



Figure S1. Fossils paravians (Xu et al., 2011) used for comparative study. (a) *Anchiornis* (Hu et al., 2009); (b) *Microraptor* (Xu et al., 2003; Li et al., 2012); (c) *Archaeopteryx* (Benton, 2005; Longrich, 2006), (d) *Jeholornis* (Zhou et al., 2002; Zhou and Zhang, 2003b; O'Connor et al., 2012; O'Connor et al., 2013), (e) *Sapeornis* (Zhou and Zhang, 2003b; Zheng et al., 2013), (f) *Zhongjianornis* (Zhou and Li, 2010) and (g) *Confuciusornis* (Gao et al., 2008; Hou et al., 1995; Chiappe et al., 1999). Subsequent specimens suggest *Sapeornis* has a long tail and a more basal phylogenetic placement than *Jeholornis* (Zheng et al., 2013; Turner et al., 2012).

Table S1. (a) Pitch static stability and equilibrium point, (b) control effectiveness in pitch using tail dorsiflexion (Figure 2b), (c) control effectiveness in pitch using symmetric wing protraction/retraction (wing sweep, Figure 2a). Results give mean \pm s.d., $n = 15$ for stability, $n = 5$ for control effectiveness; units for stability and control effectiveness are rad^{-1} .

	pitch stability, $dC_m/d\alpha$			equilibrium point	
	$\alpha = 0^\circ$	$\alpha = 15^\circ$	$\alpha = 75^\circ$	α°	equilibrium $dC_m/d\alpha$
<i>Anchiornis</i>	-0.005 \pm 0.013	-0.067 \pm 0.012	-0.13 \pm 0.03	29 \pm 2	-0.170 \pm 0.028
<i>Archaeopteryx</i>	-0.134 \pm 0.013	-0.221 \pm 0.020	-0.18 \pm 0.03	9 \pm 2	-0.190 \pm 0.012
<i>Confuciusornis</i>	0.142 \pm 0.009	0.039 \pm 0.020	-0.06 \pm 0.02	0 \pm 2	-0.030 \pm 0.073
<i>Jeholornis</i>	0.011 \pm 0.018	-0.108 \pm 0.010	-0.10 \pm 0.02	25 \pm 1	-0.120 \pm 0.044
<i>Microraptor</i>	-0.039 \pm 0.006	-0.071 \pm 0.009	-0.17 \pm 0.02	20 \pm 2	-0.070 \pm 0.029
<i>Sapeornis</i>	0.109 \pm 0.010	0.007 \pm 0.011	-0.11 \pm 0.02	5 \pm 2	0.100 \pm 0.052
<i>Zhongjianornis</i>	0.305 \pm 0.036	0.195 \pm 0.027	-0.15 \pm 0.16	5 \pm 1	0.180 \pm 0.078
<i>Alcedo</i>	0.206 \pm 0.006	0.090 \pm 0.020	-0.37 \pm 0.16	0 \pm 1	0.120 \pm 0.013
<i>Buteo</i>	0.187 \pm 0.010	-0.042 \pm 0.009	-0.13 \pm 0.02	0 \pm 3	0.140 \pm 0.030
<i>Columba</i>	0.046 \pm 0.014	-0.047 \pm 0.017	-0.18 \pm 0.16	0 \pm 6	0.050 \pm 0.088
<i>Larus</i>	0.352 \pm 0.028	0.092 \pm 0.015	-0.10 \pm 0.02	0 \pm 1	0.150 \pm 0.049
<i>Onychonycteris</i>	-0.011 \pm 0.011	-0.112 \pm 0.005	-0.12 \pm 0.02	10 \pm 2	-0.011 \pm 0.033
<i>Pteropus</i>	-0.118 \pm 0.014	-0.055 \pm 0.008	-0.10 \pm 0.02	0 \pm 2	-0.080 \pm 0.015
<i>Pteranodon</i>	0.054 \pm 0.023	0.004 \pm 0.018	-0.07 \pm 0.04	5 \pm 3	-0.050 \pm 0.029
<i>Pterodactylus</i>	-0.020 \pm 0.020	-0.050 \pm 0.009	-0.05 \pm 0.03	0 \pm 4	-0.040 \pm 0.009
<i>Rhamphorhynchus</i>	-0.062 \pm 0.013	-0.192 \pm 0.024	-0.05 \pm 0.01	15 \pm 1	-0.180 \pm 0.044
Sphere	-0.037 \pm 0.023	-0.020 \pm 0.022	-0.03 \pm 0.01		-0.050 \pm 0.006
Weathervane	-0.333 \pm 0.040	-0.347 \pm 0.020	-0.03 \pm 0.04	0 \pm 2	-0.210 \pm 0.055

	$dC_m/d\delta$, tail dorsiflexion ¹			$dC_m/d\delta$, sym protraction / wing sweep ²		
	$\alpha = 0^\circ$	$\alpha = 15^\circ$	$\alpha = 75^\circ$	$\alpha = 0^\circ$	$\alpha = 15^\circ$	$\alpha = 75^\circ$
<i>Anchiornis</i>	0.168 \pm 0.002	0.191 \pm 0.006	0.047 \pm 0.012	0.00 \pm 0.020	0.050 \pm 0.020	0.070 \pm 0.004
<i>Archaeopteryx</i>	0.219 \pm 0.007	0.190 \pm 0.010	0.065 \pm 0.024	-0.003 \pm 0.016	0.060 \pm 0.018	0.128 \pm 0.004
<i>Confuciusornis</i>	0.011 \pm 0.003	0.013 \pm 0.003	0.018 \pm 0.005	0.006 \pm 0.034	0.117 \pm 0.023	0.229 \pm 0.002
<i>Jeholornis</i>	0.268 \pm 0.019	0.223 \pm 0.001	0.068 \pm 0.005	0.042 \pm 0.009	0.072 \pm 0.006	0.088 \pm 0.002
<i>Microraptor</i>	0.174 \pm 0.023	0.125 \pm 0.002	0.089 \pm 0.014	0.018 \pm 0.008	0.037 \pm 0.003	0.051 \pm 0.004
<i>Sapeornis</i>	0.054 \pm 0.001	0.064 \pm 0.005	0.082 \pm 0.006	0.022 \pm 0.038	0.173 \pm 0.039	0.329 \pm 0.001
<i>Zhongjianornis</i>	0.023 \pm 0.004	0.019 \pm 0.004	0.012 \pm 0.026	0.025 \pm 0.027	0.119 \pm 0.023	0.221 \pm 0.001
<i>Alcedo</i>	0.011 \pm 0.004	0.012 \pm 0.005	0.044 \pm 0.007	-0.001 \pm 0.017	0.124 \pm 0.020	0.119 \pm 0.002
<i>Buteo</i>	0.018 \pm 0.003	0.033 \pm 0.012	0.049 \pm 0.006	0.043 \pm 0.034	0.142 \pm 0.021	0.213 \pm 0.001
<i>Columba</i>	0.044 \pm 0.004	0.050 \pm 0.003	0.009 \pm 0.002	0.076 \pm 0.027	0.151 \pm 0.013	0.168 \pm 0.002
<i>Larus</i>	0.014 \pm 0.008	0.016 \pm 0.003	0.014 \pm 0.008	-0.007 \pm 0.030	0.110 \pm 0.032	0.231 \pm 0.001
<i>Onychonycteris</i>	0.029 \pm 0.004	0.032 \pm 0.002	0.004 \pm 0.004	0.031 \pm 0.030	0.152 \pm 0.031	0.235 \pm 0.003
<i>Pteropus</i>	0.053 \pm 0.009	0.026 \pm 0.003	0.026 \pm 0.002	-0.005 \pm 0.041	0.131 \pm 0.030	0.230 \pm 0.002
<i>Pteranodon</i>	0.016 \pm 0.005	0.015 \pm 0.002	0.016 \pm 0.003	0.167 \pm 0.050	0.315 \pm 0.033	0.480 \pm 0.001
<i>Pterodactylus</i>	0.015 \pm 0.002	0.025 \pm 0.004	0.039 \pm 0.005	0.005 \pm 0.026	0.088 \pm 0.018	0.141 \pm 0.002
<i>Rhamphorhynchus</i>	0.347 \pm 0.016	0.245 \pm 0.032	0.029 \pm 0.010	0.012 \pm 0.025	0.045 \pm 0.020	0.175 \pm 0.001

¹movement depicted in Figure 2b

²movement depicted in Figure 2a

Table S2. (a) Roll static stability and (b) control effectiveness in roll for asymmetric wing tucking (Figure 2c). Results give mean \pm s.d. for $n = 15$; units for stability and control effectiveness are rad^{-1} . Equilibrium point in roll is at $\phi = 0^\circ$.

	roll stability, $dC_r/d\phi$		$dC_r/d\delta$, asymmetric wing tuck ¹	
	$\alpha = 15^\circ$	$\alpha = 75^\circ$	$\alpha = 15^\circ$	$\alpha = 75^\circ$
<i>Anchiornis</i>				
<i>Archaeopteryx</i>	0.009 \pm 0.06	-0.200 \pm 0.019	0.090 \pm 0.005	0.200 \pm 0.018
<i>Confuciusornis</i>	-0.020 \pm 0.02	-0.200 \pm 0.009	0.050 \pm 0.002	0.100 \pm 0.012
<i>Jeholornis</i>	0.073 \pm 0.03	-0.400 \pm 0.025	0.080 \pm 0.004	0.120 \pm 0.024
<i>Microraptor</i>	0.132 \pm 0.03	-0.300 \pm 0.019	0.050 \pm 0.007	0.170 \pm 0.021
<i>Sapeornis</i>	0.043 \pm 0.04	-0.300 \pm 0.026	0.080 \pm 0.002	0.130 \pm 0.016
<i>Zhongjianornis</i>	0.030 \pm 0.02	-0.200 \pm 0.012	0.050 \pm 0.001	0.140 \pm 0.015
<i>Alcedo</i>	0.009 \pm 0.06	-0.100 \pm 0.016	0.060 \pm 0.002	0.080 \pm 0.007
<i>Buteo</i>	0.028 \pm 0.05	-0.400 \pm 0.022	0.170 \pm 0.012	0.240 \pm 0.055
<i>Columba</i>	-0.030 \pm 0.05	-0.300 \pm 0.014	0.180 \pm 0.007	0.180 \pm 0.027
<i>Larus</i>	-0.009 \pm 0.02	-0.400 \pm 0.028	0.150 \pm 0.004	0.200 \pm 0.038
<i>Onychonycteris</i>		-1.000 \pm 0.044	0.810 \pm 0.036	0.880 \pm 0.100
<i>Pteropus</i>	-0.027 \pm 0.05	-0.700 \pm 0.064	0.680 \pm 0.020	0.830 \pm 0.088
<i>Pteranodon</i>	0.011 \pm 0.02	-0.200 \pm 0.014	0.070 \pm 0.002	0.100 \pm 0.010
<i>Pterodactylus</i>	-0.002 \pm 0.06	-0.300 \pm 0.016	0.100 \pm 0.003	0.110 \pm 0.027
<i>Rhamphorhynchus</i>	-0.069 \pm 0.03	-0.400 \pm 0.021	0.160 \pm 0.007	0.210 \pm 0.030

¹movement depicted in Figure 2c

Table S3. (a) Yaw static stability, (b) control effectiveness in yaw using tail lateral flexion (Figure 2d), (c) control effectiveness in yaw using wing pronation/supination (Figure 2e), (d) control effectiveness in yaw using lateral head flexion for pterosaurs only. Results give mean \pm s.d., $n = 15$ for stability, $n = 5$ for control effectiveness; units for stability and control effectiveness are rad^{-1} . Equilibrium point in yaw is at $\psi = 0^\circ$.

	a yaw stability, $dC_y/d\psi$		c $dC_y/d\delta$, wing pro/sup ²	d $dC_y/d\delta$, lateral head flexion		
	$\alpha = 15^\circ$	$\alpha = 75^\circ$				
<i>Anchiornis</i>	-0.097 \pm 0.003	0.006 \pm 0.006				
<i>Archaeopteryx</i>	-0.070 \pm 0.004	0.010 \pm 0.004				
<i>Confuciusornis</i>	-0.026 \pm 0.002	0.004 \pm 0.002				
<i>Jeholornis</i>	-0.091 \pm 0.003	0.002 \pm 0.001				
<i>Microraptor</i>	-0.100 \pm 0.016	0.039 \pm 0.010				
<i>Sapeornis</i>	0.002 \pm 0.003	0.005 \pm 0.001				
<i>Zhongjianornis</i>	0.021 \pm 0.003	0.008 \pm 0.002				
<i>Alectoris</i>	0.022 \pm 0.001	0.001 \pm 0.002				
<i>Buteo</i>	0.027 \pm 0.006	-0.002 \pm 0.004				
<i>Columba</i>	0.048 \pm 0.002	0.003 \pm 0.002				
<i>Larus</i>	0.017 \pm 0.004	0.002 \pm 0.002				
<i>Onychonycteris</i>	0.025 \pm 0.008	-0.040 \pm 0.007				
<i>Pteropus</i>	0.040 \pm 0.025	-0.160 \pm 0.005				
<i>Pteranodon</i>	0.026 \pm 0.002	0.002 \pm 0.001				
<i>Pterodactylus</i>	-0.002 \pm 0.001	0.002 \pm 0.001				
<i>Rhamphorhynchus</i>	-0.052 \pm 0.004	-0.034 \pm 0.004				
	b $dC_y/d\delta$, lateral tail flexion ¹		c $dC_y/d\delta$, wing pro/sup ²	d $dC_y/d\delta$, lateral head flexion		
	$\alpha = 15^\circ$	$\alpha = 75^\circ$				
<i>Anchiornis</i>	0.239 \pm 0.070	0.069 \pm 0.013	0.199 \pm 0.020	0.330 \pm 0.004		
<i>Archaeopteryx</i>	0.220 \pm 0.071	0.066 \pm 0.004	0.420 \pm 0.015	0.383 \pm 0.016		
<i>Confuciusornis</i>	0.002 \pm 0.008	-0.004 \pm 0.001	0.206 \pm 0.025	0.184 \pm 0.007		
<i>Jeholornis</i>		-0.027 \pm 0.007				
<i>Microraptor</i>	0.520 \pm 0.083	-0.076 \pm 0.010	0.259 \pm 0.013	0.373 \pm 0.008		
<i>Sapeornis</i>						
<i>Zhongjianornis</i>	-0.001 \pm 0.002	-0.007 \pm 0.001	0.296 \pm 0.015	0.262 \pm 0.015		
<i>Alectoris</i>	0.019 \pm 0.012	-0.050 \pm 0.001	0.081 \pm 0.013	0.093 \pm 0.004		
<i>Buteo</i>	-0.007 \pm 0.003	-0.029 \pm 0.003	0.565 \pm 0.060	0.431 \pm 0.025		
<i>Columba</i>	0.005 \pm 0.002	-0.022 \pm 0.001	0.455 \pm 0.042	0.204 \pm 0.003		
<i>Larus</i>		-0.012 \pm 0.002				
<i>Onychonycteris</i>	-0.011 \pm 0.005	-0.012 \pm 0.003	0.870 \pm 0.093	0.627 \pm 0.049		
<i>Pteropus</i>						
<i>Pteranodon</i>			0.271 \pm 0.013	0.234 \pm 0.004	0.120 \pm 0.002	-0.003 \pm 0.001
<i>Pterodactylus</i>			0.196 \pm 0.014	0.139 \pm 0.013	0.190 \pm 0.003	0.002 \pm 0.001
<i>Rhamphorhynchus</i>	0.170 \pm 0.008	0.128 \pm 0.002	0.279 \pm 0.027	0.319 \pm 0.024	-0.033 \pm 0.009	

¹ movement depicted in Figure 2d ² movement depicted in Figure 2e

Table S4. Fossil paravians (Xu et al., 2011) sampled for aerodynamic testing and references used during model construction.

specimen and reference	approx length $\times 10^{-2}$ m	
<i>Anchiornis</i>	LPM B00169 (Hu et al., 2009)	42
<i>Archaeopteryx</i>	Berlin (Benton, 2005; Longrich, 2006)	40
<i>Confuciusornis</i>	multiple (Hou et al., 1995; Chiappe et al., 1999)	30
<i>Jeholornis</i>	IVPP V13274, 13553 (Zhou et al., 2002; Zhou and Zhang, 2003b; O'Connor et al., 2013) ¹	65
<i>Microraptor</i>	IVPP V13352 (Xu et al., 2003; Li et al., 2012)	85
<i>Sapeornis</i>	IVPP V13275 (Zhou and Zhang, 2003a; Zheng et al., 2013)	27
<i>Zhongjianornis</i>	IVPP V15900 (Zhou and Li, 2010)	22

¹ feathers only in 13553

Table S5. Geometry data for physical models of eight fossil paravians, four extant birds, two bats, three pterosaurs, and two shapes for checking calibration. Aspect ratio (*AR*) calculated as s^2/S .

	area, <i>S</i> $\times 10^{-4}$ m ²	SVL $\times 10^{-2}$ m	TL $\times 10^{-2}$ m	span, <i>s</i> $\times 10^{-2}$ m	<i>AR</i>
<i>Anchiornis</i>	87.11	7.1	18.0	19.6	4.4
<i>Archaeopteryx</i>	94.57	8.0	10.5	17.7	3.4
<i>Confuciusornis</i>	50.53	6.8	9.2	19.9	7.8
<i>Jeholornis</i>	77.03	7.7	19.0	22.7	6.8
<i>Microraptor</i>	114.6	9.3	22.5	19.2	3.2
<i>Sapeornis</i>	54.44	6.6	7.6	20.7	7.8
<i>Zhongjianornis</i>	61.87	8.3	10.1	21.3	7.4
<i>Alectoris</i>	57.89	7.1	9.8	15.0	4.0
<i>Buteo</i>	98.55	8.3	9.9	23.8	5.8
<i>Columba</i>	80.71	7.3	9.8	19.3	4.6
<i>Larus</i>	72.62	7.9	10.5	24.0	8.0
<i>Onychonycteris</i>	194.7	9.6	13.4	29.5	4.4
<i>Pteropus</i>	201.2	8.4	12.4	35.1	6.2
<i>Pteranodon</i>	42.13	6.4	6.5	22.1	11.6
<i>Pterodactylus</i>	51.15	8.4	8.9	19.0	7.0
<i>Rhamphorhynchus</i>	78.56	8.0	18.4	29.7	11.2
Sphere	11.34		3.8	3.8	1.3
Weathervane	39.30		24.0	5.0	0.6