

Chapter 11

High Flyer or High Fashion? A Comparison of Flight Potential among Small-Bodied Paravians

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ABSTRACT

The origin of flight in birds and its relationship to bird origins itself has achieved something of a renaissance in recent years, driven by the discovery of a suite of small-bodied taxa with large pennaceous feathers. As some of these specimens date back to the Middle Jurassic and predate the earliest known birds, understanding how these potential aerofoil surfaces were used is of great importance to answering the question: which came first, the bird or the wing? Here we seek to address this question by directly comparing key members of three of the major clades of paravians: anchiornithines, *Microraptor* and *Archaeopteryx* across their known size classes to see how they differ in terms of major flight-related parameters (wing loading; disc loading; specific lift; glide speed; takeoff potential). Using specimens with snout to vent length (SVL) ranging from around 150 mm to 400 mm and mass ranging from approximately 130 g to 2 kg, we investigated patterns of inter- and intraspecific changes in flight potential. We find that anchiornithines show much higher wing- and disc-loading values and correspondingly high required minimum glide and takeoff speeds, along with lower specific lift and flapping running outputs suggesting little to no flight capability in this clade. In contrast, we see good support for flight potential, either gliding or powered flight, for all size classes of both *Microraptor* and *Archaeopteryx*, though there are differing patterns of how this shifts ontogenetically. These findings, coupled with previous findings of a lack of wing-based locomotion in early-diverging troodontids or dromaeosaurids, suggest that flight was not a synapomorphy of Paraves. This supports the contention that flight capacity and potentially powered flight itself arose convergently in at least two distinct paravian lineages, first in birds minimally 150 million years ago, then in the microraptorines 20–30 million years later. Our work indicates that the origin of flight among paravians was likely a more complex phenomenon than previously appreciated.

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INTRODUCTION

The origin of birds and the related, but not necessarily synchronous origin of powered theropod flight is an area of intense research (Agnolín and Novas, 2013; Brusatte et al., 2014, 2015; Lee et al., 2014; Puttick et al., 2014; Xu et al., 2014; Dececchi et al., 2016; Agnolín et al., 2019), including high-resolution phylogenetic analysis to identify the interrelationships among paravian clades (Brusatte et al., 2014; Cau et al., 2017; Xu et al., 2017; Cau, 2018; Hu et al., 2018; Pei et al., in press; see also Pittman et al., chapter 2). The pathway from nonavian theropods to birds has recently undergone a renaissance, including a greater understanding of the nonlinear nature of trait acquisition and the lack of a clear demarcation between “birds” and “nonavian dinosaurs” (Makovicky and Zanno, 2011; Godefroit et al., 2013; Brusatte et al., 2014; Cau, 2018; Hu et al., 2018; Pei et al., in press). What was once seen as a clear path is now understood to be a complicated series of lineage-specific specializations and convergences that makes the distillation of a single well-resolved topology difficult. This goal has been further complicated by the fact that flight—one of modern birds’ most quintessential and identifiable traits, long linked to their origins (Martin, 1983; Feduccia, 1996; Feduccia and Czerkas, 2015)—has recently been proposed to have more ancient beginnings (Xu et al., 2003, 2011, 2014; Han et al., 2014; Dececchi et al., 2016; Pei et al., in press). In that context, our work attempts to test whether the “four winged” bauplan seen in multiple paravian clades and linked to either powered or gliding flight (Xu et al., 2003, 2011; Zheng et al., 2013) is important in untangling a significant thread in this debate.

Recent finds document a suite of small-bodied taxa from suspected paravian lineages (Dromaeosauridae, Troodontidae, Avialae, and Anchiornithinae, the last one seen as birds by some and as troodontids or deinonychosaurs by others; see Pittman et al., chapter 2) with large pennaceous, often asymmetrical veined feathers on their fore-

and hind limbs (Zheng et al., 2013; Xu et al., 2017; Hu et al., 2018). As some of these specimens date to the Middle Jurassic and predate the earliest known birds (Brusatte et al., 2015; Hu et al., 2018), understanding how they used these potential airfoil surfaces and what the limits to their flight capacity were (i.e., powered flight vs. gliding) is critical to establishing the ancestral condition for later avialans, determining the palaeoecology of the Middle Mesozoic period, and reconstructing the ecological niche space available to small nonavian theropods across the origins of birds. Here we directly compare members of three of these lineages (Anchiornithinae, microraptorine dromaeosaurids, and the earliest well-accepted avialan, *Archaeopteryx*) to see how they differ in terms of major flight-related parameters and aerodynamic reconstructions. As feathered limbs become more widely recognized as the default of the various paravian clades and not a specialized feature, we need to move beyond the idea that “feathers make a wing” and understand how multiple parameters (wing size, feather structure, power output, input velocity, flapping angle and speed) interact to achieve volancy. Using multiple lines of evidence, we evaluate flight potential in both a strictly comparative, relative sense and against known physical benchmarks in the lineages bracketing the origin of birds. This knowledge will help us more accurately understand the evolution and ecological dynamics at play within small paravian theropods during the mid to late Mesozoic and begin to grapple with the question “What does it take to fly?”

METHODS

While there is still some uncertainty in the topology of the theropod tree nearest the origin of birds, especially placement of the anchiornithines, the scansoriopterygids, and what the sister group of Avialae is (Agnolín and Novas, 2013; Brusatte et al., 2014; Xu et al., 2014; Lefèvre et al., 2017; Xu et al., 2017; Cau, 2018; but see Pei et al., in press), there is little debate that birds emerged from a generalized, small-bodied paravian ancestor. With that in mind, we selected taxa whose phylogenetic placement

TABLE 1

Linear limb measurements for fossil paravian specimens

For individuals without published measurements of primary feather length, values were obtained in one of several ways: directly from images (BMNHC PH881, BMNHC PH804), from published wing length measurements (LVH 0026, *Archaeopteryx* specimens) or extrapolated from closely related taxa (CAGS 20-7-004, QV1002, V 12330, YFGP-T5197, YFGP-T5198, PKUP V1068). The value given in the original paper is inconsistent with other measures and other *Microraptor* specimens. As such we have included a second SVL based on our own measurements from the original images that are more consistent with relative and absolute values measured for the limb and tail regions as well as other *Microraptor* specimens. All measurements in mm. Abbreviations: **Fe**, femur; **Fore**, forelimb (H+ U+ Mc); **H**, humerus; **Hind**, hind limb (fe + Ti + Mt); **Mc**, metacarpal III; **Mt**, metatarsus; **Primary**, longest primary feather; **SVL**, snout to vent; **Ti**, tibia, **U**, ulna. LVH 0026 has two values in the SVL column. See text for details.

Taxon	Specimen number	SVL	H	U	MC	Primary	Fore	Wing	Fe	Ti	Mt	Hind
<i>Microraptor gui</i>	BMNHC PH881	153	47.4	44.7	31.8	140*	124	264	52.1	72.9	38.5	163.5
<i>M. gui</i>	IVPP V13320	215	57	53	31	186^	141	327	64	74	47	185
<i>M. gui</i>	IVPP V13352	297	83	70.3	45	222^	198	420	97	124.4	70.1	291.5
<i>M. gui</i>	QV1002	327	94.9	76.2	51.3	250#	222	472	108.9	143.6	75	327.5
<i>M.zhaoniaus</i>	CAGS 20-7-004	240	61.3	53.8	31.37	181#	146	327	74.8	94.2	47.76	216.8
<i>M.zhaoniaus</i>	IVPP V12330	145	42	37	22.3	113#	101	214	49.8	66	35.3	151.1
<i>M.hanqingi</i>	LVH 0026	405/360	93.5	81.9	54.9	255	230	485	111.7	137.1	75.4	324.2
<i>Anchiornis</i>	BMNHC PH804	185	45.7	39.8	23	50	109	159	50.9	69.1	41	161
<i>Anchiornis</i>	LPM-B00169	247	69	55	34	100	158	258	66.2	106.4	55.2	227.8
<i>Anchiornis</i>	PKUP V1068	275	72.2	59	32.1	110	163	273.3	90.5	117.7	56.4	264.6
<i>Eosinopteryx</i>	YFGP-T5197	166	37.9	42	21	57	101	157.8	48.5	69.5	35.5	153.5
<i>Aurornis</i>	YFGP-T5198	246	58	57	34	87	149	236	66.2	90.5	44	200.7
<i>Caihong</i>	PMoL-B00175	259	42.1	47.2	23.7	97	113	210	70.9	82.8	49	202.7
<i>Serikornis</i>	PMoL-AB00200	230	60.7	50.8	32	91	144	235	67.4	95.2	48.5	211.1
<i>Xiaotingia</i>	YFGP-T5198	295	71	65	24	107	160	267	84	-	-	-
<i>Archaeopteryx</i>	Eichstätt	154	41.5	36.5	17.8	-	96	191	37	52.5	30.2	119.7
<i>Archaeopteryx</i>	Berlin	231	63	56.2	24.8	172	144	316	52.2	68.5	37	157.7
<i>Archaeopteryx</i>	Solnhofen	300	83	72	34.3	-	189	375	67	92	47.5	206.5

bracket our current “best estimate” as to the origin of birds (Pei et al., in press) and that exemplify the paravian bauplan. We chose only well-represented and documented specimens, focusing on taxa with elongated pennaceous feathered limbs and with an estimated body mass less than 2 kg, using femur length (Christiansen and Farina, 2004), circumference (Campione et al., 2014), or published values based on 3-D or multivariate models (Chatterjee and Templin, 2007; Alexander et al., 2010; Dyke et al., 2013; Serrano et al., 2017). Based on these cri-

teria, our analysis is centered on the Anchiornithinae, *Microraptor* species complex (though there is some debate as to the interrelationships of small microraptorines: O’Connor et al., 2011), and members of the Archaeopterygidae (table 1), which have all been proposed to have aerial abilities. We did not include early-diverging troodontids as previous work has shown that similar-sized troodontids had little capability for aerodynamic force production, including for nonflight-related locomotion methods such as wing-assisted incline running (WAIR)

TABLE 2

Mass estimates for fossil paravian specimens

Based on either femur length from Christiansen and Farina (2004), femoral circumference based on Campione et al. (2014) or published reconstructions (Yalden, 1984; Chatterjee and Templin, 2007; Erickson et al., 2009; Alexander et al., 2010; Dyke et al., 2013; Serrano et al., 2017). Mass in kg. Abbreviations: **Fl**, mass derived from femoral length estimate; **Fc**, mass derived from femoral circumference estimate; **3D**, mass based on published models.

Taxon	Specimen number	Mass Fl	Mass Fc	Mass 3D
<i>Microraptor gui</i>	BMNHC PH881	0.24	0.18	-
<i>M. gui</i>	IVPP V13320	0.34	0.41	-
<i>M. gui</i>	IVPP V13352	1.30	0.88	0.95/ 0.50
<i>M. gui</i>	QV1002	1.88	1.25	-
<i>M. zhaoianus</i>	CAGS 20-7-004	0.57	0.35	-
<i>M. zhaoianus</i>	IVPP V12330	0.15	0.13	-
<i>M. hanqingi</i>	LVH 0026	2.05	-	1.23
<i>Anchiornis</i>	BMNHC PH804	0.16	0.19	-
<i>Anchiornis</i>	LPM-B00169	0.38	0.59	-
<i>Anchiornis</i>	PKUP V1068	1.04	0.61	-
<i>Eosinopteryx</i>	YFGP-T5197	0.14	0.36	-
<i>Aurornis</i>	YFGP-T5198	0.38	0.52	-
<i>Caihong</i>	PMoL-B00175	0.47	0.3	-
<i>Serikornis</i>	PMoL-AB00200	0.4	0.33	-
<i>Xiaotingia</i>	STM 27-2	0.82	0.86	-
<i>Archaeopteryx</i>	Eichstätt	-	-	0.18
<i>Archaeopteryx</i>	Berlin	-	-	0.25/0.34
<i>Archaeopteryx</i>	Solnhofen	-	-	1.09/ 0.68

or flap running (Dececchi et al., 2016), and had key aerodynamic metrics that were beyond the limits seen in extant and extinct flying animals, e.g., wing loading beyond the upper limit (Pei et al., in press). Scansoriopterygids were also excluded despite *Yi* and *Ambopteryx* being proposed as volant. This is because the wings of these taxa are believed to be patagium based rather than feather based and are thus structurally and functionally different from the wing bauplan of the earliest birds (Xu et al., 2015). We have kept species-level differentiation of the genus *Microraptor* (*M. zhaoianus*, *M. gui* and the controversial *M. hanqingi*) as well as generic differentiation of the “Yanliao” anchiornithines in accordance with Pei et al. (in press), despite recent work questioning the validity of some of these taxa

(Turner et al., 2012; Pei et al., 2017). Measurements were taken from the literature and from personal observations and communications. Element measurements not recorded in the literature or from undescribed specimens were taken from images using Inkscape software. We prioritized our own measurements when we were able to take them and found that they were within 2% of those reported in the literature. Some measurements were given through personal communications. For the details of measurement sources, see table 2.

As body size is a major determinant of behavioral ability (Dial et al., 2000), we chose to subdivide our specimens into three size classes based on snout to vent length (SVL) and reconstructed mass (table 2). For *Microraptor hanqingi*, we included a

recalculated SVL based on images of the specimens as the given value (415 mm) is 125% of the length of the similar-sized QV1002 (femoral length difference of 2.5%) is inconsistent with our measurements, both of this region and other regions of the specimen and suggests a significantly higher SVL to trunk ratio than other *Microraptor* specimens. This allowed us to compare morphometric changes with allometry both intra- and interspecifically, but also to see how they differ in terms of major flight-related linear morphometric parameters and aerodynamic reconstructions. We estimated body mass using femur length (Christiansen and Farina, 2004), femoral circumference (Campione et al., 2014), or published values based on 3-D or multivariate models (Chatterjee and Templin, 2007; Alexander et al., 2010; Dyke et al., 2013; Serrano et al., 2017; see table 2). This allowed us to bracket our estimates of flight capacity across a reasonable range of values for these key specimens. Wing length was reconstructed as the length of the longest primary added to the forelimb length (humerus + ulna + major metacarpal) with wingspan taken as $2.1 \times$ the length of a single wing, following the methodology of Dececchi et al. (2016). Wing area, unless otherwise indicated, was reconstructed using a modification of the equation in Dececchi et al. (2016), which takes the chord as only 55% of the longest primary feather length as corresponding to the difference between primary and secondary feather lengths in *Microraptor* (Li et al., 2012) and produces estimates within 2% of previous published values (see Pei et al., in press, for more details).

In reconstructing our criteria for flight ability we chose to use several metrics and methodologies to produce a more complete picture of the behavioral possibilities for the taxa in question. Wing loading denotes the mass supported by the lifting surfaces of an organism and has been shown previously to be less than 245 Nm^{-2} in flying vertebrates (Meunier, 1951). This upper maximum is thought to be a strong marker: when extant birds temporally exceed this, as during egg production, there is a corresponding loss in flight capacity (Guillemette and Ouellet, 2005). Simi-

larly, a value below this is not enough to signal flight, as pre fledging birds demonstrate (Austin and Ricklefs, 1977; Wright et al., 2006; Jackson et al., 2009; Sprague and Breuner, 2010). Nonpowered gliding taxa often have significantly lower values, commonly less than 100 Nm^{-2} (Socha et al., 2015). Higher values below this upper limit are not a direct indicator of poor flight capacity per se, but they do suggest reduced performance and maneuverability as they are often associated with higher required velocities to maintain sufficient lift (Dial et al., 2000; McGuire and Dudley, 2005, 2011; Stein et al., 2008). In addition, by including the related value of wing-disc loading, calculated as the circular area swept out by the wingspan, we have another commonly used measure that has been linked to energy expenditure, flight efficiency, and drag reduction in modern birds (Pennycuik, 1975, 1989).

Specific lift is a measure of the amount of lift generated per unit of body weight by an organism, and the vertical component of specific lift must be at least 9.8 Nkg^{-1} to overcome gravity (Marden, 1987, 1994), assuming negligible contributions from drag (which we consider to be a reasonable assumption for early birds and microraptorines). To calculate specific lift requires estimates of both muscle mass and power output, which are currently unknown in the taxa examined here. We assigned a flight muscle mass value of 10% of total body mass to our specimens rather than varying it because there is little knowledge on how this varied ontogenetically and among paravian species. This value is among the lowest known for competent living flyers (Greenewalt, 1975). Our reconstruction of flight muscle mass includes all muscles contributing to flight, not just the pectoralis musculature but muscles of the wing and back that were recruited prior to the evolution of the triosseal canal and ligamentous pulley system seen in late-diverging avialans (Baier et al., 2007). This value, while lower than seen in modern birds (Marden, 1987), is at the lower end of the range reconstructed in recent 3-D modeling of *Microraptor* and *Archaeopteryx* (Allen et al.,

2013; Heers et al., 2016). As such, we ran a second permutation using a higher value of 13% that more closely corresponds to the values seen in those analyses, facilitating more direct comparisons with them. For power output we adopted a range of values (225, 250, and 287 WKg^{-1}) corresponding to those seen in extant birds during takeoff, especially in short burst fliers (Askew et al., 2001; Guillemette and Ouellet, 2005). This allows us to examine how power output requirements would have had to vary across taxa and size classes if we assume a constant ability to achieve takeoff.

POWERED VERSUS NONPOWERED FLIGHT POTENTIAL

Beyond comparisons of simple linear metrics and ratios or empirically derived maximal and minimal thresholds to determine whether a taxon was theoretically capable of powered takeoff, we set out to examine performance across the specimens examined here under both a nonpowered (gliding) and a powered flight scenario (assuming it was possible). We chose to include both scenarios as they have been regularly proposed in the literature (Feduccia, 1996; Brusatte et al., 2014, 2015; Heers et al., 2014; Xu et al., 2014; Cau, 2018) and permit the possibility of arboreal and terrestrial launch sites, given ongoing debate into the ecology of theropod flight origins (Dececchi and Larsson, 2011; Dyke et al., 2013). For gliding flight, we chose two metrics as proxies for performance: minimum glide speed and minimum turning radius (see Longrich, 2006, for a more in-depth discussion). For both of these metrics we chose coefficient of lift (CL) values of 1 and 1.5, which correspond to the upper and lower range of values seen in extant avian flight and flapping-based locomotion (Longrich, 2006; Tobalske and Dial, 2007; Usherwood, 2009; Heers et al., 2011). For turn radius we chose a constant bank of 60° following Longrich (2006). As some previous reconstructions have suggested that feathered paravian hind

limbs may have had a role in gliding flight (Chatterjee and Templin, 2007; Alexander et al., 2010; Koehl et al., 2011; Dyke et al., 2013), we ran permutations with and without factoring in the hind limbs. For this we ran our specimens at an abduction angle of 45° from the vertical plane, which was probably beyond their possible range (Brougham and Brusatte, 2010; Manafzadeh and Padian, 2018). However, this mimics the “sprawled” leg position that has been previously modeled (Longrich, 2006; Alexander et al., 2010; Koehl et al., 2011; Dyke et al., 2013), permitting more direct comparisons with those studies. As there is little data on the area of the “hind wings” and as most specimens show incomplete preservation in this region we chose to model the areas based on scaling from previously published reconstructions (Longrich, 2006; Chatterjee and Templin, 2007; Dyke et al., 2013). For anchiornithines, for which there were no previous estimates, we chose to bracket our reconstructions using the forewing to hind-wing area ratio with values for *Microraptor* (around 50% of forewing area: Chatterjee and Templin, 2007; Dyke et al., 2013) as an upper bounds and *Archaeopteryx* (20% of forewing: Longrich, 2006) as the lower bound since this taxon lacks elongate feathers on the metatarsals (Foth et al., 2014). Given the length and distribution of plumage seen in the hind limbs of anchiornithines, it is more likely that their values approach the lower bounds, but we included both to be conservative. This does not mean they are not useful, as it allows us to estimate upper and lower bounds of capacity in these taxa to determine the limits of aerial behavior. We did not include the tail in our calculations as it is suspected that it functioned primarily in pitch control rather than as a high vertical force-generating surface in paravians (Han et al., 2014). However, it should be noted that this ignores any potential tail-body interactions, which could make our performance estimates more conservative, especially for taxa with more proximally located tail fans (i.e., shorter tails).

Unlike the gliding reconstructions, our flap-ping-based powered flight scenarios do not include lift generation from the hind limbs as they would have been held relatively vertically in these scenarios and thus would not present sufficient area to be considered active airfoils. Here we focused on reconstructing the minimal forward speed required to achieve takeoff, especially in a terrestrial setting. This required reconstructing a flap angle (70°) within the range of adduction possible for paravians based on shoulder morphology (Turner et al., 2012) and a minimal flapping speed derived from modified equations based on extant bird values, following Dececchi et al. (2016). We further examined whether these taxa could achieve takeoff using the flap running technique for thrust generation described by (Burgers and Chiappe, 1999). For this analysis we performed two major permutations of flap angle and CL to see how they would influence takeoff ability across our study group. First we ran the analysis using the CL (2) and flap angle (50°) (following Burgers and Chiappe, 1999), modifying only flapping frequency to our early equation to account for allometry. We then reduced CL to 1.5 to better approximate the value seen in living avians, and extended the flap angle to 70° to account for the greater excursion angles permitted by the paravian shoulder joint. We note that a CL of 2.0 may be generous for early avialan wings. By contrast, juvenile chukars can generate a maximum CL of nearly 1.5 just 49 days posthatching (dph), which is the stage suggested to mimic the wing development seen in *Microraptor* and *Archaeopteryx* (Heers et al., 2014), with values over 1 seen in 10 dph age class and above (Heers et al., 2011). We suggest that wing performance of these subadult galliform birds represents a more realistic model of paravian wing performance than the CL of 2 proposed by Burgers and Chiappe (1999). Interestingly, at this life stage, chukars show high wing effectiveness but low aerodynamic efficiency (i.e., high maximum CL and low lift to drag ratio (L:D)—a feature that seems to align with independent models of paravian performance (Palmer, 2014).

RESULTS

MORPHOMETRIC PATTERNS

Examination of the linear measurements across taxa and size classes indicates several significant patterns. First, there appears to be no correlation between relative forelimb length and increasing size in either *Microraptor* or anchiornithines (slope -0.0005 , $p = 0.37$). This does not change if we use the longer SVL for *M. huanqingi* (slope -0.0006 , $p = 0.07$), our new estimate of SVL (slope -0.0004 , $p = 0.18$), or if we exclude it altogether (slope -0.0005 , $p = 0.29$). We also find that, while anchiornithines show slightly reduced forelimb lengths compared to either *Microraptor* or *Archaeopteryx* if we use SVL, they are within the range seen in both groups (table 3). We see a similar lack of decreasing relative forelimb length if we use femoral length as opposed to SVL (*Microraptor* slope $= -0.003$, $p = 0.28$; anchiornithines slope $= -0.008$, $p = 0.23$), but interestingly some members of the anchiornithines show slightly higher forelimb to femur ratios, though the difference is not significant (t test $= 0.616$, $p = 0.55$). This may be due to the relatively longer hind limbs seen in *Microraptor* compared to the other taxa examined here, something previously reported (Dececchi and Larsson, 2013) and may hint at ecological differences. Compared to both anchiornithines and *Microraptor*, *Archaeopteryx* has a notably larger forelimb to femur ratio, and one that suggests positive allometry, but this pattern is not present when we use SVL. We in fact see a slight decrease in hind-limb length with size in this taxon, which may influence the forelimb to femur value. This pattern of divergence in forelimb and hind-limb scaling is different from the other two clades, but is similar to a larger pattern observed in early birds compared to nonavian maniraptoran theropods (Dececchi and Larsson, 2013).

While there was little differentiation between anchiornithines and *Microraptor* using forelimb length, this is not the case if we use total wing length. Here we see a distinctly larger wing length in microraptorines using

TABLE 3

Morphometrics for fossil paravian specimens

Note that we included two separate values for the SVL reconstruction of *M. hanqingi* due to the uncertainty in the original published values (see text for description). We treat these as a minimum SVL (our own reconstruction represented by ¹) and a maximum SVL (² per Gong et al. (2012)). We have run permutations with both extremes (see text) to determine how using either estimate affects the overall results of limb length scaling with increasing body size.

The original reconstruction of *M. hanqingi* and our own reconstruction are both included to determine how they affect the overall results with increasing body size. Abbreviations: **Fe**, femur; **FL**, forelimb; **H**, humerus; **HL**, humeral length; **SVL**, snout to vent length; **W**, wing length (forelimb + longest primary); **U**, ulna.

Taxon	Specimen number	SVL	FL/ SVL	HL/ SVL	W / SVL	FL/ Fe	W / Fe	H/ Fe
<i>M. zhaoianus</i>	IVPP V12330	145	0.70	1.04	1.48	2.03	4.30	0.84
<i>M. gui</i>	BMNHC PH881	153	0.81	1.07	1.72	2.38	5.07	0.91
<i>Archaeopteryx</i>	Eichstätt	153.5	0.62	0.78	1.24	2.59	5.15	1.12
<i>Eosinopteryx</i>	YFGP-T5197	165.8	0.61	0.93	0.95	2.08	3.25	0.78
<i>Anchiornis</i>	BMNHC PH804	185	0.59	0.87	0.86	2.13	3.11	0.90
<i>M. gui</i>	IVPP V13320	215	0.66	0.86	1.52	2.20	5.11	0.89
<i>Serikornis</i>	PMoL-AB00200	230	0.62	0.92	1.02	2.13	3.48	0.90
<i>Archaeopteryx</i>	Berlin	231	0.62	0.68	1.37	2.76	6.05	1.21
<i>M. zhaoianus</i>	CAGS 20-7-004	240	0.61	0.90	1.36	1.96	4.38	0.82
<i>Aurornis</i>	YFGP-T5198	246	0.61	0.82	0.96	2.25	3.56	0.88
<i>Anchiornis</i>	LPM-B00169	246.9	0.64	0.92	1.04	2.39	3.90	1.04
<i>Caihong</i>	PMoL-B00175	259	0.44	0.78	0.81	1.59	2.96	0.59
<i>Anchiornis</i>	PKUP V1068	275	0.59	0.96	0.99	1.80	3.02	0.80
<i>Xiaotingia</i>	STM 27-2	295	0.54	-	0.90	1.90	3.17	0.85
<i>M. gui</i>	IVPP V13352	297	0.67	0.98	1.42	2.04	4.33	0.86
<i>Archaeopteryx</i>	Solnhofen	300	0.63	0.69	1.25	2.83	5.60	1.24
<i>M. gui</i>	QV1002	327	0.68	1.00	1.44	2.04	4.34	0.87
<i>M. hanqingi</i>	LVH 0026 ¹	360	0.64	0.90	1.35	2.06	4.34	0.84
<i>M. hanqingi</i>	LVH 0026 ²	405	0.57	0.80	1.20	2.06	4.34	0.84

either SVL (mean of 1.47× SVL compared with 0.94 for anchiornithines, $t = 9.87$, $p < 0.001$) or femur (mean = 4.55× femur length compared with 3.31, $t = 7.04$, $p < 0.001$). Notably, we do have some evidence that wing length decreases with increased SVL, though this is only significant if we use the larger measure for *M. hanqingi* ($p = 0.03$) and it is not seen if we use femoral length ($p = 0.21$). In direct comparisons across size classes we consistently see much longer wings in *Microraptor* species than in either anchiornithine or *Archaeopteryx* specimens using SVL as a measure, but not when using femoral length, again suggesting a bifurcation in the trajectory of the fore- and hind limbs in early avialans.

LOADING AND LIFT GENERATIONS

We find all wing-loading values below the maximum value of 245 Nm^{-2} seen in extant volant taxa, with the exception of *Eosinopteryx* when its body mass is estimated using femoral circumference. These values are significantly different between clades and with increasing body size, using the forewing only when fore- and hind-wing areas are combined (table 4). In a comparable size class using the same mass estimator, anchiornithines have wing-loading values 260%–680% larger than a similar-sized *Microraptor* and 230%–610% larger than a similar-sized *Archaeopteryx*. This pattern also occurs if we include hind-limb wing area. When we are reconstructing anchiornithines with hind-wing areas proportional to those seen in *Microraptor* we are likely underestimating the magnitude of this difference. The reason is that the forewing:hindwing area ratio is likely overestimated in anchiornithines relative to *Microraptor*. In the former, the tibial feathers (95%–150% of femoral length, FL) and metatarsal feathers (45%–70% of FL) are proportionally significantly shorter than those seen in *Microraptor*, which have tibial feathers 170% of FL and metatarsal feathers 200%–210% of FL respectively. Thus the wing-loading difference between these two clades is likely only exacerbated if we include the hind wing's influence. Across size categories within *Microraptor* we see a trend of increasing wing loading in larger individuals (table 5). We do not see a clear pattern in anchiornithines, though generic level differences in wing use and behavior may be masking underlying ontogenetic trends. In *Archaeopteryx* we see the lowest loading values in intermediate sized individuals, with both smaller and larger size classes showing similar levels of loading. While this is intriguing, it requires larger sampling to confirm its validity. For disc loading we see something of an increase in loading with size, though this is most apparent between the largest individuals and not between small and medium size classes. We see a separation between anchiornithines and *Microraptor*,

with the former showing values above what is expected in a gliding lineage (Sprague and Breuner, 2010), but all taxa show values within the range of extant powered fliers (Nudds and Bryant, 2000; Tobalske and Dial, 2000; Askew et al., 2001).

A similar trend is seen among specific lift numbers, though these values do appear to suggest a more restrictive subset of flight capable taxa and specimens. Using a 10% flight muscle mass fraction we find only 10 of 48 reconstructions for anchiornithines result in lift generation values sufficient to permit flight from the ground, of which 7 of them come using the femoral length mass estimation method. In contrast, 34 of a possible 51 permutations in *Microraptor* and 11 of 15 for *Archaeopteryx* show ground launch and climb-out capability. Again, we see a significant effect of increasing body size; in both *Microraptor* and *Archaeopteryx* the largest individuals in our sample require the highest levels of power output to generate sufficient lift for takeoff. One possible reason for the low number of successful launches in the latter two groups could be that a 10% flight muscle fraction is simply too low an estimate. Three-dimensional volumetric work has suggested a higher value closer to 12% or 13% in *Archaeopteryx* and *Microraptor* (Allen et al., 2013; Heers et al., 2016), which is supported by osteological evidence such as the larger sternum in *Microraptor*. Using this higher estimate, we find 43 of 48 iterations for *Microraptor* and 14 out of 15 for *Archaeopteryx* achieve the necessary lift for flight.

GLIDING FLIGHT

As glide speed is intimately linked with wing loading, we see a similar pattern of increased minimal glide speed both across the clades and with increasing size (table 6, fig. 1). While we cannot make a clear statement of a speed beyond that expected from a gliding animal, in similar environments (i.e., terrestrial tree to tree locomotion) glide speed ranges between 5 and 13 ms^{-1} across tetrapods (Emerson and Koehl, 1990;

TABLE 4

Wing loading and disc loading for fossil paravian specimens

For *Microraptor gui* IVPP V13352 two different wing area reconstructions were used to capture the range of published estimates adopted in previous aerodynamic investigations: area estimates following Chatterjee and Templin (2007) are indicated by ¹ and those following Dyke et al. (2013) are indicated by ². There are several different mass estimates for the *Archaeopteryx* specimens studied here. Our analysis involved permutations based on these previously published values. Values accompanied by ³ correspond to those from Serrano et al. (2017), ⁴ for those from Yalden (1984) and ⁵ following Erickson et al. (2009). Abbreviations: **Fl**, mass derived from femoral length estimate; **Fc**, mass derived from femoral circumference estimate, **3D**, mass based on published models.

A. Calculated values for wing loading using the forewing area only (FW) and using forewing + hindwing area (TW)									
Taxa	Specimen	FW	TW	Wing loading FW			Wing loading TW		
				Fl	Fc	3D	Fl	Fc	3D
<i>M. gui</i>	BMNHC PH881	0.04	0.06	55.1	41.3	-	36.7	27.6	-
	IVPP V13320	0.07	0.11	47.4	57.2	-	31.6	38.1	-
	IVPP V13352 ¹	0.09	0.13	143.1	96.9	104.6	96.5	65.3	70.5
	IVPP V13352 ²	0.09	0.14	141.7	95.9	54.5	93.2	63.1	35.8
	QV1002	0.14	0.20	135.1	89.8	-	90.0	59.9	-
<i>M. zhaoianus</i>	CAGS 20-7-004	0.07	0.10	81.6	50.1	-	54.4	33.4	-
	IVPP V12330	0.03	0.04	52.2	45.3	-	34.8	30.2	-
<i>M. hanqingi</i>	LVH 0026 ³	0.14	0.28	142.5	-	85.5	70.7	-	42.4
<i>Anchiornis</i>	BMNHC PH804	0.01	0.01	171.3	203.4	-	114.2	135.6	-
	LPM-B00169	0.03	0.04	125.0	194.0	-	83.3	129.4	-
	PKUP V1068	0.03	0.05	293.5	172.2	-	195.7	114.8	-
<i>Eosinopteryx</i>	YFGP-T5197	0.01	0.02	132.5	340.6	-	88.3	227.1	-
<i>Aurornis</i>	YFGP-T5198	0.02	0.04	157.0	214.9	-	104.7	143.3	-
<i>Caihong</i>	PMoL-B00175	0.02	0.04	195.8	125.0	-	130.5	83.3	-
<i>Serikornis</i>	PMoL-AB00200	0.02	0.04	159.0	131.2	-	106.0	87.5	-
<i>Xiaotingia</i>	STM 27-2	0.03	0.05	245.1	257.1	-	163.4	171.4	-
<i>Archaeopteryx</i>	Eichstätt	0.02	0.03	-	-	74.3	-	-	62.0
	Berlin ⁴	0.05	0.06	-	-	44.9	-	-	38.2
	Berlin ⁵	0.06	0.07	-	-	55.4	-	-	46.2
	Solnhofen ⁴	0.12	0.15	-	-	86.3	-	-	71.9
	Solnhofen ⁵	0.12	0.15	-	-	68.1	-	-	56.7

B. Calculated values for disc loading (Nm⁻²)

Taxa	Specimen	Disc	Disc loading		
			Fl	Fc	3D
<i>M. gui</i>	BMNHC PH881	0.24	9.8	7.3	-
	IVPP V13320	0.37	9.0	10.8	-
	IVPP V13352 ¹	0.69	14.1	20.8	13.4
	IVPP V13352 ²	0.58	14.1	20.8	8.4
	QV1002	0.77	23.9	15.9	-

TABLE 4 continued

Taxa	Specimen	Disc	Disc loading		
			Fl	Fc	3D
<i>M. zhaoianus</i>	CAGS 20-7-004	0.37	15.0	9.1	-
	IVPP V12330	0.16	9.3	8.0	-
<i>M. hanqingi</i>	LVH 0026	0.82	24.6	-	14.8
<i>Anchiornis</i>	BMNHC PH804	0.09	18.3	21.4	-
	LPM-B00169	0.23	16.1	24.9	-
	PKUP V1068	0.26	39.3	23.2	-
<i>Eosinopteryx</i>	YFGP-T5197	0.09			-
<i>Aurornis</i>	YFGP-T5198	0.19	19.3	26.6	-
<i>Caihong</i>	PMoL-B00175	0.15	30.3	19.5	-
<i>Serikornis</i>	PMoL-AB00200	0.19	20.7	16.9	-
<i>Xiaotingia</i>	STM 27-2	0.25	32.5	34.3	-
<i>Archaeopteryx</i>	Eichstätt ³	0.13	-	-	13.7
	Berlin ⁴	0.28	-	-	8.7
	Berlin ³	0.28	-	-	12.0
	Solnhofen ³	0.48	-	-	22.1
	Solnhofen ⁵	0.48	-	-	13.9

Socha et al., 2015) with higher speeds of 10–20 ms⁻¹ in soaring specialists and seabirds (Alerstam et al., 1993; Koehl et al., 2011). Using the forewings only at a CL of 1.5 we find glide speed estimates of less than 10 ms⁻¹ for most of the *Microraptor* and *Archaeopteryx* reconstructed at less than 1 kg, while members of the anchiornithines show values ranging from 11.6 to 19 ms⁻¹. This places the anchiornithines at the upper range of what is seen in extant gliders. If we use a CL of 1, this range is increased to between 14.3 and 26 ms⁻¹ and is comparable to speeds seen in dynamic seabirds soaring in high-wind conditions (Alerstam et al., 1993) and beyond what is seen in terrestrial taxa (Socha et al., 2015). As previously noted, our estimates of hind-wing influence are likely overstated, but we included them to mimic the “four winged” scenario that has been suggested. We find that in this scenario the minimum glide speeds are significantly reduced, though are still very high in anchiornithines compared to modern gliders ranging from 10–16.5 ms⁻¹ under the *Microraptor* hindwing

model and 11–18 ms⁻¹ under the *Archaeopteryx* model (under a CL of 1.5 and a hip angle of 45°). Our estimates are for equilibrium gliding, for the sake of comparison with powered-flight performance characteristics. We note that in living taxa glides are often short and do not reach an equilibrium state. However, we also note that with an animal as large as *Microraptor* (~1 kg), small gaps could likely be easily cleared with leaping alone, making long distance glide performance more relevant.

We contend that minimum turning radius is a proxy of the maneuverability of an individual during gliding flight and was likely highly important in navigating forested parts of their habitats (Wang et al., 2006; Burnham, 2007; Gong et al., 2012). Given that this exact value would vary based on multiple parameters, such as the exact placement and angling of both the hind limbs and tail (Longrich, 2006), and is notoriously difficult to model accurately even in extant birds, whose characteristics often violate some of the key assumptions of this equation (Warrick et al.,

TABLE 5

Specific lift values for fossil paravian specimens

Values above 9.8 Nkg⁻¹ indicate flight capability. Abbreviations: **Fl**, mass derived from femoral length estimate; **Fc**, mass derived from femoral circumference estimate; **3D**, mass based on published models.

A. Specific lift in Nkg ⁻¹ using a flight muscle mass estimate of 10% of total mass muscle mass for <i>Microraptor</i> and <i>Archaeopteryx</i>										
Taxa	Specimen	Fl			Fc			3D		
		225	250	287	225	250	287	225	250	287
<i>M. gui</i>	BMNHC PH881	11.1	12.3	14.1	12.6	14.0	16.1	-	-	-
<i>M. gui</i>	IVPP V13320	11.4	12.7	14.5	10.5	11.7	13.4	-	-	-
<i>M. gui</i>	IVPP V13352	9.3	10.3	11.8	7.8	8.7	10.0	11.7/ 9.5	13.0/ 10.5	14.9/ 12.1
<i>M. gui</i>	QV1002	7.3	8.1	9.3	8.8	9.7	11.2	-	-	-
<i>M. zhaoianus</i>	CAGS 20-7-004	9.1	10.1	11.6	11.3	12.6	14.4	-	-	-
<i>M. zhaoianus</i>	IVPP V12330	11.4	12.7	14.6	12.2	13.5	15.5	-	-	-
<i>M. hanqingi</i>	LVH 0026	7.2	8.0	9.2	-	-	-	9.0	10.1	11.5
<i>Anchiornis</i>	BMNHC PH804	8.6	9.5	10.9	8.0	8.9	10.2	-	-	-
<i>Anchiornis</i>	LPM-B00169	8.9	9.9	11.3	7.3	8.2	9.4	-	-	-
<i>Anchiornis</i>	PKUP V1068	6.0	6.7	7.6	7.6	8.4	9.6	-	-	-
<i>Eosinopteryx</i>	YFGP-T5197	9.1	10.1	11.6	6.0	6.7	7.7	-	-	-
<i>Aurornis</i>	YFGP-T5198	8.3	9.2	10.5	7.2	7.9	9.1	-	-	-
<i>Caihong</i>	PMoL-B00175	6.8	7.5	8.7	8.2	9.2	10.5	-	-	-
<i>Serikornis</i>	PMoL-AB00200	8.0	8.9	10.2	8.8	9.7	11.2	-	-	-
<i>Xiaotingia</i>	STM 27-2	6.5	7.2	8.3	6.4	7.1	8.1	-	-	-
<i>Archaeopteryx</i>	Eichstätt	-	-	-	-	-	-	9.6	10.7	12.3
<i>Archaeopteryx</i>	Berlin	-	-	-	-	-	-	11.6	12.9	14.8
<i>Archaeopteryx</i>	Berlin	-	-	-	-	-	-	10.1	11.2	12.9
<i>Archaeopteryx</i>	Solnhofen	-	-	-	-	-	-	7.6	8.5	9.8
<i>Archaeopteryx</i>	Solnhofen	-	-	-	-	-	-	9.4	10.4	12.0
B. Specific lift in Nkg ⁻¹ using a flight muscle mass estimate of 13% flight muscle fraction for <i>Microraptor</i> and <i>Archaeopteryx</i>										
Taxa	Specimen	Fl			Fc			3D		
		225	250	287	225	250	287	225	250	287
<i>M. gui</i>	BMNHC PH881	12.8	14.3	16.4	14.6	16.2	18.6	-	-	-
<i>M. gui</i>	IVPP V13320	13.2	14.7	16.8	12.2	13.5	15.6	-	-	-
<i>M. gui</i>	IVPP V13352	10.7	11.9	13.7	9.1	10.1	11.6	13.5/ 11.0	15.0/ 12.1	17.2/ 14.0
<i>M. gui</i>	QV1002	8.5	9.4	10.8	10.2	11.3	12.9	-	-	-
<i>M. zhaoianus</i>	CAGS 20-7-004	10.6	11.7	13.5	13.1	14.6	16.7	-	-	-

TABLE 5 continued

<i>M. zhaoianus</i>	IVPP V12330	13.2	14.7	16.9	14.1	15.6	18.0	-	-	-
<i>M. hanqingi</i>	LVH 0026	8.4	9.3	10.7	-	-	-	10.5	11.6	13.4
<i>Archaeopteryx</i>	Eichstätt	-	-	-	-	-	-	11.2	12.4	14.3
<i>Archaeopteryx</i>	Berlin	-	-	-	-	-	-	13.5	15.0	17.2
<i>Archaeopteryx</i>	Berlin	-	-	-	-	-	-	11.7	13.0	14.9
<i>Archaeopteryx</i>	Solnhofen	-	-	-	-	-	-	8.9	9.8	11.3
<i>Archaeopteryx</i>	Solnhofen	-	-	-	-	-	-	10.9	12.1	13.9

TABLE 6

Minimum glide speed for fossil paravians under coefficient of lift reconstructions of 1.0 and 1.5

Abbreviations: **CL**, coefficient of lift; **FL**, mass derived from femoral length estimate; **Fc**, mass derived from femoral circumference estimate; **3D**, mass based on published models. Minimum glide speed (= stall speed) in ms⁻¹. Estimates following Chatterjee and Templin (2007) are indicated by ¹ and those following Dyke et al. (2013) by ².

Taxa	Specimen	CL=1.5			CL=1.0		
		FL	Fc	3D	FL	Fc	3D
<i>M. gui</i>	BMNHC PH881	7.7	6.7	-	9.5	8.2	-
<i>M. gui</i>	IVPP V13320	7.2	7.9	-	8.8	9.6	-
<i>M. gui</i>	IVPP V13352	11.6	9.4	10.7 ¹	14.1	11.5	13.1 ¹
<i>M. gui</i>	IVPP V13352	11.6	9.4	7.7 ²	14.1	11.5	9.4 ²
<i>M. gui</i>	QV1002	12.1	9.9	-	14.9	12.1	-
<i>M. zhaoianus</i>	CAGS 20-7-004	9.4	7.3	-	11.5	9.0	-
<i>M. zhaoianus</i>	IVPP V12330	7.6	7.1	-	9.3	8.6	-
<i>M. hanqingi</i>	LVH 0026	12.1	-	14.9	9.9	-	12.1
<i>Anchiornis</i>	BMNHC PH804	13.8	14.9	-	16.9	18.2	-
<i>Anchiornis</i>	LPM-B00169	11.6	14.5	-	14.3	17.7	-
<i>Anchiornis</i>	PKUP V1068	17.9	13.7	-	21.9	16.8	-
<i>Eosinopteryx</i>	YFGP-T5197	12.0	19.2	-	14.7	23.6	-
<i>Aurornis</i>	YFGP-T5198	13.1	15.4	-	16.0	18.8	-
<i>Caihong</i>	PMoL-B00175	14.6	11.7	-	17.9	14.4	-
<i>Serikornis</i>	PMoL-AB00200	13.2	11.9	-	16.1	14.6	-
<i>Xiaotingia</i>	STM 27-2	16.3	16.7	-	20.0	20.5	-
<i>Archaeopteryx</i>	Eichstätt	-	-	9.0	-	-	11.0
<i>Archaeopteryx</i>	Berlin	-	-	7.0	-	-	8.6
<i>Archaeopteryx</i>	Berlin	-	-	7.8	-	-	9.6
<i>Archaeopteryx</i>	Solnhofen	-	-	9.7	-	-	11.9
<i>Archaeopteryx</i>	Solnhofen	-	-	7.7	-	-	9.4

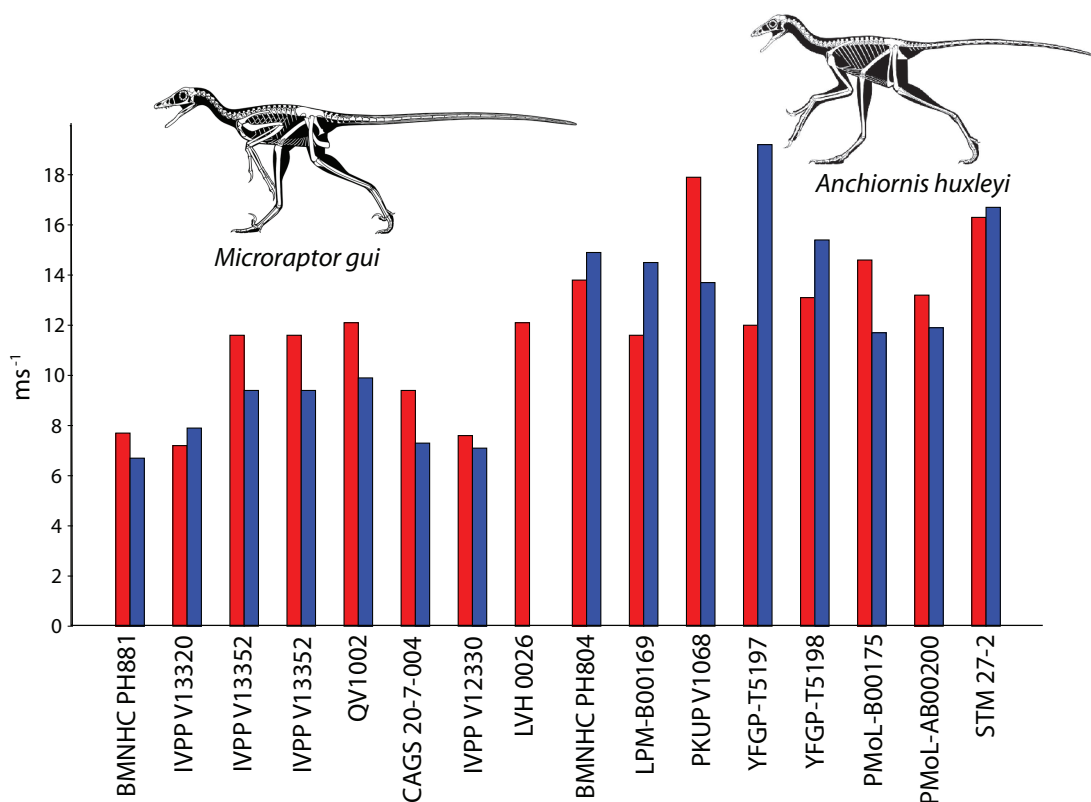


FIG. 1. Minimum glide speed (= stall speed) at $CL = 1.5$ for *Microraptor* specimens compared with those for anchiornithine specimens. Red bars represent masses from femoral length estimates, blue from femoral circumference. Note the higher average score, especially at comparable size classes for anchiornithines. Illustration used with the permission of Scott Hartman.

2002), we advocate using our values as relative scores rather than absolute values. Looking at the data we see that *Microraptor* specimens of similar size have a turning radius significantly smaller than anchiornithines, but similar to that of *Archaeopteryx*. For example, *Microraptor* specimen BMNHC PH881 shows a turning radius between 20% and 31% of that seen in the similar-sized *Anchiornis* specimen BMNHC PH804 and 55%–75% of that seen in the Eichstätt *Archaeopteryx* specimen (table 7). This comparatively smaller turning radius in *Microraptor* is observed even at larger size classes, e.g., the *M. gui* type specimen (IVPP V13352), as all mass estimates display values that are half those seen in the similar-sized anchiornithine *Xiaotingia* and are below those seen in any anchiornithine specimen

regardless of size. This level of reduction implies significantly lower levels of maneuverability in anchiornithines than in *Microraptor* that, when coupled with their higher glide speed, would make maneuvering very difficult and inefficient.

POWERED FLIGHT AND TAKEOFF

Unlike gliding, flapping-based takeoff methods require a significantly lower—often around 50% lower—minimal speed to achieve lift values sufficient to support the body (table 8). Again we see a pattern of increased takeoff velocity needed at larger sizes among *Microraptor* specimens, but the pattern is less clear in the other two clades. Interestingly in *Archaeopteryx* the highest required speed is found in the Eichstätt specimen, the smallest in

TABLE 7

Banking radius estimates for fossil paravians based on the criteria of Longrich (2006)

Abbreviations: **Fl**, mass derived from femoral length estimate; **Fc**, mass derived from femoral circumference estimate; **3D**, mass based on published models. Radii in °. Estimates following Chatterjee and Templin (2007) are indicated by ¹ and those following Dyke et al. (2013) by ².

Taxa	Specimen	Fl	Fc	3D
<i>M. gui</i>	BMNHC PH881	7.1	5.3	-
<i>M. gui</i>	IVPP V13320	7.3	6.1	-
<i>M. gui</i>	IVPP V13352	15.5	10.5	13.4 ¹
<i>M. gui</i>	IVPP V13352	15.5	10.5	7.0 ²
<i>M. gui</i>	QV1002	17.4	11.5	-
<i>M. zhaoianus</i>	CAGS 20-7-004	10.4	6.4	-
<i>M. zhaoianus</i>	IVPP V12330	6.8	5.9	-
<i>M. hanqingi</i>	LVH 0026	11.0	18.3	-
<i>Anchiornis</i>	BMNHC PH804	22.3	26.1	-
<i>Anchiornis</i>	LPM-B00169	16.0	24.7	-
<i>Anchiornis</i>	PKUP V1068	37.6	22.2	-
<i>Eosinopteryx</i>	YFGP-T5197	16.9	43.6	-
<i>Aurornis</i>	YFGP-T5198	20.1	27.8	-
<i>Caihong</i>	PMoL-B00175	25.3	16.2	-
<i>Serikornis</i>	PMoL-AB00200	20.5	16.7	-
<i>Xiaotingia</i>	STM 27-2	31.3	33.0	-
<i>Archaeopteryx</i>	Eichstätt	-	-	9.5
<i>Archaeopteryx</i>	Berlin	-	-	5.8
<i>Archaeopteryx</i>	Berlin	-	-	7.2
<i>Archaeopteryx</i>	Solnhofen	-	-	11.0

our dataset, while the lowest values are in the mid-sized Berlin specimen. The subclass of small *Microraptor* specimens show the lowest minimum takeoff speed of any taxon. The similar sized Eichstätt *Archaeopteryx* has values 140%–220% higher and comparable anchiornithines have speeds 220%–450% greater than *Microraptor*. In fact, across *Microraptor* specimens we see relatively low minimal speed values, with the highest for the 2 kg reconstruction of LVH 0026 (8.3 ms⁻¹) still below the lowest value seen in any anchiornithine.

We compared these values to estimates of maximum sprint speed based on either reconstructions from Froude number (Pontzer et al., 2009) or body mass (Hirt et al., 2017) to see whether they were achievable from an unaided terrestrial

run (fig. 2). We chose Froude numbers of 10 and 15 to mimic sprint speed capacity. While these numbers are high they are within the range seen in extant terrestrial birds and previously estimated for theropod dinosaurs (Hutchinson and Garcia, 2002; Sellers and Manning, 2007). These values are realistic even for small-bodied taxa such as those examined here, as modern roadrunners (*Geococcyx californianus*) have been recorded running at 5.3–6.7 ms⁻¹ (Stewart, 1958), which at a hip height of around 0.16 m (Halsey, 2013) gives Froude values of 18–28. Using Froude values we find that 12 of 16 permutations of *Microraptor* achieve running speeds greater than minimum takeoff values, as do all cases using Hirt et al.’s (2017) body-mass estimates for top speed. The

TABLE 8

Minimum speed required for takeoff based under a powered flapping regime

Note that for the anchiornithines all minimum values are higher than the maximum potential sprint speed using either a Froude number (Fr) or body mass based running speed estimate. See text for description. Estimates following Chatterjee and Templin (2007) are indicated by ¹ and those following Dyke et al. (2013) by ². Abbreviations: **Fl**, mass derived from femoral length estimate; **Fc**, mass derived from femoral circumference estimate; **3D**, mass based on published models. Speeds in ms⁻¹.

Taxa	Specimen	Flapping takeoff speed			Running speed		Speed based on Hirt et al. (2017)		
		Fl	Fc	3D	Fr=10	Fr=15	Fl	Fc	3D
<i>M. gui</i>	BMNHC PH881	4.1	2.8	-	4.0	4.9	4.9	4.5	-
<i>M. gui</i>	IVPP V13320	3.0	3.8	-	4.3	5.2	5.4	5.6	-
<i>M. gui</i>	IVPP V13352	7.5	5.1	6.1 ¹	5.3	6.5	7.6	6.9	7.0 ¹
<i>M. gui</i>	IVPP V13352	7.5	5.1	2.9 ²	5.3	6.5	7.6	6.9	5.9 ²
<i>M. gui</i>	QV1002	8.1	5.4	-	5.7	6.9	8.4	7.5	-
<i>M. zhaoianus</i>	CAGS 20-7-004	5.6	3.2	-	4.2	5.1	6.1	5.4	-
<i>M. zhaoianus</i>	IVPP V12330	4.2	3.6	-	3.9	4.7	4.3	4.2	-
<i>M. hanqingi</i>	LVH 0026	8.3	-	5.0	5.6	6.9	7.5	-	8.5
<i>Anchiornis</i>	BMNHC PH804	11.3	12.5	-	4.0	4.9	4.4	4.6	-
<i>Anchiornis</i>	LPM-B00169	8.4	11.5	-	4.7	5.8	5.5	6.2	-
<i>Anchiornis</i>	PKUP V1068	15.1	10.6	-	5.1	6.2	7.2	6.2	-
<i>Eosinopteryx</i>	YFGP-T5197	9.5	17.2	-	3.9	4.8	4.2	5.4	-
<i>Aurornis</i>	YFGP-T5198	10.1	12.6	-	4.4	5.4	5.5	6.0	-
<i>Caihong</i>	PMoL-B00175	12.1	8.9	-	4.5	5.5	5.8	5.2	-
<i>Serikornis</i>	PMoL-AB00200	10.3	8.8	-	4.6	5.6	5.6	5.3	-
<i>Xiaotingia</i>	STM 27-2	13.5	14.0	-	-	-	6.7	6.8	-
<i>Archaeopteryx</i>	Eichstätt	-	-	6.1	3.4	4.2	-	-	4.5
<i>Archaeopteryx</i>	Berlin	-	-	3.1	3.9	4.8	-	-	4.9
<i>Archaeopteryx</i>	Berlin	-	-	4.1	3.9	4.8	-	-	5.4
<i>Archaeopteryx</i>	Solnhofen	-	-	6.0	4.5	5.5	-	-	7.2
<i>Archaeopteryx</i>	Solnhofen	-	-	3.6	4.5	5.5	-	-	6.4

four reconstructions that do not all rely on body-mass reconstructions taken using femoral length produce values 40%–70% greater than the value for other metrics using the same specimen and may be considered overestimations based on known elongation of the femur in this taxon (Dececchi and Larsson, 2013). Among *Archaeopteryx* representatives, the smallest specimen (Eichstätt) fails to achieve sufficient speed through running under either scenario as does the largest specimen under its heaviest reconstruction using

Froude values. No anchiornithine achieves a running speed within 2 ms⁻¹ of the minimal value needed to achieve takeoff. As running speed relies solely on thrust generated by the hind limbs, we also ran reconstructions to account for the possibility that flap-generated thrust during the run could overcome the barrier of getting airborne (Burgers and Chiappe, 1999). We find among *Microraptor* specimens that only the largest mass estimates for the largest specimens under the 50° flap angle fail to

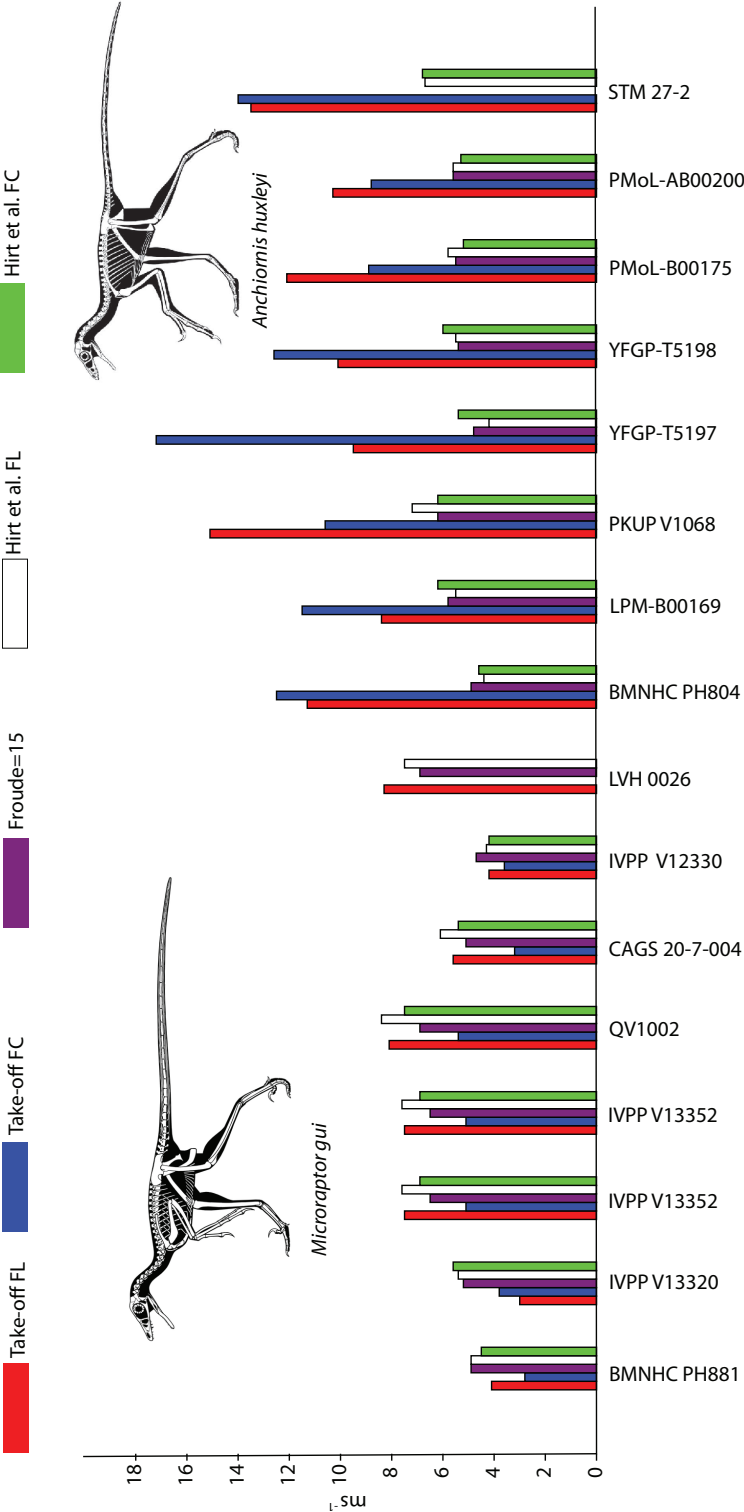


FIG. 2. Comparison of minimum flapping-based takeoff speed under mass reconstructions using femur length and circumference for *Microaptor* and anchiornithine specimens. Femoral length (FL) in red; femoral circumference (FC) in blue. These values are mapped against maximum sprint speed calculated using a Froude number of 15 (purple) or using body mass based on the equation of Hirt et al., 2017 (FL = white, FC = green). In all cases the anchiornithines show running speeds significantly too slow to allow them to achieve a ground-based takeoff. Illustration used with the permission of Scott Hartman.

TABLE 9

Takeoff potential through flap running based on the criteria of Burgers and Chiappe (1999) under several potential coefficient of lift values and flap angles

Coefficient of lift (CL) values used: 2.0 and 1.5. Flap angles (FA) used: 50° and 70°. A run was considered a success if it achieved a body weight (bw) support value of above 100% of mass in 10 seconds or less. Estimates following Chatterjee and Templin (2007) are indicated by ¹ and those following Dyke et al. (2013) by ². Abbreviations: **Gr**, grounded, not able to achieve support of 1.0 bw or above; **TO**, achieved values above 1.0 bw; **Fl**, mass derived from femoral length estimate; **Fc**, mass derived from femoral circumference estimate; **3D**, mass based on published models.

Taxa	Specimen	CL = 2, FA = 70°			CL = 2, FA = 50°			CL = 1.5, FA = 70°			CL = 1.5, FA = 50°		
		Fl	Fc	3D	Fl	Fc	3D	Fl	Fc	3D	Fl	Fc	3D
<i>M. gui</i>	BMNHC PH881	TO	TO	-	TO	TO	-	TO	TO	-	TO	TO	-
<i>M. gui</i>	IVPP V13320	TO	TO	-	TO	TO	-	TO	TO	-	TO	TO	-
<i>M. gui</i>	IVPP V13352	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	Gr ¹
<i>M. gui</i>	IVPP V13352	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO	TO ²
<i>M. gui</i>	QV1002	TO	TO	-	Gr	TO	-	Gr	TO	-	Gr	TO	-
<i>M. zhaoianus</i>	CAGS 20-7-004	TO	TO	-	TO	TO	-	TO	TO	-	TO	TO	-
<i>M. zhaoianus</i>	IVPP V12330	TO	TO	-	TO	TO	-	TO	TO	-	TO	TO	-
<i>M. hanqingi</i>	LVH 0026	TO	-	TO	Gr	-	TO	Gr	-	TO	Gr	-	TO
<i>Anchiornis</i>	BMNHC PH804	Gr	Gr	-	Gr	Gr	-	Gr	Gr	-	Gr	Gr	-
<i>Anchiornis</i>	LPM-B00169	TO	Gr	-	Gr	Gr	-	Gr	Gr	-	Gr	Gr	-
<i>Anchiornis</i>	PKUP V1068	Gr	Gr	-	Gr	Gr	-	Gr	Gr	-	Gr	Gr	-
<i>Eosinopteryx</i>	YFGP-T5197	TO	Gr	-	Gr	Gr	-	Gr	Gr	-	Gr	Gr	-
<i>Aurornis</i>	YFGP-T5198	Gr	Gr	-	Gr	Gr	-	Gr	Gr	-	Gr	Gr	-
<i>Caihong</i>	PMoL-B00175	Gr	TO	-	Gr	TO	-	Gr	TO	-	Gr	TO	-
<i>Serikornis</i>	PMoL-AB00200	Gr	TO	-	Gr	Gr	-	Gr	Gr	-	Gr	Gr	-
<i>Xiaotingia</i>	STM 27-2	Gr	Gr	-	Gr	Gr	-	Gr	Gr	-	Gr	Gr	-
<i>Archaeopteryx</i>	Eichstätt	-	-	TO	-	-	TO	-	-	TO	-	-	TO
<i>Archaeopteryx</i>	Berlin	-	-	TO	-	-	TO	-	-	TO	-	-	TO
<i>Archaeopteryx</i>	Berlin	-	-	TO	-	-	TO	-	-	TO	-	-	Gr
<i>Archaeopteryx</i>	Solnhofen	-	-	TO	-	-	TO	-	-	TO	-	-	TO
<i>Archaeopteryx</i>	Solnhofen	-	-	TO	-	-	TO	-	-	TO	-	-	TO

takeoff (table 9), with those specimens having body weights supporting lift values well above 1 under all other permutations. Under all scenarios, the smaller specimens achieve lift off. The Solnhofen *Archaeopteryx* fails to achieve sufficient body support under the CL 1.5 and 50° flap angle reconstruction, but succeeds under all others, as do the Berlin and Eichstätt individuals in all versions. In contrast, the anchiornithines (*Eosinopteryx*, *Caihong*, *Serikiornis*, and *Anchiornis* specimen LPM-B00169) that achieve takeoff capacity do so only under the least stringent per-

mutation ($CL = 2$, 70° flap angle), using the lower mass estimates with the highest body weight support value shown after 10 seconds at only 67% of that needed to achieve takeoff. No anchiornithines show this capacity with a CL of 1.5, a value that is similar to that seen in modern avians.

DISCUSSION

By looking at these three similar-sized small bodied paravians close to the origins of birds, each with a similar bauplan of elongated forelimbs and long pennaceous feathered fore- and hind limbs, we get a sense of how flight potential extends across this region of the phylogeny. Often all three have been lumped together as “four-winged” dinosaurs, under the assumption that they show similar ecological and behavioral strategies (Dyke et al., 2013; Xu et al., 2014). What is apparent from our data is that there is a distinct difference in flight capacity that may not be immediately discernable from simple linear osteological measurements alone. While any single value may be considered insufficient to draw larger conclusions on an integrated function such as flight, the combined data of these various methods of reconstruction paint a picture of significantly different aerodynamic capabilities among similar-sized paravian lineages.

We find some intriguing patterns across size classes within each of our clades. The first is there is little constant size-related change within the anchiornithines for any of our factors related to flight potential. We view this as perhaps an indication that the wings were not used for flight, as there seems to be little compensation for the rapid increase in mass that would be expected in a creature that needs to overcome gravity at larger and larger sizes. This lack of compensation is especially relevant as several of these markers such as specific lift and takeoff speed are beyond the range seen in modern volant taxa even at small sizes, where wing size may be able to overcome reduced muscle fraction for wing-assisted locomotion (Dececchi et al., 2016; Heers et al., 2018). In addition, this

clade shows a combination of high wing loadings concurrent with high disc loadings. The former suggests high-speed and nonmaneuverable wings, as anchiornithines possess values that are higher than those seen in modern gliding animals (Thorington and Heaney, 1981; McGuire and Dudley, 2011; Socha et al., 2015). The latter are more in line with what we see in short-winged burst fliers (Tobalske and Dial, 2000) whose wings are energetically inefficient and require more power input to perform flight, but these insufficiencies can be overcome with larger wing muscle fractions and emarginated wing feathers (Tobalske and Dial, 2000; van Oorschot et al., 2017). Neither of those compensatory features are found in anchiornithines (Pei et al., 2017). Anchiornithines' combination of wing features, poorly designed for gliding or powered flight, is not compatible with the reconstruction of a clade that regularly used volant modes of transport: this clade had wings (including or excluding the hind limbs), but they were poorly designed for passive gliding (high glide speeds, high wing and disk loadings, and poor turn radii) and they lacked signs of strong short- or burst-flight capabilities (large muscle volumes with high power outputs) while they had symmetrical wing feathers (Hu et al., 2009; Saitta et al., 2018) that reduce aerodynamic efficiency further still (Feo et al., 2015). The combined weight of these data suggest that the “wings” of anchiornithines were not used in flight, though they could have had some aerodynamic role in other types of terrestrial behavior such as WAIR or leap assistance (Heers et al., 2014; Dececchi et al., 2016).

While we cannot rule out some gliding capability in anchiornithines, the high wing loadings, high minimum glide speeds, and larger turning radii compared to the other clades do not suggest very strong aerial mobility in this group, if it was possible. While wing-loading values are below the maximal level seen in flying animals, it should be noted that nonvolant hatchling-aged birds can also show wing-loading values below 245 Nm^{-2} (Austin and Ricklefs, 1977; Wright et

al., 2006; Sprague and Breuner, 2010; Heers and Dial, 2015). Also, given that the osteological signals in this clade are inconsistent with a reconstruction of arboreality such as long distal limbs, low claw curvature, and lack of ankle or hip flexibility, one can further argue against gliding as a locomotion strategy in this group (Dececchi and Larsson, 2011; Lefèvre et al., 2017). This, coupled with the low support for any ground-based take-off capacity, makes flight highly unlikely. We only see 21% of permutations achieve minimal specific lift levels in this clade, with no cases of running speed sufficient to achieve minimal takeoff speed and only 6% of cases, all under the most lenient conditions with a CL higher than modern bird wings, where flap running produces sufficient thrust to achieve takeoff. In no specimen, at any size class, are constant and consistent signs of flight potential shown in the clade.

We see very different patterns in the *Microraptor* and *Archaeopteryx* as both show characteristic metrics expected of animals that were aerial, though not necessarily identical patterns. Within *Microraptor* specimens we see a clear decrease in flight potential, including higher loadings, lower specific lift values, higher minimal speeds (under powered or passive gliding scenarios) and less success at flap running as we increase body size. This becomes especially apparent if we use femoral length as a proxy for size (though see Dececchi and Larsson, 2013, for evidence that this may not be an accurate proxy for this group, as under some permutations it moves the larger individuals from volant to flightless). While we understand the methods used here have limitations in their use of scaling and estimates for reconstructing wing area, thus introducing some uncertainty in the observed pattern, our results suggest that ontogeny may have a role to play in flight capacity in this clade. While none of the specimens examined here are considered to be very young juveniles, we capture 10-fold body-size changes that likely took several years to achieve (Erickson et al., 2009). Therefore, at each stage in our continuum there would be a prolonged exposure to selective pressures on wing parameters. This finding of propor-

tionally larger and more aerodynamically effective wings in juveniles is similar to what is seen in some modern birds where there is a delay in muscle growth that is compensated for by wing area (Heers et al., 2018). The finding of juveniles outpacing adults in or even being the major exploiters of aerial locomotion would not be a completely novel finding as juvenile flight capacity that is reduced or lost in adults has previously been proposed in another paravian *Deinonychus* (Parson and Parson, 2015) and is seen in extant avians across locomotion strategy (Heers et al., 2011; Heers and Dial, 2015).

In contrast to what is seen in *Microraptor*, in *Archaeopteryx* we see an n-shaped curve with optimality at the midsize range and similar levels seen at smaller and larger sizes. This is similar to what is seen in some modern birds such as chukars, where early fledglings to subadults show lower wing loadings than either prefledglings or mature adults (Jackson et al., 2009). What is potentially different in the case of the chukar is that while adults have lower wing loadings and wing areas than fledglings and subadults, they have larger flight muscle fractions, which may overcome this difference (Dececchi et al., 2016). We have little evidence that this occurred in *Archaeopteryx*, but if so it would suggest that perhaps among the earliest flying members of Avialae the pressure to gain larger wings outpaced the evolution of larger muscles. This is a pattern that is seen in the ontogeny of some modern avians (Heers et al., 2014, 2016). What is interesting is that while the pattern of proportionally larger wings appears early in the ontogeny of *Microraptor* compared with a delayed peak in *Archaeopteryx*, both seem to show this “wings first” approach, suggesting that the traditional focus on large pectoral muscles as prerequisites for flight may be incorrect. Perhaps the major consideration is gaining sufficient wing area to achieve full body weight support, with muscle mass increase becoming more important both as size increased ontogenetically and as flight became more a canalized and centralized life-history trait phylogenetically.

CONCLUSIONS

We find that despite the generalized paravian bauplan and the shared feature of elongated hind limbs giving them a “four-winged” appearance similar to proposed models of flight origins (Beebe, 1915; Xu et al., 2003, 2014), our data strongly suggest that anchiornithines were not using their wings as an aerodynamic flight surface as they lack the features required to efficiently behave as either a gliding or a powered flapping structure. Such poor aerodynamic performance cannot be explained by a lack of selection in a vacant niche space because *Anchiornis* lived in the presence of better-performing gliding mammals (Meng et al., 2006, 2017; Luo et al., 2017) and powered-flying pterosaurs. If *Anchiornis* or its sister lineages were attempting to use their feathered limbs to fly, they were too awkward to catch prey or avoid becoming prey on the wing, lacked the ability to achieve precision landing or crash avoidance, and their nonarboreal body plan would have made climbing to a sufficient height difficult, moving among branches to launch dangerous, and landing from a glide near impossible. This does not preclude them from using their wings for some aerodynamic functions such as WAIR, flap running, or leaping (Dececchi et al., 2016), but this along with hind-limb structure and proportions (Dececchi and Larsson, 2011; 2013) argues for a terrestrial, nonvolant life history for this clade.

The lack of signs of flight among the most ancient members of the paravians does not mean that their feathered limbs did not have had some functional significance. They may have facilitated ground-based behaviors such as WAIR or increased leaping distance as suggested previously (Dececchi et al., 2016). In addition, we know that they possessed striking coloration, even iridescence, and frond-shaped tails (Li et al., 2010; Hu et al., 2018), suggesting that display was a likely major life-history trait. If we restrict anchiornithines from flight capability, we see similarities in the potential for wing use primarily or in conjunction with terrestrial flapping-

based locomotion strategies, for display or signaling behaviors as proposed for other feathered theropods (Pittman et al., 2013; Person et al., 2014; Xing et al., 2016; Hu et al., 2018). Combined with developmental work suggesting that hind-limb feathers may have evolved due to constraints to evolve large forelimb feathers (Domyan et al., 2016), evidence suggests the origins of the “four-winged” state lies not in the air, but on the ground.

As early-diverging avialans predating the oldest-known *Archaeopteryx* specimen (see Pittman et al., chapter 1), our anchiornithine results suggest that flight was not present in the paravian common ancestor. While this conclusion is partially dependent on the phylogenetic hypothesis used to reconstruct the ancestral state, it is reinforced by other work showing little evidence of flight capability in troodontids, some of which also had elongate hind-limb feathers (Xu et al., 2017), and in most dromaeosaurids (Dececchi et al., 2016; Hartman et al., 2019; Pei et al., in press). Thus, regardless of whether anchiornithines were early-diverging troodontids (Hu et al., 2009), sister to both troodontids and dromaeosaurids (Hu et al., 2018), or early-diverging members of the avialans (Foth and Rauhut, 2017; Cau, 2018; Rauhut et al., 2019), the conclusion remains consistent. The only possible configuration that allows for a single origin in the literature is if microraptorines are not members of the Dromaeosauridae, but a separate, later-diverging clade (Agnolín and Novas, 2013; Agnolín et al., 2019). Yet, even in this case, flight capacity is lacking in the larger, earlier-diverging members of this group such as *Tianyuraptor* and *Zhenyuanlong* (Pei et al., in press) and achieved only in the *Microraptor* species complex itself (Dececchi et al., 2016; Pei et al., in press), suggesting it is not an ancestral trait for this lineage nor plesiomorphic for Averaptora (Agnolín and Novas, 2013). The different pattern of optimization of flight-related characters also suggests different strategies to achieve volancy in *Microraptor* and *Archaeopteryx*, while their hind-limb metrics suggest perhaps different ecological roles for each (Dececchi and Larsson, 2013; Pei et al., in press).

This strongly supports the contention that flight capacity and potentially powered flight itself arose convergently in at least two distinct paravian lineages, first in birds minimally 150 million years ago, then in the microraptorines 20–30 million years later. If true, this finding leads to new avenues of investigation that look at the place of each taxon within its ecosystem, in regards to both its terrestrial and aerial interactions. It also gives us a greater glimpse into the requirements for achieving flight from a theropod body, with both the convergent and the unique solutions to the physical problems of aerial travel giving us valuable information on what it takes to fly. These findings also help reinforce the notion that the nonavian theropod to bird transition was not a simple linear path and that the behavioral and ecological roles of players on both sides of the transition were likely diverse. We see clearly that among members of the Deinonychosauria developing flight worthiness was only one of multiple trends in niche expansion in this clade (Turner et al., 2011; Lü and Brusatte, 2015; Cau et al., 2017; Xu et al., 2017; Torices et al., 2018) and complex in a way not previously appreciated.

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REFERENCES

- Agnolín, F., and F.E. Novas. 2013. Avian ancestors: a review of the phylogenetic relationships of the theropods Unenlagiidae, Microraptorina, *Anchiornis* and Scansoriopterygidae. Berlin: Springer Netherlands.
- Agnolín, F.L., M.J. Motta, F. Brissón Egli, G. Lo Coco, and F.E. Novas. 2019. Paravian phylogeny and the dinosaur-bird transition: an overview. *Frontiers in Earth Science* 6: 252. [doi.org/10.3389/feart.2018.00252]
- Alerstam, T., G.A. Gudmundsson, and L. Bertil. 1993. Flight tracks and speeds of Antarctic and Atlantic seabirds: radar and optical measurements. *Philosophical Transactions of the Royal Society B* 340: 55–67.
- Alexander, D.E., E. Gong, L.D. Martin, D.A. Burnham, and A.R. Falk. 2010. Model tests of gliding with different hindwing configurations in the four-winged dromaeosaurid *Microraptor gui*. *Proceedings of the National Academy of Sciences of the United States of America* 107: 2972–2976.
- Allen, V., K.T. Bates, Z. Li, and J.R. Hutchinson. 2013. Linking the evolution of body shape and locomotor biomechanics in bird-line archosaurs. *Nature* 497: 104.
- Askew, G.N., R.L. Marsh, and C.P. Ellington. 2001. The mechanical power output of the flight muscles of blue-breasted quail (*Coturnix chinensis*) during take-off. *Journal of Experimental Biology* 204: 3601–3619.
- Austin, G.T., and R.E. Ricklefs. 1977. Growth and development of the rufous-winged sparrow (*Aimophila carpalis*). *Condor* 79: 37–50.
- Baier, D.B., S.M. Gatesy, and F.A. Jenkins, Jr. 2007. A critical ligamentous mechanism in the evolution of avian flight. *Nature* 445: 307–310.
- Beebe, W.A. 1915. Tetrapteryx stage in the evolution of birds. *Zoologica* 2: 39–52.
- Brougham, J., and S.L. Brusatte. 2010. Distorted *Microraptor* specimen is not ideal for understanding the origin of avian flight. *Proceedings of the National Academy of Sciences of the United States of America* 107: E155–E156.
- Brusatte, S.L., G.T. Lloyd, S.C. Wang, and M.A. Norell. 2014. Gradual assembly of avian body plan culminated in rapid rates of evolution across the dinosaur-bird transition. *Current Biology* 24: 2386–2392.
- Brusatte, S.L., J.K. O'Connor, and E.D. Jarvis. 2015. The origin and diversification of birds. *Current Biology* 25: R888–R898.
- Burgers, P., and L.M. Chiappe. 1999. The wing of *Archaeopteryx* as a primary thrust generator. *Nature* 399: 60–62.
- Burnham, D.A. 2007. *Archaeopteryx* – a re-evaluation suggesting an arboreal habitat and an intermediate

- stage in trees down origin of flight. *Neues Jahrbuch für Geologie und Paläontologie* 245: 33–44.
- Campione, N.E., D.C. Evans, C.M. Brown, and M.T. Carrano. 2014. Body mass estimation in non-avian bipeds using a theoretical conversion to quadruped stylopodial proportions. *Methods in Ecology and Evolution* 5: 913–923.
- Cau, A. 2018. The assembly of the avian body plan: a 160-million-year long process. *Bollettino della Società Paleontologica Italiana* 57: 1–25.
- Cau, A., et al. 2017. Synchrotron scanning reveals amphibious ecomorphology in a new clade of bird-like dinosaurs. *Nature* 552: 395.
- Chatterjee, S., and R.J. Templin. 2007. Biplane wing planform and flight performance of the feathered dinosaur *Microraptor gui*. *Proceedings of the National Academy of Sciences of the United States of America* 104: 1576–1580.
- Christiansen, P., and R.A. Farina. 2004. Mass prediction in theropod dinosaurs. *Historical Biology* 16: 85–92.
- Dececchi, T.A., and H.C. Larsson. 2011. Assessing arboreal adaptations of bird antecedents: testing the ecological setting of the origin of the avian flight stroke. *PLoS One* 6: e22292.
- Dececchi, T.A., and H.C. Larsson. 2013. Body and limb size dissociation at the origin of birds: uncoupling allometric constraints across a macroevolutionary transition. *Evolution* 67: 2741–2752.
- Dececchi, T.A., H.C. Larsson, and M.B. Habib. 2016. The wings before the bird: an evaluation of flapping-based locomotory hypotheses in bird antecedents. *PeerJ* 4: e2159.
- Dial, K.P., E. Greene, and D.J. Irischick. 2000. Allometry of behaviour. *Trends in Ecology and Evolution* 23: 394–401.
- Domyan, E.T., et al. 2016. Molecular shifts in limb identity underlie development of feathered feet in two domestic avian species. *eLife* 5: e12115.
- Dyke, G., et al. 2013. Aerodynamic performance of the feathered dinosaur *Microraptor* and the evolution of feathered flight. *Nature Communications* 4: 2489.
- Emerson, S.B., and M.A.R. Koehl. 1990. The interaction of behavioural and morphological change in the evolution of a novel locomotor type: “flying” frogs. *Evolution* 44: 1931–1946.
- Erickson, G.M., et al. 2009. Was dinosaurian physiology inherited by birds? Reconciling slow growth in *Archaeopteryx*. *PLoS One* 4: e7390.
- Feduccia, A. 1996. *The origin and evolution of birds*. New Haven, CT: Yale University Press.
- Feduccia, A., and S. Czerkas. 2015. Testing the neoflightless hypothesis: propatagium reveals flying ancestry of oviraptorosaurs. *Journal of Ornithology* 156: 1067–1074.
- Feo, T.J., D.J. Field, and R.O. Prum. 2015. Barb geometry of asymmetrical feathers reveals a transitional morphology in the evolution of avian flight. *Proceedings of the Royal Society of London B, Biological Sciences* 282(1803): 20142864.
- Foth, C., and O.W.M. Rauhut. 2017. Re-evaluation of the Haarlem *Archaeopteryx* and the radiation of maniraptoran theropod dinosaurs. *BMC Evolutionary Biology* 17: 236.
- Foth, C., H. Tischlinger, and O.W.M. Rauhut. 2014. New specimen of *Archaeopteryx* provides insights into the evolution of pennaceous feathers. *Nature* 511: 79.
- Godefroit, P., et al. 2013. Reduced plumage and flight ability of a new Jurassic paravian theropod from China. *Nature Communications* 4: 1394.
- Gong, E., L.D. Martin, D.A. Burnham, A.R. Falk, and L.H. Hou. 2012. A new species of *Microraptor* from the Jehol Biota of northeastern China. *Palaeoworld* 21: 81–91.
- Greenewalt, C.H. 1975. The flight of birds: the significant dimensions, their departure from the requirements for dimensional similarity, and the effect on flight aerodynamics of that departure. *Transactions of the American Philosophical Society* 65: 1–67.
- Guillemette, M., and J.F. Ouellet. 2005. Temporary flightlessness in pre-laying Common Eiders *Somateria mollissima*: are females constrained by excessive wing-loading or by minimal flight muscle ratio? *Ibis* 147: 293–300.
- Halsey, L.G. 2013. The relationship between energy expenditure and speed during pedestrian locomotion in birds: a morphological basis for the elevated y-intercept? *Comparative Biochemistry and Physiology Part A, Molecular and Integrative Physiology* 165: 295–298.
- Han, G., et al. 2014. A new raptorial dinosaur with exceptionally long feathering provides insights into dromaeosaurid flight performance. *Nature Communications* 5: 4382.
- Hartman, S., et al. 2019. A new paravian dinosaur from the Late Jurassic of North America supports a late acquisition of avian flight. *PeerJ* 7: e7247.
- Heers, A.M., and K.P. Dial. 2015. Wings versus legs in the avian bauplan: development and evolution of alternative locomotor strategies. *Evolution* 69: 305–320.

- Heers, A.M., B. Tobalske, and K.P. Dial. 2011. Ontogeny of lift and drag production in ground birds. *Journal of Experimental Biology* 214: 717–725.
- Heers, A.M., K.P. Dial, and B.W. Tobalske. 2014. From baby birds to feathered dinosaurs: incipient wings and the evolution of flight. *Paleobiology* 40: 459–476.
- Heers, A.M., D.B. Baier, B.E. Jackson, and K.P. Dial. 2016. Flapping before flight: high resolution, three-dimensional skeletal kinematics of wings and legs during avian development. *PLoS One* 11: e0153446.
- Heers, A.M., J.W. Rankin, and J.R. Hutchinson. 2018. Building a bird: musculoskeletal modeling and simulation of wing-assisted incline running during avian ontogeny. *Frontiers in Bioengineering and Biotechnology* 6: 140. [doi.org/10.3389/fbioe.2018.00140]
- Hirt, M.R., W. Jetz, B.C. Rall, and U. Brose. 2017. A general scaling law reveals why the largest animals are not the fastest. *Nature Ecology and Evolution* 1: 1116–1122.
- Hu, D., L. Hou, L. Zhang, and X. Xu. 2009. A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus. *Nature* 461: 640.
- Hu, D., et al. 2018. A bony-crested Jurassic dinosaur with evidence of iridescent plumage highlights complexity in early paravian evolution. *Nature Communications* 9: 217.
- Hutchinson, J.R., and M. Garcia. 2002. *Tyrannosaurus* was not a fast runner. *Nature* 415: 1018.
- Jackson, B.E., P. Segre, and K.P. Dial. 2009. Precocial development of locomotor performance in a ground-dwelling bird (*Alectoris chukar*): negotiating a three dimensional terrestrial environment. *Proceedings of the Royal Society B, Biological Sciences* 276: 3457–3466.
- Koehl, M.A.R., D. Evangelista, and K. Yang. 2011. Using physical models to study the gliding performance of extinct animals. *Integrative and Comparative Biology* 51 (6): 1002–1018.
- Lee, M.S., A. Cau, D. Naish, and G.J. Dyke. 2014. Sustained miniaturization and anatomical innovation in the dinosaurian ancestors of birds. *Science* 345: 562–566.
- Lefèvre, U., et al. 2017. A new Jurassic theropod from China documents a transitional step in the macrostructure of feathers. *Science of Nature* 104: 74.
- Li, Q., et al. 2010. Plumage color patterns of an extinct dinosaur. *Science* 327: 1369–1372.
- Li, Q., et al. 2012. Reconstruction of *Microraptor* and the evolution of iridescent plumage. *Science* 335: 1215–1219.
- Longrich, N. 2006. Structure and function of hindlimb feathers in *Archaeopteryx lithographica*. *Paleobiology* 32(3): 417–431.
- Lü, J.C., and S.L. Brusatte. 2015. A large, short-armed, winged dromaeosaurid (Dinosauria: Theropoda) from the Early Cretaceous of China and its implications for feather evolution. *Scientific Reports* 5: srep11775.
- Luo, Z.X., et al. 2017. New evidence for mammaliaform ear evolution and feeding adaptation in a Jurassic ecosystem. *Nature* 548: 326.
- Makovicky, P.J., and L.E. Zanno. 2011. Theropod diversity and the refinement of avian characteristics. In G. Dyke and G. Kaiser (editors), *Living dinosaurs: the evolutionary history of modern birds*: 9–29. Wiley, Hoboken.
- Manafzadeh, A.R., and K. Padian. 2018. ROM mapping of ligamentous constraints on avian hip mobility: implications for extinct ornithodirans. *Proceedings of the Royal Society B, Biological Sciences* 285: 20180727.
- Marden, J.H. 1987. Maximum lift production during takeoff in flying animals. *Journal of Experimental Biology* 130: 235–258.
- Marden, J.H. 1994. From damselflies to pterosaurs: how burst and sustainable flight performance scale with size. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* 266: R1077–R1084.
- Martin, L.D. 1983. The origins of birds and avian flight. In R.F. Johnston (editor), *Current Ornithology* 1: 105–129.
- McGuire, J.A., and R. Dudley. 2005. The cost of living large: comparative gliding performance in flying lizards (Agamidae: *Draco*). *American Naturalist* 166: 93–106.
- McGuire, J.A., and R. Dudley. 2011. The biology of gliding in flying lizards (Genus *Draco*) and their fossil and extant analogs. *Integrative and Comparative Biology* 51: 983–990.
- Meng, J., Y.M. Hu, Y.Q. Wang, X.L. Wang, and C.K. Li. 2006. A Mesozoic gliding mammal from northeastern China. *Nature* 444: 889.
- Meng, Q.J., et al. 2017. New gliding mammaliaforms from the Jurassic. *Nature* 548: 291.
- Meunier, K. 1951. Korrelation und Umkonstruktion in den grössenbeziehungen zwischen Vogelflügel und Vogelkörper. *Biologia Generalis* 19: 403–443.
- Nudds, R.L., and D.M. Bryant. 2000. The energetic costs of short flights in birds. *Journal of Experimental Biology* 203: 1561–1572.

- O'Connor, J.K., Z.H. Zhou, and X. Xu. 2011. Additional specimen of *Microraptor* provides unique evidence of dinosaurs preying on birds. *Proceedings of the National Academy of Sciences of the United States of America* 108: 19662–19665.
- Palmer, C. 2014. The aerodynamics of gliding flight and its application to the arboreal flight of the Chinese feathered dinosaur *Microraptor*. *Biological Journal of the Linnean Society* 113: 828–835.
- Parson, W.L., and K.M. Parson. 2015. Morphological variation with the ontogeny of *Deinonychus antirrhopus* (Theropoda, Dromaeosauridae). *PLoS One* 10: e0121476.
- Person, W.S., P. Currie, and M.A. Norell. 2014. Oviraptorosaur tail forms and functions. *Acta Palaeontologica Polonica* 59: 553–567.
- Pei, R., Q.G. Li, Q.J. Meng, M.A. Norell, and K.Q. Gao. 2017. New specimens of *Anchiornis huxleyi* (Theropoda: Paraves) from the Late Jurassic of northeastern China. *Bulletin of the American Museum of Natural History* 411: 1–66.
- Pei, R., et al. In press. Potential for powered flight neared by most close avialan relatives but few crossed its thresholds. *Current Biology*.
- Pennycuik, C.J. 1975. Mechanics of flight. *Avian Biology* 5: 1–73.
- Pennycuik, C.J. 1989. *Bird flight performance: a practical calculation manual*. Oxford: Oxford University Press.
- Pittman, M., S.M. Gatesy, P. Upchurch, A. Goswami, and J.R. Hutchinson. 2013. Shake a tail feather: the evolution of the theropod tail into a stiff aerodynamic surface. *PLoS One* 8: e63115.
- Pontzer, H., V. Allen, and J.R. Hutchinson. 2009. Biomechanics of running indicates endothermy in bipedal dinosaurs. *PLoS One* 4: e7783.
- Puttick, M.N., G.H. Thomas, and M.J. Benton. 2014. High rates of evolution preceded the origin of birds. *Evolution* 68: 1497–1510.
- Rauhut, O.W.M., H. Tischlinger, and C. Foth. 2019. A non-archaeopterygid avialan theropod from the Late Jurassic of southern Germany. *eLife* 8: e43789.
- Saitta, E.T., R. Gelernter, and J. Vinther. 2018. Additional information on the primitive contour and wing feathering of paravian dinosaurs. *Palaeontology* 61: 273–288.
- Sellers, W.I., and P.L. Manning. 2007. Estimating dinosaur maximum running speeds using evolutionary robotics. *Proceedings of the Royal Society B, Biological Sciences* 274: 2711–2716.
- Serrano, F.J., P. Palmqvist, L.M. Chiappe, and J.L. Sanz. 2017. Inferring flight parameters of Mesozoic avians through multivariate analyses of forelimb elements in their living relatives. *Paleobiology* 43: 144–169.
- Socha, J.J., F. Jafari, Y. Munk, and G. Byrnes. 2015. How animals glide: from trajectory to morphology. *Canadian Journal of Zoology* 93: 901–924.
- Sprague, R.S., and C.W. Breuner. 2010. Timing of fledging is influenced by glucocorticoid physiology in Laysan Albatross chicks. *Hormones and Behavior* 58: 297–305.
- Stein, K., C. Palmer, P.G. Gill, and M.J. Benton. 2008. The aerodynamics of the British late Triassic *Kuehneosauridae*. *Palaeontology* 51: 967–981.
- Stewart, P.A. 1958. Locomotion of wood ducks. *Wilson Bulletin* 70: 184–187.
- Thorington, R.W., Jr., and L.R. Heaney. 1981. Body proportions and gliding adaptations of flying squirrels (Petauristinae). *Journal of Mammalogy* 62: 101–114.
- Tobalske, B.W., and K.P. Dial. 2000. Effects of body size on take-off flight performance in the Phasianidae (Aves). *Journal of Experimental Biology* 203: 3319–3332.
- Tobalske, B.W., and K.P. Dial. 2007. Aerodynamics of wing-assisted incline running in birds. *Journal of Experimental Biology* 210: 1742–1751.
- Torices, A., R. Wilkinson, V.M. Arbour, J.I. Ruiz-Omeñaca, and P.J. Currie. 2018. Puncture-and-pull biomechanics in the teeth of predatory coelurosaurian dinosaurs. *Current Biology* 28: 1467–1474.
- Turner, A.H., D. Pol, and M.A. Norell. 2011. Anatomy of *Mahakala omnogovae* (Theropoda: Dromaeosauridae), Tögrögiin Shiree, Mongolia. *American Museum Novitates* 3722: 1–66.
- Turner, A.H., P.J. Makovicky, and M.A. Norell. 2012. A review of dromaeosaurid systematics and paravian phylogeny. *Bulletin of the American Museum of Natural History* 371: 1–206.
- Usherwood, J.R. 2009. The aerodynamic forces and pressure distribution of a revolving pigeon wing. *Experiments in Fluids* 46: 991–1003.
- van Oorschot, B.K., H.K. Tang, and B.W. Tobalske. 2017. Phylogenetics and ecomorphology of emarginate primary feathers. *Journal of Morphology* 278: 936–947.
- Wang, Y.D., X.J. Yang, W. Zhang, S.L. Zheng, and N. Tian. 2006. Biodiversity and palaeoclimate of the Middle Jurassic floras from the Tiaojishan Formation in western Liaoning, China. *Progress in Natural Science* 16: 13–20.

- Warrick, D., M.W. Bundle, and K.P. Dial. 2002. Bird maneuvering flight: blurred bodies, clear heads. *Integrative and Comparative Biology* 42: 141–148.
- Wright, J., S. Markman, and S.M. Denney. 2006. Facultative adjustment of pre-fledging mass loss by nestling swifts preparing for flight. *Proceedings of the Royal Society B, Biological Sciences* 273: 1895–1900.
- Xing, L.D., et al. 2016. A feathered dinosaur tail with primitive plumage trapped in mid-Cretaceous amber. *Current Biology* 26: 3352–3360.
- Xu, X., et al. 2003. Four-winged dinosaurs from China. *Nature* 421: 335–340.
- Xu, X., H.L. You, K. Du, and F.L. Han. 2011. An *Archaeopteryx*-like theropod from China and the origin of Avialae. *Nature* 475: 465.
- Xu, X., et al. 2014. An integrative approach to understanding bird origins. *Science* 346: 1253293.
- Xu, X., et al. 2015. A bizarre Jurassic maniraptoran theropod with preserved evidence of membranous wings. *Nature* 521: 70–73.
- Xu, X., et al. 2017. Mosaic evolution in an asymmetrically feathered troodontid dinosaur with transitional features. *Nature communications* 8: 14972.
- Yalden, D.W. 1984. What size was *Archaeopteryx*? *Zoological Journal of the Linnean Society* 82: 177–188.
- Zheng, X.T., et al. 2013. Hind wings in basal birds and the evolution of leg feathers. *science* 339: 1309–1312.