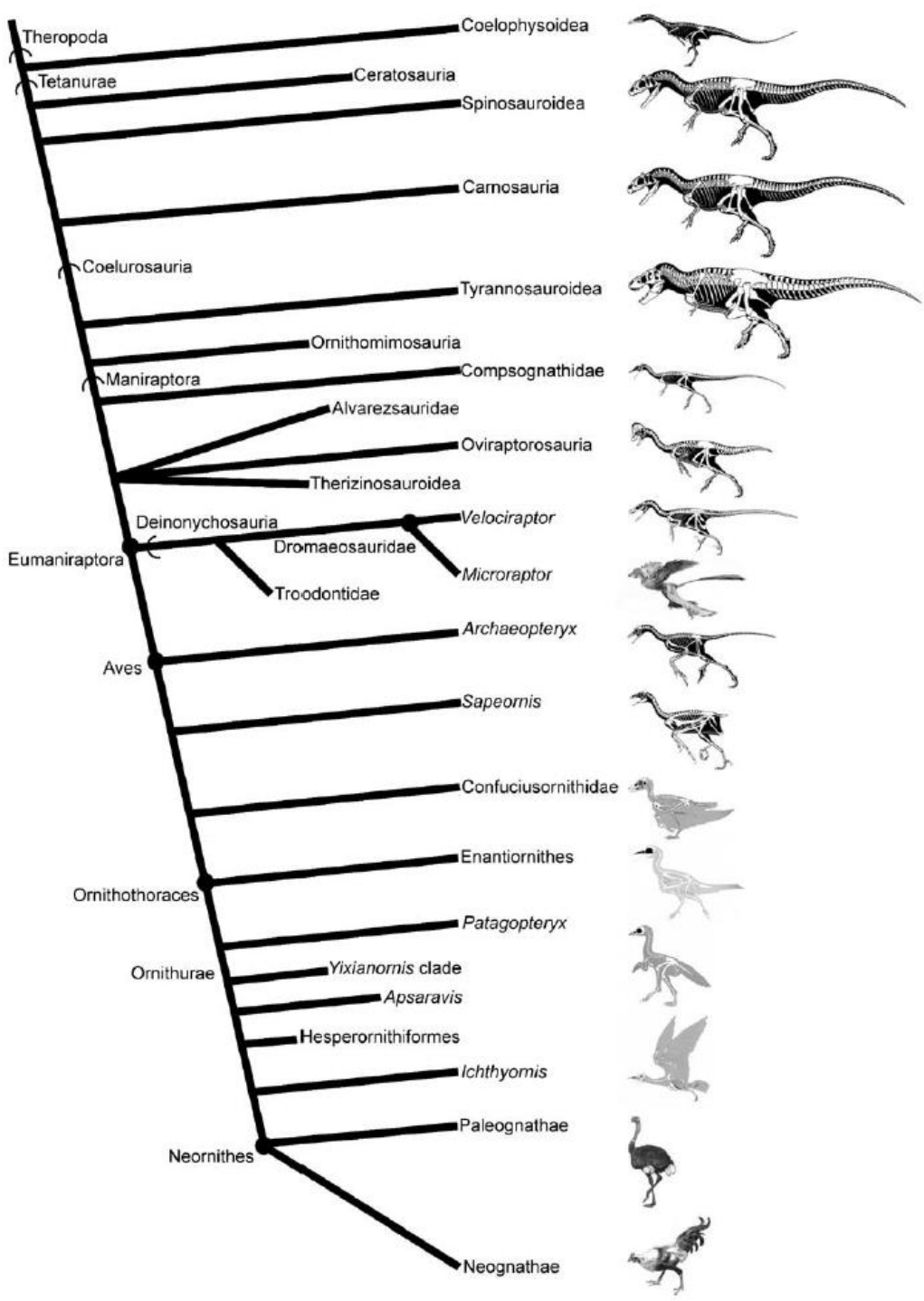
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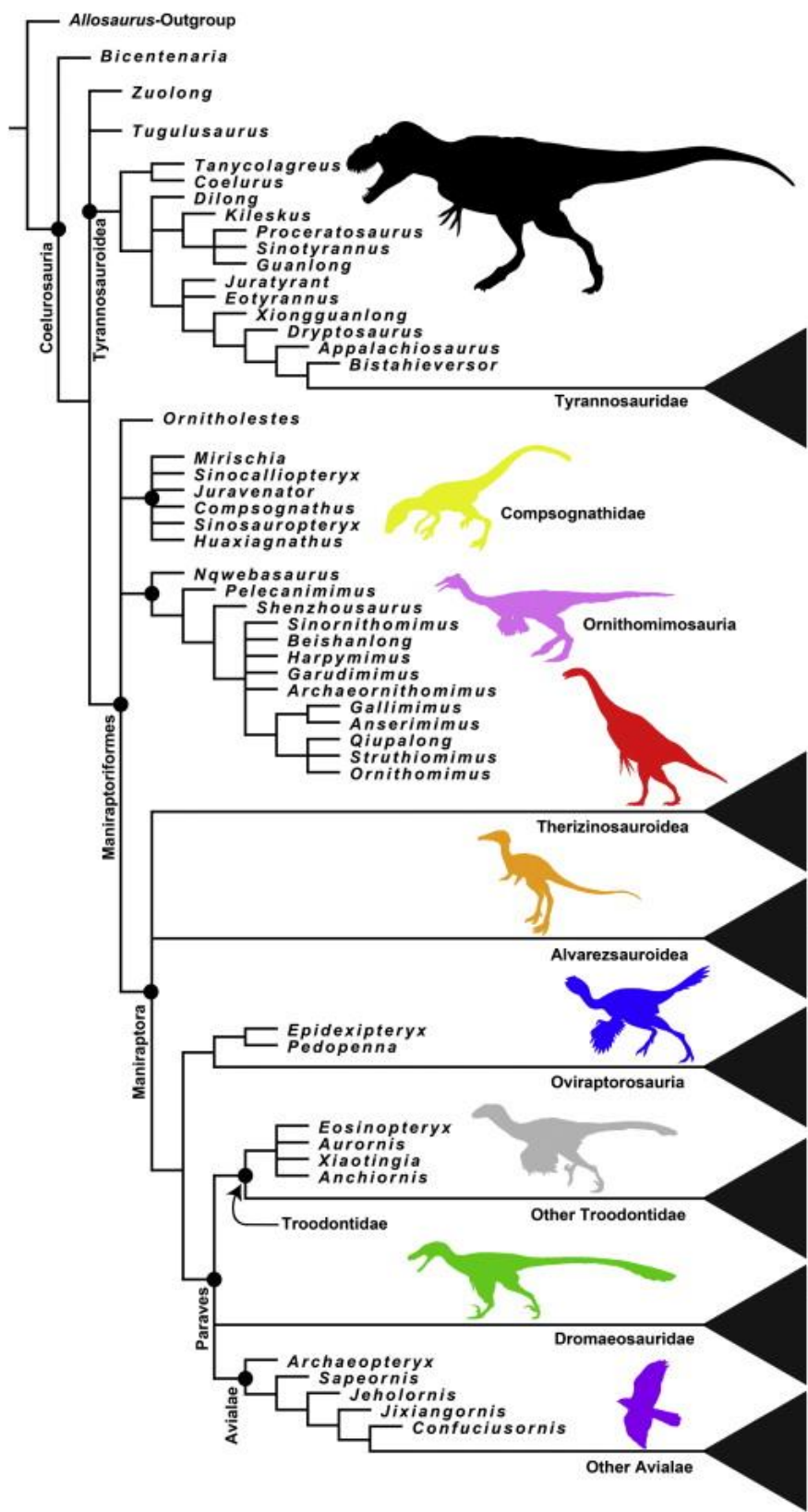
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Appendix A: Bird Phylogenies

Phylogeny of Theropoda. Reprinted from: Hutchinson and Allen, 2009.

Allosaurus-Outgroup
Bicentenaria
Zuolong
Tugulusaurus
Tanycolagreus
Coelurus
Dilong
Kileskus
Proceratosaurus
Sinotyrannus
Guanlong
Juratyrant
Eotyrannus
Xiongguanlong
Dryptosaurus
Appalachiosaurus
Bistahieversor

Tyrannosauridae

Coelurosauria

Tyrannosauroidea

Ornitholestes
Mirischia
Sinocalliopteryx
Juravenator
Compsognathus
Sinosauropteryx
Huaxiagnathus

Compsognathidae

Nqwebasaurus
Pelecanimimus
Shenzhousaurus
Sinornithomimus
Beishanlong
Harpymimus
Garudimimus
Archaeornithomimus
Gallimimus
Anserimimus
Qiupalong
Struthiomimus
Ornithomimus

Ornithomimosauria

Maniraptoriformes

Therizinosauroidea

Alvarezsauroidea

Maniraptora

Epidexipteryx
Pedopenna

Oviraptorosauria

Eosinopteryx
Aurornis
Xiaotingia
Anchiornis

Troodontidae

Other Troodontidae

Paraves

Dromaeosauridae

Archaeopteryx
Sapeornis
Jeholornis
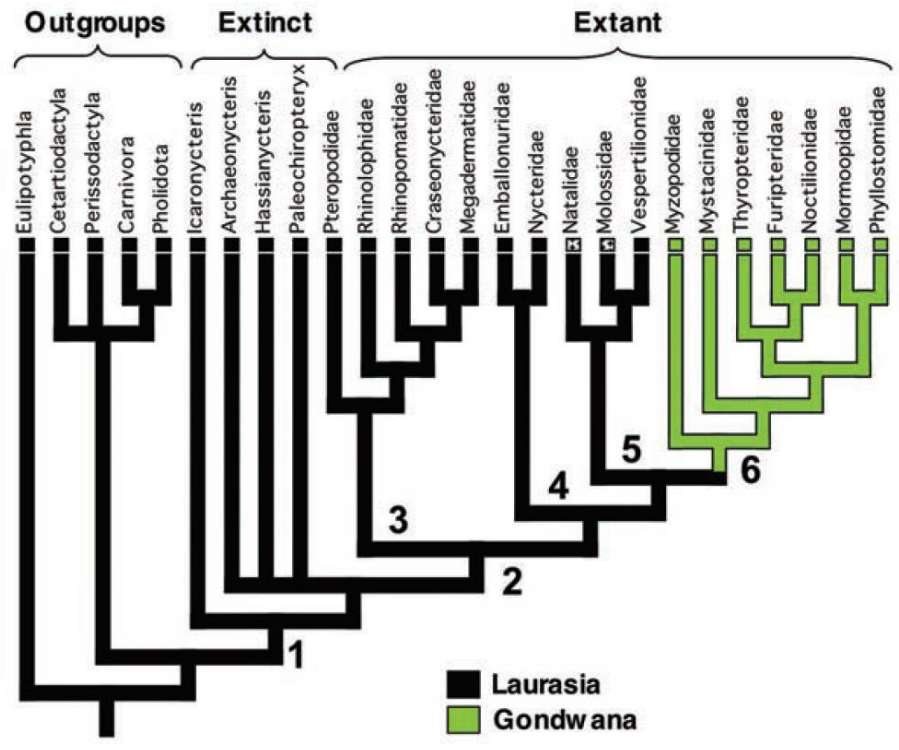*Jixiangornis*
Confuciusornis

Avialae

Other Avialae

Morphological phylogeny of Coelurosauria. Reprinted from: Brusatte, et al., 2014.

Appendix B: Bat Phylogenies
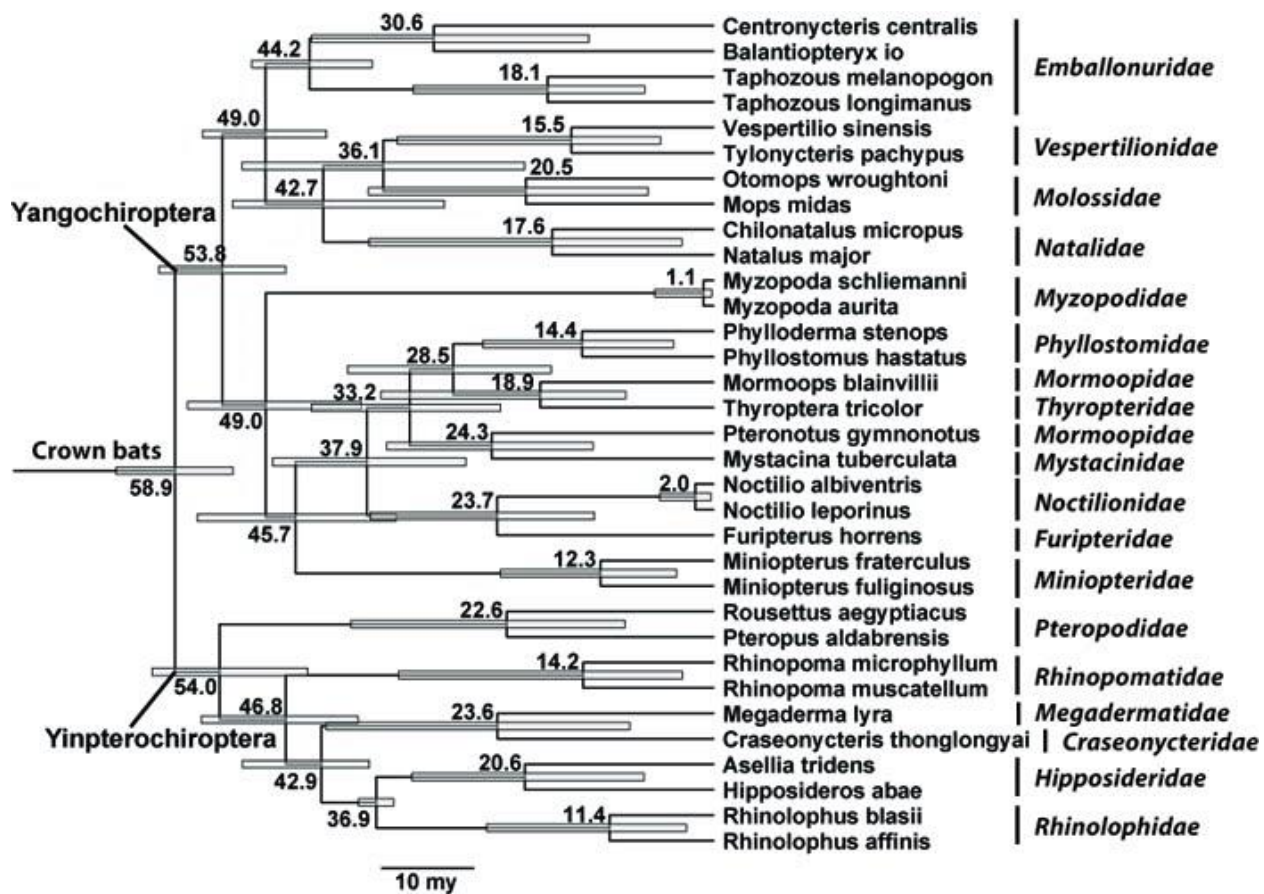
Molecular phylogeny of crown Chiropterans. Reprinted from Agnarsson et al., 2011.

Molecular phylogeny of extinct and extant Chiropterans. Nodes are labeled as follows: 1-Chiroptera, 2-Yangochiroptera, 3-Yinpterochiroptera, 4-Emballonuroidea, 5-Vespertilionoidea, and 6-Noctilionoidea. Reprinted from Teeling, 2005.