



**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 3b), (c) control effectiveness in pitch using symmetric wing protraction/retraction (wing sweep, Figure 3a). Results give mean  $\pm$  s.d.,  $n = 15$  for stability,  $n = 5$  for control effectiveness; units for stability and control effectiveness are  $\text{rad}^{-1}$ .

	pitch stability, $dC_m/d\alpha$			equilibrium point	
	$\alpha = 0^\circ$	$\alpha = 15^\circ$	$\alpha = 75^\circ$	$\alpha^\circ$	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	0.142 $\pm$ 0.009
<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>Allectoris</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>	0.200 $\pm$ 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	-0.018 $\pm$ 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 <sup>1</sup>			$dC_m/d\delta$ , sym protraction / wing sweep <sup>2</sup>		
	$\alpha = 0^\circ$	$\alpha = 15^\circ$	$\alpha = 75^\circ$	$\alpha = 0^\circ$	$\alpha = 15^\circ$	$\alpha = 75^\circ$
<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>Allectoris</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

<sup>1</sup>movement depicted in Figure 3b

<sup>2</sup>movement depicted in Figure 3a

**Table S2.** (a) Roll static stability and (b) control effectiveness in roll for asymmetric wing tucking (Figure 3c). Results give mean  $\pm$  s.d. for  $n = 15$ ; units for stability and control effectiveness are  $\text{rad}^{-1}$ . Equilibrium point in roll is at  $\phi = 0^\circ$ .

	roll stability, $dC_r/d\phi$		$dC_r/d\delta$ , asymmetric wing tuck <sup>1</sup>	
	$\alpha = 15^\circ$	$\alpha = 75^\circ$	$\alpha = 15^\circ$	$\alpha = 75^\circ$
<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>Allectoris</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

<sup>1</sup>movement depicted in Figure 3c

**Table S3.** (a) Yaw static stability, (b) control effectiveness in yaw using tail lateral flexion (Figure 3d), (c) control effectiveness in yaw using wing pronation/supination (Figure 3e), (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  $\text{rad}^{-1}$ . Equilibrium point in yaw is at  $\psi = 0^\circ$ .

a						
yaw stability, $dC_y/d\psi$						
	$\alpha = 15^\circ$		$\alpha = 75^\circ$			
<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		-0.004 $\pm$ 0.007			
<i>Pteropus</i>	0.040 $\pm$ 0.025		-0.016 $\pm$ 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 <sup>1</sup>						
	$\alpha = 15^\circ$		$\alpha = 75^\circ$			
<i>Anchiornis</i>	0.239 $\pm$ 0.070		0.069 $\pm$ 0.013			
<i>Archaeopteryx</i>	0.220 $\pm$ 0.071		0.066 $\pm$ 0.004			
<i>Confuciusornis</i>	0.002 $\pm$ 0.008		-0.004 $\pm$ 0.001			
<i>Jeholornis</i>			-0.027 $\pm$ 0.007			
<i>Microraptor</i>	0.520 $\pm$ 0.083		-0.076 $\pm$ 0.010			
<i>Sapeornis</i>						
<i>Zhongjianornis</i>	-0.001 $\pm$ 0.002		-0.007 $\pm$ 0.001			
<i>Alectoris</i>	0.019 $\pm$ 0.012		-0.050 $\pm$ 0.001			
<i>Buteo</i>	-0.007 $\pm$ 0.003		-0.029 $\pm$ 0.003			
<i>Columba</i>	0.005 $\pm$ 0.002		-0.022 $\pm$ 0.001			
<i>Larus</i>			-0.012 $\pm$ 0.002			
<i>Onychonycteris</i>	-0.011 $\pm$ 0.005		-0.012 $\pm$ 0.003			
<i>Pteropus</i>						
<i>Pteranodon</i>				0.271 $\pm$ 0.013	0.234 $\pm$ 0.004	0.120 $\pm$ 0.002
<i>Pterodactylus</i>				0.196 $\pm$ 0.014	0.139 $\pm$ 0.013	0.190 $\pm$ 0.003
<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	-0.003 $\pm$ 0.001

  

c						
$dC_y/d\delta$ , wing pro/sup <sup>2</sup>						
	$\alpha = 15^\circ$		$\alpha = 75^\circ$			
<i>Anchiornis</i>	0.199 $\pm$ 0.020		0.330 $\pm$ 0.004			
<i>Archaeopteryx</i>	0.420 $\pm$ 0.015		0.383 $\pm$ 0.016			
<i>Confuciusornis</i>	0.206 $\pm$ 0.025		0.184 $\pm$ 0.007			
<i>Jeholornis</i>						
<i>Microraptor</i>	0.259 $\pm$ 0.013		0.373 $\pm$ 0.008			
<i>Sapeornis</i>						
<i>Zhongjianornis</i>	0.296 $\pm$ 0.015		0.262 $\pm$ 0.015			
<i>Alectoris</i>	0.081 $\pm$ 0.013		0.093 $\pm$ 0.004			
<i>Buteo</i>	0.565 $\pm$ 0.060		0.431 $\pm$ 0.025			
<i>Columba</i>	0.455 $\pm$ 0.042		0.204 $\pm$ 0.003			
<i>Larus</i>						
<i>Onychonycteris</i>	0.870 $\pm$ 0.093		0.627 $\pm$ 0.049			
<i>Pteropus</i>						
<i>Pteranodon</i>						
<i>Pterodactylus</i>						
<i>Rhamphorhynchus</i>						

  

d						
$dC_y/d\delta$ , lateral head flexion						
	$\alpha = 15^\circ$		$\alpha = 75^\circ$			
<i>Anchiornis</i>						
<i>Archaeopteryx</i>						
<i>Confuciusornis</i>						
<i>Jeholornis</i>						
<i>Microraptor</i>						
<i>Sapeornis</i>						
<i>Zhongjianornis</i>						
<i>Alectoris</i>						
<i>Buteo</i>						
<i>Columba</i>						
<i>Larus</i>						
<i>Onychonycteris</i>						
<i>Pteropus</i>						
<i>Pteranodon</i>						
<i>Pterodactylus</i>						
<i>Rhamphorhynchus</i>						

<sup>1</sup> movement depicted in Figure 3d <sup>2</sup> movement depicted in Figure 3e

**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) <sup>1</sup>	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

<sup>1</sup> 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> $\times 10^{-4} \text{ m}^2$	SVL $\times 10^{-2} \text{ m}$	TL $\times 10^{-2} \text{ m}$	span, <i>s</i> $\times 10^{-2} \text{ m}$	<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