

Original Article

## Aerial ability in basal Deinonychosauria

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**Abstract:** Previously proposed hypothesis that flightless derived members of the maniraptoriform clade Deinonychosauria (Dinosauria: Theropoda) evolved from volant ancestors is evaluated by reviewing relevant publications subsequent to that of the hypothesis. Functional morphology and computer and physical modeling indicate that basal Dromaeosauridae microraptorine *Microraptor* and unenlagiine *Rahonavis* were volant, the former being capable of gliding and powered flight utilizing long pennaceous feathers on fore and hind limbs and scansorial locomotion, supporting the hypothesis that the more derived flightless dromaeosaurids evolved from volant ancestors. Phylogenetic relationships between the short-armed basal dromaeosaurids *Tianyuraptor* and *Mahakala* and the longer-armed dromaeosaurids and troodontids indicate that short fore limbs and inferred lack of aerial and scansorial ability of the former are autapomorphies and do not contradict the above conclusion.

Functional morphology indicates that basal Troodontidae *Anchiornis* and *Xiaotingia* were capable of gliding flight utilizing long pennaceous feathers on both fore and hind limbs and scansorial locomotion, supporting the hypothesis that the more derived flightless troodontids evolved from volant ancestors. Functional morphology indicates that microraptorine *Sinornithosaurus* and unenlagiine *Buitreraptor* and basal troodontid (or more basal paravian) *Eosinopteryx* represent transitional forms between the volant and scansorial basal dromaeosaurids and troodontids (or more basal paravians) and the more derived flightless and terrestrial ones. Scansorial and four-winged gliding ability in basal members of both Dromaeosauridae and Troodontidae and morphology of basal paravians *Pedopenna* and *Archaeopteryx* suggest that the most recent common ancestors of both Deinonychosauria and Paraves were also scansorial four-winged gliders.

Morphology and phylogenetic position of yet unknown members of the maniraptoriform clade Oviraptorosauria whose future discovery would support or falsify previously proposed hypothesis that known flightless oviraptorosaurs evolved from volant ancestors are speculated on.

**Key Words :** Deinonychosauria, secondary flightlessness, flight adaptations, climbing adaptations

### Introduction

Prior to discovery of non-avian members of the coelurosaurian clade Maniraptoriformes (Dinosauria: Theropoda) capable of aerial locomotion, Paul (1988, 2002) has argued based on skeletal flight adaptations found in the then known flightless members of maniraptoriform clades other than Avialae (Deinonychosauria, Oviraptorosauria, Therizinosauroidea, Alvarezsauridae, and Ornithomimosauria) that their ancestors possessed aerial ability, possibly more developed than that of basal avialan *Archaeopteryx*. The purpose of this paper is to evaluate Paul's hypothesis for the maniraptoriform clade Deinonychosauria based on relevant publications subsequent to Paul (2002). Given the close phylogenetic relationship between Deinonychosauria and Avialae (including living birds), which form the clade Paraves (Senter, 2007; Turner *et al.*, 2012), support or falsification of this hypothesis would provide new insight into evolution of bird flight. The hypothesis suggests the following prediction (hinted at but never articulated by Paul, 2002, p. 255): members of each of the two deinonychosaurian clades Dromaeosauridae and Troodontidae would be discovered exhibiting skeletal and (if preserved) soft tissue morphology indica-

tive of aerial ability and occupying a phylogenetic position more basal than the known members of these clades lacking aerial ability.

### Abbreviations

AMNH, American Museum of Natural History, USA. BMNH, Beijing Museum of Natural History, China. CAGS, Chinese Academy of Geological Sciences, China. IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, China. LPM, Liaoning Paleontological Museum, China. LVH, Department of Land and Resources of Liaoning Province, China. STM, Shandong Tianyu Museum of Nature, China. UA, Université d'Antananarivo, Madagascar. YFGP, Yizhou Fossil and Geology Park, China.

### Materials and Methods

The illustrations in this paper represent illustrations from cited references edited (by removing background and adding labels) using Adobe Photoshop 7.0, except Figures 5E, 6I, and 7. Figures 5E and 6I are based on two-dimensional X-rays taken

by the author with the assistance of AMNH staff using a Bruker In-Vivo DXS PRO X-ray machine. Figure 7 is based on a photograph taken by the author using an HP Photosmart 318 digital camera.

Both paleontological (Xu *et al.*, 2009a) and embryological (Tamura *et al.*, 2011) evidence indicates that the three digits of coelurosaurian manus represent digit I, II, and III identities imposed on digits II, III, IV, justifying the use of either numbering system for identifying those digits. The former system (manual digits I, II, and III with digit I being the pollex) is used in this paper for consistency with the majority of references.

### Aerial Ability in Basal Dromaeosauridae

#### *Microaptor zhaioianus* – a volant basal dromaeosaurid

*Microaptor zhaioianus* has been described (Xu *et al.*, 2000) prior to the publication of Paul (2002). Both the initial (Xu *et al.*, 2000) and subsequent (Senter *et al.*, 2004; Turner *et al.*,

2012) phylogenetic analyses indicate that this genus together with other members of Microraptorinae is among the most basal dromaeosaurids (Fig. 1). Microraptorines, including *Microraptor*, from the Early Cretaceous Jehol group are also among the earliest members of Dromaeosauridae known from adequate remains (Zheng *et al.*, 2010) together with the more derived *Utahraptor* (Turner *et al.*, 2007). However, the features of skeletal and soft tissue (feather) morphology indicative of its aerial ability were not apparent until the discovery of additional specimens described as “*Cryptovolans pauli*” (Czerkas *et al.*, 2002) and *M. “gui”* (Xu *et al.*, 2003), which were synonymized with *M. zhaioianus* by Senter *et al.*, (2004).

There is a consensus (Xu *et al.*, 2003; Paul, 2003; Chatterjee and Templin, 2007; Alexander *et al.*, 2010) based on functional morphology and computer and physical modeling that *Microraptor* was capable of gliding using its long fore (relative to hind) limbs (Table 1) with long pennaceous feathers attached to ulna and manus. There is also an emerging consensus (Paul,

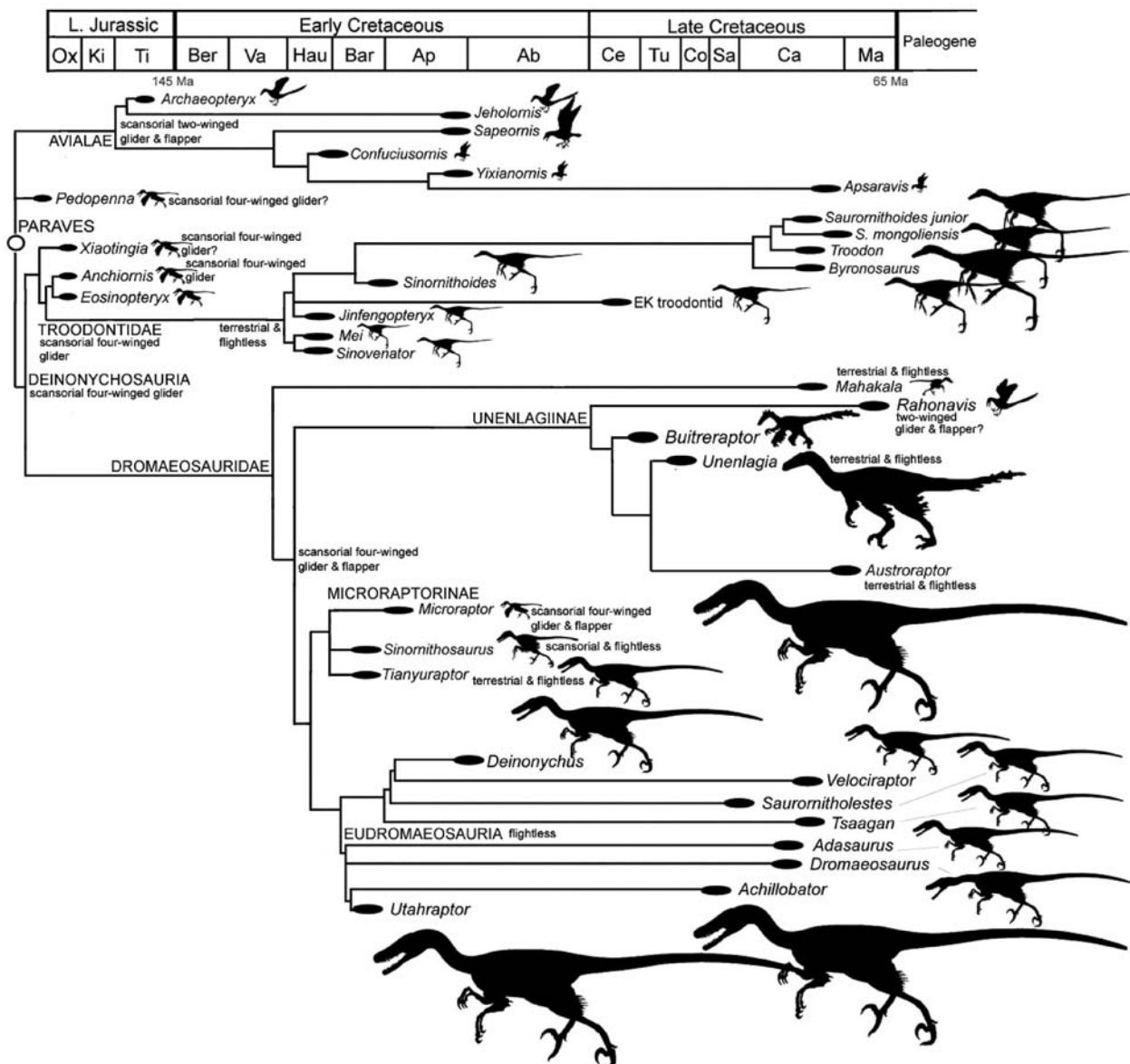


Figure 1. Phylogeny of Paraves with geologic ages and relative sizes of individual genera. Scansorial and aerial ability of selected genera and the most recent common ancestors of major clades are also indicated. Modified from Turner *et al.*, 2007, fig. 3.

2003; Longrich and Currie, 2009; Alexander *et al.*, 2010; Gong *et al.*, 2012; *contra* Chatterjee and Templin, 2007) that during aerial locomotion *Microaptor* strongly abducted its hind limbs with long pennaceous feathers attached to femur, tibia and metatarsus (metatarsal feathers >200% femoral length, Xu *et al.*, 2003) and used them to supplement lift generated by the forelimbs bearing similarly long pennaceous feathers. Such abduction was made possible by dorsolateral opening of the acetabulum (due to reduced supra-acetabular crest of the ilium, Longrich and Currie, 2009; Alexander *et al.*, 2010; Gong *et al.*, 2012; Fig 2A)

and femoral head with a short neck (Paul, 2003; Gong *et al.*, 2012; Fig. 3A) in microraptorines, *contra* Padian and Dial (2005) and Brougham and Brusatte (2010), who questioned the capacity of microraptorines for strong femoral abduction based on pelvic and femoral morphology of the more derived flightless dromaeosaurids.

The capacity of *Microaptor* for powered (flapping) flight is more controversial. Both Paul (2003) and Chatterjee and Templin (2007) independently listed numerous adaptations for powered flight present in this dromaeosaurid (Fig. 4): long (270% hu-

Table 1. Limb proportions in basal Deinonychosauria.

Taxon	Reference	forelimb/ hind limb	ilium/ hind limb	ilium/ femur+tibia+mt III	humerus/ femur	ulna/ femur	radius/ femur
<i>Velociraptor</i>	Zheng <i>et al.</i> , 2010	0.75					
<i>Microaptor</i>	Zheng <i>et al.</i> , 2010	0.80-0.81			0.78-0.85		0.68-0.73
	Hwang <i>et al.</i> , 2002		0.16	0.18	0.83-0.84	0.72	
<i>Sinornithosaurus</i>	Zheng <i>et al.</i> , 2010	0.83			0.91		0.72
	Xu <i>et al.</i> , 1999		0.19	0.23	0.91	0.74	
<i>Tianyuraptor</i>	Zheng <i>et al.</i> , 2010	0.53			0.65		0.49
<i>Rahonavis</i>	Forster <i>et al.</i> , 1998a			0.26		1.51	1.45
<i>Buitreraptor</i>	Makovicky <i>et al.</i> , 2005				0.90	0.77	
<i>Mahakala</i>	Turner <i>et al.</i> , 2007						0.46
<i>Anchiornis</i>	Hu <i>et al.</i> , 2009	0.82	0.14	0.16	1.04	0.83	0.82
	Xu <i>et al.</i> , 2009b	0.78			0.96	0.86	
<i>Xiaotingia</i>	Xu <i>et al.</i> , 2011				0.85	0.77	0.75
<i>Eosinopteryx</i>	Godefroit <i>et al.</i> , 2013a	0.75	0.14	0.16	0.78	0.87	0.81
basal Coelurosauria	Paul, 2002		≥0.20				
<i>Archaeopteryx</i> and more derived avialans	Paul, 2002 Xu <i>et al.</i> , 2011	≥1.00			≥1.18		

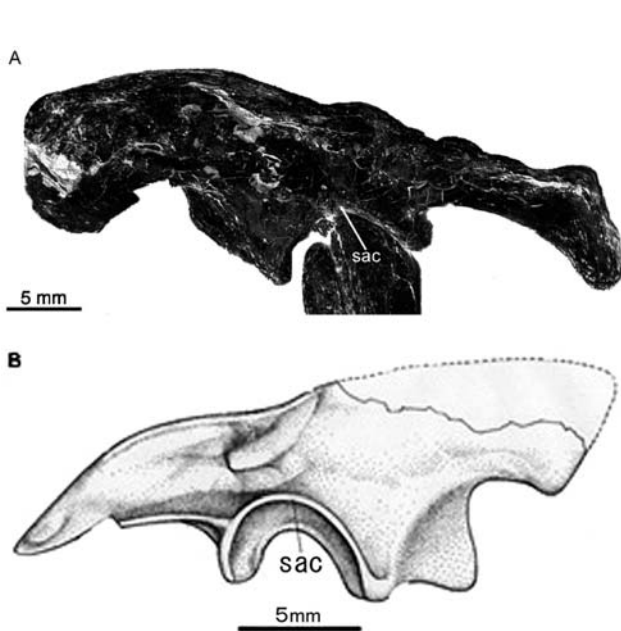


Figure 2. Ilium of basal Deinonychosauria in lateral view, showing reduced supra-acetabular crest (sac). A. *Microaptor zhaoianus*, CAGS 20-8-001, left, with femoral head in articulation with acetabulum; modified from Hwang *et al.*, 2002, fig. 24. B. *Anchiornis huxleyi*, IVPP V14378, right; modified from Xu *et al.*, 2009b, fig. 4c.

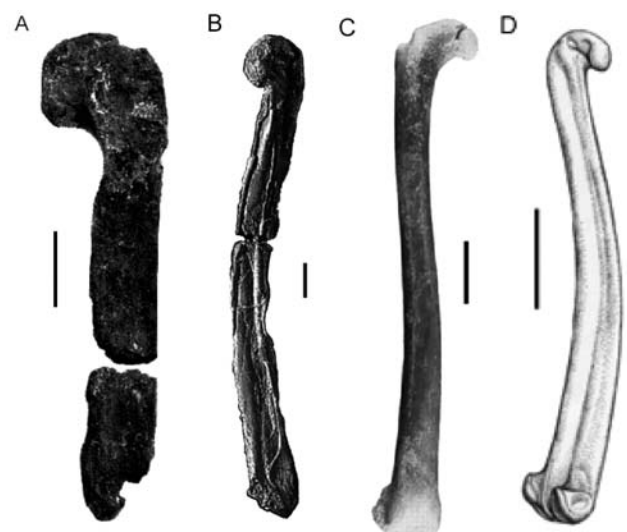


Figure 3. Femora of basal Deinonychosauria. A. *Microaptor zhaoianus*, CAGS 20-7-004, left, proximal end, anterior view, scale = 5 mm; modified from Hwang *et al.*, 2002, fig. 27b. B. *Sinornithosaurus millenii*, IVPP V12811, left, distal end missing, anterior view, scale = 10 mm; modified from Sloan, 1999. C. *Rahonavis ostromi*, UA 8656, right, anterior view, scale = 10 mm; modified from Forster *et al.*, 1998a, fig. 4b. D. *Anchiornis huxleyi*, IVPP V14378, left, posteromedial view, scale = 10 mm; modified from Xu *et al.*, 2009b, fig. 4d.



Figure 4. Adaptations for powered flight in *Microraptor zhaoianus*, IVPP V13352. A. Long pennaceous feathers with asymmetrical vanes attached to the manus. B. Strongly bowed metacarpal III. C. Flattened proximal phalanx of manual digit II. D. Scapula and coracoid joined at an acute angle. E. Single large ossified sternum. F. Ossified sternal ribs. G. Uncinate processes on dorsal ribs. Scale = 5 cm. Modified from Hone *et al.*, 2010, fig. 1.

meral length, Xu *et al.*, 2003) pennaceous feathers with asymmetrical vanes (to resist twisting while generating lift and thrust) attached to the manus (the primaries) and strongly bowed metacarpal III & flattened proximal phalanx of manual digit II to support them, scapula and coracoid joined at an acute angle (to shorten fiber length of proximoventral flight muscles), as well as a single large ossified sternum (for attachment of flight muscles; present in *M. gui* and “*Cryptovolans pauli*” specimens, sternal plates are unfused in other, smaller *M. zhaoianus* specimens (Gong *et al.*, 2012) possibly representing younger individuals), ossified sternal ribs, and uncinat processes on dorsal ribs (to resist compression force on the thoracic cavity imposed during downstroke). However, Chatterjee and Templin (2007) argued that *Microraptor* was incapable of ground takeoff because it lacked the triosseal canal (=“supracoracoideus pulley”) for the tendon of the supracoracoideus muscle, which plays a key role in the wing recovery stroke of living birds, and did not discuss its capacity for powered flight any further.

Yet, the inability to take off from the ground does not render a member of Paraves incapable of powered flight, as demonstrated by the living kakapo (*Strigops habroptilus*), a nocturnal parrot endemic to New Zealand. Although incapable of ground takeoff or sustained level flight (and therefore considered flightless), the kakapo is capable of gliding and brief, weak powered flight to gain altitude (Livezey, 1992). Moreover, some living birds retain the ability to take off from the ground even when the supracoracoideus muscle is disabled (Sy, 1936 and Sokoloff, *et al.*, 1994 cited in Paul, 2002). The hind limb “wings” of *Microraptor* would not have necessarily been an obstacle to ground takeoff, either, since the fore limb wings do not prevent the common vampire bat (*Desmodus rotundus*) from using its fore limbs to make vertical flight-initiating jumps from the ground (Schutt *et al.*, 1997). Therefore, given its adaptations for powered flight, *Microraptor* was probably capable of this form of aerial locomotion and possibly even of ground takeoff, as

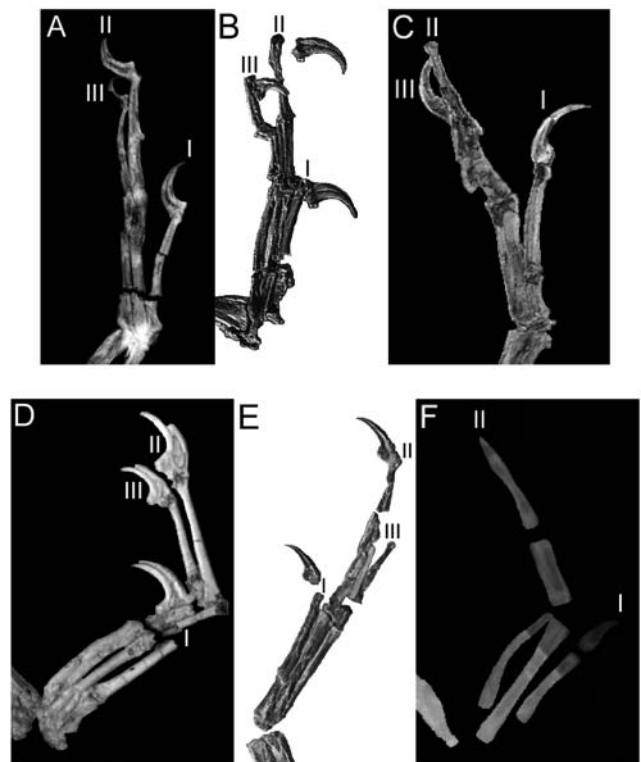


Figure 5. Manus of Paraves, showing clawed digits I, II, and III (see Materials and Methods for discussion of digit numbering).

A. *Microraptor hanqingi*, LVH 0026, right, X-ray; modified from Gong *et al.*, 2012, fig. 6. B. *Sinornithosaurus millenii*, IVPP V12811, right; modified from Sloan, 1999. C. *Anchiornis huxleyi*, BMNHC PH828, right, the counterpart; modified from Li *et al.*, 2010, fig. S3. D. *Xiaotingia zhengi*, STM 27-2, left; modified from Xu *et al.*, 2011, fig. 2d. E. *Eosinopteryx brevipenna*, YFGP-T5197, right; modified from Godefroit *et al.*, 2013a, fig. S2. F. *Opisthocomus hoazin*, male juvenile study skin AMNH 804812, right; X-ray edited to show bones only. Not to scale.

argued by Paul (2003).

The well-developed aerial ability and basal phylogenetic position of *Microraptor* within Dromaeosauridae support Paul's (1988, 2002) hypothesis that the more derived flightless dromaeosaurids (=Eudromaeosauria *sensu* Longrich and Currie, 2009, which include all dromaeosaurids known at the time of publication of Paul, 1988) evolved from volant ancestors.

Although the holotype of *Microraptor* does not preserve evi-

dence of aerial ability, the features of skeletal morphology it does preserve have led Xu *et al.*, (2000) to ascribe substantial scansorial ability to this basal dromaeosaurid, an inference supported by discovery of additional specimens. Climbing adaptations of *Microraptor* include long fore limbs with clawed manual digits (Fig. 5A), short (relative to hind limb) ilium (Table 1) indicative of reduced thigh musculature (Paul, 2002), elongated distal phalanges & slender, curved unguals of pedal

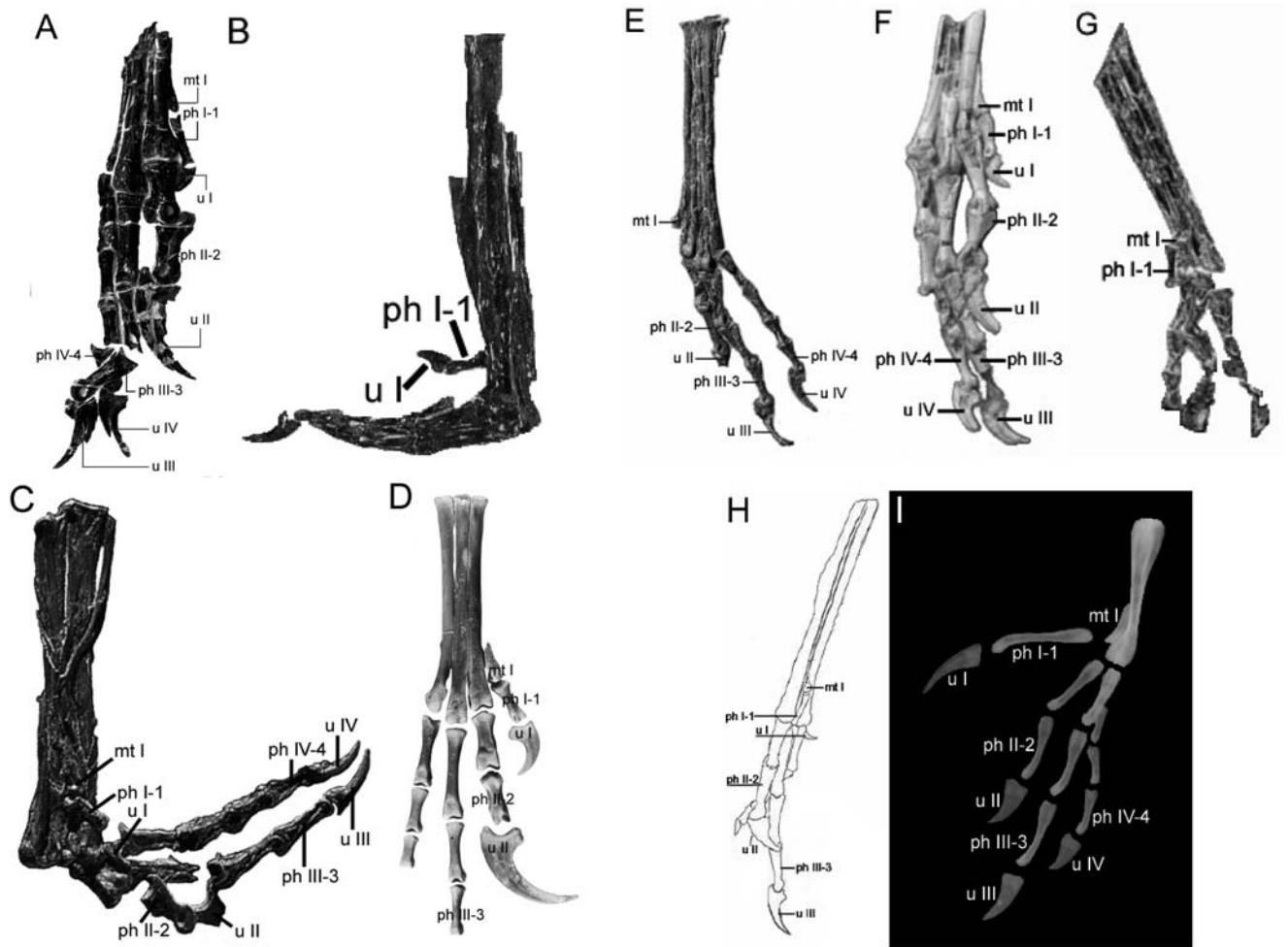


Figure 6. Pedes of Paraves, showing elongated distal phalanges (ph) & slender, curved unguals (u) of pedal digits III & IV and distally positioned hallux (digit I) & its metatarsal (mt I). A. *Microraptor zhaioanus*, CAGS 20-8-001, right; modified from Hwang *et al.*, 2002, fig. 30a. B. *Microraptor* sp., BMNHC PH881, right; modified from Li *et al.*, 2012, fig. 1a. C. *Sinornithosaurus millenii*, IVPP V12811, right; modified from Sloan, 1999. D. *Rahonavis ostromi*, UA 8656, left; modified from Ankizy Fund Anatomical Comparisons and Other Visuals @ flickr. E. *Anchiornis huxleyi*, LPM-B00169, left; modified from Hu *et al.*, 2009, fig. S4. F. *Xiaotingia zhengi*, STM 27-2, left; modified from Xu *et al.*, 2011, fig. 2e. G. *Eosinopteryx brevipenna*, YFGP-T5197, left; modified from Godefroit *et al.*, 2013a, fig. 1a. H. *Pedopenna daohugouensis*, IVPP V12721, right; modified from Xu and Zhang, 2005, fig. 1b. I. *Opisthocomus hoazin*, male juvenile study skin AMNH 804812, left; X-ray edited to show bones only. Not to scale.

Table 2. Pedal digit III phalanx lengths in basal Deinonychosauria and juvenile hoatzin.

Taxon	Reference	Specimen	Pedal digit III phalanx length (mm)						
			1	2	3	4 (ungual)	2/1	3/2	4/3
<i>Microraptor</i>	Hwang <i>et al.</i> , 2002	CAGS 20-8-001 right	9.74	8.20	8.10	9.37	0.84	0.99	1.16
<i>Anchiornis</i>	Hu <i>et al.</i> , 2009	LPM-B00169	12.9	11.1	10.5	13.7	0.86	0.95	1.30
<i>Eosinopteryx</i>	Godefroit <i>et al.</i> , 2013a	YFGP-T5197 right	8.8	7.1	6.5	6	0.81	0.92	0.92
<i>Opisthocomus</i>	Fig. 6I, this paper	AMNH 804812 left					1.11	1.01	0.79

digits III–IV (Fig. 6A; Table 2), and distally positioned pedal digit I/hallux (Fig. 6A, B) indicative of improved ability to grasp branches with the pes relative to basal Coelurosauria. Orientation of the hallucal ungual is reversed in those specimens in which the hallux is preserved in articulation with the rest of the pes (Fig. 6A, B) and metatarsal I attaches to the plantar surface of metatarsal II (Xu *et al.*, 2000; Fig. 6A). In contrast, metatarsal I attaches to the medial surface of metatarsal II in most non-avian theropods and even in the basal avialan *Archaeopteryx* (Mayr *et al.*, 2005), although the orientation of the hallucal ungual in the latter is reversed, as in *Microraptor*, and the hallux extends further distally and is more robust relative to other pedal digits than in the dromaeosaurid (based on Mayr *et al.*, 2005, fig. 3). Observations on the juveniles of the hoatzin (*Opisthocomus hoazin*), which are the only living birds to use clawed digits I & II (also present in a wide variety of other extant bird species, Fisher, 1940) for quadrupedal scansorial locomotion, confirm that a paravian with clawed manual digits (Fig. 5F) can be a competent climber without the specialized pedal morphology of the highly arboreal perching birds (Passeriformes) and parrots (Psittaciformes) (Paul, 2002; Fig. 6I; Table 2).

### *Sinornithosaurus millenii* – a transitional form between volant and flightless dromaeosaurids

*Sinornithosaurus millenii* was the first microraptorine to be described (Xu *et al.*, 1999). Its remains were found in the same geographic region (Liaoning, China) but in slightly older Early Cretaceous Yixian Formation than those of *Microraptor* (Jiufotang Formation; Zhou and Wang, 2000). Paul (2002) reconstructed *Sinornithosaurus* as a scansorial but flightless dromaeosaurid. The climbing ability of *Sinornithosaurus* is indicated by its long fore (relative to hind) limbs (Table 1) with clawed manual digits (Fig. 5B), short (relative to hind limb) ilium (Table 1), elongated distal phalanges & slender, curved unguals of pedal digits III & IV (Paul, 2002; Fig. 6C) and distally positioned hallux with metatarsal I attached to the plantar surface of metatarsal II (Fig. 6C). Ilium length intermediate between *Microraptor* and basal Coelurosauria (Table 1) and less elongated phalanx 1 of the hallux (Fig. 6C) suggest that *Sinornithosaurus* was less specialized for scansorial locomotion than *Microraptor*.

The inability of *Sinornithosaurus* to fly is indicated by the absence of long pennaceous feathers on the fore limbs. All integumental filaments associated with the right ulna of the holotype specimen are less than 50% the length of the bone (based on a high resolution photograph of the specimen in Sloan, 1999). In contrast, the pennaceous feathers associated with the left ulna of *Microraptor* IVPP V13352 (the secondaries) are more than 100% ulnar length and the ones associated with the left manus (the primaries) are more than 300% ulnar length (Fig. 4). Also unlike that of some *Microraptor* specimens (or species) and like those of flightless Eudromaeosauria, the sternum of *Sinornithosaurus* consists of two separate plates (Xu *et al.*, 1999). Yet, *Sinornithosaurus* does share with *Microraptor* the scapula and coracoid joined at an acute angle, laterally faced glenoid fossa, strongly bowed metacarpal III & flattened proximal phalanx of manual digit II (Xu *et al.*, 1999; Paul, 2002; Xu *et al.*, 2003), and femoral head with a short neck (Fig. 3B). The presence of these flight adaptations, absent in the more derived flightless

dromaeosaurids, suggests that a recent ancestor of *Sinornithosaurus* possessed well-developed aerial ability (Paul, 2002). Therefore, evidence of aerial ability in *Microraptor* supports Paul's (2002) view (based on functional morphology) that *Sinornithosaurus* represents a transitional form between the volant basal dromaeosaurids (though, obviously, not the more recent *Microraptor* itself) and the flightless derived ones (Eudromaeosauria), though, obviously, not a common ancestor of the latter (eudromaeosaur *Utahraptor* was roughly contemporary with *Sinornithosaurus*; Turner *et al.*, 2007). Notably, the phylogenetic analysis by Xu *et al.* (2000), performed prior to discovery of microraptorines other than *Sinornithosaurus* and *Microraptor* and establishment of the clade Microraptorinae, found *Microraptor* to be a dromaeosaurid more basal than the clade made up of *Sinornithosaurus* and the rest of Dromaeosauridae known at the time of publication (=Eudromaeosauria), supporting transitional status of *Sinornithosaurus*.

### *Rahonavis ostromi*

#### – another volant basal dromaeosaurid

*Rahonavis ostromi* (= "*Rahona*" *ostromi*) was described (Forster, *et al.*, 1998a, b) prior to the publication of Paul (2002), but was not recognized as a member of Dromaeosauridae until several years later (Makovicky *et al.*, 2005). Together with other Gondwanan dromaeosaurids, *Rahonavis* forms the clade Unenlagiinae, which occupies an even more basal phylogenetic position within Dromaeosauridae than Microraptorinae (Makovicky *et al.*, 2005; Senter, 2007; Turner *et al.*, 2012; Fig. 1).

Long (relative to femur) ulna (Table 1) with quill knobs for attachment of long pennaceous feathers (the secondaries) (Forster *et al.*, 1998a), suggest that *Rahonavis* possessed substantial aerial ability. *Rahonavis* parallels avialans more derived than *Archaeopteryx* in having a scapula with an articular facet for the coracoid, indicating a mobile joint between the two bones, and a synsacrum composed of more than five (six) vertebrae (Forster *et al.*, 1998a), suggesting that the scapula and coracoid of the unenlagiine joined at a more acute angle (further shortening proximoventral flight muscles) and its trunk was stiffer than in *Archaeopteryx*. Therefore, despite its limited ability to abduct the hind limb (and use long hind limb feathers, if present, to generate lift) indicated by femoral head with a long neck (Fig. 3C), *Rahonavis* may have been a more capable flier than *Microraptor*, in which the ulna is shorter (Table 1), the scapula and coracoid are fused together at a large (though still acute) angle, and the synsacrum is composed of five vertebrae (Xu *et al.*, 2000, 2003). A longer ilium (Table 1) and shortened distal phalanges of pedal digits III & IV (Fig. 6D) suggest that *Rahonavis* was a less capable climber than *Microraptor* or *Sinornithosaurus*. A more robust (relative to other pedal digits) hallux with a larger and more strongly curved reversed ungual than in either microraptorine (Fig. 6D) suggest that *Rahonavis* did possess some scansorial ability.

### Aerial ability in unenlagiines other than *Rahonavis*

In contrast to *Rahonavis*, short fore (relative to hind) limbs and much larger size of *Unenlagia comahuensis* (= *U. paynemili* and = *Neuquenraptor argentinus*) and *Austroraptor cabazai* (No-

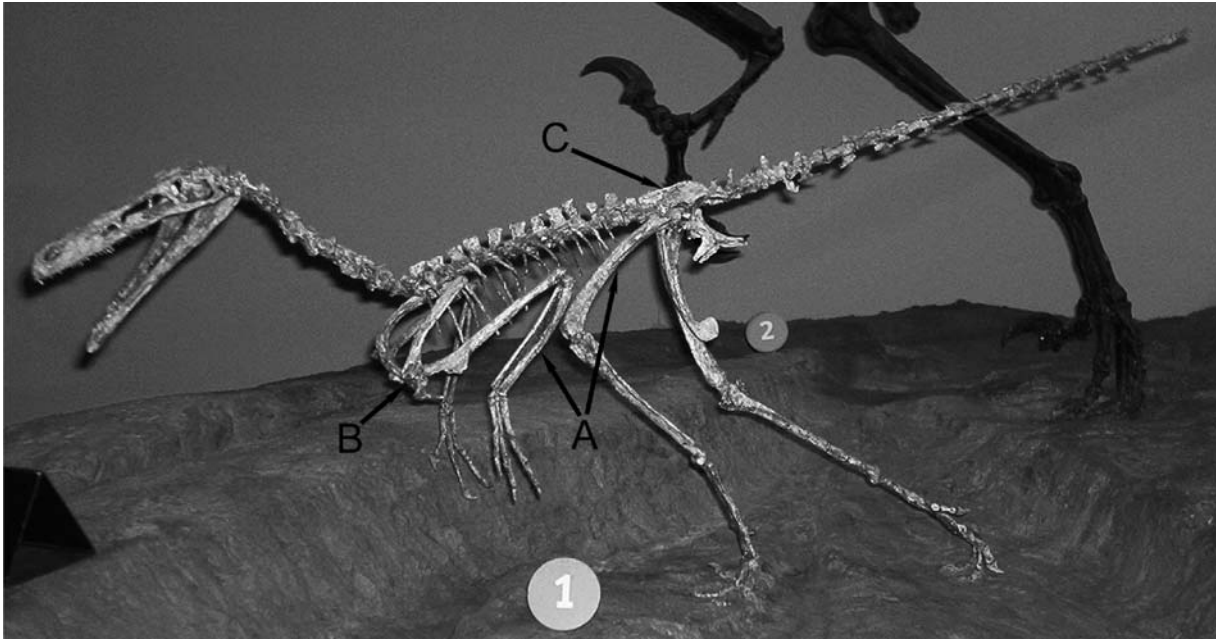


Figure 7. Flight and climbing adaptations in *Buitreraptor gonzalezorum* mounted skeletal reconstruction at the Field Museum (Chicago, IL, USA). All labeled bones are preserved in the known specimens and described by Makovicky *et al.* (2005). A. Long fore (relative to hind) limb (as indicated by the high ulna/femur ratio). B. Scapula and coracoid joined at an acute angle. C. Short (relative to hind limb) ilium.

vas and Puerta, 1997; Makovicky *et al.*, 2005; Novas *et al.*, 2009) indicate that these unenlagiines were incapable of aerial or scansorial locomotion. The aerial and scansorial ability of unenlagiine *Buitreraptor gonzalezorum* is less certain. While its fore limbs are shorter than those of *Rahonavis*, *Buitreraptor* is still as long-armed as *Microraptor* and *Sinornithosaurus* (Table 1). *Buitreraptor* also shares with the two microraptorines the scapula and coracoid joined at an acute angle (Makovicky *et al.*, 2005; Fig. 7) and short ilium (Fig. 7). The estimated adult body mass of *Buitreraptor* (3 kg) is also similar to that of *Sinornithosaurus* (3 kg) and of the same order of magnitude as that of *Rahonavis* (1 kg) (Paul, 2010), low enough for scansorial and even aerial locomotion (body masses of largest extant scansorial mammals and volant birds are 120 kg and 19 kg, respectively, Paul, 2002). Aerial and scansorial ability of *Buitreraptor* cannot be fully evaluated until morphology of its ribs, sternum, manual & pedal phalanges, and forelimb feathers is fully known. Available functional morphological data suggest that *Buitreraptor* either possessed substantial aerial and scansorial ability (though was probably a less capable flier than *Rahonavis*) or was a transitional form between the volant & scansorial and the flightless & terrestrial unenlagiines.

Analyses of phylogenetic relationships within Unenlagiinae indicate that either *Rahonavis* (Senter, 2007; Longrich and Currie, 2009; Turner *et al.*, 2012) or *Buitreraptor* (Makovicky *et al.*, 2005; Novas *et al.*, 2009) is the most basal known member of the clade. Given the above discussed evidence of aerial & scansorial ability of *Microraptor* and the evolutionary grade of *Sinornithosaurus* as a scansorial transitional form between volant and flightless dromaeosaurids, available data suggest that the most recent common ancestor of Unenlagiinae, Microraptorinae, and Eudromaeosauria was capable of both scansorial and

aerial locomotion, including active flight (Fig. 1). This provides further support for the hypothesis that Eudromaeosauria evolved from volant ancestors and suggests that the same was true of derived unenlagiines *Unenlagia* and *Austroraptor*. The alternative scenario would require independent evolution of several flight and climbing adaptations (long ulna with long penna-ceous feathers, scapula and coracoid joined at an acute angle, short ilium) in both basal unenlagiines and basal microraptorines and is, clearly, less parsimonious.

#### *Tianyuraptor ostromi* and *Mahakala omnogovae* – flightless basal dromaeosaurids

*Tianyuraptor ostromi* is the only member of Microraptorinae (Zheng *et al.*, 2010; Turner *et al.*, 2012), other than *Microraptor* and *Sinornithosaurus*, known from remains complete enough to evaluate its aerial and scansorial ability. Its short fore (relative to hind) limb and small furcula (relative to femur and scapula) indicate that it was incapable of aerial or scansorial locomotion (Zheng *et al.*, 2010). However, the fore/hind limb ratios of eudromaeosaurs are closer to those of other microraptorines than to that of *Tianyuraptor* (Table 1), suggesting that the most recent common ancestor of Microraptorinae and Eudromaeosauria was also longer-armed than *Tianyuraptor*. The long fore limbs of the basal unenlagiines *Rahonavis* and *Buitreraptor* (Table 1) suggest that the same was true of the most recent common ancestor of Unenlagiinae and the Microraptorinae + Eudromaeosauria clade, making the short forelimbs of *Tianyuraptor* an autapomorphy.

Though much less complete than those of *Tianyuraptor*, the known skeletal remains of *Mahakala omnogovae* indicate that its fore limbs were too short for aerial or scansorial locomotion

(Table 1). *Mahakala* is the most basal known member of Dromaeosauridae (Turner *et al.*, 2007; Turner *et al.*, 2012; Fig. 1). The fact that *Mahakala* is shorter-armed than basal troodontids *Anchiornis*, *Xiaotingia*, and *Eosinopteryx* discussed in the following section, basal unenlagiines *Buitreraptor* and *Rahonavis*, microraptorines *Sinornithosaurus* and *Microraptor*, and eudromaeosaur *Velociraptor* (Table 1) suggests that short fore limbs is an autapomorphy of this dromaeosaurid (as argued above for *Tianyuraptor*). This scenario does require independent evolution of short fore limbs (radius/femur = 0.5) in *Mahakala* and *Tianyuraptor*. However the alternative scenario requires independent evolution of long fore limbs (radius/femur  $\geq$  0.7) in basal Troodontidae, basal Unenlagiinae, Microraptorinae other than *Tianyuraptor*, and Eudromaeosauria and is, clearly, less parsimonious. Therefore, the short fore limbs and inferred lack of aerial and scansorial ability in *Mahakala* and *Tianyuraptor* do not contradict the presence of aerial and scansorial ability in the most recent common ancestor of Dromaeosauridae.

## Aerial Ability in Basal Troodontidae

### *Anchiornis huxleyi* and *Xiaotingia zhengi* – volant basal troodontids

The phylogenetic analysis based on the holotype (IVPP V 14378) of the late Jurassic paravian *Anchiornis huxleyi* indicated that it was a basal member of Avialae (Xu *et al.*, 2009b). However, a majority of phylogenetic analyses utilizing a more complete specimen (LPM-B00169) indicate that *Anchiornis* and its contemporary *Xiaotingia zhengi* are the most basal (and earli-

est) members known from adequate remains of either Troodontidae (Hu *et al.*, 2009; Turner *et al.*, 2012; Godefroit *et al.*, 2013a; Fig. 1) or Deinonychosauria as a whole (Xu *et al.*, 2011). The implications of the phylogenetic analysis by Godefroit *et al.* (2013b), which indicates that *Anchiornis* and *Xiaotingia* are basal avialans, will be discussed in the Aerial Ability of Basal-most Deinonychosauria and Paraves section.

*Anchiornis* resembles *Microraptor* in possessing fore limbs  $\approx$  80% hind limb length (Table 1) with long pennaceous feathers attached to both ulna and manus (the longest  $\approx$  150% humeral length) and tibia (the longest  $>$ 100% femoral length) & metatarsus (presence of such feathers on the femur is uncertain, Hu *et al.*, 2009), as well as reduced supra-acetabular crest of the ilium & femoral head with a short neck (Figs. 2B, 3D) which would have allowed strong abduction of the hind limb. The area of hind limb “wing” in *Anchiornis* is further increased by shorter pennaceous feathers attached to pedal phalanges (Hu *et al.*, 2009). However, the distal fore limb (the primaries) and the metatarsal feathers of the basal troodontid are shorter, have thinner rachises, and symmetrical vanes as compared to those of the basal dromaeosaurid, indicating inferior aerial ability in the former (Hu *et al.*, 2009). Moreover, *Anchiornis* and the more derived Troodontidae lack the skeletal adaptations for powered flight present in *Microraptor* and Eudromaeosauria: ossified sternum & sternal ribs & uncinat processes on dorsal ribs (Paul, 2002, 2010; Hu *et al.*, 2009). In both *Anchiornis* and *Microraptor* the long metatarsal feathers would have interfered with terrestrial locomotion (Xu *et al.*, 2003; Hu *et al.*, 2009). The long forelimbs with clawed manual digits (Fig. 5C), short ilium (Table 1), elongated distal phalanges & slender, curved unguals of pedal digits III & IV (Fig. 6E; Table 2), and distally positioned hallux (Fig. 6E) of *Anchiornis* indicate that it possessed substantial scansorial ability.

Paul (2010) argued that the aerial ability of *Anchiornis* was

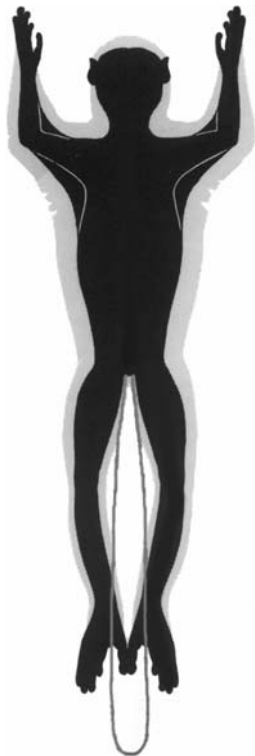


Figure 8. *Propithecus verreauxi* (Indriidae) in mid-leap, showing greatest frontal body area. Grey area indicates fur, outline indicates tail. Modified from Demes *et al.*, 1991, fig. 4.

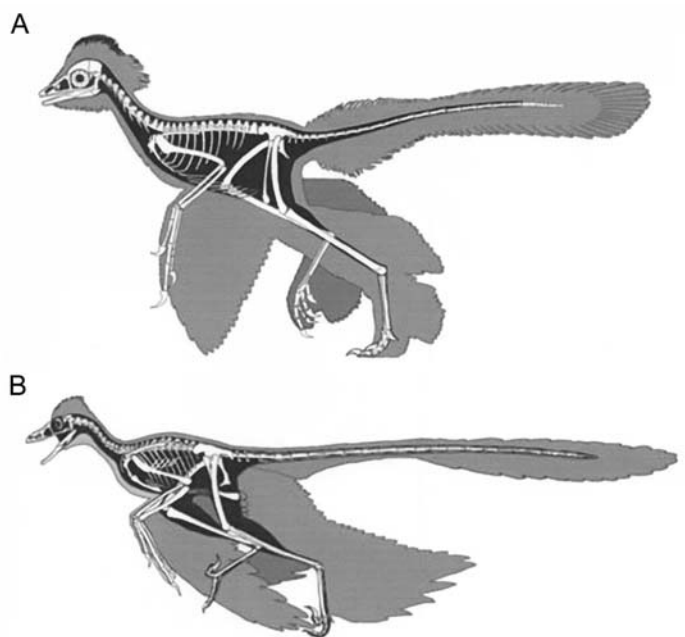


Figure 9. Skeletal reconstructions with body (black) and feather (grey) outlines of *Anchiornis huxleyi* (A) and *Microraptor zhaoianus* (B). Not to scale. Modified from Hu *et al.*, 2009, fig. 1.



limited to parachuting. However, analysis of leaping aerodynamics in bushbabies (Lorisidae: *Galago* spp.) and lemurs of the family Indriidae (Mammalia: Primates) by Demes *et al.* (1991) indicates that even integumentary structures far less extensive and complex than the fore and hind limb pennaceous feathers of basal deinonychosaurians can contribute significantly to the aerial ability of a scansorial amniote. Unlike gliding mammals of the marsupial order Diprotodontia (Pseudocheiridae and Petauridae) and of the placental orders Rodentia (Sciuridae) & Dermoptera which all have broad patagia (skin folds) between fore and hind limbs and the trunk (Nowak, 1999), *Galago* spp. and Indriidae have very narrow patagia at the armpit and the former – at the junction between thigh & trunk (Fig. 8). Instead, their long hair increases the frontal body area and thereby the contribution of lift to leaping distance, in the case of Indriidae – by up to 46%. Observations on *Galago moholi* indicate that lift increases its leaping distance by at least 10%. The gliding model of *Microraptor* used by Alexander *et al.* (2010) represented an individual weighing 0.41 kg and had a combined fore & hind wing area of 0.284 m<sup>2</sup>, 32 times that of the entire frontal body area (including hair) of a 0.2 kg *Galago* (Demes *et al.*, 1991). With body mass (0.25 kg, Paul, 2010) and wing area (Fig. 9) comparable to those of *Microraptor*, it seems certain that lift increased leaping distance in *Anchiornis* by a much greater percentage than in *Galago*. The structure of the forelimb wing in *Anchiornis* is consistent with rapid gliding (Longrich *et al.*, 2012). Thus, available evidence suggests that, although incapable of powered flight, *Anchiornis* was capable of gliding but its gliding performance was inferior to that of *Microraptor* (due to lack of twist-resistant asymmetrical primary feathers).

Poor feather preservation on the only known specimen makes aerial ability of *Xiaotingia* more difficult to evaluate. Like *Anchiornis* and the more derived Troodontidae, it lacks any skeletal adaptations for powered flight (Xu *et al.*, 2011). Preserved feather impressions indicate the presence of pennaceous feathers on ulna & manus and femur & pedal phalanges, with the presence of such feathers on tibia & metatarsus uncertain (Xu *et al.*, 2011). Comparison of known pennaceous feather distribution between *Anchiornis* and *Xiaotingia* suggests that the former did possess such feathers on the femur and the latter – on the tibia and the metatarsus and that both basal troodontids were capable of gliding. However, a shorter (relative to femur) humerus of *Xiaotingia* (Table 1) suggests that its aerial ability was inferior to that of *Anchiornis*. Clawed manual digits (Fig. 5D) and elongated distal phalanges & slender, curved unguals of pedal digits III & IV and distally positioned hallux (Fig. 6F) suggest that *Xiaotingia* possessed substantial scansorial ability. However, like *Anchiornis* and unlike *Microraptor*, its metatarsal I attaches to the medial side of metatarsal II (Fig. 6F). Also unlike *Microraptor*, the orientation of the hallux ungual in *Xiaotingia* is unreversed, suggesting that the same was true of *Anchiornis*.

Whether *Anchiornis* and *Xiaotingia* are basal troodontids or lie outside the Troodontidae + Dromaeosauridae clade, their aerial ability supports Paul's (1988, 2002) hypothesis that the more derived flightless Troodontidae evolved from volant ancestors. The more limited capacity for aerial locomotion in the two basal deinonychosaurians as compared to *Microraptor* is consistent with the lower "potentially neoflightless character score & grade"

(indicating probability of descent from volant ancestors) of Troodontidae (17.5 and 45) as compared to Dromaeosauridae (38.25 and 83) calculated by Paul (2002, table 11.1) based on the number of skeletal flight adaptations present in flightless derived troodontids and dromaeosaurids prior to discovery (or recognition of aerial ability) of volant basal members of the two deinonychosaur clades.

### *Eosinopteryx brevipenna*

#### – a transitional form between volant and flightless paravians

The phylogenetic analysis by Godefroit *et al.* (2013a; Fig. 1) indicates that, together with its contemporaries *Anchiornis* and *Xiaotingia*, *Eosinopteryx brevipenna* is the most basal and earliest member of Troodontidae known from adequate remains. In contrast, the subsequent phylogenetic analysis by Godefroit *et al.* (2013b) indicates that *Eosinopteryx* is a basal paravian lying outside the Dromaeosauridae + Troodontidae + Avialae clade (referred to as Eumaniraptora by the authors).

*Eosinopteryx* shares with *Anchiornis* and *Xiaotingia* long pennaceous feathers attached to ulna & manus (the longest  $\approx$  150% humeral length). However, the fore limb of *Eosinopteryx* is shorter (relative to hind limb) than that of *Anchiornis* and the humerus of *Eosinopteryx* is shorter (relative to femur) than those of both *Anchiornis* and *Xiaotingia* (Table 1). *Eosinopteryx* also shares with *Anchiornis* and *Xiaotingia* pennaceous feathers attached to femur & tibia, but in *Eosinopteryx* the tibial feathers are shorter than in *Anchiornis* and there are no feathers on metatarsus and pedal phalanges, reducing the area of hind limb "wing". Moreover, the tail feathers of *Eosinopteryx* are shorter than those of *Anchiornis*, reducing the tail's aerodynamic utility. Therefore, feather morphology indicates that aerial ability of *Eosinopteryx* was greatly inferior to those of *Anchiornis* and *Xiaotingia* (Godefroit *et al.*, 2013) and was probably limited to parachuting. Yet, the presence of long pennaceous feathers on the fore limb of *Eosinopteryx*, which would have interfered with its grasping function, suggests that a recent ancestor of this flightless basal troodontid was capable of aerial locomotion.

Shorter fore limbs, lesser curvature of manual unguals (Fig. 5E), and shorter pedal unguals (relative to distal phalanges, Table 2) indicate that scansorial ability of *Eosinopteryx* was inferior to those of *Anchiornis* and *Xiaotingia* (Godefroit *et al.*, 2013). However, the curvature of manual unguals and the relative length of pedal unguals in *Eosinopteryx* are similar to those of juvenile hoatzin (Fig. 5E, F; Table 2), suggesting that the basal troodontid did possess limited scansorial ability, perhaps comparable to that ascribed by Paul (2002) to eudromaeosaurs. The short ilium (Table 1) and distally positioned hallux (Fig. 6G) of *Eosinopteryx* suggest that a recent ancestor of this predominantly terrestrial basal troodontid possessed well-developed scansorial ability.

Thus, whether *Eosinopteryx* is a basal troodontid or lies outside the Dromaeosauridae + Troodontidae + Avialae clade, its functional morphology suggests that it is a transitional form between the volant & scansorial basal paravians (though, obviously, not the contemporary *Anchiornis* and *Xiaotingia*) and the more derived flightless & terrestrial ones, though not necessarily a common ancestor of the latter.

## Aerial Ability in Basalmost Deinonychosauria and Paraves

The fact that adaptations for scansorial locomotion and four-winged gliding, including elongated distal phalanges & slender, curved unguals of pedal digits III & IV and distally positioned hallux, fore limbs with clawed manual digits  $\approx 80\%$  hind limb length, long pennaceous feathers attached to both the fore (the longest  $\geq 150\%$  humeral length) and the hind limbs (the longest  $> 100\%$  femoral length), reduced supra-acetabular crest of the ilium, and femoral head with a short neck, are present in both a basal dromaeosaurid (*Microaptor*) and a basal troodontid (*Anchiornis*) makes it probable that these characteristics (and the scansorial & aerial ability they indicate) are present in the most recent common ancestor of Deinonychosauria (Fig. 1). Moreover, elongated distal phalanges & slender, curved unguals of pedal digits III & IV, distally positioned hallux (with unreversed unguinal orientation), and long pennaceous feathers with symmetrical vanes on tibia and metatarsus of the basal paravian *Pedopenna daohugouensis* (Xu and Zhang, 2005; Fig. 6H; similar to the condition in *Anchiornis* and *Xiaotingia*) suggest that the most recent common ancestor of Paraves is also a scansorial four-winged glider (Xu and Zhang, 2005; Longrich, 2006; Chatterjee and Templin, 2007; Hu *et al.*, 2009; Fig. 1). This evolutionary scenario is further supported by the presence of long pennaceous feathers with asymmetrical vanes on femur & tibia of the basal avialan *Archaeopteryx* (Longrich, 2006).

The above evidence for the presence of scansorial & aerial ability in the basalmost Deinonychosauria provides further support for interpreting the short fore limbs (and the lack of scansorial & aerial ability they indicate) of basal dromaeosaurids *Tianyuraptor* and *Mahakala* as autapomorphies. The absence of adaptations for powered flight in the gliding basal deinonychosaur *Anchiornis* suggests that the more advanced aerial ability of the basal deinonychosaur *Microaptor* (gliding & active flight) evolved independently from the members of Avialae more derived than *Archaeopteryx*. *Archaeopteryx* lacks most of the skeletal adaptations for powered flight present in *Microaptor* and retained in flightless Eudromaeosauria (Paul, 1988, 2002), though it was probably capable of this form of aerial locomotion (reviewed in Paul, 2002). The above evidence for the structure of flight apparatus in the basalmost Deinonychosauria and Paraves suggests that the volant unenlagiine *Rahonavis* evolved from a *Microaptor*-like four-winged glider & flapper and that the reduced contribution of *Rahonavis*' hind limbs to the flight apparatus (as indicated by its longer fore limbs and reduced ability to abduct the hind limbs compared to *Microaptor*) evolved independently from *Archaeopteryx* and the more derived avialans.

The above discussion is based on the phylogeny of Paraves (Fig. 1) supported by Senter (2007), Hu *et al.* (2009), Turner *et al.* (2012), and Godefroit *et al.* (2013a). Godefroit *et al.* (2013b) support a very different paravian phylogeny, in which *Rahonavis*, *Anchiornis*, and *Xiaotingia* are basal avialans, Troodontidae is a sister group of Avialae (rather than Dromaeosauridae), and *Eosinopteryx* is a basal paravian lying outside the Dromaeosauridae + Troodontidae + Avialae clade (referred to as Eumaniraptora by the authors). However, as Godefroit *et al.* (2013b) point out, this alternative phylogeny is consistent with the most recent

common ancestor of Dromaeosauridae, Troodontidae, and Avialae being a four-winged glider, and, therefore, with secondary flightlessness of troodontids and dromaeosaurids other than *Microaptor*.

Thus, available comparative anatomical and phylogenetic data and computer and physical modeling support Paul's (1988, 2002) hypothesis that flightless derived members of Dromaeosauridae and Troodontidae evolved from volant ancestors. Paul (1988, 2002) argued that not only did flightless members of Deinonychosauria and the rest of maniraptoriform clades other than Avialae evolve from volant ancestors, but that these ancestors were phylogenetically closer to the living birds than the basal avialan *Archaeopteryx*, but the latter hypothesis was not supported by subsequent phylogenetic analyses.

## Aerial Ability in Basal Oviraptorosauria

The values of "potentially neoflightless character score and grade" of 7.5-24 and 49-66 calculated by Paul (2002, table 11.1) for basal (*Protarchaeopteryx*, *Caudipteryx*, *Avimimus*) and derived (Oviraptoridae) members of Oviraptorosauria are second only to those for Dromaeosauridae (38.25 and 83) among the non-avian Theropoda. This makes it probable that the ancestors of the presently known flightless members of Oviraptorosauria pos-

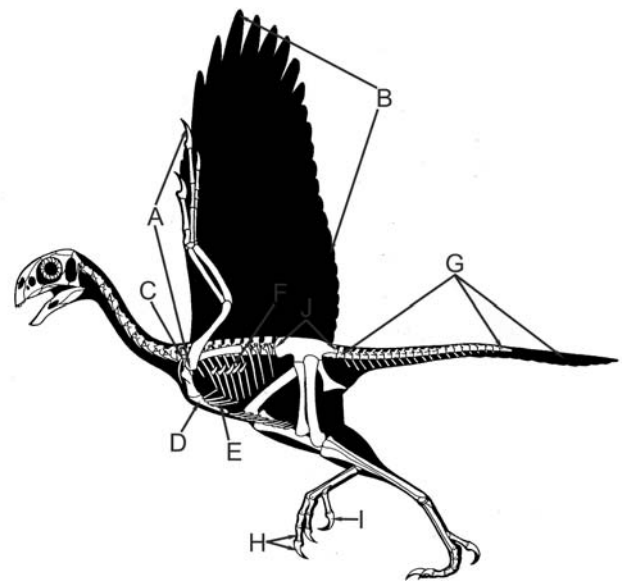


Figure 10. Morphology of "*Oviraptorovolans*", a hypothetical basal member of Oviraptorosauria capable of aerial locomotion, showing flight and climbing adaptations. Skeletal reconstruction with body outline kindly produced by G. S. Paul. Labels added by the author. A. Fore limbs  $\geq 80\%$  hind limb length. B. Long asymmetrical pennaceous feathers (the primaries) attached to the manus and shorter, more symmetrical ones (the secondaries) attached to the ulna. C. Scapula and coracoid joined at an acute angle. D. Single large ossified sternum. E. Ossified sternal ribs. F. Uncinate processes on dorsal ribs. G. Tail consisting of fewer than 28 caudal vertebrae with posterior-most 2-5 caudals fused into a pygostyle supporting long pennaceous feathers in a fan-like arrangement. H. Pedal digits II-IV with elongated distal phalanges & slender, curved unguals. I. Distally positioned hallux with reversed unguinal orientation. J. Ilium  $< 20\%$  hind limb length.

sessed aerial ability superior to that of *Anchiornis* (“potentially neoflightless character score & grade” for the more derived Troodontidae = 17.5 and 45). This hypothesis can only be tested by future discoveries of oviraptorosaurs more basal than *Protarchaeopteryx robusta* (and its sister species *P. = “Incisivosaurus” gauthieri*; Senter *et al.*, 2004), the most basal member of Oviraptorosauria presently known from adequate remains (Xu *et al.*, 2002; Senter, 2007; Turner *et al.*, 2012). Since *Protarchaeopteryx* and Caudipteridae, both among the most basal and the earliest oviraptorosaurs (Xu *et al.*, 2002; Senter, 2007; Turner *et al.*, 2012), were discovered in the Liaoning province of northeastern China (Ji *et al.*, 1998; Xu *et al.*, 2002; He *et al.*, 2008), more basal members of Oviraptorosauria will probably also be discovered in northeastern Asia. Both *Protarchaeopteryx* and Caudipteridae were discovered in strata of Aptian age (125-120 Ma; Xu *et al.*, 2002; Zhonghe, 2006; He *et al.*, 2008). More basal oviraptorosaurs must have existed during earlier ages of the Early Cretaceous (and, possibly, the Late Jurassic) period but may have survived to and be discovered in strata of Aptian and even later ages.

Paul’s (1988, 2002) hypothesis that the presently known flightless members of Oviraptorosauria evolved from volant ancestors would be supported by a discovery of an oviraptorosaur more basal than *Protarchaeopteryx* that possessed substantial aerial ability. This hypothetical member of Oviraptorosauria will be referred to as “*Oviraptorovolans*” in the following reconstruction of its morphology (Fig. 10) based on morphology of presently known oviraptorosaurs and volant paravians.

“*Oviraptorovolans*” would be as small as or smaller than the smallest known oviraptorosaurs with adult body mass <2 kg, as in volant deinonychosaur (*Anchiornis*, *Rahonavis*, and *Micro-raptor*) and *Archaeopteryx* (body mass estimates from Paul, 2010). The fore limbs of a volant basal oviraptorosaur would have clawed manual digits and be  $\geq 80\%$  hind limb length (Fig. 10A) as in *Micro-raptor*, *Anchiornis*, *Archaeopteryx* and more derived avialans. The fore limbs of known oviraptorosaurs are  $\leq 67\%$  hind limb length (Ji *et al.*, 1998). “*Oviraptorovolans*” would have long asymmetrical pennaceous feathers (the primaries) attached to the manus and shorter (but still  $>100\%$  ulnar length), more symmetrical ones (the secondaries) attached to the ulna (Fig. 10B), as in *Micro-raptor*, *Archaeopteryx* and more derived avialans. In the absence of soft tissue preservation, the presence of secondaries may be indicated by quill knobs on the ulna (as in *Rahonavis*). The scapula and coracoid of “*Oviraptorovolans*” would be joined at an acute angle (Fig. 10C) as in Microraptorinae, *Archaeopteryx* and more derived avialans. The two bones are joined at an obtuse angle in known oviraptorosaurs (Paul, 2002). “*Oviraptorovolans*” would possess a single ossified sternum (Fig. 10D, as in *Micro-raptor*) with an area as large as or larger than (adjusted for body mass) that of the paired sterna of oviraptorids (Paul, 2002), ossified sternal ribs (Fig. 10E), and uncinat processes on dorsal ribs (Fig. 10F). Ossified sternal ribs and uncinat processes are known to be present in both *Caudipteryx* and Oviraptoridae among Oviraptorosauria (Paul, 2002).

A volant basal oviraptorosaur would possess a short tail consisting of fewer than 28 caudal vertebrae, (as in *Protarchaeopteryx*, Caudipteridae, and derived oviraptorosaur *Nomingia gobiensis*, Ji *et al.*, 1998; Barsbold *et al.*, 2000; He *et al.*, 2008) with posteriormost 2-5 caudals fused into a pygostyle (as in cau-

dipterid *Similicaudipteryx yixianensis* and derived oviraptorosaur *Nomingia gobiensis*, Barsbold *et al.*, 2000; He *et al.*, 2008), supporting long pennaceous feathers in a fan-like arrangement (Fig. 10G) as in *Protarchaeopteryx* and Caudipteridae (Ji *et al.*, 1998; Xu, *et al.*, 2010). “*Oviraptorovolans*” would possess pedal digits II-IV with elongated distal phalanges & slender, curved unguals (Fig. 10H, as in *Protarchaeopteryx*, Paul, 2002) and a distally positioned hallux (Fig. 10I, as in Oviraptoridae, based on Paul, 2002, plate 15) with reversed unguual orientation (as in *Protarchaeopteryx* and *Caudipteryx*, based on Ji *et al.*, 1998, fig. 1; Zhou *et al.*, 2000). Another climbing adaptation likely to be present in “*Oviraptorovolans*” is an ilium <20% hind limb length (Fig. 10J), as in Caudipteridae (Ji *et al.*, 1998; He *et al.*, 2008). “*Oviraptorovolans*” may possess long pennaceous feathers on its hind limbs, since the supra-acetabular crest is reduced in the most recent common ancestor of Oviraptorosauria and Paraves, allowing stronger hind limb abduction than in more basal maniraptoriforms (Longrich, 2006).

As reconstructed above, a volant basal oviraptorosaur would have been capable of both gliding and powered flight and would have possessed substantial scansorial ability (the latter has been postulated for the ancestor of *Caudipteryx* by Zhou *et al.*, 2000).

Paul (2010) has argued that *Sapeornis chaoyangensis* was a volant basal oviraptorosaur. However, he provided no phylogenetic analysis to support this assertion and all recent phylogenetic analyses of Coelurosauria (Senter, 2007; Hu *et al.*, 2009; Turner *et al.*, 2012; Godefroit *et al.*, 2013a,b) have placed *Sapeornis* as an avialan more derived than *Archaeopteryx*. Paul himself (2010) has pointed out that *Sapeornis* lacked adaptations for powered flight (ossified sternum & sternal ribs and uncinat processes on dorsal ribs) present in flightless Oviraptorosauria and expected to be present in their volant ancestor.

If no basal oviraptorosaur fitting the description of “*Oviraptorovolans*” is discovered and, instead, flightless transitional forms between basal Coelurosauria and Oviraptorosauria are discovered, Paul’s (1988, 2002) hypothesis of volant ancestry of known oviraptorosaurs would be falsified. This is what happened to Paul’s (2002) hypothesis of volant ancestry of Alvarezsauridae with the discovery of *Haplocheirus sollers*, the earliest and the most basal known member of the more inclusive clade Alvarezsauridae (Choiniere *et al.*, 2010). This falsification is not unexpected, given the low “potentially neoflightless character score & grade” of 9.25 and 23 (much lower than for Dromaeosauridae, Troodontidae, and Oviraptorosauria, see above), calculated by Paul (2002) for Alvarezsauridae.

The implications of the recently discovered oviraptorosaur *Ningyuansaurus wangi* for the volant ancestry of Oviraptorosauria are uncertain. Short fore (relative to hind) limbs indicate that it was incapable of aerial or scansorial locomotion. A more elongated skull with a greater number of teeth suggests that *Ningyuansaurus* is a more basal oviraptorosaur than its contemporaries *Caudipteryx* and *Protarchaeopteryx* (Ji *et al.*, 2012). If confirmed by a quantitative phylogenetic analysis, the basal position of *Ningyuansaurus* within Oviraptorosauria would suggest that the short fore limbs (and the inferred lack of aerial & scansorial ability) also present in Caudipteridae and *Avimimus portentosus* (Paul, 2002; He *et al.*, 2008) is a basal condition within the clade, falsifying volant ancestry of caudipterids and

*Avimimus*. However, short fore limbs in the most recent common ancestor of Oviraptorosauria would require independent evolution of long fore limbs ( $\geq 60\%$  hind limb length, Ji *et al.*, 1998) in basal (*Protarchaeopteryx*) and derived (Oviraptoridae) oviraptorosaurs (based on oviraptorosaur phylogeny in Turner *et al.*, 2012). Alternatively, long fore limbs may be a basal condition within Oviraptorosauria and *Ningyuansaurus* converged with Caudipteridae and *Avimimus* in evolving short fore limbs and elongated distal segments (tibia and metatarsus, Ji *et al.*, 1998, 2012; Paul, 2002; He *et al.*, 2008) of hind limbs, probably as cursorial adaptations. The latter evolutionary scenario is supported by the presence in *Ningyuansaurus* of a shorter ilium (17% femur+tibia+metatarsal III, Ji *et al.*, 2012) than in either *Caudipteryx* or *Protarchaeopteryx* (22% and 26% femur+tibia+metatarsal III, Ji *et al.*, 1998), suggesting that a recent ancestor of *Ningyuansaurus* possessed well-developed scansorial ability and, therefore, long fore limbs.

## Conclusions

- 1.) Microraptorine dromaeosaurid *Microraptor* was capable of both gliding and powered flight that utilized long pennaceous feathers on both fore and hind limbs and possessed substantial scansorial ability. Its basal phylogenetic position and early appearance in the fossil record within Dromaeosauridae support the hypothesis that the more derived and, mostly, later appearing flightless Eudromaeosauria evolved from volant ancestors.
- 2.) Microraptorine dromaeosaurid *Sinornithosaurus* possessed substantial scansorial but no aerial ability, despite possessing a number of adaptations for active flight. It therefore appears to represent a transitional form between the volant basal dromaeosaurids and the more derived flightless ones.
- 3.) Unenlagiine dromaeosaurid *Rahonavis* possessed substantial aerial ability possibly superior to that of *Microraptor* despite reduced contribution of hind limbs to flight apparatus. Unenlagiine dromaeosaurid *Buitreraptor* either possessed substantial aerial and scansorial ability or was a transitional form between the volant & scansorial and the flightless & terrestrial unenlagiines. The basal phylogenetic position of *Rahonavis* and *Buitreraptor* within Dromaeosauridae supports the hypothesis that flightless Eudromaeosauria and unenlagiines more derived than *Rahonavis* evolved from volant ancestors.
- 4.) The short fore limbs and the inferred lack of aerial & scansorial ability of basal dromaeosaurids *Tianyuraptor* and *Mahakala* are autapomorphies of these two taxa and do not contradict the descent of flightless Eudromaeosauria and unenlagiines more derived than *Rahonavis* from volant ancestors.
- 5.) Troodontids *Anchiornis* and *Xiaotingia* were capable of gliding flight that utilized long pennaceous feathers on both fore and hind limbs and possessed substantial scansorial ability. Their basal phylogenetic position and early appearance in the fossil record within Troodontidae support the hypothesis that the more derived and later appearing flightless troodontids evolved from volant ancestors.
- 6.) Basal troodontid (or a more basal paravian) *Eosinopteryx* possessed little or no aerial or scansorial ability, despite possessing a number of gliding and climbing adaptations. It therefore appears to represent a transitional form between the volant & scansorial basal troodontids (or more basal paravians), and the more derived flightless & terrestrial ones.
- 7.) It is highly probable that the most recent common ancestor of Deinonychosauria was a scansorial four-winged glider. It is also probable, though less certain, that the same was true of the most recent common ancestor of Paraves.
- 8.) Flight adaptations present in the known flightless Oviraptorosauria suggest that they evolved from a volant ancestor. The above hypothesis of volant ancestry of Oviraptorosauria would be supported by future discovery of an oviraptorosaur more basal than those presently known possessing the following characteristics: adult body mass  $< 2$  kg, fore limbs  $\geq 80\%$  hind limb length with clawed manual digits and long asymmetrical pennaceous feathers attached to the manus & shorter, more symmetrical ones attached to the ulna, scapula and coracoid joined at  $< 90^\circ$ , single large ossified sternum, ossified sternal ribs, uncinat processes on dorsal ribs, short tail consisting of  $< 28$  vertebrae with posteriormost 2-5 caudals fused into a pygostyle supporting long pennaceous feathers in a fan-like arrangement, ilium  $< 20\%$  hind limb length, pedal digits II-IV with elongated distal phalanges & slender, curved unguis, and distally positioned hallux with reversed unguis orientation.

The above hypothesis of volant ancestry of Oviraptorosauria would be falsified by future discovery of transitional forms between basal Coelurosauria and Oviraptorosauria lacking the above characteristics.

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## 基盤的デイノニコサウルス類の飛行能力

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**要旨:** これまでに提唱されてきた、無飛翔性を獲得したマニラプトル形類クレード Maniraptoriform clade に属するデイノニコサウルス類が飛行能力を持つ祖先から進化したとする仮説について、仮説の提唱以降に公表された関連する研究を元に再検討した。

機能形態、ならびにコンピュータモデルや物理モデルを用いた研究によると、基盤的ドロマエオサウルス科 basal Dromaeosauridae のミクロラプトル類 Microraptorine に属する *Microraptor*、ならびにウネンラギア類 Unenlagiine に属する *Rahonavis* は飛行能力を有しており、前者は、前肢と後肢に備わった長い羽軸を持つ木の葉形の羽毛を用いた滑空と羽ばたき飛行、それに木登りができたと考えられる。これは飛行能力の無い、より派生的なドロマエオサウルス類が飛行能力を持つ祖先から進化したとする仮説を支持する。基盤的ドロマエオサウルス科の *Tianyuraptor* 及び *Mahakala* と、長い腕を持つドロマエオサウルス科及びトロオドン科 Troodontid の系統関係を考慮すると、前者が短い前肢を有することから推定される飛行能力の欠如は彼らの系統の固有派生形質であり、上述の結論と矛盾しない。

機能形態的に見て、基盤的トロオドン科 basal Troodontidae に属する *Anchiornis* と *Xiaotingia* は、前肢と後肢に備わった長い羽軸を持つ木の葉形の羽毛を用いた滑空と木登りができたと考えられる。これは、より派生的な飛行能力の無いトロオドン類が飛行能力を持つ祖先から進化したとする仮説を支持する。さらに、ミクロラプトル類に属する *Sinornithosaurus* とウネンラギア類の *Buitreraptor*、それに基盤的トロオドン科 (もしくは、より基盤的なパラヴェス類 paravian) に属する *Eosinopteryx* は、基盤的ドロマエオサウルス科及び基盤的トロオドン科 (もしくは、より基盤的なパラヴェス類) の両系統の中において、飛行能力を持つ、あるいは木登りができる種類と飛行能力を持たない陸生の種類との中間的な形態を持っていることが機能形態学的な研究により示唆された。

ドロマエオサウルス科及びトロオドン科の両者の基盤的なグループが有する木登りの能力と四枚羽根による滑空の能力、ならびに基盤的パラヴェス類に属する *Pedopenna* と *Archaeopteryx* に見られる形態的特徴から、デイノニコサウルス類とパラヴェス類の最も新しい共通祖先も木登りのできる四枚羽根の滑空性の動物であったと示唆される。

その形態的特徴やマニラプトル形類の中での系統学的な位置付けがよくわからないオヴィラプトロサウルス類 Oviraptorosauria は、従来の仮説では飛行能力を持つ祖先から飛行能力の無いオヴィラプトロサウルス類が進化したと推定されているが、将来の新たな発見がこの仮説が支持されるかどうか明らかにするだろう。

**キーワード:** デイノニコサウルス類、飛行能力の二次的喪失、飛行適応、木登り適応