

# A review of the Early Cretaceous Jehol Group on northeastern China and a revision of concerning the origin of flight paradigm

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**ABSTRACT** - The unusual preservation and evolutionary significance of the avian and non-avian dinosaur fossils from western Liaoning Province in China exemplifies rare conservation deposits. Described as the Jehol Biota, the fauna includes such remarkable discoveries such as feathers and wings associated with dinosaurs as well as many new species of fossil birds preserved in abundance. Volcanic activity during the Mesozoic was crucial to the preservation of the Early Cretaceous Jehol Biota by acting as a mechanism that killed organisms en masse from volatile emissions and voluminous ash falls. One of the crucial specimens documented in the Liaoning deposits is *Microraptor gui*, a four-winged glider. Described as a feathered, non-avian dinosaur, the evolution of such an animal in a group closely related to birds necessitates revision of the origin of flight paradigm.

**Key words:** dromaeosaur, origin of flight, Jehol Group, Cretaceous, volcanism.

**Le Groupe Jehol (Crétacé inférieur) du Nord-Est de la Chine et une révision du paradigme de l'origine du vol** - La conservation inhabituelle et la signification évolutive des fossiles de dinosaures aviens et non-aviens de l'Ouest de la province du Liaoning, en Chine, sont liées à des dépôts à préservation exceptionnelle. Décrite sous le nom de « Jehol Biota », cette faune comprend des spécimens remarquables, avec notamment des plumes et des ailes associées à des dinosaures, ainsi que de nombreuses nouvelles espèces d'oiseaux fossiles en grande abondance. L'activité volcanique mésozoïque a été cruciale pour la préservation de cette faune, en tant que mécanisme ayant causé la mort d'organismes en masse du fait d'émissions gazeuses et de volumineuses chutes de cendres volcaniques. Un des spécimens cruciaux provenant des dépôts du Liaoning est *Microraptor gui*, un planeur à quatre ailes décrit comme un dinosaure non-avien pourvu de plumes. L'évolution d'un tel animal dans un groupe étroitement apparenté aux oiseaux nécessite une révision du paradigme de l'origine du vol.

**Mots-clés:** dromaeosaure, origine du vol, Groupe Jehol, Crétacé, volcanisme.

## INTRODUCTION

This paper reviews the geological context of the Early Cretaceous Jehol Group with emphasis on the volcanology. It also provides additional insights concerning the new paradigm for the origin of flight through comparison of the functional morphology between the maniraptoran dinosaurs, *Microraptor gui* (the four-winged glider from the Early Cretaceous of China) and *Bambiraptor feinbergi* (the cursorial, birdlike dinosaur from the Late Cretaceous of North America). This study considers these two animals as representing arboreal and cursorial forms, respectively. Study of both forms may place the origin of flight paradigm in a stratigraphic context since *Bambiraptor* is geologically younger. Sources of information for this paper include a review of current geological literature and direct observations of specimens and outcrops.

China has been the location of many recent discoveries of exceptionally preserved fossils representing a major biological radiation in the Early Cretaceous (Luo, 1999; Zhou *et al.*, 2003; Zhou, 2004b) and fossils from this area have been collectively termed the Jehol Biota (Chang *et al.* 2003). The fossils are found within the volcanic and volcanoclastic rocks in this area suggesting that these are mass kills resulting from volcanism (Martin *et al.*, 1998; Burnham *et al.*, 2000). Considered one of the world's premier fossil regions (Gee, 2001; Chang *et al.*, 2003, Zhou *et al.*, 2003), western Liaoning Province (fig. 1) provides a rare glimpse into Early Cretaceous life with both plant and animal remains abundantly preserved. Many of the vertebrate fossils are articulated skeletons with soft tissues, stomach contents, and integument (Zhou *et al.*, 2003). The release of chemical constituents from the alteration of the volcanic ash and bacterial films may have enhanced fossilization during diagen-



**Figure 1** - Study area showing fossil localities from the Jehol Group in western Liaoning Province, China.

esis (Davis & Briggs, 1995; WoldeGabriel *et al.*, 2000).

Tuff layers within the fossil-bearing strata provide isotopic (Swisher *et al.*, 1999, 2002; He *et al.*, 2004a) and magnetic polarity ages (Pan *et al.*, 2001) of Cretaceous. This dating is critical to understanding paleoenvironment, paleoecology, and evolution of the faunal and floral elements (Wang *et al.*, 2000; Chang *et al.*, 2003) as well as the timing of geologic events that were previously reported as the Late Jurassic.

## TECTONIC SETTING

The Turgai Strait separated Mesozoic landmasses now part of modern Eurasia. The eastern part, the Asiatic Plate, was an isolated area and contained the Jehol Biota. This plate included northeastern China, Mongolia (Transbaikalia region), Siberia, Korea, and Japan (Chen, 1992; Chang *et al.*, 2003) and bordered what is now the Pacific Ring of Fire. During the Paleozoic, collision of the Pacific plate with the Asiatic plate induced a pattern of complicated movements. These movements included east-west compression in the early Mesozoic to north-northeast extension during the late Mesozoic (Zhu *et al.*, 2002; Meng *et al.*, 2003). Consequently, plate boundaries became over-thickened with extensive and voluminous magmatism associated with this process. These tectonic changes may have promoted extension of the crust by thermal weakening (Meng *et al.*, 2003). Subsequently, volcanic chains and basins formed along faults developed during this process. Additionally, in regions of highly extended crust, volcanogenic sedimentary rocks commonly accumulate in basins formed during this process (Gaylord *et al.*, 2001).

There was also north-south trending left-lateral shearing stress resulting from the northward movement of the Pacific plate. This caused a gigantic sinistral wrench fault close to the margin of the continent (Chen, 1992). Named the Tancheng-Lujiang fault, it trends north-northeast across eastern China extending 2400 km and was active during the Mesozoic with about 740 km of strike-shear movement (Chen, 1992). Chen (1992) described a volcanic belt west of the fault, in Liaoning Province, which produced the intermediate to mafic volcanoclastics, while the volcanism east of the

fault was intermediate to silicic. All the fossil occurrences exhibiting unusual preservation are reported in basins west of this fault. The Fuxian-Yixian basin is one of the largest and it trends northeast to north-northeast. In this basin, volcanism was most intense during the Late Jurassic and Early Cretaceous, forming basalt-andesitic rocks. The activity at this earlier time was very strong and accompanied by plutonism (Xu, 1990).

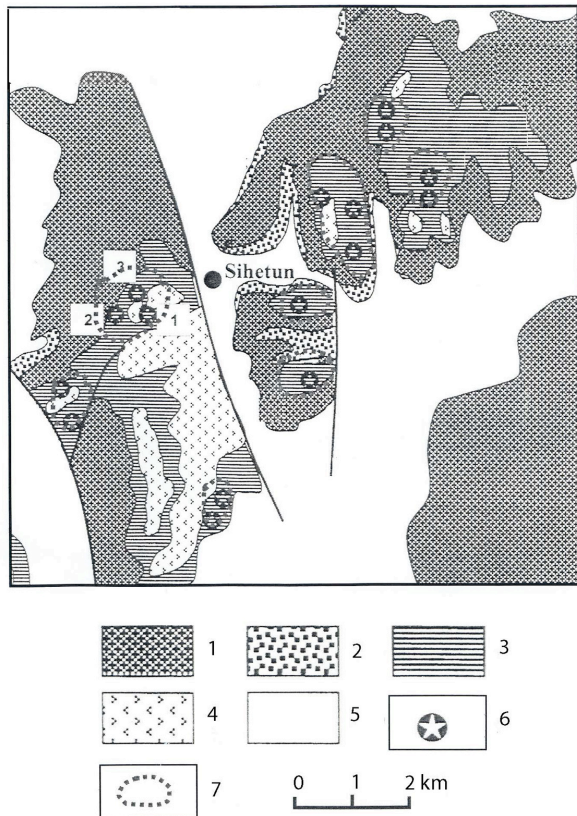
The resulting fault belts trend northeast and north-northeast. Volcanic eruption belts developed along the faults. The mountain building (Yanshan orogeny) and volcanism filled the basins with fluvial and lacustrine volcanoclastic sediments after the displacement of the Tancheng-Lujiang fault (Chen, 1992).

The study area (fig. 1), a series of northeast basins (fig. 2), were topographically low areas and filled with thick Mesozoic deposits. The common type of basin in the study area had been downwarped and faulted. There are at least 11 basins in western Liaoning Province. They are monoclinical and dip to the southeast.

## GEOLOGIC SETTING

Early Cretaceous Jehol Group strata mainly crop out in western Liaoning Province, northern Hebei Province, and southeastern Inner Mongolia in northeastern China (fig. 1) (Wang *et al.*, 1998, 1999, 2000; Chang *et al.*, 2003: fig. 11). These rocks have Early Cretaceous ages ranging from approximately 128.4 Ma to 110 Ma (Swisher *et al.*, 1999, 2002; Chang *et al.*, 2003). Wang *et al.*, (2001) reported U-Pb age of 125 Ma and the isotopic age inferred by Smith *et al.* (1999) was Aptian. Additionally, paleomagnetic age data suggest an Early Cretaceous Barremian M3n zone (Pan *et al.*, 2001). These dates refute previous determinations of a Jurassic-Cretaceous boundary (Hou *et al.*, 1995; Chen *et al.*, 1998) or a late Jurassic age suggested by Ren *et al.* (1997), Chiappe *et al.* (1999), and Ji *et al.* (2001).

The early Cretaceous Jehol Group in the study area includes the Yixian Formation and overlying rocks of the Jiufotang Formation (fig. 3). But the Jehol Group has been defined poorly and some authors have placed additional formations into the group, both above and below the Yixian



**Figure 2** - Geologic map of Sihetun area (from WANG *et al.*, 2000; CHANG *et al.*, 2003); Dotted lines represent possible maars (CHU, G. 2005 pers. comm.). 1. basalt and andesite (lava); 2. conglomerate and volcanic breccia; 3. shale and tuff; 4. subvolcanic rock; 5. Tuccongzi Formation; 6. fossil localities; 7. maars outline.

and Jiufotang Formations; others authors have used different formation names extending the group from Upper Jurassic to Lower Cretaceous (Lucas and Estep 1998; Sun *et al.*, 1998; Chiappe *et al.*, 1999; Chang and Park, 2003). For the purpose of this paper, nomenclature and stratigraphy of Wang *et al.* (2000) and Chang *et al.* (2003) is retained (fig. 3).

The Jehol Group was divided into the Yixian and Jiufotang Formations with five vertebrate fossil beds recognized as members that occur between four thick lava flows A, B, C, and D (fig. 3) (Chang *et al.*, 2003). The Jehol Group is 1590 to 2,570 meters thick (Chang *et al.*, 2003) and overlies unconformably the Late Jurassic Tuchengzi Formation (Wang *et al.*, 1999), upper part of which has, however, been dated as 139.4 Ma (Swisher *et al.*, 2002) (fig. 3).

The lower portion of the Jehol Group, the Yixian Formation, consists of four basaltic units [lava] and four sedimentary units (fig. 3). Initially, it was divided into 3 beds (Wang *et al.*, 1998, 1999, 2000), but a fourth set of beds in the lowermost portion was recognized more recently (Chang *et al.*, 2003). The beds in the Yixian Formation have been formally designated from lowest to uppermost: (I) Lujiatun Beds, (II) Jianshagou Beds, (III) Dawangzhangzi Beds, (IV) Jingangshan Beds (fig. 3).

The Sihetun locality, south of Beipao City, is the type section (figs. 1, 2, 5) of the Yixian Formation (Wang *et al.*, 1998, 1999). It is approximately 790 to 1370 meters thick (Chang *et al.*, 2003). The Jiufotang Formation, with the type section in the Jiufotang village, also exposed at the

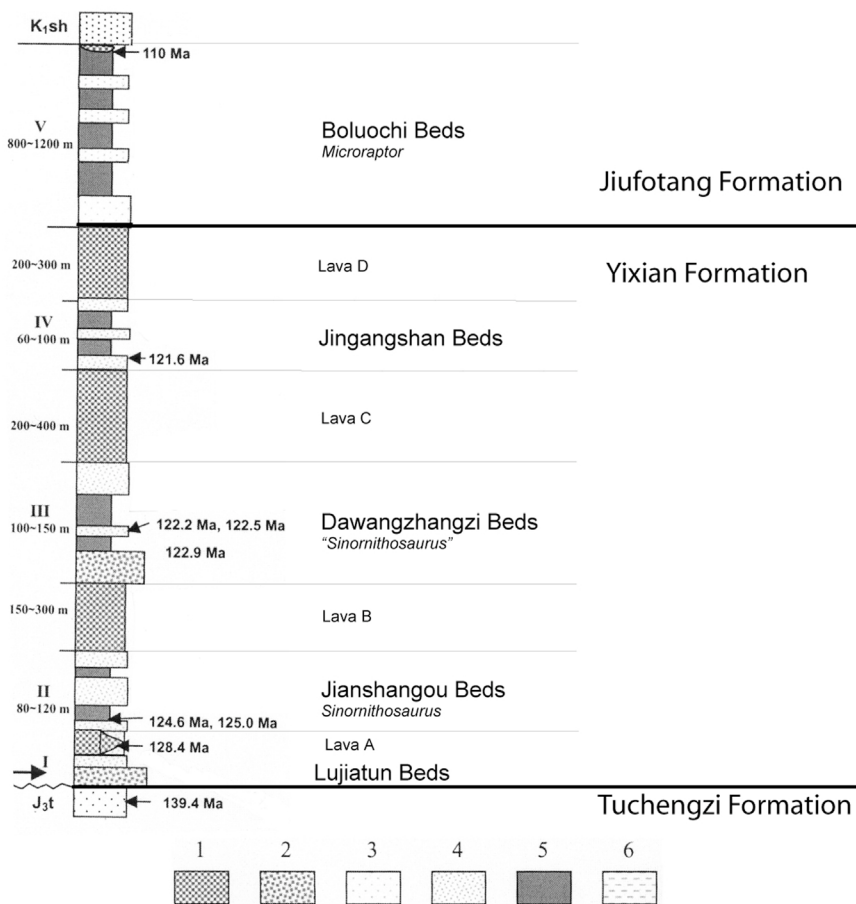
Shangheshou and Buluochi localities near Chaoyang City, comprises the fifth unit of the Jehol Group. This formation contains 800 to 1,200 meters of lacustrine shales intercalated with tuffs (figs. 1, 2, 3) (Chang *et al.*, 2003).

The Lujiatun Beds (I in fig. 3—lowest Yixian and most recently added segment of the Jehol Group) comprises tuffaceous conglomerate, sandstones, and silty mudstones in alluvial deposits (Wang *et al.*, 1998, 2000). The beds contain a vertebrate fauna consisting of such small, ornithischian dinosaurs as *Psittacosaurus*, *Jeholosaurus*, and *Liaoceratops*; the small theropod dinosaurs *Sinovenator* (a basal dromaeosaurid) and *Incisivosaurus*; *Mei*, *Dilong*, and mammals and frogs (Wang *et al.*, 1999, Chang, 2003, Zhou *et al.*, 2003). Few plant fossils and no invertebrates are known from this bed. These beds overly unconformably Jurassic fluvial deposits dated at 139.4 Ma and underly 128.4 Ma beds (Chang *et al.*, 2003).

It is unclear whether the Lujiatun Beds of the Yixian can be correlated to the Daohugou Beds in Inner Mongolia. The Daohugou Beds were once considered to be the southward extension of lowest portion of the Yixian Formation in Inner Mongolia (Wang *et al.*, 1998). Described as a lacustrine deposit, they comprise gray tuffaceous shales and mudstones with tuffaceous breccia at the bottom. Various tuff layers are intercalated with shales and mudstones (He *et al.*, 2004). They have also been described as conglomeritic tuff that may be correlated with Lujiatun (Chang *et al.*, 2003). The beds contain also an arboreal coelurosaurian,

## Jehol Group

**Figure 3** - Stratigraphic column of the Jehol Group (modified from CHANG *et al.*, 2003).



Legend: 1, basalt and andesite with volcanic breccia (lava); 2, conglomerate with volcanic breccia; 3, sandstone conglomerate; 4, tuffaceous sandstone and tuff; 5, Shale and tuff; 6, silt and silty mudstone

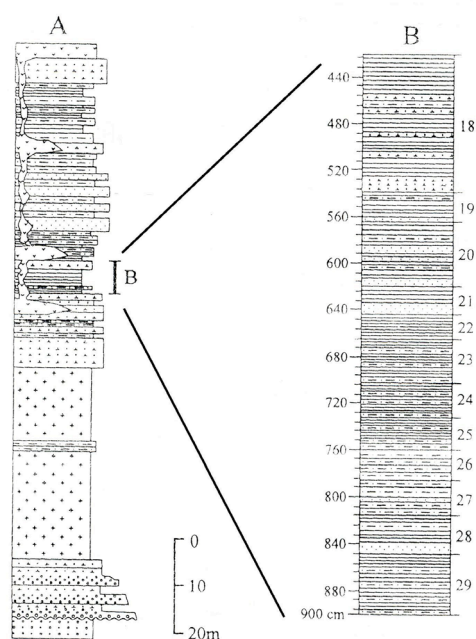
*Epidendrosaurus* (Zhang *et al.*, 2002) and *Pedopenna* (Xu and Zhang, 2005). The Daohuguo Beds overly an ignimbrite with a  $^{40}\text{Ar}/^{39}\text{Ar}$  date of 159.8 Ma (He *et al.*, 2004). He *et al.* (2004) consider the Daohuguo Beds as upper Jurassic or higher.

The Jianshangou Beds (II in fig. 3) of the Yixian Formation comprise gray to black sandstone, shale, and mudstone rich in tuff. Chang *et al.* (2003) consider it to be the most significant bed for the evolution of birds since it contains the *Confuciusornis* paleoavifauna and the feathered dinosaurs *Sinosauropteryx*, *Sinornithosaurus*, *Caudipteryx*, *Beipiaosaurus*, and *Protoarchaeopteryx*. Many other such fossils as mammals, pterosaurs, fish, the angiosperm *Archaeofructus* (Sun *et al.*, 1998), and invertebrates are abundant as well. Isotopic age dates were found to be 125.0 Ma (Swisher *et al.*, 2002) and are between Barremian and Aptian.

At the locality of Sihetun Village, Beipiao City, Wang *et al.* (1998) numbered 37 quarry layers (fig. 4) in an

excavation of the lower part of the Jianshangou Bed (II in fig. 3) of the Yixian Formation (fig. 4). The layers have been numbered from upper to lower. This quarry comprises thin, horizontal layers of lacustrine deposits intercalated with volcanic ash (Plate 1). Some of the reported sedimentary structures are varves (fig. 5) also found in the excavation profile of the Sihetun section. These are thin laminations thought to represent annual cycles (Liu *et al.*, 2000; Chu, G. personal communication, 2004) and contain also charcoal and ash. Mass death assemblages and individual fossil discoveries have been referred to this numbered sequence (Wang *et al.*, 2000; Chang *et al.*, 2003; Lu, 2002). Most of the vertebrate fossils associated with tuffs are concentrated in layers 25, 28, and 29. The lower part of layer 29 is significant because it contains an abundant and diverse vertebrate fauna consisting of feathered dinosaurs and fossil birds (Wang *et al.*, 1999). Concentrations of volatile emissions from volcanic eruptions have also been correlated to these numbered layers (Guo *et*





**Figure 4** - The composite stratigraphic section A and the excavating profile B of the lower Yixian Formation in Sihetun and neighboring area, western Liaoning (from WANG *et al.*, 1998).

*al.* 2003). An intermediate to basic sub-volcanic dike intrudes bed 6 at the Sihetun excavating site. The dike baked adjacent rocks: a shale-sandstone-siltstone-silty mudstone with layers of tuffaceous sandstone and mudstone. Tuffs in layer 5 and layers 2,3, and 4 contain intermediate basic lava (basalt, andesite) and overlie the dike (Wang *et al.*, 1998, 1999).

The Dawangzhangzi Beds (III in fig. 3) comprise horizontally bedded, gray to black sandstone, shale and mudstone with a tuffaceous component. Feathered theropod dinosaurs, including the microraptorine cf. *Sinornithosaurus* (NGMC 91) (Ji *et al.*, 2001) dominate the fauna (Chang *et al.*, 2003). Other fossils include fishes, birds, mammals, and angiosperms.

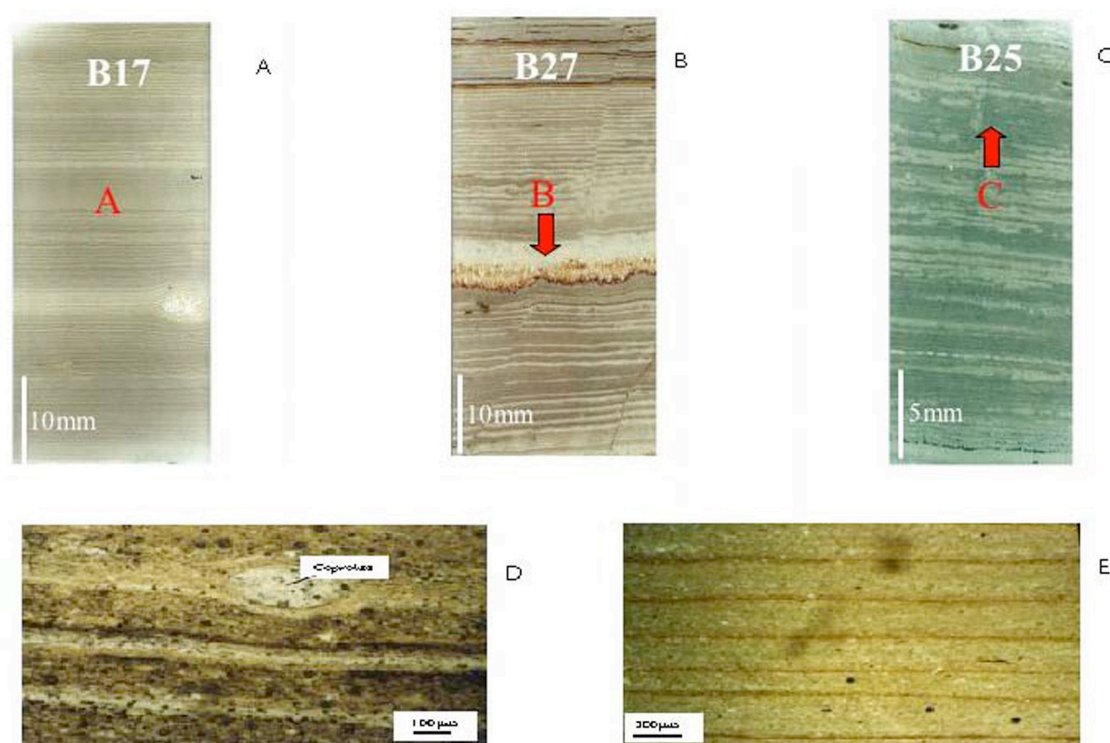
Lake deposits of the upper Yixian Formation comprise the Jingangshan Beds (IV in fig. 3). The black and gray sandstone, mudstone, and shale are rich in tuff. The fish *Lycoperoptera muroii* is the only abundant component of the vertebrate fauna, although birds and pterosaurs are known (Chang *et al.*, 2003).

The Buluoichi Beds (V of fig. 3) of the Jiufotang Formation include a thick sequence of sandstone and conglomerate at the base that thin upwards and become interbedded with shale and tuff. The top of the formation is a thin conglomerate containing volcanic breccia (Wang *et al.*, 1999, 2000; Chang *et al.*, 2003). The tuffs in the Shangheshou section have been dated 120.3 Ma (Aptian) using  $^{40}\text{Ar}/^{39}\text{Ar}$  (He *et al.*, 2004). *Microraptor* specimens have been collected from this bed (Xu *et al.*, 2000; Xu, 2002; Czerkas *et al.*, 2002; Chang *et al.*, 2003; Xu *et al.*, 2003).

## VOLCANIC ACTIVITY

The volcanic rocks of the Jehol Group contain basalt and andesite that is basic to intermediate-basic (Xing *et al.*, 2004). Nearly all well-preserved fossils in the Jehol Group are in tuff or tuffite. Many such tuff layers exist, and the strata are intercalated with lava and flow breccia (fig. 3). Explosive and effusive volcanic activity was common in the area for 35 to 45 Ma (Chang *et al.*, 2003; Guo *et al.*, 2003). Volcanism related to plate tectonics is usually restricted to the edges of plates but also occurs at hot spots and zones of extrusion. Mantle plumes explain the volcanism that occurred during the late Mesozoic in western Liaoning since this did not occur at the plate boundaries. The basalt in western Liaoning is of mantle-plume origin caused by upwelling of heat from far below the MOHO discontinuity (Zhu *et al.*, 2002). Differences of temperature and density due to delamination of the mantle and upward movement of hotter asthenosphere accounts for this type of magmatism and can produce such local mantle convections (Qian *et al.*, 2003). This in turn produces volcanism, and in eastern China this manifested itself in massive volcanic eruptions (Zhu *et al.*, 2002).

Geochemical data of Guo *et al.* (2003) associated with the intercalated tuff layers in the lower Yixian Formation show large -and small-scale ash falls associated with more frequent gassing (fig. 6). The volcanic activity may include series of phreatomagmatic eruptions forming maar lakes (Guo *et al.*, 2003). Maximum eruption height from the plume of the volcano in western Liaoning was estimated to



**Figure 5** - Varves from Sihetun area excavating profile in lower Yixian Formation. A, coprolite; B, ash layer; C, burrow; D, coprolite; E, clastic varves. (from CHU, G. 2005 pers. comm.)

be 18 to 38 km, and the volume of fallout ash covered 200 to 320 km<sup>3</sup> (Guo *et al.*, 2003). The distribution area was approximately 5 by 14 km (Chu, G. personal communication, 2004).

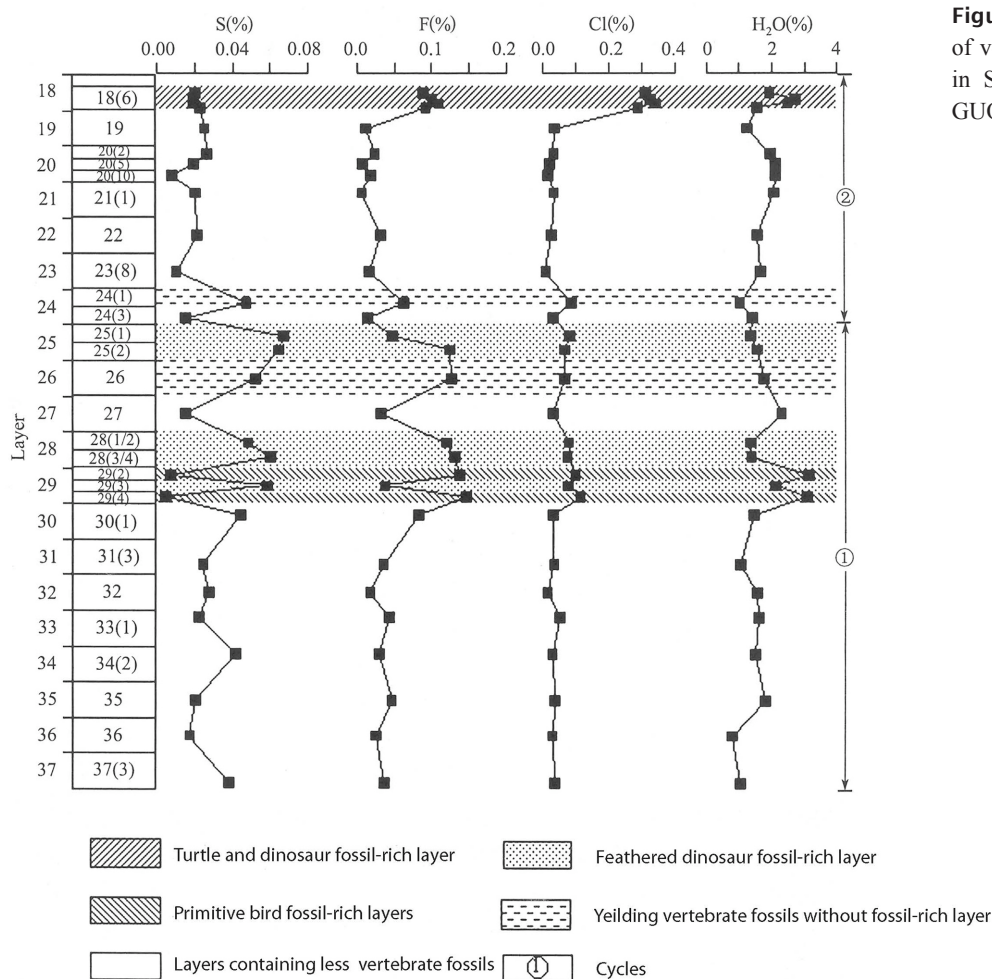
## DISCUSSION

Wang *et al.* (2000) and Chang *et al.* (2003) interpreted the Early Cretaceous Jehol Group as alluvial (conglomerates with volcanic breccia at the base) to lacustrine facies (horizontally bedded shales). This interpretation is supported by the sedimentary cycles found in the lower Yixian Formation in which the Jianshangou Beds record coastal lakes, shallow lakes, semi-deep lakes, and deep lakes (Chang *et al.*, 2003: fig. 16). Wang *et al.* (2000) proposed that the lake was a wide pan basin with periods when water was deep and volcanism affected the sedimentation. Volcanism included lava flows and ash falls and intrusive igneous activity occurred as well. Chen *et al.* (2002) reported volcanic bombs, pillow lava, tephra, and volcanic ash in the fossil beds at Sihetun. The pillow lava indicates the volcanic activity was not exclusively subaerial. Guo *et al.* (2003) suggested alternatively that the Sihetun locality was the site of small and deep maar lakes rather than a single, large lake. Pan *et al.* (2001) also suggested a quiet lake environment with the fossil-bearing sediments at Sihetun deposited in a closed lake with minimal

drainage.

Without extensive fieldwork to map the lateral extent of the stratigraphy, it is difficult to differentiate between maar lakes, shallow flood-plain lakes, and lakes with long-lived basins. The conglomerates with volcanic breccia are not well described, which raises the question that they may be surge deposits. On the other hand, the maar lake interpretation of Guo *et al.* (2003), as shown on their map, has eight maars oriented along the fault lines in a southeast to northeast direction (fig. 2). Some of the volcanic deposits appear to have concentric outlines fitting the pattern expected from a series of maar lakes. There is no evidence, however, of the characteristic tuff ring structures that typically encircle the maar lakes. Guo *et al.* (2003) suggested that they were eroded away but were able to provide estimates of the surface areas of the maars at 0.6 km<sup>2</sup> to 10 km<sup>2</sup> based on geologic structures (Chu, G. personal communication, 2004). They argued against a large lake since few lacustrine-border facies are present in the study area. There is also geologic evidence of underwater eruption (Chu, G. personal communication, 2004). They cited fine-grain size, considerable thickness of horizontal bedding, varves, and low concentration of magnetic minerals as evidence against a large lake fed by rivers.

The small areal extent of the fallout deposits reported by Guo *et al.* (2003) suggests relatively small scale eruptions. It may be possible that the volcanic activity in western



**Figure 6** - Graph of concentration of volatiles emitted with fossil layers in Sihetun excavating profile (from GUO *et al.*, 2003).

Liaoning consisted of many small eruptions including maars and possibly a large Plinian-style eruption from a nearby volcano. It may be reasonable to assume that the thickness of these basalt and andesite layers indicate more than a single lava flow per unit. It is also possible that the system of faults and basins provided groundwater for phreatomagmatic eruptions. These factors along with the lack of cross-bedded sedimentary structures within either the Yixian or Jiufotang Formations, except for the presence of varves, seem to support a maar lake interpretation or a large, closed lake. These environments would have provided a restricted physical environment and deep, anoxic conditions (Liu *et al.*, 2002). Without geological evidence of tuff rings, tuff cones, or surge deposits, the localities in this region remain ambiguous as to whether there were hydrovolcanic eruptions.

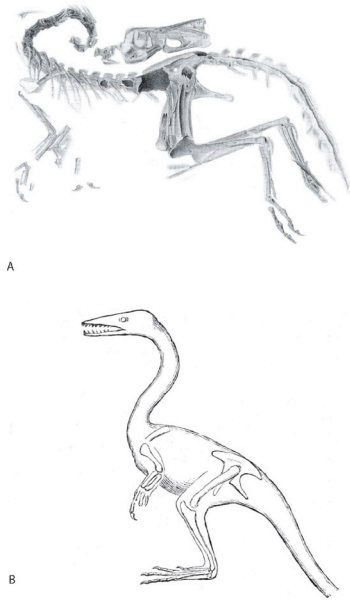
## VOLCANOES AS KILLERS

The Liaoning volcanoes may have killed their victims in several ways, producing the mass death assemblages found in the Jehol Group directly through exposure to poisonous gases as evidenced by the analysis of the volatiles

(Guo *et al.*, 2003), asphyxiation from volcanic ash (Francis, 1994; Burnham *et al.* 2003), and indirectly through abrupt climate changes. The fossiliferous layers are coincident with the pyroclastic tephra. Since the deposits in western Liaoning comprises ash layers at or below the level of the fossils, the massive assemblage of early birds and dinosaurs can be associated with local intensive volcanic eruptions.

The exposure to volatile gases may have had a tremendous effect on the biota. Guo *et al.* (2003) showed that there is a correlation between volatiles released by the intermediate-acid eruptions in their samples and the mass-death layers. Crystals separated from the volcanic rocks were analyzed using an electron microprobe for major oxides, sulfur, chlorine, and fluorine in the melt inclusions and matrix glasses (Guo *et al.*, 2003). The layers associated with the fossil assemblages have higher concentrations of different volatiles (fig. 6). Guo *et al.* (2003) concluded that frequent, explosive; high-volatile-release eruptions caused the mass mortality layers. Furthermore, the volatiles consisted of three types, each with a different but fatal effect on the biota. Guo *et al.* (2003) postulated that sulfur gases killed the feathered dinosaurs directly, while hydrogen chloride

**Figure 7** - *Compsognathus longipes* A, fossil skeleton (from WAGNER, 1861); B, birdlike life restoration (from MARSH, 1895).



and hydrogen fluoride caused deleterious effects on the environment and climate resulting in mass mortalities found in the other layers.

Hydrogen sulfide is a lethal gas known to impact modern populations. For instance, the Toba eruption produced  $H_2SO_4$  aerosols with a six-year residence time and likely dropped regional temperatures up to  $15\text{ }^{\circ}\text{C}$  (Rampino and Ambrose 2000). Such loading of the atmosphere caused a global volcanic winter with more severe local effects to vegetation and animals. Hydrogen fluoride (HF) is a lethal gas and was likely hazardous to the local Jehol populations since the concentration of the gas was found to be highest coincident with the bird fossil-tuff horizons (layer 29—*Confuciusornis* avifauna). But there is no evidence this had a regional effect on the paleoclimate or paleoenvironment during that time.

Sulfur-rich gases were postulated by Guo *et al.* (2003) to form acid rain and lower surface temperature, thereby causing mass mortalities of the dinosaurs in the Sihetun quarry layers 25 (1), 25 (2), 28 (1/2), 28 (3/4), and 29 (3). Unfortunately, there is no mention of indicators in the fossil flora showing acid rain effects that damaged vegetation (Grattan *et al.*, 2003) or reduced thickness of annual growth in tree rings (Schmincke, 2004). Also, the resulting greenhouse effect may actually cause an improvement in the foliage, and the flora would flourish for a period of time afterwards (Schmincke, 2004). Cooling phenomena from the sulfur gases are thought to have killed the dinosaurs on the assumption they had a cold-blooded metabolism.

Possibly analogous, is the Laki Fissure eruption in Iceland in 1783 that was notorious for its devastating impact mostly due to gases (Grattan *et al.*, 2003). Grattan *et al.*

(2003) linked air pollution to increases in human mortality rates at that time. Two factors that induced environmental forcing were acidic gases (the infamous sulphurous dry fog) and aerosols that damaged vegetation and caused human sickness and death. Secondly, the extremely high surface temperatures were certainly lethal.

The lowest part of the Jehol Group has the most diverse fossil assemblage and related probably to the most disruptive volcanism (Guo *et al.*, 2003). The strata of the upper members of the Jehol Group indicate further volcanic activity but perhaps less violent (Chang *et al.*, 2003; Guo *et al.*, 2003; Zhou, 2004a).

The most important layer (29) is in the Jianshangou Beds of the lower Yixian Formation since it preserves birds and feathered dinosaurs (Chang *et al.*, 2003). Mass death assemblages of the primitive bird *Confuciusornis* occur here and it is estimated that more than one thousand specimens have been collected from layer 29. The density of the *Confuciusornis* skeletons ranging from one individual every 1 to  $6\text{ m}^2$  indicates that a mass-mortality event occurred (Hou *et al.*, 1995; Guo *et al.*, 2003). The fossils were preserved articulated with intact feathers. This *Confuciusornis* layer lies within a tuffaceous mudstone and fine ash tuff.

## UNUSUAL PRESERVATION

The well-preserved Jehol fauna suggest strongly more than rapid burial (Wang *et al.*, 2000). A plethora of soft-tissue preservation types occurs in this area (Chang *et al.*, 2003; Zhou *et al.*, 2003) and soft-tissue preservation is associated usually with chemical diagenetic mineralization (Allison & Briggs, 1991). A low degree of decay prior to





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**Figure 8** - *Bambiraptor feinbergi* reconstructed skeleton (from S. HARTMAN, 2003).

fossilization allows carbonized volatile soft tissues to be preserved. Certainly decay had been inhibited by a higher than normal sedimentation rate because the organisms were quickly buried in anoxic conditions, but the preservation process continued during diagenesis aided by the constituents of the volcanic ash. This factor affected the organic remains by leaving them uncrushed and articulated, since the minerals from the breakdown of the volcanic ash filled the hollow spaces of the bones and reinforced the bone structure itself possibly by infiltration of the bone fabric.

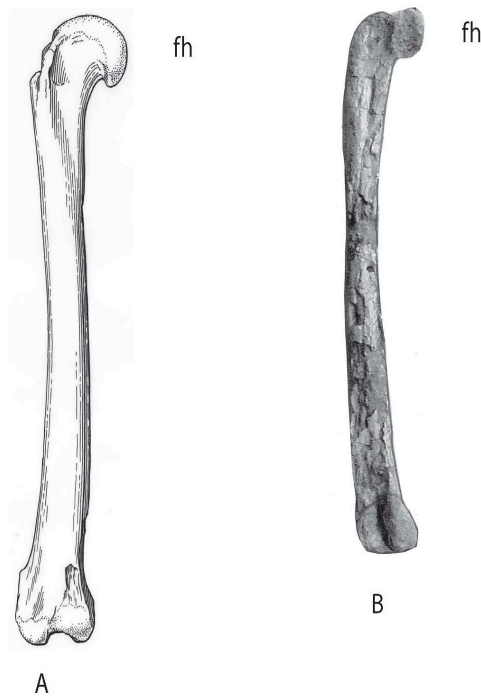
The fossils of feathered dinosaurs occur only in the Yixian and Jiufotang Formations (Wang *et al.*, 2000; Ji *et al.*, 2001; Norell *et al.*, 2002; Xu *et al.*, 2003; Zhou *et al.*, 2003). The remarkable preservation in this area of articulated fossils with feathers suggests strongly that burial was rapid and transportation was minimal. The lithologic components that surrounded them provided an excellent matrix allowing details of the feathers to be preserved. Strata containing intact fossils may have resulted from deposition from suspension. The volcanic source of the sediments enhanced preservation by providing necessary components during diagenesis allowing petrification and permineralization of hard parts (Lucas & Prevot, 1991). Infilling of vertebrates by diagenetic minerals may preserve three-dimensional structure. The precipitation of additional diagenetic mineral phases as clays, zeolites, and carbonates resulting from clastic and volcanic fragments also provides necessary components that enhance preservation (WoldeGabrial *et al.*, 2000). Preservation of feathers is a special case since it usually involves bacterial autolithification (Davis & Briggs 1995) seen also in the maar lake deposits of Messel, Germany *Lagerstätte*. Additionally, the low rate of decay in anoxic conditions allowed

organic remains to survive long enough to undergo diagenetic alteration. Chiappe *et al.* (1999) described the preservation of feathers of *Confuciusornis* as carbonization but gave no methodology of how this analysis was determined. Kellner (2002) also mentioned that the feathers preserved from these deposits were probably carbonized remains but based this on their dark color contrasting with lighter matrix. Xu (2002) mentioned that the feathers of *Microraptor* were carbonizations as well. Such carbon films are usually bacterial species specific to feathers (Davis & Briggs, 1998). Additional work is needed to discern if all the varying preservational patterns described as protofeather morphologies (plumes, filaments, etc.) represent feathers or other kinds of filaments (Prum & Brush, 2002; Wellnhofer, 2004). Most importantly, the unique preservation allows a revision of the origin of flight paradigm. Without feathers *Microraptor* would not have been recognized as a four-winged glider that shifts the focus of the origin of flight back into the trees.

## REVISION OF THE ORIGIN OF FLIGHT PARADIGM

The small Jurassic theropod *Compsognathus* (fig. 7a, b) was historically the first dinosaur linked to the evolution of birds and their flight since the discovery of the first fossil bird, the Jurassic *Archaeopteryx* (Desmond, 1976; Witmer, 1991). Anatomical similarities between the gracile and birdlike *Compsognathus* and *Archaeopteryx* showed how flight might have evolved in a morphological context, but the argument polarized on how this may have come about. Williston (1879) first proposed that flight evolved from the *ground up* by cursorial animals. Marsh (1880), countered

**Figure 9** - Anterior view of right femora of A, adult *Bambiraptor* FIP 007; B, *Microraptor* sp. IVPP V 126662.



with the *trees down* concept involving an arboreal lifestyle. Nopcsa (1907) restored *Compsognathus* as a cursorial biped surmising that the flight stroke had evolved from predatory motions of the arms and that running was efficient enough for the animal to achieve eventually powered flight. This assumption is still under investigation (Ostrom, 1976; Padian, 1986, 2003; Burgers & Chiappe, 1999). Beebe (1915) proposed that the arboreal origin of flight passed through a gliding, four-winged Tetrapteryx stage (Witmer, 1991; Xu et al., 2003; Prum, 2003). Heilman (1926), influenced by the bird-features of the small coelurosaurian *Compsognathus*, proposed Proavis—a hypothetical arboreal ancestor. Bock (1965) revisited the arboreal theory and detailed the evolutionary steps with adaptations necessary to achieve flight.

Another theropod dinosaur is linked to *Archaeopteryx* and the origin of flight. The impact of Ostrom's work on the Early Cretaceous dromaeosaur *Deinonychus*, with even closer anatomical similarities to *Archaeopteryx*, seemed to solidify the cursorial origin of flight theory. Since *Deinonychus* had elongated arms and a folding wrist it allowed refinement of the prey-capturing model as a precursor to flight mechanisms. Padian (1985) attempted to constrain the origin of flight argument within three criteria: phylogenetic, functional, and aerodynamic. Phylogeny coincided with cladistic analysis showing terrestrial dromaeosaurs leading to a crown group Aves (Gauthier, 1986). The Late Cretaceous *Bambiraptor* was the next significant discovery—a small, birdlike dromaeosaur with a furcula (fig. 8). This virtually complete,

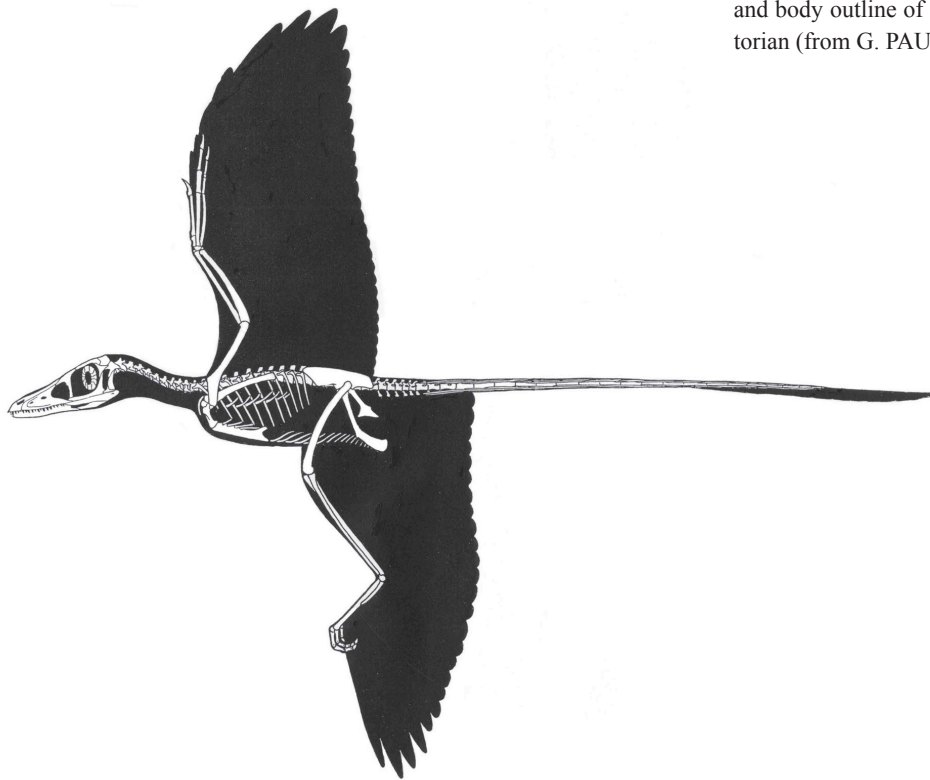
three-dimensionally preserved fossil skeleton allowed functional morphology studies regarding dromaeosaur locomotion (Burnham, 2004).

Finally, new discoveries feature the smallest known theropod, *Microraptor*, in the debate over the origin of flight. *Microraptor* is a four-winged dromaeosaurid dinosaur (fig. 10) that seems to fulfill Beebe's *trees down* Tetrapteryx postulate (Xu et al., 2003; Prum, 2003). With direct fossil evidence of hindlimb feathers on a dromaeosaur, the paradigm shifts from cursorial phase towards a gliding phase during the evolution of flight.

Further supporting feathered hindlimbs, a recent study has reconfirmed the preservation of the hindlimb feathers on *Archaeopteryx* that were ignored largely for over a century (Christiansen & Bonde, 2004). Although, hindlimb feathers seem out of context with cladistic analyses (Padian, 2003), the report of an enantiornithine bird with elongate leg feathers provides more support for the evolution of hindlimb feathers (Zhang & Zhou, 2004).

The following sections investigate the functional morphology of new four-winged microraptorians, their mode of locomotion, and the changes that evolved in their skeletal systems as a result of their lifestyles. Ji et al. (2001), Xu (2002), Xu et al., (2000, 2003), Czerkas et al. (2002), and Hwang et al. (2002) have described the osteology of different specimens of microraptorians, including *Microraptor*. Taxonomic references to the specimens retain some of the phylogeny of Senter et al. (2004) in which the group con-

**Figure 10** - Skeletal reconstruction with wings and body outline of a generalized Jehol microraptorian (from G. PAUL, 2005).



taining *Microraptor*, *Sinornithosaurus*, NGMC 91 *Sinornithosaurus*, and *Bambiraptor feinbergi* is called Microraptoria—sister taxon to Dromaeosauridae. *Microraptor gui* and *Cryptovolans pauli* are considered junior synonyms of the type species, *Microraptor zhaoianus*. Since the Microraptoria are not well known and appear to be very speciose, some of the undescribed specimens are lumped in a generic *Microraptor*.

## FUNCTIONAL ANATOMY

The pectoral girdle of a typical microraptorian is constructed solidly with fused scapulocoracoids, large, ossified sternal plates, and a flat, rigid furcula (Xu *et al.*, 2003: fig. 1). This unit is tied to a rib cage overlapped dorsally by scapulae and ventrally by sternal ribs and gastralia. Uncinate processes overlap the thoracic ribs (Ji *et al.*, 2001; Xu, 2002; Xu *et al.*, 2003). The sternum and furcula provide ample surface area for the attachment of pectoral musculature.

In lateral view the L-shaped scapular arch (scapulocoracoid) of *Microraptor* is similar to that of *Bambiraptor feinbergi*. This is due mostly to the morphology of the coracoid in which the neck bends posteriorly (LPM 0824). But the angle on which the scapular blades reside on the rib cage differs, although the glenoid remains laterally positioned on both. In *Microraptor*, the shoulder socket sits high on the back, anterior to the first dorsal rib (Xu *et al.*, 2003: fig. 1b), and the ridge outlining the glenoid is indistinct with most of

the articular surface on the scapula (Xu, 2002). In *B. feinbergi*, the glenoid also resides forward of the first dorsal rib but is lower on the ribcage. The glenoid of *B. feinbergi* is also formed mostly by the scapula; it is cup shaped, and there is a lip situated posteriorly and anteriorly on the articular surfaces of the glenoid.

The long forelimbs of the Jehol microraptoria are preserved usually in an avian-like folding posture (Ji *et al.*, 2001: fig. 1, 2; Czerkas *et al.*, 2002: fig. 1, 2, 17; Xu, 2002: fig. 15, 57; Xu *et al.*, 2003: fig. 2). The humerus has a prominent humeral head with a large pectoral crest with an internal tuberosity (Hwang *et al.*, 2002: fig. 20). There are at least three, possibly four carpals in the wrist (Ji *et al.*, 2001: fig. 2; Xu, 2002) including a semi-lunate carpal that caps the first metacarpal and part of the middle metacarpal in an arrangement very similar to *Archaeopteryx*. The distal ginglymoid articular surface of metacarpal I (Hwang *et al.*, 2002) is similar to that of *Bambiraptor* and allows some range of motion towards the palmar aspect of the other fingers (Gishlick, 2001; Burnham, 2004). The manual phalanges are long and slender, except for digit II that is thicker (Ji *et al.*, 2001; Czerkas *et al.*, 2002; Xu *et al.*, 2003) and represents the longest digit in the hand (Hwang *et al.*, 2002). The manual unguals have large flexor tubercles and are recurved strongly, with the curvature even more pronounced with the keratinous claw sheaths preserved (Hwang *et al.*, 2002: fig. 22; Czerkas *et al.*, 2002: fig. 17).

*Microraptor* has long remiges aligned similar to a

modern bird wing and both primary and secondary feathers are preserved (Xu *et al.*, 2003: fig. 2f). Some of the primary feathers are asymmetrical on the holotype of *Microraptor gui*, and the longest ones appear to be attached to the ulna and manus (Xu *et al.*, 2003). Primary and secondary feathers attached along the forelimb down to the manus, and there are small feathers attached to manual digit I (Xu *et al.*, 2003: fig. 2i).

*Microraptor* and *Archaeopteryx* have similar rib cages and body outlines. The lack of pleurocoels in the anterior dorsal centra of Jehol microraptorians (Hwang *et al.*, 2002) is also similar to that of *Archaeopteryx* (Wellnhofer, 1976) and unlike *Bambiraptor feinbergi*, in which all the presacral vertebrae have pleurocoels (Burnham, 2004). The rib cage, outlined by the sternum and gastralia on articulated skeletons, is deepest at the 6<sup>th</sup> or 7<sup>th</sup> dorsal rib, but tapers posteriorly and does not extend ventrally past the distal tip of the ischium on *Microraptor*. The body outline is congruent with such arboreal and gliding animals that have flattened bodies, such as the lizard *Draco*.

The tail is long and stiff due to the bony rods that occur in all dromaeosaurids and microraptorians, but there is flexibility at the base of the tail since the rods do not extend cranially over the proximal caudals. Some specimens have feathers attached to the tail, forming a fan-like frond extending well beyond the tip (Ji *et al.*, 2001; Hwang *et al.*, 2002; Czerkas *et al.*, 2002: fig. 1; Xu, 2002: fig. 57; Xu *et al.*, 2003). These retrices are attached from about the mid tail region to the tip. The tail feathers lengthen distally, and are widest just beyond the tip of the tail (Xu *et al.*, 2003: 2d, e).

The pelvic girdle in *Microraptor* has some important differences from other deinonychosaurs. The ilium has a reduced dorsal rim over the acetabulum, and this rim does not overhang the head of the femur (Hwang *et al.*, 2002). The ilium also has a weakly developed antitrochanter and a reduced antiliac shelf (Xu, 2002; Hwang *et al.*, 2002, also see figs. 9, 24, 25). The pubes exhibit a posterior bend in lateral view and a reduced pubic boot (Xu *et al.*, 2003; Hwang *et al.*, 2002). In *Bambiraptor*, there is a large pubic boot, and no bend in the pubic shaft. *B. feinbergi* has a stronger antitrochanter and iliac shelf (Burnham *et al.*, 2000: fig. 4). In both, the ischia are half as long as the pubes and are distally unfused.

The femora of *Microraptor* are very long and have an inclined femoral head (Hwang *et al.*, 2002: fig. 27B; fig. 11). In *Microraptor*, the shape of the femoral head is blocky, fuller, and more robust. In contrast, *Bambiraptor*'s femoral head is much more rounded and less robust (fig. 9). The femoral shaft of *Microraptor* is much straighter and longer than that of *Bambiraptor*. There is no indication of a fourth trochanter in *Microraptor* (Xu, 2002; Hwang *et al.*, 2002) or *Bambiraptor* (Burnham, 2004).

The tibia is described as bowed in *Microraptor* by Xu *et al.* (2003: fig. 1) but appears to be straight in the specimens described by Hwang *et al.* (2002: fig. 3). Tibia length of *Microraptor* is 126 percent to 130 percent that of

the femur (Xu, 2002; Hwang *et al.*, 2002). In comparison, the tibia length on *Bambiraptor* is 141 percent the length of the femur. This shows the long femoral length characteristic of the Jehol Microraptorina.

The ankle joint of *Microraptor* is very different from that of other deinonychosaurs with the proximal articular surface of tarsus-metatarsus sloped posteromedially (Hwang *et al.*, 2002: fig. 29; L. Martin, personal communication, 2005). In *Bambiraptor feinbergi*, the ankle joint is a simple, horizontal hinge (fig. 8).

Metatarsal I's distal displacement is present in *Archaeopteryx* and *Microraptor* and does not occur in an articulated foot of *Velociraptor* (Norell & Makovicky, 1999: fig. 16). My observations show that the hallux is also reversed on some Jehol microraptorians as well as CAGS 20-8-001 (Hwang *et al.*, 2002: fig. 30A). The placement of metatarsal I on *Bambiraptor* remains ambiguous since the feet were not articulated, nor is there a scar or facet to indicate the attachment site.

Another feature of the *Microraptor* tarsus is the ginglymoid articular surfaces of the distal ends of the metatarsals II and III (Hwang *et al.*, 2002). Xu (2002) describes metatarsal III as 71 percent of femoral length. In contrast, *Bambiraptor*'s metatarsal III is 68 percent of femoral length.

The arrangement of feathers on the hindlimb can be described as wing-like (Xu *et al.*, 2003: fig. 2g). The longest feathers are attached to the metatarsus and have asymmetrical vanes. There are also shorter, symmetrical feathers on the tibia. Coverts were also described by Xu *et al.* (2003) as being attached to the metatarsus.

## FUNCTIONAL ANALYSIS

It is apparent from the skeletal construction of *Microraptor* that this skeletal anatomy was powered by a strong muscular system in the chest and upper arms (Senter *et al.*, 2004). In fact, the body outline in the pectoral area and forelimbs far exceeds that of the pelvic area and hindlimbs. The pectoral girdle is built strongly and the shoulder socket was open with no prominent ridge surrounding the glenoid to restrict motions. The glenoid was positioned high on the back and forward. This places the center of gravity in a position giving the animal a high center of mass at the shoulders. The articular surface of the humeral head, allowed the arms to reach overhead. This allowed a range of motion for this animal to reach forward only with its lower arms. Similar to *Bambiraptor*, it could not adduct the humeri towards the midline of the body (Burnham, 2004), but the lower arms could be adducted. The long forelimbs were also powerful as indicated by the large pectoral crest and large shaft diameter of the humerus. The arm was able to fold like a bird's wing because of the arrangement of the wrist bones. The radius and ulna were also heavily built. The entire arm could reach forward as the hands pivoted on the wrist in an up and down motion useful for climbing (Chatterjee and Templin, 2003).



Digit II on the hand was the longest and most heavily built of the fingers. All fingers had large, strongly curved claws. This could function easily as a grappling device useful for an arboreal animal.

Additionally, the range of motion described above also enabled *Microraptor* to spread its forelimbs to glide, and it is quite possible it could flutter to soften landings. Most likely, gliding was tree to tree and *Microraptor* probably could use its forelimbs for landing as well. The furcula helped brace the pectoral girdle during the impact of landings allowing use of the strong arms for this purpose as well. Again, the long, curved claws and strong middle finger would be useful as arboreal mechanisms acting as grappling hooks. It is possible that this second metacarpal is somewhat fused with the outer metacarpal since most specimens that were examined have these two metacarpals appressed. Modern birds fuse all the metacarpals, and lose the claws.

The pelvic girdle is another major functional component for locomotion. It is curious to note that the pelvic girdle is secondary to the pectoral girdle in terms of size in the described specimens of *Microraptor* and the girdle is small in terms of area for muscle attachment because of the small ilium. The upper portion of the acetabulum (ilium) has a reduced dorsal rim, iliac shelf, and antitrochanter. This allows the femur a tremendous range of motion, especially sprawling. The femur, with its large, inclined head was able to splay outwards, due to the open arrangement of the hip socket. In fact, *Bambiraptor*, which has a significant acetabular rim (Burnham *et al.*, 2000: fig. 4), also had lateral range of motion for its femur, although more limited. Using three-dimensional casts of *Bambiraptor*'s femur and pelvis, I found that adjusting the ilium with a small tilt increased the splaying range of motion dramatically.

*Microraptor* was described as arboreal based on phalangeal proportions (Xu *et al.*, 2003), reflexed hallux, and large, curved pedal unguals (Hou *et al.*, 1996). Further evidence can be found in the ginglymoid digits of the foot. This additional range of movements in the toes does not seem functionally sound for a cursorial animal. It suggests the animal could use its toes for climbing by changing their angles to accommodate the curved climbing surfaces of tree trunks or branches.

Arboreal and cursorial morphotypes have contrasting hindlimb morphology and proportions as shown by the comparison of *Microraptor* to *Bambiraptor*. A plot of hindlimb proportions places *Bambiraptor* with other bipedal cursorial animals using Coomb's (1978: fig.9; Holtz, 1994) graph while *Microraptor* falls below this range. The long femora of *Microraptor* have relatively straight shafts and inclined femoral heads. The pes was proportionally smaller than the metatarsals with highly curved claws on each pedal digit, and the hallux was reversed. Long, vaned feathers were preserved attached to the femur, tibia, and along the entire length of the metatarsus on some specimens. The hindlimb of *Bambiraptor* had curved femora, shorter metatarsi, and flattened pes unguals (certainly a cursorial adaptation). The

hallux was probably not reversed and was positioned more proximally on the metatarsus than *Microraptor*. Both dromaeosaurids have elongated penultimate phalanges on pes digits II and IV, although more so in *Microraptor*.

The feathered wings of *Microraptor* were arranged in birdlike positions on the forelimbs, but the hindlimb wings are unusual and are not represented in any known modern analog. As seen from the published figures and direct examination of some of the specimens the hindlimb feathers are attached to the posterior surface of the femora and tibiae (Xu *et al.*, 2003; Czerkas *et al.*, 2002; personal observation). Apparently, the long, asymmetrical feathers on the metatarsi were attached to the posterior surface as well. When the hindlimb folded, the feathers on the femur and tibia collapsed in a parallel, fan like fashion overlapping the feathers on the metatarsus. The overlapping was facilitated by the angled ankle joint and prevented the proximal hindlimb feathers from brushing into the distal ankle feathers. This arrangement allowed the animal to climb without the leg feathers encumbering its locomotion but would not have been efficient for locomotion on the ground as the forward motion of the foot would brush the hindwing tips on the ground.

## DISCUSSION

Controversies surrounding evolution of flight are framed usually around the forelimb rather than the structure of the hindlimb because flapping flight is found in modern birds and it is assumed that this is the only relevant factor concerning the origin of flight (Padian, 2003). The morphology of the microraptorians is similar to that shown in Heilmann's 1927 illustration of the skeleton of a hypothetical arboreal form representing the gliding phase in the origin of flight. The contrasting morphologies that occur within the microraptorian lineage support two different locomotory lifestyles: arboreal for *Microraptor* and cursorial for *Bambiraptor*. The importance of hindlimbs to the origin of flight is also supported by the presence of feathers on the legs of *Archaeopteryx*. This changes the running capabilities of this animal as well. It has been argued that *Archaeopteryx* overcame the physical problems of a running takeoff through the generation of thrust from its wings (Burgers and Chiappe, 1999; Chatterjee and Templin, 2003). Neither study had considered the additional drag or encumbrance of motion due to the leg feathers (Note: the naked legs in fig. 1 & 2 of Burgers and Chiappe, 1999). The feathers of *Archaeopteryx* hindlimbs are at least 3 centimeters long and possibly formed some sort of wing (Christiansen and Bonde, 2004). Since they are not simply contour feathers, the leg feathers would affect likely the ground speed, adding more drag and perhaps encumbering locomotion. This raises the question whether *Archaeopteryx* could run fast enough to achieve sufficient lift to enable flight.

Chatterjee and Templin (2003) suggested phugoid gliding as a lifestyle for *Archaeopteryx* as a more efficient means of aerial locomotion. Elzanowski (2001) suggested

multiple lifestyles with alternative methods to achieve lift without running as the sole mechanism. This is not only more realistic but certainly makes it more likely the origin of flight was from the trees down since *Archaeopteryx* may have had both a terrestrial and an arboreal lifestyle.

Padian (2003) argued that birds evolved the flight stroke by using the arms to capture prey. The old paradigm transforms these prey-capturing motions into flight mechanisms. But recent work has shown that the closest relatives of birds, the dromaeosaurs (including *Microraptor*), were arboreal animals (Zhou, 2004a). This forces consideration of a new paradigm such as fluttering or tree-climbing motions as the precursors to the modern flight stroke. Primitive flyers are known to occur in all the major groups of fossil birds in the Mesozoic (Zhou, 2004a). Truly modern flight is determined by high frequency flapping in which the furcula becomes flexible, the wrist is able to lock (Vasquez, 1992), and the supracoracoideus pulley system occurs within a triosseal canal twisting the humerus to orient the wing for the downstroke (Poore *et al.*, 1997). The elongation of the coracoid and formation of the triosseal canal to accommodate high-frequency powered flight is found in all modern flight mechanisms.

The relationships of birds to dinosaurs and the origin of flight can seem polarized with differing interpretations of *Archaeopteryx* anatomy and life habits. Burgers and Chiappe (1999) provided an argument for the additional thrust component necessary for ground up flight for *Archaeopteryx*. The terrestrial origin of flight fits current cladistic phylogenies but physical laws seem not to comply (Long *et al.*, 2004) and the hypothesis may be untestable philosophically (Zhou, 2004a). Ultimately, bits of morphology from the four-winged dinosaurs yield phylogenetic information, giving new direction to character states whereby existing polarities in cladograms may actually be reversed.

Anatomical problems and physical forces seem to defy the ground up theory. Newtonian physics makes it unlikely that a protoflyer could generate the thrust needed to take off (Long *et al.*, 2004). Additionally, slow flight requires refinement of such anatomical features as a locking wrist and a pulley system for the arms, both needed for the recovery of the flight stroke and high frequency flapping flight. Much less fine control is needed for fast flight or gliding. This implies that fast-flying evolved first, especially with the fossil evidence of a gliding dinosaur that had preadapted primitive flight mechanics possibly capable of fluttering to control landings.

## CONCLUSIONS

The Liaoning volcanism in the Early Cretaceous provided exceptional preservation of the feathered dinosaurs and birds that it killed to produce the Jehol Biota. Cycles of volcanism repeated over the course of 40 million years. Between eruptions the paleoenvironment was probably a lush forest dominated by conifers (Ho *et al.*, 1995; Chang *et al.*,

2003; Zhou *et al.*, 2003) surrounding deep lakes. During that time, dinosaurs and birds were part of the fauna in an environment that was conducive to arboreal lifestyles (Zhou, 2004b). This included the four-winged *Microraptor*, demonstrating the existence of gliding phase during the origin of flight. This shifts the focus of the origin of flight into a new paradigm that must include arboreal, gliding forms. Closer examination of this paradigm aligns the fossil forms within a stratigraphic context. Study of the functional morphology of this genus confirms locomotory lifestyles, but this result seems to contradict current cladistic phylogenies. Future work will test these phylogenies by analyzing the polarity of character states within the new paradigm of the trees down origin of flight.

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