PALEOENVIRONMENT, PALEOECOLOGY, AND EVOLUTION OF MANIRAPTORAN “DINOSAURS”

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ABSTRACT

Maniraptora is a taxonomic group that includes the well-known primitive bird, *Archaeopteryx*, that is thought to have had limited power of flight, the small, four-winged, feathered glider, *Microraptor* and the terrestrial runner *Bambiraptor*. All are herein considered important links in the origin of flight and a subsequent transition to terrestriality in some forms. In cladistic classifications, dromaeosaurid "dinosaurs" were only considered terrestrial cursors. The discovery of a gliding stage within the dromaeosaurs, a group purportedly closest to birds, confounds the currently suggested biologic framework. Any evolutionary framework lacking predictability for origin of flight scenarios must be fundamentally flawed.

Paleoclimate was a significant factor for evolution of birds and birdlike dinosaurs during the Mesozoic. It is characterized by faunal and floral changes reflecting climatic change. For instance, the first known birds such as *Archaeopteryx* were arboreal and evolved during a warm period in the Late Jurassic. The Solnhofen quarries that produced *Archaeopteryx* have a windblown faunal and floral component from a forested area indicating a typical Jurassic forest with large trees. During the Early Cretaceous, the Jehol Biota climate was warm and forested providing a suitable arboreal habitat for *Microraptor*. The cooling trend at end of the Cretaceous opened up the environment making it difficult for poor fliers or gliders as forested areas

became less dense. Terrestrial forms and birds with full flight capabilities could survive best in these new environments.

Furthermore, birds with specialized manus claws for tree climbing were common in the Early Cretaceous and are so far unknown in the Late Cretaceous. This indicates a change in the avian community with fliers developing an increased ability to take off from flat surfaces. Dromaeosaurs survived well after their initial radiation during the Jehol Biota. Only terrestrial forms, such as *Bambiraptor*, have been found during the Late Cretaceous. Birds of modern aspect probably replaced the primitive dromaeosaurs, *Microraptor* and its kin, since they were more efficient fliers.

A majority of cladistic analyses show *Microraptor* as the plesiomorphic sister group to the more terrestrial dromaeosaurs. The geologically younger *Bambiraptor* provides examples of the morphological changes necessary for the transition to ground dwelling and how this transition was accomplished.

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“*Archaeopteryx*—a re-evaluation suggests an arboreal habitat and an intermediate stage in the origin of flight”; the Thermopolis *Archaeopteryx* image was provided by G. Mayr/Forschungsinstitut Senckenberg; N. Longrich allowed use of his reconstruction of *Archaeopteryx*, the most current and accurate to date; X. Xing allowed the use of a *Microraptor* photo; U. Göhlich and L. Chiappe provided images of *Juravenator* for study.

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CHAPTER 1

Introduction

The focus of this dissertation is to unravel the evolution of bird flight by examining the paleoenvironment, paleoecology, functional morphology, and evolutionary relationships of maniraptoran “dinosaurs” a lineage related to modern birds. A historical review of pertinent origin of flight arguments can be found in the introductory section as well as a brief review of maniraptorans. This dissertation is comprised of three manuscripts, presented here as chapters, with a summary and conclusions as a final chapter. The scope of this project covered three research areas—the Late Jurassic Solnhofen Formation (Bavaria, Germany), the Early Cretaceous Jehol Group (Liaoning Province, China), and the Late Cretaceous Two Medicine Formation (Montana, USA). These areas provide well-preserved maniraptoran taxa that record the evolution of flight and the secondary loss thereof.

The origin of flight occurred in stages, similar to a hypothesis proposed by Beebe (1915), that included primitive gliders. However, secondarily flightless forms have evolved (Paul 2002), throughout avian history. The origin of flight for birds has always been a contentious issue and presented as either a *trees down* or *ground up* hypothesis. Because evolution of the flight stroke was thought to be the central problem in determining the origin of flight (Padian, 2003), this dissertation began testing the hypothesis that the flight stroke was developed from climbing mechanisms in a quadrupedal, arboreal ancestor rather than from prey-capture strokes in a bipedal, cursorial form. However, it was soon evident that hindlimb morphology made a critical contribution to evolution of flight. Moreover, the series of stages leading to modern flapping flight began with a small, arboreal, quadrupedal ancestor. The thesis of this dissertation is that flight evolved from the *trees down* incrementally through stages involving changes in both the forelimbs and hindlimbs of birds. During the evolutionary sequence leading to flight, secondarily flightless forms evolved as well. These secondarily flightless forms retain morphologic features inherited from their arboreal ancestors. Furthermore, maniraptoran "dinosaurs" are considered birds. Cladistic phylogenies that were examined were not broad enough to encompass alternative hypotheses for the origin of flight other than *ground up*.

Williston (1879) was the first to propose that flight was achieved from the *ground up* by bipedal cursors exemplified by the small, theropod dinosaur *Compsognathus*. Marsh (1880) countered with *trees down* origin involving a quadrupedal, arboreal lifestyle. Osborn (1900) concluded birds diverged from theropods early in the Triassic based on the arboreal characteristics of *Archaeopteryx* including a reversed hallux (perching foot) and long middle digit on a tridactyl hand. Nopsca (1907) surmised that the flight stroke evolved from predatory motions of the arms and a bipedal runner produced enough speed for it to leap into the air eventually evolving powered flight from the *ground up*. Beebe (1915) proposed a series of stages leading to modern flight. The most important evolutionary step in the sequence leading to flapping flight was called the Tetrapteryx stage. It represented a primitive, gliding bird that had in addition to forelimb wings, passive pelvic wings and a feathered tail. The hindlimb wings reduce in later stages as the forelimb wings developed flapping flight. Lastly, the tail is lost when the forelimb wings develop a modern flight stroke giving birds the ability to take flight without an elevated launch platform.

Heilman (1926) presented an eloquent argument for arboreality in his detailed work on the origin of birds. Heilman compared the long forelimbs of *Archaeopteryx* to shorter ones in theropods and surmised dinosaurs became terrestrial before "the hypothetic Proavis" evolved flight. Instead of hindlimb wings, Heilman proposed the forelimbs and tail as a parachute for Proavis. Although Proavis was bipedal with parasagittal hindlimbs, the arms would lengthen after becoming arboreal. The main evidence Heilman used to determine a bipedal role for his Proavis was the taphonomy of the two known *Archaeopteryx* specimens during that time (the London *Archaeopteryx* was disarticulated and Berlin specimen was preserved in lateral view). Heilman noted that if *Archaeopteryx* was sprawled it would be preserved as such. Arboreal theory remained in favor for nearly half a century.

A long hiatus without a *ground up* challenge followed until the well-documented dinosaur renaissance in the early 1970s began to unfold (Bakker, 1975). Spurred by the discovery of *Deinonychus* (Ostrom, 1969a, b), the first relatively complete dromaeosaur, Ostrom (1974, 1976) revived the birds-are-dinosaurs theory based on what he thought were similarities in osteology and metabolism. Ostrom also supported Nopsca's (1907) claim that the origin of flight was found in the preadaptation of the predatory movements of the arms in conjunction with bipedal running and the development of feathers. Hence, the *ground up* theory of flight was also reborn. Padian (1986) championed further the cursorial origin of flight, but was challenged by Newtonian Physics demonstrating there was truly a physical barrier preventing a running takeoff (Long et al., 2003). Burgers and Chiappe (1999) countered with a postulate that *Archaeopteryx*, using the wings as a primary thrust generator, could overcome the physical problems with the *ground up* model. More recently, Dial (2003) introduced another hypothesis termed wing-assisted inclined running (hence, the acronym WAIR). Dial showed modern birds could run up inclined tree trunks assisted by wing thrust, melding both theories. Paul (2002) suggested that such maniraptorans as *Deinonychus* and *Bambiraptor* were secondarily flightless and advocated evolution of flight from the *trees down*, thereby making efficient use of gravity and resolving the temporal sequence for maniraptorans.

Although, the origin of flight in birds has been argued for over a century using evolutionary, ecological and anatomical concepts as either evolving from the *trees down* or the *ground up*, neither argument has had substantive proof until recently. New fossil evidence for *trees down* now seriously outweighs the *ground up* origin of flight and challenges the evolutionary framework surrounding it as well. Dromaeosaurids from China question the currently accepted scenario for the origin of flight (Xu et al., 2000; Norell et al., 2002; Xu, 2002; Xu et al., 2003; Xu and Zhang, 2005). Not only are these Chinese maniraptorans feathered, but also the new dromaeosaurids are described as gliders (Xu et al., 2003; Chatterjee and Templin, 2007). This is contrary to work that concentrates on the origin-of-flight hypothesis through a cursorial ancestor (Ostrom, 1986; Burgers and Chiappe, 1999; Padian and Chiappe, 1999). In addition, the birds-are-dinosaurs hypothesis has always seemed temporally incongruent (Feduccia, 1999; Martin, 2004) since cladistic phylogenies show the youngest fossils, such as *Deinonychus* and *Bambiraptor* (bipedal cursors) as the progenitors of birds. An arboreal phase before a terrestrial phase may actually reconcile the evolutionary sequence with the stratigraphic record (Paul, 2002).

Recent arguments for the *ground up* origin of flight, assume that cladistic phylogenies provide a framework that outweighs biological parameters and physical sense. A similar situation had also obfuscated the origin of flight in pterosaurs (Geist and Feduccia, 2000). Eventually, fossil evidence (body and track) demonstrated the origin of flight in pterosaurs was from the *trees down* confounding the cladistic version of pterosaur evolutionary history. Although today the most widely accepted hypothesis is that birds arose from dinosaurs, as Huxley first argued in 1868, this argument was based on philosophical arguments (Gauthier, 1986) similar to the unsuccessful ones for the pterosaurs. In that view the precise details and timing of avian divergence from dinosaurs are presumed missing from the fossil record. This dissertation assumes the geologic record contains the best information available and examining fossils is still the most legitimate method in determining evolutionary history (Bennu, 2004). The core of my work presented here is based on direct examination of fossil specimens and mounting three-dimensional cast skeletons from three areas of study. This method provided new information concerning functional morphology, especially of bone joints and girdle systems, for *Archaeopteryx*, *Microraptor* and *Bambiraptor*.

Microscopic study of *Archaeopteryx* specimens included part and counterpart slabs that are reposited in Eichstätt, Solnhofen, Berlin, and Munich. Casts of the London, Tyler, and Maxberg *Archaeopteryx* specimens, as well as the skeletal cast based on the London exemplar by Larry Martin, were studied at the University of Kansas. Information on the Thermopolis exemplar of *Archaeopteryx* was based on the descriptive publications and digital images provided by G. Mayr. *Compsognathus* specimens were studied in Munich and Paris. *Juravenator* was examined while on exhibit at the Bishop's Seminary, Eichstätt, Germany.

Holotypes of *Microraptor*, housed at the Institute of Vertebrate Palaeontology and Paleoanthroplology (IVPP), People's Republic of China, were examined with a binocular microscope. A specimen of a small, feathered dromaeosaurid (cf. *Microraptor*) was transfer prepared at the University of Kansas. Additionally, stereo x-rays and 3-D skeletal casts were produced. *Sinornithosaurus* was examined at the Explorer's Club in Washington, D.C. and at the Florida Institute of Paleontology (aka. Graves Museum—now defunct).

Cryptovolans (=*Microraptor*) and several specimens referable to cf. *Microraptor*, were examined at the San Diego Museum of Natural History (SDMNH) during the "Feathered Dinosaurs and Origin of Flight" traveling exhibit (©The Dinosaur Museum). Another specimen, cf. *Microraptor*, was examined during Chicago's DinoFest Exhibit.

The holotype of *Bambiraptor feinbergi* was prepared microscopically and cast as a privately owned specimen. Skeletal models were constructed for study and display at the University of Kansas (KU Natural History Museum). *B. feinbergi* was graciously donated to the American Museum of Natural History (AMNH).

Two specimens of small dromaeosaurs, *Saurornitholestes* and *Atrocirapto*r, were examined at the Royal Tyrrell Museum of Palaeontology (RTMP). The Museum of the Rockies (MOR) houses a maxilla referable to *Bambiraptor* (D. Varicchio, pers. comm.) and postcranial remains of a nearly complete, undescribed cf. *Saurornitholestes*. *Deinonychus* material is also housed at MOR and was examined as well. The AMNH collection includes the type specimens of *Dromaeosaurus* and *Ornitholestes* (only the skulls were examined). A *Deinonychus* skeletal mount on exhibit, *Velociraptor* skulls, and the "Dave" specimen, cf. *Saurornitholestes*, were also studied at the AMNH. Harvard Museum of Comparative Zoology (MCZ) houses a *Deinonychus* skeleton on exhibit and skeletal material in the collections. All available material of *Deinonychus* was examined at the MCZ.

What are Maniraptoran "Dinosaurs"?

Dinosaurs have been known for centuries and their fossil record has been traced back to the Triassic (Sereno, 1999, Weishampel et al., 2004, Benton, 2006). Nested within the Dinosauria, are the Theropoda and Coelurosauria, respectively. Both groups date back to the Late Triassic as well (Currie, 1997; Hutchinson and Padian, 1997). The Coelurosauria are theropods that have been considered as the precursors to modern birds and relevant to flight origins in birds (Witmer, 1991).

Maniraptoran dinosaurs, the oldest known is Late Jurassic (*Archaeopteryx*), have been represented as the most birdlike coelurosaurs and the naming of Maniraptora reflects the advent of cladistic methodology in vertebrate paleontology (Gauthier, 1986; Feduccia et al., 2005). Maniraptora is a clade that includes birds and the dinosaurs most closely related to them. Differing nuances in various evolutionary schemes (Holtz, 1994, 1995, 1996; Norell et al., 2001; Xu et al., 2000, Xu et al., 2003; Hwang et al., 2002; Makovicky, 2005; Kirkland et al., 2005; Senter et al., 2004, Burnham et al., 2004; Martin, 2004; Kurochkin, 2006) result in definitional changes for the Maniraptora (Benton, 2000). Maniraptoran "dinosaurs" interpreted as derived birds (Martin, 2004; Feduccia et al., 2005), contra Gauthier's (1986) Avialae, would make them "dinosaur-like" birds. Using this definition, Maniraptora would no longer nest with Cretaceous non-avian theropod dinosaurs but may actually be related to an ancestor nearer the base of Dinosauria and further back in geologic time, perhaps in the Triassic.

Much of the answer to the origin and evolution of flight lie in the Maniraptora, especially the dromaeosaurs, including feathered, arboreal forms reported as the primitive sister group to birds (Xu et al., 2000; Norell et al., 2001; Xu et al. 2003; Hwang et al., 2002, Senter et al., 2004, Makovicky et al., 2005). Maniraptoran fossils occur worldwide, but the most notable are from Europe, North America, and Asia. The most significant Asian taxa are Barremian in age (lower Cretaceous) and include *Microraptor*, a small, feathered arboreal form found in lake deposits in China (Xu et al., 2000). The geologically younger taxon from North

America, the holotype of *Bambiraptor feinbergi* (in a *lapsis*, probably due to incomplete knowledge of ICZN rules, some authors refer to the holotype as *B. feinbergorum*), represents one of the most birdlike dinosaurs (Burnham et al.,, 2000, Burnham, 2004—Chapter 2) and may be the best preserved representative of a secondarily flightless radiation (Burnham, 2006). *Archaeopteryx* has further significance in this study since it represents the earliest record (Jurassic) of any known bird although bird tracks are reported from the Triassic (Melchor and De Valais, 2006).

As discussed above, this research resulted in a paradigm shift, *sensu* Kuhn (1962), from my previous work on a birdlike theropod dinosaur, presented in here as Chapter 2. Chapter two on *Bambiraptor feinbergi*, focused on description of the osteology with interpretation of important anatomical features. My original interpretations on *Bambiraptor* were constrained by evolutionary relationships that showed dinosaurs as the precursors to birds (Burnham et al. 2004; Senter et al., 2004). Furthermore, these phylogenies were not broad enough to encompass alternative hypotheses for the origin of flight.

Finally, conclusions in this dissertation demonstrate overwhelming evidence for the *trees down* origin of flight, which is a paradigm shift away from *ground up* theories supported mostly by cladistic phylogenies. Moreover, *Bambiraptor, Microraptor, Archaeopteryx*, and their kin should be considered birds so their evolutionary history is consistent with *trees down* origin of flight.

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CHAPTER 2

NEW INFORMATION ON *BAMBIRAPTOR FEINBERGI* (THEROPODA: DROMAEOSAURIDAE) FROM THE LATE CRETACEOUS OF MONTANA

Chapter Summary

Aspects of the osteology of *Bambiraptor feinbergi,* a velociraptorine dromaeosaurid from the Upper Cretaceous Two Medicine Formation of Montana, are described. The holotype consists of a nearly complete skull and skeleton of an immature animal found in association with at least two other individuals of the same species, one of which is larger. Barely a meter in total length, the holotype probably weighed only two kilograms. As in most sub-adults, the orbits and braincase seem disproportionately large when compared with those of most dromaeosaurids. An endocast suggests that *Bambiraptor* had one of the largest dinosaurian brains known. The scapula and coracoid are unfused, the scapula has a pronounced acromion for contact with the furcula, and the glenoid is oriented posterolaterally. The coracoid articulates with a relatively large sternal plate. The arm-to-leg-length ratio (0.69) is one of the highest known for any non-avian dinosaur. The pelvis is opisthopubic, and the pubis has a well-developed pubic boot. The functionally didactylous foot supported a large, strongly curved raptorial claw, like that of other dromaeosaurids.

Introduction

In recent years, new discoveries have elucidated the evolutionary relationships between dinosaurs and birds. Much of this research centers on the Dromaeosauridae, a family of lightly built, agile, carnivorous maniraptorans that is believed by most workers to be closely related to the ancestors of birds. Some controversy remains, owing to a lack of unequivocal interpretation of morphological characters found in the two groups (Martin, 1991; Martin and Feduccia, 1998; Feduccia, 1996; Ruben et al., 1997). However, many of the arguments surrounding this debate have focused more on systematic methodology (Gauthier, 1986; Sereno, 1999; Norell et al., 2001; Xu et al., 2002) and less on functional aspects of the skeleton. The purpose of this paper is to describe *Bambiraptor feinbergi* and previously unknown aspects of dromaeosaur anatomy, as well as to provide new insight into dromaeosaurid functional morphology and bird origins.

Bambiraptor feinbergi was briefly reported as a small, birdlike, predatory dinosaur (Burnham et al., 2000). While this fossil is geologically too young to be the progenitor of birds, analysis of the specimen reveals a sequence of character acquisitions that may have culminated in the earliest members of Aves. It also shows that fundamental avian features existed within dromaeosaurids prior to the origin of birds. Additionally, the holotype is well preserved, and an assessment of its functional morphological adaptations indicates it was a highly developed, birdlike predator with an advanced brain and well-coordinated skeletal system.

The holotype of *Bambiraptor* represents a small, sub-adult theropod dinosaur less than one meter long and weighing approximately two kilograms in life (fig. 3.1). *Bambiraptor* is assigned to the Maniraptora (Gauthier, 1986) on the basis of having a forelimb that is more than 75 percent as long as the presacral vertebral column, a hand which is longer than the foot, a posteriorly bowed ulna, a semilunate carpal, and a thin, bowed third metacarpal. It conforms to the typical dromaeosaurid design with a retroverted pubis, a large, retractable pedal ungual on digit II, and a tail modified with bony extensions of the prezygapophyses and chevrons. It also has relatively long, slender limbs, a shoulder girdle with a laterally facing glenoid, a furcula, and large sternals. It can be identified as a velociraptorine dromaeosaurid because the anterior tooth denticles are significantly smaller than the denticles on the posterior carina (Currie et al., 1990). The skeleton is important because it is reasonably complete, well preserved, and represents a life stage that is not well represented in other small theropods. *Bambiraptor feinbergi* provides new insights into anatomy, functional morphology, and life habits of dromaeosaurid theropods.

One of the most influential descriptions of any theropod is the revolutionary monograph on *Deinonychus* (Ostrom, 1969). This fossil material was crucial to understanding the evolutionary changes necessary for determining the probable ancestry of *Archaeopteryx* (Ostrom, 1976) and other birds. It precipitated the dinosaur-bird debate with the discovery of a folding wrist mechanism (involving a semilunate carpal) in conjunction with a shoulder girdle that was an evolutionary precursor to the modern avian condition. Ostrom’s description of dromaeosaurid osteology also enhanced our understanding of the killing mechanism of the foot, the rod-stiffened tail, and the overall *bauplan* for dromaeosaurids. Although specimens of *Deinonychus* are well preserved, some crucial skeletal elements, including cranial bones, remain unknown. Additionally, *Deinonychus* is larger and apparently less derived (Ostrom, 1969) than the geologically younger *Bambiraptor.*

Figure 1. *Bambiraptor feinbergi*. (Sculpture ©2003 Tom Swearingen)

Well-preserved discoveries in Mongolia led workers to focus on *Velociraptor* (Osborn, 1924; Sues, 1977; Paul, 1988). The discovery of a specimen with a furcula (Norell et al., 1997) fulfilled an important criterion required by Heilmann (1927) to be present in an avian ancestor. Recently described material from Mongolia includes articulated skulls (Barsbold and Osmólska, 1999) and postcrania (Norell and

Makovicky, 1997, 1999).

The Yixian deposits (Upper Jurassic or Lower Cretaceous) of China have produced non-avian theropods that include some of the most primitive and smallest representatives of the Dromaeosauridae. Featherlike integumentary structures are preserved on nearly all of the dromaeosaurids from these localities. The dromaeosaurid *Sinornithosaurus* (Xu et al., 2000) is based on a semi-articulated, incomplete skeleton with a furcula and sternal plates. Another specimen of *Sinornithosaurus* has long feather plumes near the tail and hindlimb (Norell, 2001). Closely related is a juvenile dromaeosaurid (Ji et al., 2001; Norell, 2001). Less known is *Microraptor* (Xu et al., 2000), which is the smallest dromaeosaurid known.

Only partial dromaeosaurid skeletons are known from Canada. *Dromaeosaurus* Matthew and Brown 1922 is based on a specimen with a fairly complete skull and associated foot. The skull (Colbert and Russell, 1969; Currie ,1995) may be more primitive than other members of the group. *Saurornitholestes* Sues 1978 was initially established on less than 10 percent of a skeleton, which lacks many of the diagnostic features for this group. More recently collected specimens of *Saurornitholestes* in the collections of the Museum of the Rockies (MOR 660) and the Royal Tyrrell Museum of Palaeontology (TMP 88.128.1) will better define this taxon when described.

Other fossils have been assigned to the Dromaeosauridae, but remain poorly known because they are so incomplete. Nonetheless, these specimens help establish the geographic and temporal ranges of this family. They include the larger-bodied forms *Utahraptor* (Kirkland et al., 1993) from North America and *Achillobator* (Perle et al., 1999) from Asia. Additional occurrences include partial skeletons of *Adasaurus* (Barsbold, 1983) and *Hulsanpes* (Osmólska, 1982) from Mongolia, *Pyroraptor* (Allain and Taquet, 2000) from France, and possibly *Unenlagia* (Novas, 1998) from Argentina. The Cretaceous of Madagascar has produced *Rahonavis ostromi*, which was described as a bird (Forster et al., 1998) but shares with small maniraptorans the sickle claw on the foot and some other features.

Geology, Taphonomy, and Preservation

Bambiraptor was recovered from the Two Medicine Formation, which crops out along the flanks of the Rocky Mountains in northwestern Montana. Especially at Egg Mountain, the formation is famous for its dinosaur nesting grounds (Horner and Gorman, 1988). This rock unit is approximately 600 meters thick (Lorenz, 1981) and comprised of fluvial sediments deposited 83 to 74 million years ago (Rogers, 1997) adjacent to the Cretaceous interior seaway. The sediments were deposited in a series of westward-dipping beds. The holotype of *Bambiraptor* was found north of the Willow Creek anticline in a non-marine, gray-green mudstone. A thin layer of ankerite surrounded the bones.

The stratigraphy of the Two Medicine formation is well documented, though no precise stratigraphic data was collected with the holotype of *Bambiraptor.* It is estimated that the site is 360 meters (±50m) above the base of the Virgelle Sandstone/Two Medicine contact (D. Trexler pers. comm. 1999). Its association with a *Maiasaura* bone bed supports this stratigraphic interval because this hadrosaur is restricted to a narrow zone within the Two Medicine Formation (J. Horner pers. comm. 2001).

The *Bambiraptor* specimens, which include the holotype (AMNH 001) and isolated adult bones (AMNH 002–036), were collected from a single locality. A small outcrop is exposed along the northern edge of Blackleaf Creek (S 18, T 26 N, R 7 W) about 11 miles north of Bynum, Montana on the Jones (Tee Six, Inc.) Ranch. The site has been quarried for many years as a bone bed composed mostly of isolated hadrosaur bones with some partially articulated skeletons (Burnham et al., 1997). Large theropods have also been found, including the articulated skull and partial skeleton of the tyrannosaurid *Gorgosaurus*, now in the Children's Museum of Indianapolis, along with a *Maiasaura* skeleton from the same site. Most of the fossils from this quarry have not yet been adequately studied, but initial observations show an interesting sample representing the Two Medicine fauna (Horner et al., 2001; Trexler, 2001). Fish, amphibian, and non-dinosaurian reptiles are not known from the quarry although these fossils are reported from MOR sites thought to be part of the same bone bed (Horner et al., 2001). The only other materials collected are isolated theropod teeth and different types of eggshell fragments. It has not been determined if the dinosaur skeletons occur at different horizons than the isolated bones or whether it is a mixed assemblage of bones and skeletons in one interval. Because some of the material consists of portions of articulated skeletons of different dinosaurs interspersed with many isolated bones, the question remains whether a single event concentrated this material. Until the entire site can be studied and documented in more detail, the data herein must be considered preliminary. However, the occurrence of the holotype of *Bambiraptor* within a small outcrop with other well-preserved skeletons may represent a single catastrophic event.

As determined from the quarry maps (Burnham et al., 2000), the holotype of *Bambiraptor feinbergi* was found near a large hadrosaur skull. It was partially articulated, and was spread out over an area of less than one square meter. The degree of disarticulation shows that the skeleton was disturbed before burial (Weigelt, 1989). Major portions of the right side of the skeleton were crushed, and there was considerable disturbance between the skull and the limbs. The nearly complete skull and lower jaws formed a collapsed mass of closely associated bones. The thin cranial bones are well preserved with intact delicate processes. The left side of the muzzle had been separated, twisted, and displaced. The lower jaws were joined at the symphysis and remained in articulation with the quadrates. Remarkably, these areas remained intact after the muzzle and dentaries were deflected onto the rest of the skull. This kind of disarticulation strongly suggests these elements were held together by soft tissues (muscles and integument) until shortly after death. Subsequent to this damage, teeth floated out of the jaws, the podials disassociated, and the skeleton separated into units. Loose teeth, some with roots, were found in the matrix surrounding the skull. The disassociation of the skeleton may have been accomplished by flowing water.

The axial skeleton was preserved as closely associated and articulated vertebral segments, although some were disarticulated in the neck and chest region. The anterior cervicals were in position behind the skull, although a fragment of the braincase (proximal portion of the exoccipital) was found under the cervical centra. The positions of the mid-to-posterior cervicals and anterior dorsals were not clearly recorded. The posterior dorsals and sacrals were articulated, but a small gap separated them from the first four caudals, which were preserved, articulated in an upward curve. Most caudal vertebrae were held together by the bony rods of their prezygapophyses and hemal arches, and all but the most distal portion of the tail was recovered. At mid-point, the tail was upturned and slightly twisted, and curved anterodorsally almost 180°.

The appendicular elements were arranged on either side of the axial skeleton close to their positions in life. The scapulae lay in their respective positions, but were separated from the paired sternals. The right coracoid was crushed and partly folded near the right sternal although the glenoid articulation was never found. The nearly complete left coracoid was in close association with the left sternal. Unfortunately, the furcula was not in articulation and was found near the pelvis. Ribs and gastralia lay strewn about the sternal plates although a series of posterior ribs lay in articulation with the dorsal vertebrae. The arms, carpus, and manus were laid out in loose association. The pelvis lay collapsed on its right side, and a single, loose dorsal centrum was found lying under the ventral side. An anterior chevron was found between the ischia, which were in contact distally. The hindlimbs lay close to the pelvis, but neither femur was in the acetabulum. The tibia, fibula, and metatarsals were associated, whereas the pedal elements were in disarray with some missing bones. The metatarsals on the right side were still articulated.

Preservation of the bones was excellent due, in part, to spar calcite filling in the hollow spaces. The bones are black in color (similar to other Two Medicine fossil bones), and their surfaces show foramina and minute details of texture. Crushing was minimal and most bones are three-dimensional.

Sub-Adult Features of the Holotype

Growth series are relatively rare in the fossil record, but various workers have used bone fusion, delayed ossification of some elements, tooth counts, relative dimensions, and histology to determine ages at death of fossil tetrapods. These estimates are rarely accurate, because trends vary among dinosaurs (Varricchio, 1997) and are influenced by many different factors. For example, the large heads and eyes of juvenile archosaurs become relatively smaller as the animals grow, but even mature modern birds have large skulls.

The extremes of the size range known for *Bambiraptor* specimens are close, and allometric trends cannot be determined without reference to related animals. Reid (1993) did histological work on the velociraptorine *Saurornitholestes,* and this kind of work may ultimately produce a method to estimate the age of dromaeosaurids. Carpenter and Smith (2001) believe femur length is more reliable for estimating age, especially when multiple specimens are available. Such is the case in *Bambiraptor,* in which the femora of three individuals were recovered from the same bone bed. The femur of the holotype of *Bambiraptor* is 69 percent of the length of the largest velociraptorine femur from the same site, which is presumably a more mature individual of the same species. Comparison of lengths between humeri suggests the holotype is 70 percent grown, and between the tibiae shows the holotype tibia is 74 percent that of the longest tibia. At least one other dromaeosaurid femur is known from the Two Medicine Formation (MOR 660). It lacks a femur, but the tibia of the holotype of *Bambiraptor* is 67 percent of the length of this tibia, and the humerus is only 63 percent of the length. Without cranial material, it is difficult to know if MOR 660 is *Bambiraptor*, *Saurornitholestes*, or a new type of dromaeosaurid.

The bones of the braincase are separate in the holotype of *Bambiraptor*, which is a clear indication of immaturity. Incomplete fusion, evident in the neural arches by the presence of visible "zigzag" sutures between posterior dorsal neural arches and centra, is another clue suggesting the sub-adult nature of the holotype at the time of death. Although this specimen is not mature, the presence of sternal plates and fusion of some skeletal elements show that it was not a hatchling either. At this time, it cannot be determined exactly how old the holotype was at the time of death. Its small size, along with associated characters such as relatively large orbits and brain, may be at least partially attributable to immaturity.

Materials and Methods

Most of the original bones of the holotype of *Bambiraptor* were molded and cast. A variety of silicone molding materials were used because of their capacity to record surface details (down to a microscopic level), to maintain dimensionality (very low shrinkage), and to release easily from delicate fossil bones. Casts were then poured using urethane plastic (Pro Cast 10) that also has low shrinkage and retains fine detail. Two sets of casts representing the holotype were produced: a research set of unaltered elements, and a working set restored and straightened to assemble a skeleton of the animal. The skull was assembled using casts of the individual elements. Missing portions (supraoccipital, right premaxilla) were sculpted. The nasals were restored posteriorly, although there is some uncertainty as to their total length and their contact with the frontals because of postmortem damage. The dentaries and posterior regions of the jaws were cast as found, but restoration was necessary near the intramandibular joints. The size and shape of the mandibular fenestra were not preserved. The resulting cast of the skull and jaws was straightened, missing teeth were added, and re-molded. Little sculpting or restoration was necessary for the postcranial skeleton, although some bones (sacrum, tail, some podials) were straightened or partially restored (some vertebrae, right ilium, right coracoid, tips of manual unguals). Missing paired elements were reproduced as mirror images of their counterparts from the opposite side (phalanges, unguals). Rib shafts were sculpted based on information from *Velociraptor* and *Saurornitholestes* (MOR 660). Casts of the appendicular elements were articulated to help in determining their ranges of motion.

The cranial elements of *Bambiraptor feinbergi* were so well preserved that casts of the braincase were easily articulated and an endocast (fig. 2A) of silicone rubber rendered.

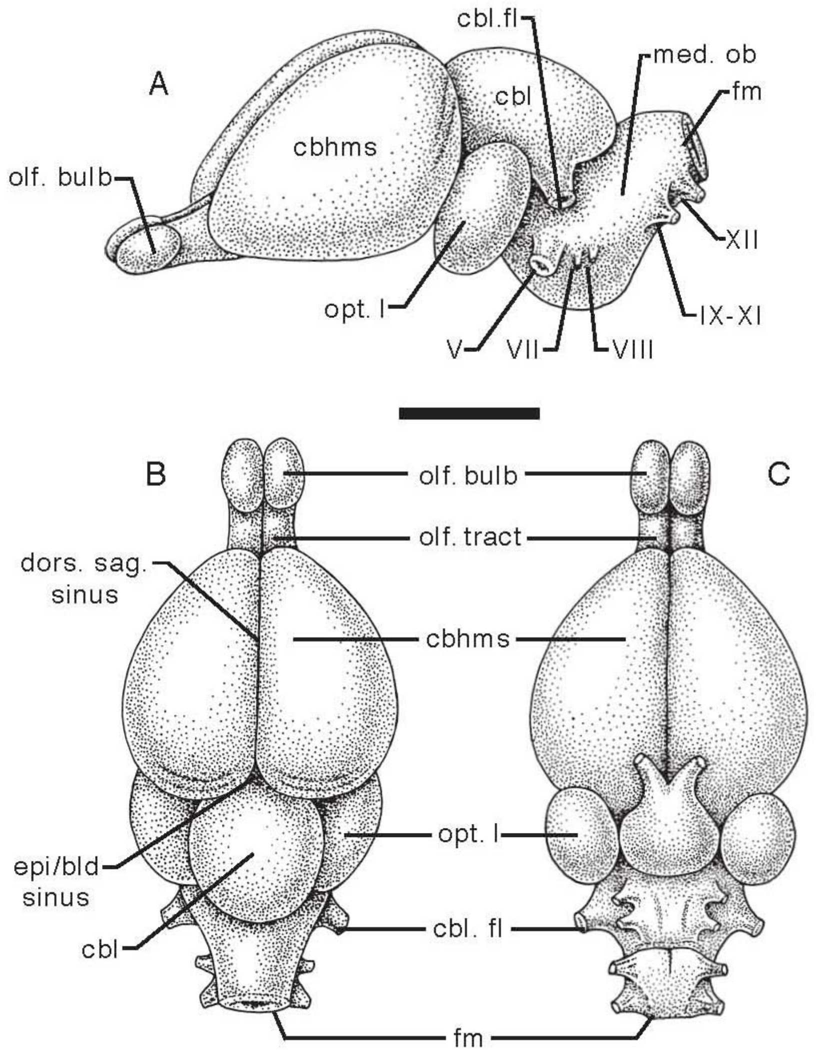


Figure 2. Reconstructed endocranial cast *Bambiraptor feinbergi* (KUVP 129737) in left lateral view (A), with cranial nerves visible in Roman numerals, V—trigeminal, VII—facial, VIII—cochlear, IX–XI—vagus, glossopharyngeal, accessory spinal nerves, XII—hypoglossal (missing: II, III, IV, VI); dorsal view (B), and ventral view

(C). Abbreviations: olfactory bulb (olf. bulb), olfactory tract (olf. tract), cerebral hemispheres (cbhms), cerebellum (cbl), optic lobe (opt. l), cerebellar flocculi (cbl. fl), dorsal sagittal sinus (dors. sag. sinus), epiphysis/blood sinus (epi/bld sinus), medulla oblongata (med. ob), foramen magnum (fm). Scale bar = 1 cm.

Institutional abbreviations: AMNH, American Museum of Natural History, New York; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; MOR, Museum of the Rockies, Bozeman; NGMC, National Geological Museum of China, Beijing; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller.

Systematic Paleontology

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Maniraptora Gauthier, 1986

Dromaeosauridae Matthew and Brown, 1922

Velociraptorinae Barsbold, 1983

Bambiraptor feinbergi Burnham, Derstler, Currie, Bakker, Zhou, and Ostrom, 2000.

Holotype: American Museum of Natural History AMNH 001, virtually complete skull and postcranium.

Horizon: Two Medicine Formation (Upper Cretaceous) *Locality and age:* Teton County, Montana.

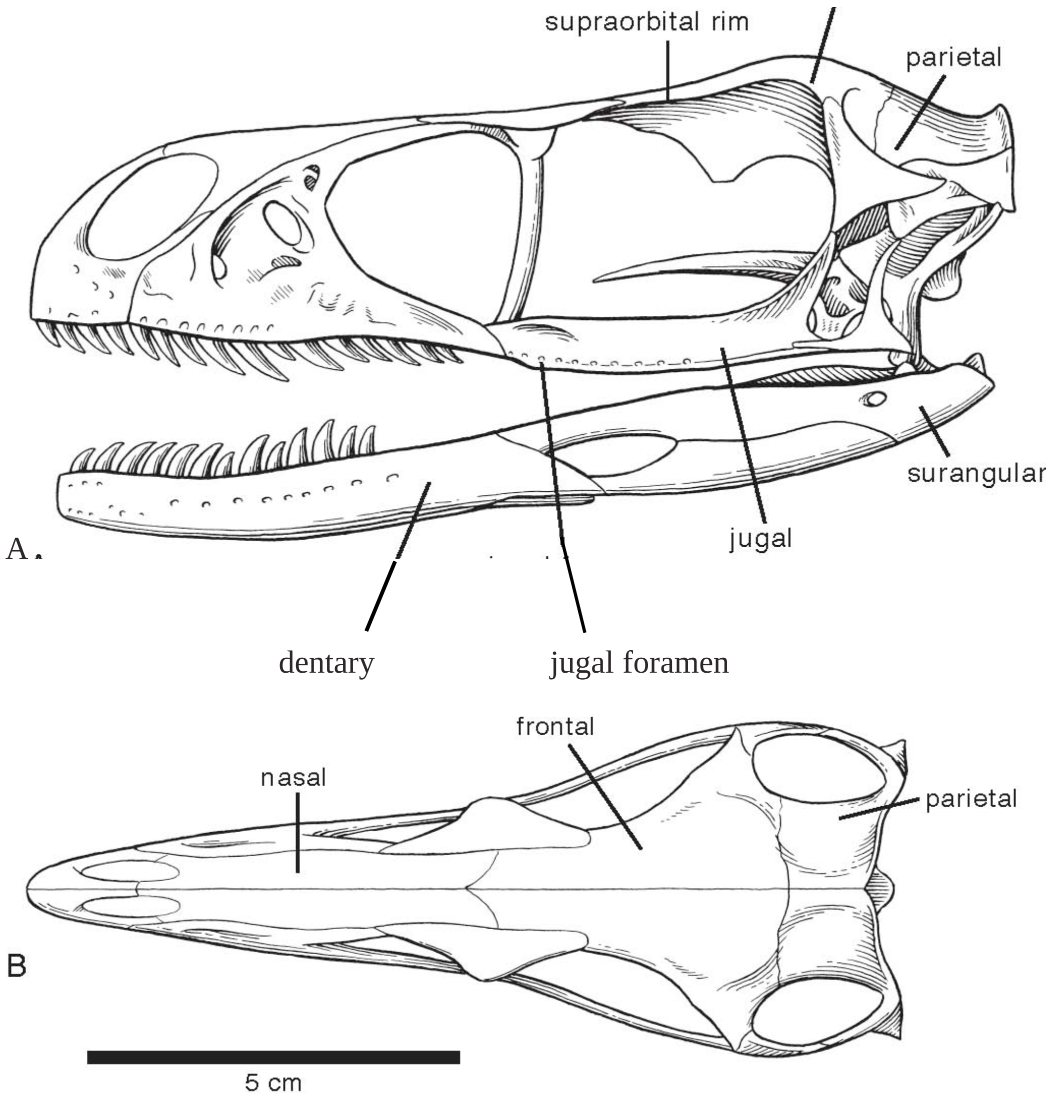


Figure 3. Reconstructed skull of *Bambiraptor feinbergi* in left lateral (A), and dorsal views (B). Scale bar = 5 cm.

Description

The holotype of *Bambiraptor feinbergi* consists of a nearly complete skull and skeleton. The skull (table 1) measures 125 mm from the tip of the snout to the occipital condyle, and 55 mm maximum width across the posterior cranium. It has large, almost rectangular orbits (fig. 3). The snout is narrow (fig. 3B), allowing for a degree of forward, possibly stereoscopic, vision. The antorbital region comprises only 55 percent of the maximum skull length, which is relatively shorter than that of *Velociraptor.* The oval shape of the nares and premaxilla give the snout a small anterior bump in lateral view similar to, but less distinct than, that of *Velociraptor*. The temporal region of the skull is relatively short. The lightly built skeleton is less than 0.5 m tall and is about 1 meter long from the tip of snout to the end of the tail. The tail itself is 350 mm long.

TABLE 1. Skull measurements of *Bambiraptor feinbergi*.

Element Measured	Measurement (in mm)
Maximum length of skull (paraoccipital process–tip of snout	127
Maximum width (across postorbitals)	60
Length of snout (rostral margin of orbit–tip of snout)	70
Maximum depth (skull roof–quadratic condyle)	53
Width of snout (in front of lacrimals)	25
Maxillary tooth row length	43
Upper tooth row length	57
Orbit height	35

Orbit length	36
Lower jaw length	122
Dentary tooth row length	47

Skull

The left premaxilla was found in close association with the left maxilla. No complete tooth is preserved in the four alveoli, but a tooth crown was found less than a centimeter away. The premaxilla is otherwise complete (fig. 4) and has a length to height index (Kirkland et al., 1993) of 150, which is closest to *Velociraptor* (164) among dromaeosaurids. The length of the tooth row is 15 mm. The superior (nasal) process is almost parallel to the inferior (maxillary) process, but is longer, more slender, and tapers to a point. The nasal process is straight and is directed posterodorsally at 45°. The maxillary process is stouter, and is concave ventrally for its contact with the maxilla.

There is an isolated crown of a premaxillary tooth, but there are roots within the alveoli of the left premaxilla. The crown has seven serrations per millimeter along the posterior keel, whereas the anterior carina lacks denticles.

The left maxilla (fig. 5) is well preserved, but the right maxilla is in two pieces. The triangular maxilla is relatively tall and foreshortened compared to that of *Velociraptor.* Anteriorly, the maxilla is bluntly squared-off where it contacts the premaxilla. The area anterior to the antorbital fenestra has at least two subsidiary fenestrae (fig. 5). The teeth are recurved and laterally compressed. The tooth count is at least nine, based on stereo x-ray examination of the alveoli (fig. 6) of the left maxilla, but there could have been as many as twelve if more alveoli

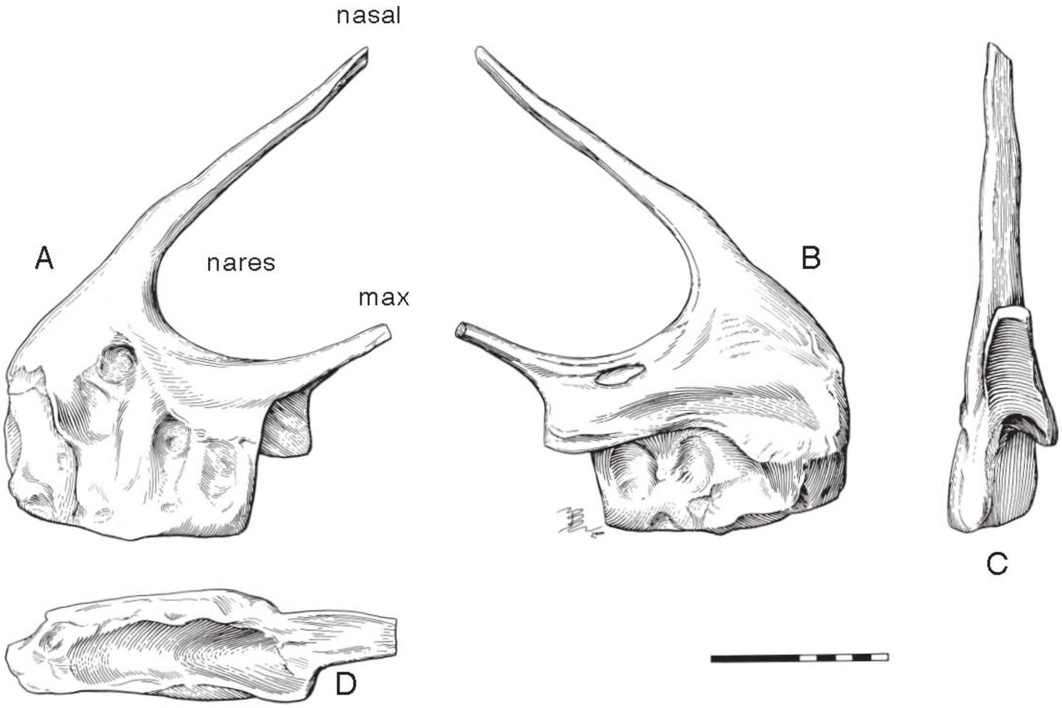


Figure 4. Left premaxilla of *Bambiraptor feinbergi* in lateral (A), medial (B), posterior (C), ventral (D) views. Scale bar in mm.

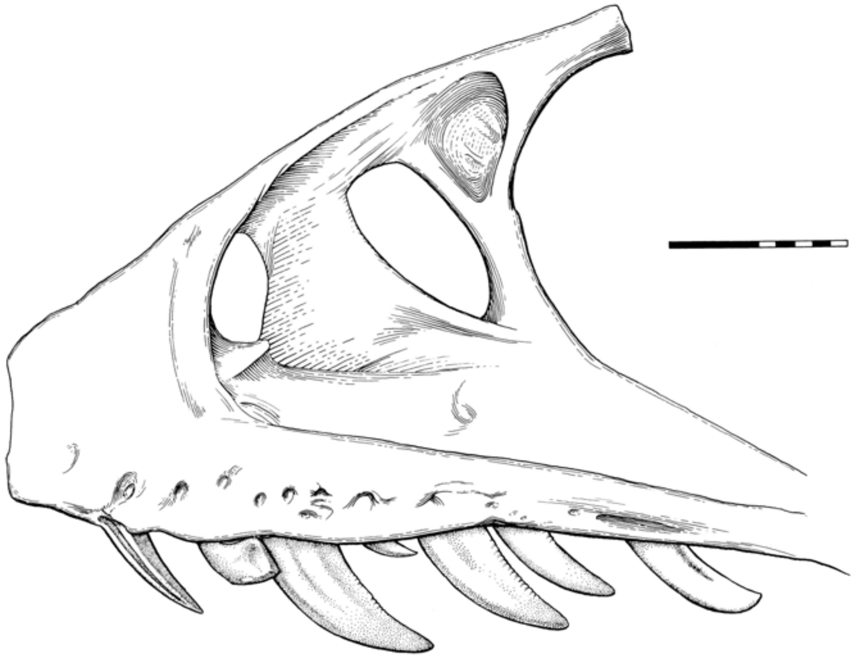


Figure 5. Left maxilla of *Bambiraptor feinbergi* in lateral view. Abbreviations: maxillary fenestra (fen max), promaxillary fenestra (fen promax). Scale bar in mm.

Figure 6. Stereo x-rays of left maxilla of *Bambiraptor feinbergi* lateral view.

were added as the animal grew. The largest teeth are positioned mid-length in positions 4, 5, and 6. Serrations are larger on the posterior carina than the anterior, and are sometimes completely absent anteriorly. The interdental plates seem to be separate from each other.

Both nasals suffered postmortem damage when they were separated from the rest of the skull. This long, thin bone bifurcated anteriorly to contact the premaxilla posterodorsal to the external naris.

The left frontal is nearly complete and measures 45 mm along the midline and 22 mm wide just behind the orbits. The anteriorly tapering, triangular shape resembles that of *Velociraptor, Saurornitholestes,* and *Archaeopteryx* more than *Dromaeosaurus,* which is squared off anteriorly (Currie, 1995). The relatively longer orbital rim of the holotype of *Bambiraptor* with its raised lateral margin (Burnham et al., 2000) distinguishes it from *Saurornitholestes,* although this may be just an allometric growth feature associated with the relatively large orbit of the juvenile. Exposed dorsally along the anterolateral edge of the *Bambiraptor* frontal is an articular surface for the lacrimal. The suture with the parietal is thickened and grooved, forming a stout, immobile contact between the two bones. Brain morphology can be seen on the ventral surface of the frontals, with distinct depressions for the olfactory lobes and the cerebrum. Small convolutions reflect undulations in the tissues covering the brain. These attest to the tight fit of the brain and associated tissue to the skull roof.

The parietals were found in close association with the frontals and laterosphenoids as separate unfused right and left elements. A suture also separates the parietals in *Sinornithosaurus,* but presumably represents immaturity, because all mature dromaeosaurids have fused parietals. In *Bambiraptor* the parasagittal crest bifurcates behind the parietal-frontal contact. The nuchal crest across the back of the parietals curves laterally downward to form a process that inserts between the squamosal and exoccipital. There is no evidence of a paraparietal process in the holotype as reported for *Sinornithosaurus* (Xu et al., 1999). The ventral surface of paired parietals has a large depression for the cerebellum.

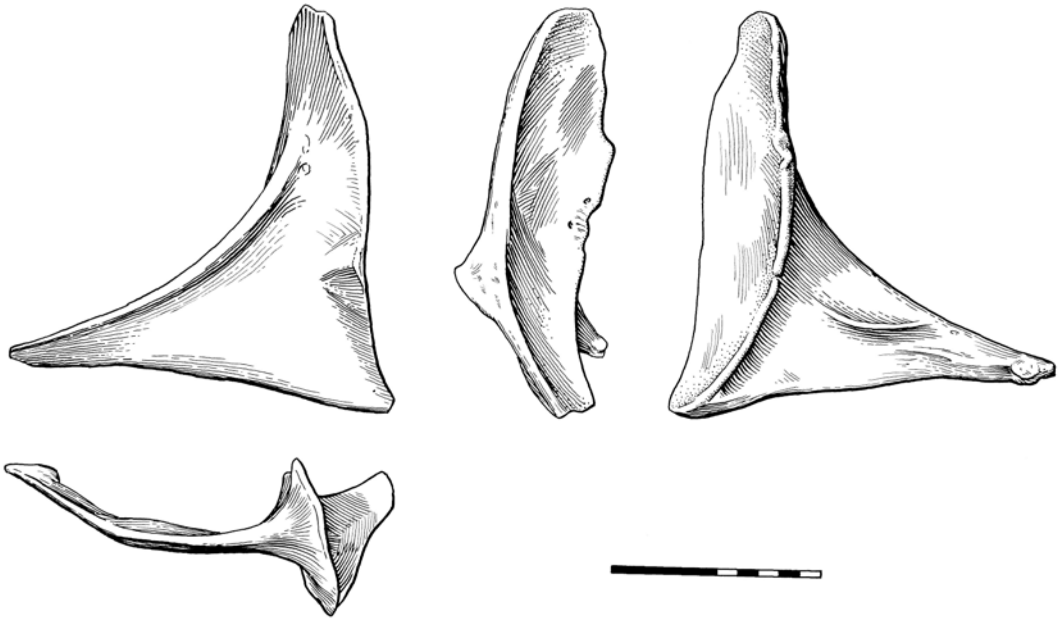


Figure 7. Right postorbital of *Bambiraptor feinbergi* in lateral (A), anterior (B), medial (C), and posterior (D) views. Scale bars (above and below) in mm.

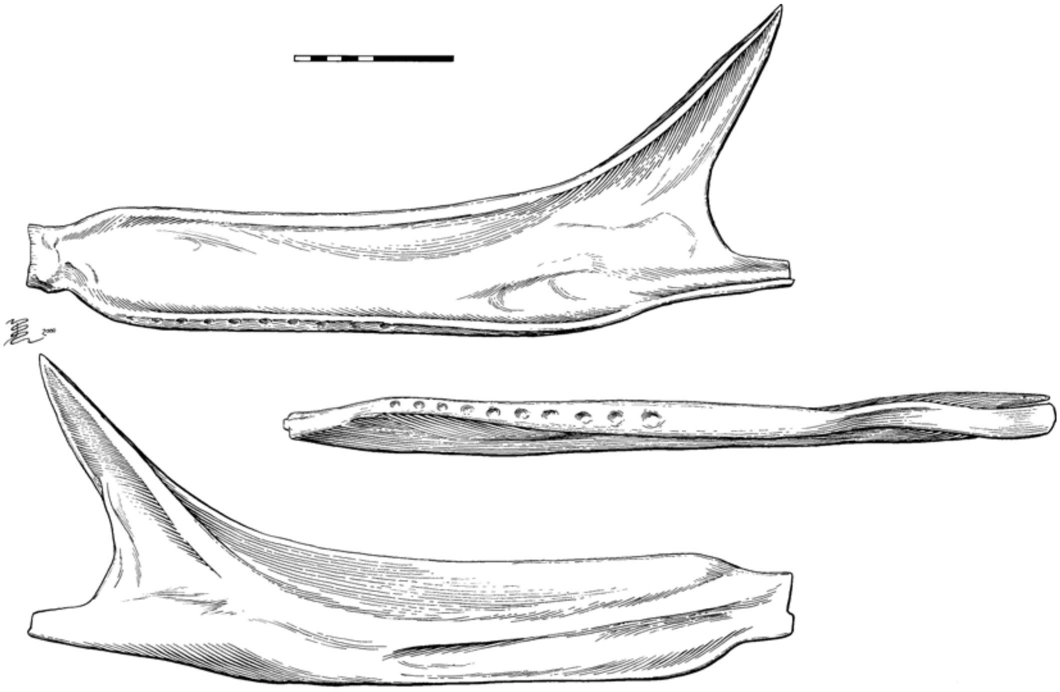


Figure 8. Left jugal of *Bambiraptor feinbergi* in lateral, ventral, and medial views.

The postorbital is almost triangular in outline (fig. 7), like that of *Sinornithosaurus* (Xu et al., 2000). In *Velociraptor* and *Dromaeosaurus,* the postorbital has better-defined processes and is triradiate rather than triangular. *Deinonychus* displays an intermediate condition. A thickened flange forms the back of the orbit and descends to partially overlap the jugal. The posterior process fits into a slot in the squamosal.

The parallel dorsal and ventral edges of the jugal (fig. 8) are laterally keeled. There is a row of eight tiny foramina on the ventral surface of each jugal (fig. 8c). This feature has not been reported in dromaeosaurids, but was also observed on the MOR specimen of *Deinonychus.* The bone is similar in overall shape to those of *Velociraptor* and *Dromaeosaurus,* but is unlike the jugal of *Deinonychus* in which the suborbital bar expands posteriorly in lateral view (Ostrom, 1969).

The lacrimals are T-shaped bones in lateral aspect (fig. 3). The anterior nasal process is shorter than the frontal process. The upright preorbital process is channeled, giving it an I-beam appearance in cross section. The shaft of the lacrimal curves medially, clearing the line of sight for the eye. Ventrally, the shaft of the lacrimal flares out into a small boot-shaped contact with the jugal. The dorsal portion of the lacrimal is triangular, tapers anteriorly and posteriorly, and overlaps the frontal. In dorsal view, this bone has a lateral boss that is also found on *Velociraptor.* It has been suggested that the lacrimal is a compound element fused with the prefrontal as in *Deinonychus* (Witmer and Maxwell, 1996; Currie and Dong, 2001). However, there is no evidence for this in *Bambiraptor,* a sub-adult specimen. The lacrimal in

Velociraptor is relatively longer anteroposteriorly, but is otherwise very similar to that of *Bambiraptor*.

The squamosal is a rectangular bone with a posterolaterally projecting process that contacts exoccipital and supraoccipital. Anteriorly there is a triangular slot for the postorbital. The contact with the quadratojugal appears loose as preserved.

Both quadratojugals are well preserved. Each is a delicate, triradiate bone (fig. 9) with an inverted T-shape (Paul, 1988). It is similar to that of *Velociraptor,* but is more lightly built than the quadratojugals of *Deinonychus* (Ostrom, 1969) and *Dromaeosaurus* (Currie, 1995). The squamosal process is an ascending, curved, thin rod that is anteroposteriorly constricted dorsally where it inserts between the squamosal and quadrate. The curvature has not been reported in other known dromaeosaurid skulls (fig. 9c). The posteroventral quadrate process is short and stout as in all dromaeosaurids (Barsbold and Osmólska, 1999) and attaches to the lateral condyle of the quadrate. The anteriorly projecting jugal process overlaps the lateral surface of the jugal as in all theropods.

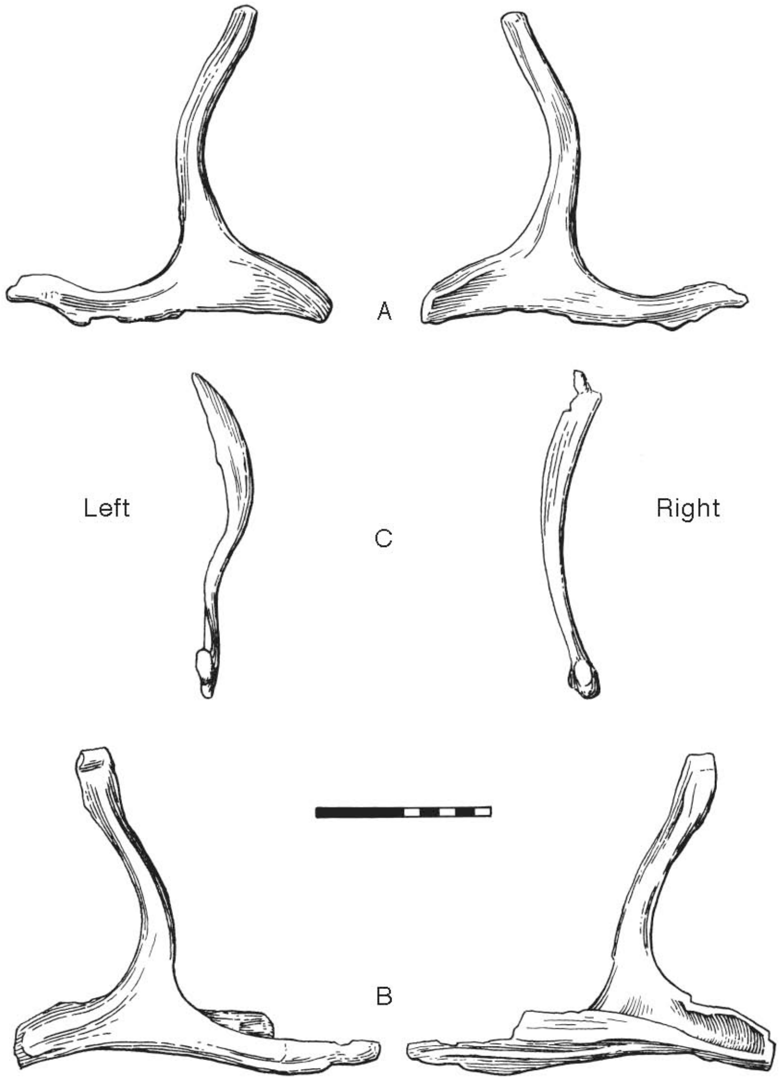


Figure 9. Left and right quadratojugals of *Bambiraptor feinbergi* in lateral (A), medial (B), and anterior (C) views. Scale bar in mm.

Right and left quadrates were recovered in articulation with the lower jaws, quadratojugals, and squamosals. As in *Velociraptor*, *Dromaeosaurus,* and *Deinonychus,* there is a single-headed otic process (fig. 10). There is no evidence of any pneumatic foramina. The medial and lateral condyles for the mandibular articulation are separated by a shallow sulcus.

The palate consists of very thin elements that lie inside the crushed skull. A fissure in the matrix extended alongside the palate and caused some damage to these bones. The pterygoid and palatine are apparently comparable with those of *Deinonychus* (Ostrom, 1969). Both ectopterygoids were found with the skull, and are distinctively like those of most other theropods in design, with robust upwardly curved processes that meet the jugal. Remnants of a small portion of the sclerotic ring were found in the left orbit. These bones indicate an approximate diameter of 15 mm for the eyeball. With the exception of the supraoccipital, all elements of the braincase were found in close association. The prootic is notched for the exit of cranial nerve V, the front margin of which was formed by the laterosphenoid. The basisphenoid-parasphenoid complex (parabasisphenoid) is pneumatic, with deep pockets along its lateral and ventral surfaces (fig. 11). The anterior tip of the elongate cultriform process is not preserved, and is probably missing a few millimeters. The basioccipital (fig. 12), which formed most of the occipital condyle, participated in the floor of the foramen magnum. The occipital condyle is only one-third the diameter of the foramen magnum. As in *Velociraptor,* the articular surface of the condyle is well rounded, and the basitubera flare out posteriorly (fig. 12a). The basitubera are separated by a cleft, and diverge ventrolaterally, unlike the condition in *Velociraptor* and *Dromaeosaurus* in which they are parallel. Pneumatic recesses penetrate the basioccipital-basisphenoid suture. The paroccipital process (exoccipital plus opisthotic) projects posterolaterally as in *Deinonychus* (Brinkman et al., 1998), but contrasts with the posteroventrally oriented process of the London *Archaeopteryx*.

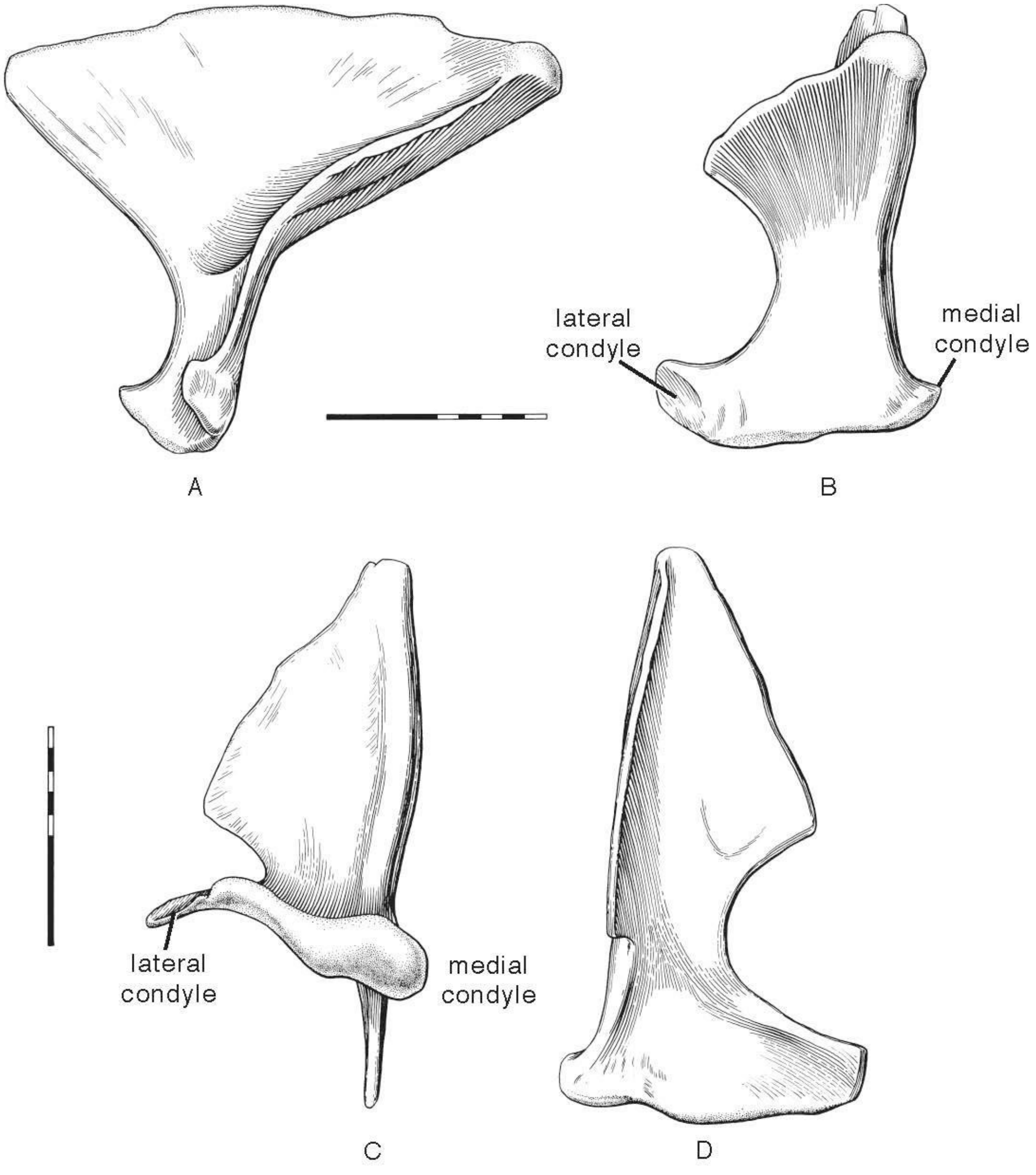


Figure 10. Left quadrate of *Bambiraptor feinbergi* in lateral (A), Posterior (B), dorsal (C), and anterior views. Scale bar in mm.

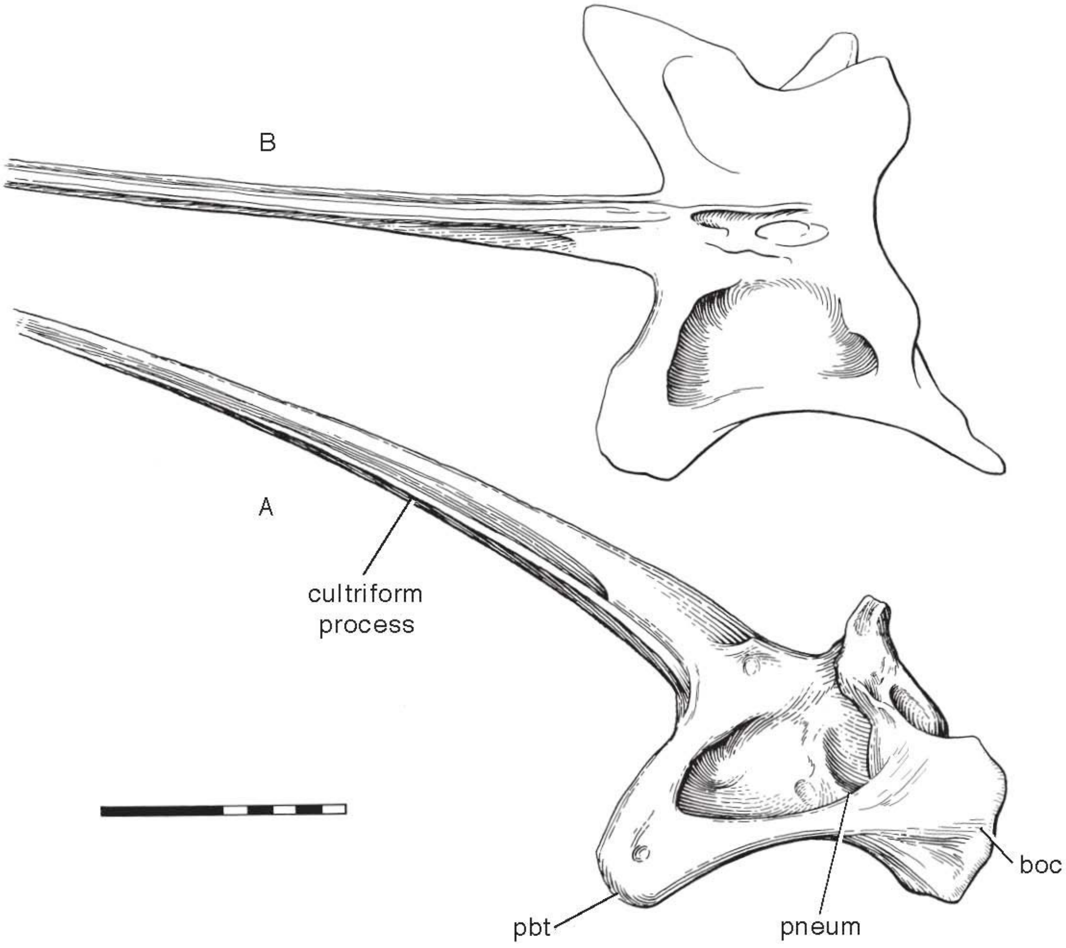


Figure 11. Parasphenoid of *Bambiraptor feinbergi* in lateral (A), and ventral (B) views. Scale bar in mm.

An elongate, slender stapes, found along the side of the exoccipital, is broken lengthwise and is poorly preserved.

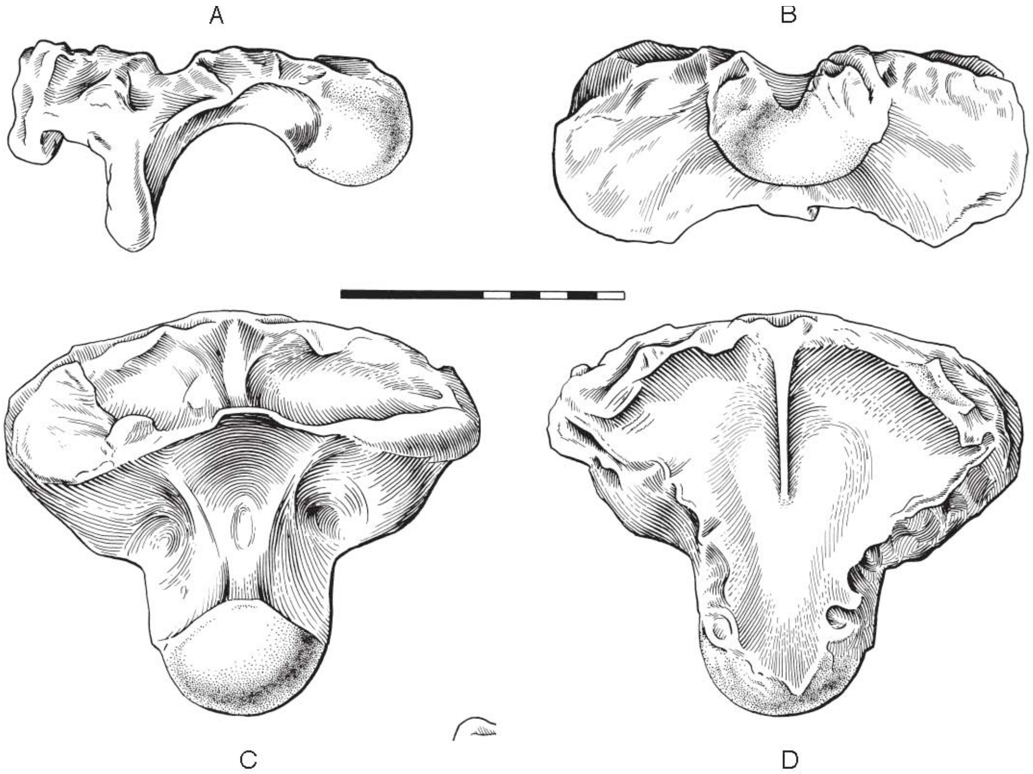


Figure 12. Basioccipital of *Bambiraptor feinbergi* in lateral (A), posterior (B), ventral (C), and (D) views. Scale bar in mm.

The dentaries were recovered in a separate block of matrix from the posterior mandibular bones, and were apparently displaced before burial. The dentaries lack their posterior margins, but include complete alveolar margins (fig. 13). In dorsal view (fig. 13c) the anterior ends of the dentaries curve toward the midline to meet in a symphysis, which is a small, flat, roughened area. The left dentary has 12 tooth positions. The anterior sockets are empty, but most of positions 6 through 12 have teeth in situ. Along the lateral surface, there is a row of foramina that are larger anteriorly, as well as a lower parallel row of smaller foramina. There are fused interdental plates as reported by Currie (1987) for other dromaeosaurids. The dentary tooth crowns show some wear. They fit the basic velociraptorine denticle pattern of having approximately seven denticles per mm on the posterior carina, but lack denticles on the anterior keel (Currie et al., 1990).

The left splenial was found separated from the dentary and other jaw elements, whereas the right splenial was recovered near the right jaw articulation. The splenial is similar to that of *Deinonychus* (Ostrom, 1969) in lateral and medial views. Both surangulars were recovered but are missing their anterior portions. The posterior surangular foramen is a small opening positioned anterior to the jaw articulation. The angular is flat and fan-shaped where it overlaps the surangular as a thin sheet. Anteriorly, the dorsal margin is clearly evident and forms the margin of the external mandibular fossa. The external mandibular fenestra was probably large, as described for *Deinonychus* (Ostrom, 1969) and *Velociraptor* (Barsbold and Osmólska, 1999). A small, flat, triangular bone found on the medial surface of the dorsal process of the right jugal is tentatively identified as a coronoid. The posterior end of the pre-articular is exposed along the medial side of the surangular, but is covered anteriorly by portions of the palate. Right and left articulars were found in place on both surangulars and are unfused. Each is a robust bone with a prominent downwardly curved retroarticular process. A posterior buttress is present, as in *Dromaeosaurus* (Colbert and Russell, 1969) and *Deinonychus* (Ostrom, 1969).

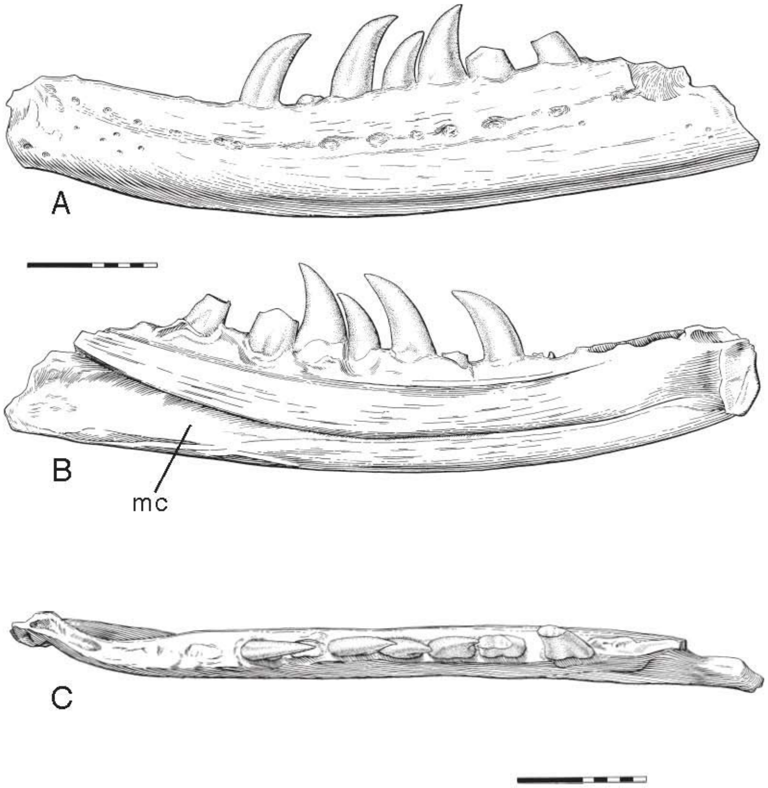


Figure 13. Left dentary of *Bambiraptor feinbergi* in lateral (A), medial (B), and dorsal (C) views. Abbreviation: Meckelian canal (mc). Scale bar in mm.

The slightly expanded posterior end of the thin, rod-like right ceratohyal was in close association with the posterior end of the surangular. The bone is 45 mm long and 1mm in diameter, and is similar to the hyoid figured for *Sinornithosaurus* (Xu and Wu, 2001).

Loose teeth recovered from the matrix surrounding the skull range from isolated crowns to perfectly preserved teeth with roots. Like all velociraptorine dromaeosaurids, the denticles are larger on the posterior carina than they are on the anterior ridge.

Paleoneurology

The only previously described endocast of a small, non-avian theropod is that of *Troodon,* which has a high degree of encephalization (Russell, 1969; Currie, 1985). The endocast taken from the holotype of *Bambiraptor* is detailed enough (fig. 2) to show vascular imprints on the ventral surface of the skull roof. Because this suggests that the brain of the living animal occupied the entire braincase cavity, the endocast is a good indicator of how large the brain actually was (Jerison, 1973). The three main areas of the brain (Cobb and Edinger, 1962) are evident in the endocast. Whereas the optic lobe is relatively pronounced, the paired olfactory tracts are relatively small in comparison with *Troodon* and tyrannosaurids. Cranial nerves II, III, IV, and VI cannot be seen on the endocast, but V and VII–XII are represented.

The brain lies mostly behind the orbits, with the olfactory structures extending anteriorly toward the snout. The olfactory bulbs lie above and slightly anterior to the orbit (approximately at the frontal-nasal suture). The optic lobes are readily distinguished in the midbrain region and reside in a ventrolateral position, as in birds. There is some flexure in the brain (fig. 2a), but is not as pronounced as in modern birds.

The endocast, measured from the olfactory lobe to the foramen magnum, is 55.2 mm long; its maximum height is 31.3 mm; and at its widest point across the anterior portion of the cerebellum it is 27.5 mm. The endocast of the holotype of *Bambiraptor* displaced 14 cm^3 of water. If we assume that the brain had a specific gravity of 0.9, then the original brain weighed an estimated 12.6 g. Body mass is estimated to range from 1.86 to 2.24 kg (estimated using the circumference of the femur shaft in the formula developed by Anderson et al. 1985). This yields an REQ (Reptilian Encephalization Quotient, Jerison, 1973) of 12.5 to 13.8 and a BEQ (Bird Encephalization Quotient, Jerison, 1973) of 1.2 to 1.4, figures well above values found not only in dinosaurs, but birds as well (Wharton, 2001). This estimate may even be conservative because the endocast does not preserve the portion of the brain bordered by the supraoccipital. However, the estimated EQs may be somewhat inflated because of the immaturity of the holotype (brain size shows negative allometry during growth in all tetrapods). Nevertheless, the estimate is high enough to suggest that the relative brain size of *Bambiraptor* was as large or larger than that of *Troodon* (Currie and Zhao, 1993) and other coelurosaurs, which puts it in the lower part of the range of modern birds. Additionally, the posterior enlargement of the brain is also atypical of other coelurosaurs and is more birdlike.

Comparison of spinal cord data shows similarities in the cervicodorsal region between the holotype *Bambiraptor* and those of other dromaeosaurids. This cross-sectional area was described by Giffin (1990) as especially enlarged in this region. Spinal cord anatomy has been described for *Deinonychus* and *Saurornitholestes* by Giffin (1990). Other lines of evidence, referred to as the spinal quotient (SQ), indicate the biggest difference in brain size occurs between very young individuals and adults (Giffin, 1990). SQ measure versus basal skull length for alligators showed that it was higher only for hatchlings, but medium-sized and large individuals were “remarkably constant" (Giffin, 1990).

Axial Skeleton

Nearly the entire vertebral column (table 2) was recovered for the holotype of *Bambiraptor feinbergi.* The anterior cervicals (up to C 4) were loosely articulated, after which the fifth cervical to the sixth dorsal vertebrae were disarticulated. Behind the position of the sternal plates, the vertebral column is continuous almost to the end of the tail.

TABLE 2. Vertebral measurements for *Bambiraptor feinbergi* (in millimeters).

Vertebra position	Maximum length	Posterior width	Width at transverse process	Maximum height of neural canal	Maximum width of neural canal
C-1 (atlas)	___	___	___	___	___
C-2 (axis)	13	5	16.9	5	6.1
C-3	13.5	11.2	24a	5.8	7.9
C-4	13.5	10.8	22.4	5.7	7
C-5	16	10	___	7	7.7
C-6	14.5	7.4	___	6.7	5.8
C-7	15a	9.4	___	7	7

C-8	12	11.3	___	___	7.4
C-9	13	___	___	___	___
C-10	___	___	___	___	___
D-1	11	9.7	34a	8	8.4
D-2	12	12.7	29.5	7.2	7.5
D-3	12	___	___	___	___
D-4	11.8	___	___	___	___
D-5	11	___	___	___	___
D-6	13	___	___	___	___
D-7	10	___	___	___	___
D-8	10.5	___	___	___	___
D-9	9.5	___	___	___	___
D-10	10	___	___	___	___
D-11	10.5	___	___	___	___
D-12	10.8	___	___	___	___
D-13	10.5	___	___	___	___
S-1	11	___	___	6	7
S-2	15	___	___	?	?
S-3	15	___	___	?	?
S-4	13	___	___	?	?
S-5	11.5	31	___	5.7	6

CA-1	9.1	8.6	25a	3.6	6.3
CA-2	12.6	8.4	28a	___	___
CA-3	13.1	7.3	28.7a	___	___
CA-4	14.5	7.9	29.a	3.5a	4a
CA-5	15.6	___	___	___	___
CA-6	16.1	___	___	___	___
CA-7	17.9	___	___	___	___
CA-8	20.3	___	___	___	___
CA-9	21.6	___	___	___	___
CA-10	24.2	___	___	___	___
CA-11	24.6	___	___	___	___
CA-12	26	___	___	___	___
CA-13	27a	___	___	___	___
CA-14	27	___	___	___	___
CA -15	26a	___	___	___	___
CA-16	24a	___	___	___	___
CA-17	23	___	___	___	___
CA-18	22	___	___	___	___
CA-19	?	___	___	___	___
CA-20	?	___	___	___	___
CA-21	?	___	___	___	___

CA-22	?	——	——	——	——

a = denotes approximation.

The cervical vertebrae strongly resemble those described for *Deinonychus* (Ostrom, 1969) in having large divergent zygapophyses and relatively short centra. The centra are angled differentially along the cervical column to form an S-shaped neck. Each pneumatic centrum has lateral pleurocoels, and pneumatopores penetrate the neural arch below the diapophysis. The relatively large neural canal increases in diameter posteriorly until the cervicodorsal transition. At this point, the canal is larger in diameter than it is in any of the dorsal vertebrae, indicating a prominent brachial plexus and extensive innervation of the forelimbs (Giffin, 1995).

The disarticulated atlas neural arch, centrum, intercentrum, and odontoid were found closely associated in the anterior cervical region. The axis was recovered from the matrix near the back of the skull behind the atlas elements. It closely resembles that of *Deinonychus.* However, in ventral view the centrum tapers posteriorly and does not have a distinct keel. The axis includes parapophyses and diapophyses for cervical ribs, even though no ribs were recovered.

The complete cervical series is presumed to number ten, although this cannot be ascertained because some vertebrae were badly damaged when collected. Cervical 7 is the worst-preserved vertebra in the specimen and cannot be reconstructed. Cervical centra are wider than tall and have somewhat heterocoelous articular surfaces. The laterally positioned pleurocoels increase in size posteriorly, and are subdivided by struts in the ninth and tenth cervical centra. Fragmentary anterior cervical ribs were found crushed onto the lateral surfaces of the centra.

Some anterior dorsals are crushed, and are missing spines and transverse processes. Neural arches on some dorsals have distinct, interdigitating sutures with the centra, although these elements are not completely fused. The anterior dorsals have large neural canals and prominent ventral keels. Pleurocoels are present on all dorsal centra, with the most anterior ones having multiple openings on each side. The parapophyses are cupped, circular facets anteroventral to the transverse processes. They diminish in size posteriorly and move up in position along the neural arch. The tall neural spines of the posterior dorsals are rectangular in shape and are about twice the height of the centra. The centra of the posterior dorsals are rounded in cross section and are best described as amphiplatyan, although they are slightly platycoelus as in *Deinonychus* (Ostrom, 1969). These vertebrae have centra that are constricted at mid-length, and transverse processes that arch posterodorsally.

The sacrum, composed of five vertebrae, was crushed between the ilia. This resulted in the loss of most of the sacral ribs and posterior neural spines, even though the centra are well preserved. The sacrum described for *Velociraptor* (Norell and Makovicky, 1997) is similar in morphology to that of *Bambiraptor.* The third, fourth, and last sacrals have fused ribs. There are foramina on the lateral surfaces of the centra just under the transverse sacral ribs as reported for *Saurornitholestes* (Norell and Makovicky, 1997) but in contrast with *Velociraptor*, which lacks pleurocoels in the fifth sacral. The ventral surface of the third sacral has a deep sulcus.

TABLE 3. Pectoral girdle measurements (in millimeters).

Element	Maximum Length	Maximum Width
Right sternal plate	63	29
Left sternal plate	67	29
Right scapula	85	—
Left scapula	83*	—
Right coracoid	19*	28*
Left coracoid	22	33

*Approximation

As with most non-avian coelurosaurs, the caudals increase in length until the middle of the series. The first few caudal centra have small foramina on their lateral surfaces, but there are no pneumatopores. The articular surfaces of the pre- and postzygapophyses are offset 45°to the neural spine. Transverse processes protrude from low on the arch and are directed lateroventrally. The elongate extensions of the prezygapophyses of more distal vertebrae extend anteriorly onto the third and fourth caudals.

Elongate anterior zygapophyses and chevrons stiffened the distal part of the tail as described in detail for *Deinonychus* (Ostrom, 1969). However, there is a degree of flexibility of this system that was not apparent initially. The stiffening rods in the holotype of *Bambiraptor* and several *Saurornitholestes* specimens from Alberta (Currie pers. comm., 2000) bent enough to allow the distal part of the tail to curve gently dorsally. In short, the stiffening rods restricted the mobility of the distal part of the tail, but did not stop it entirely from bending.

A single proximal hemal arch was discovered in the matrix between the articulated ischia. The chevron is tall and thin in comparison with the anteroposteriorly elongate ones associated with more posterior caudals.

Appendicular Skeleton

Proximally, the scapula (fig. 14) is robust and almost triangular in cross section (table 3). There was no fusion with the coracoid, and the sutural contact is smooth. Most of the glenoid articular surface is smoothly concave, but the convex edges form a lip or buttress anterodorsally. There is a prominent anteromedially directed acromion process with a roughened surface, presumably for the attachment of the furcula (Norell and Makovicky, 1999). Distally, the elongate, strap-like scapular blade becomes mediolaterally thinner. It curves gently dorsoposteriorly to conform to the rib cage. Compared with *Deinonychus* (Ostrom, 1969) and recently described dromaeosaurids (Norell and Makovicky, 1999), the scapular blade of *Bambiraptor* is more gracile and tapers distally. The acromion in *Bambiraptor* is relatively longer

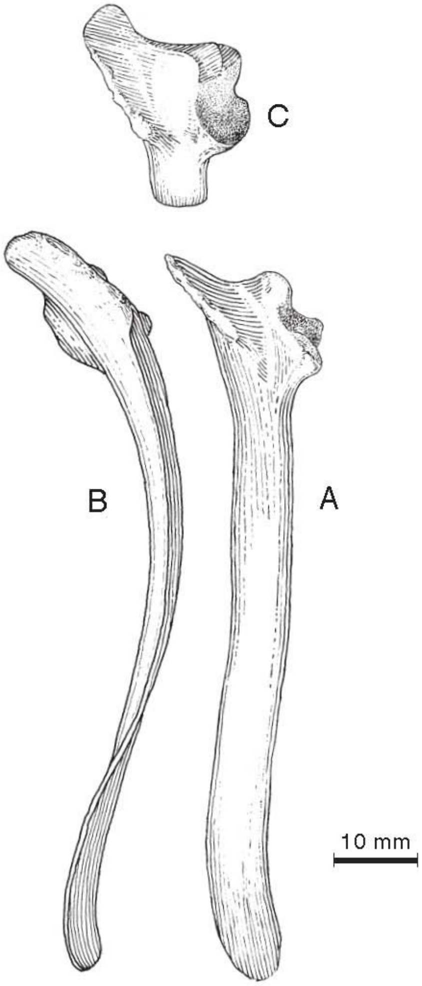


Figure 14. Right scapula of *Bambiraptor feinbergi* in lateral (A), dorsal (B), and anterior (C) views. Scale bar equals 10 mm.

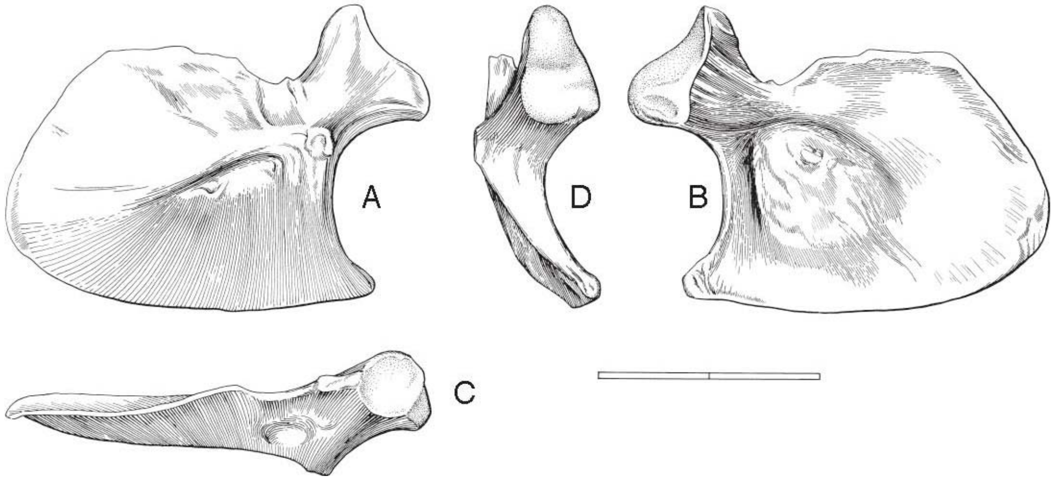


Figure 15. Left coracoid of *Bambiraptor feinbergi* in anterior (A), posterior (B), dorsal (C), and ventral (D) views. Scale bar equals 5 mm.

and wraps around the front of the chest (fig. 14c). In *Sinornithosaurus* (Xu et al., 1999) the elongate scapula is also strap-like and has a large, forwardly directed acromion.

The left coracoid is complete (fig. 15), but the right one was crushed, and lacks the sutural contact for the scapula. Overall, the coracoid is similar in shape to the larger, quadrangular ones described for other dromaeosaurids by Norell and Makovicky (1999). However, it is longer anteroposteriorly than tall dorsoventrally, the glenoid seems to be supported on a prominent strut-like neck, and there is no coracoid foramen. The absence of the latter can be attributed to the presence of a deep notch in the bone, and may represent an immature state. The recovery of a more mature *Bambiraptor* coracoid will be necessary to determine whether this is an autapomorphy of the genus. The biceps or coracoid tubercle is positioned anteroventral to the glenoid.

Both sternal plates are well preserved and three-dimensional, although the right one is crushed at the coracoid-sternal articulation. When found, the two plates were touching on the midline posteriorly, but were slightly displaced anteriorly. Each elongate sternal is thin and sub-rectangular (fig. 16), and is similar in shape to the dromaeosaurid sternals described by Norell and Makovicky (1997, 1999). There is a transverse groove for the coracoid along the thick anterior margin. The lateral margins are scalloped with facets for the attachment of four, possibly five, sternal ribs. The anteroventral surface of each sternal plate is shallowly concave, probably for muscle attachment.

The furcula (fig. 17) is a well-preserved bone shaped like a flared “U” or boomerang. It has a flattened cross section with a grooved dorsal surface. Within this channel, a nutrient foramen can be found on each ramus of the radiale (fig. 17b), about 10 mm from the apex. The angle between the rami is approximately 80°. The distal ends of the rami taper and have striated attachment surfaces, which are especially prominent on the ventral side. Near the midline of the furcula, the bone thickens on the dorsal surface (fig. 17a), although there is no hint of a hypocleidium. This bone is in sharp contrast to the robust, V-shaped furcula of *Velociraptor* (Norell et al., 1997), and is closer in appearance to that of *Archaeopteryx*, which is also U-shaped and flattened, has a low clavicular angle, and lacks a hypocleidium.

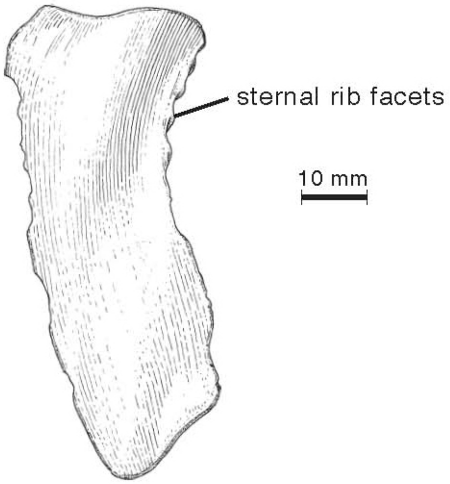


Figure 16. Left sternal of *Bambiraptor feinbergi* in ventral view.

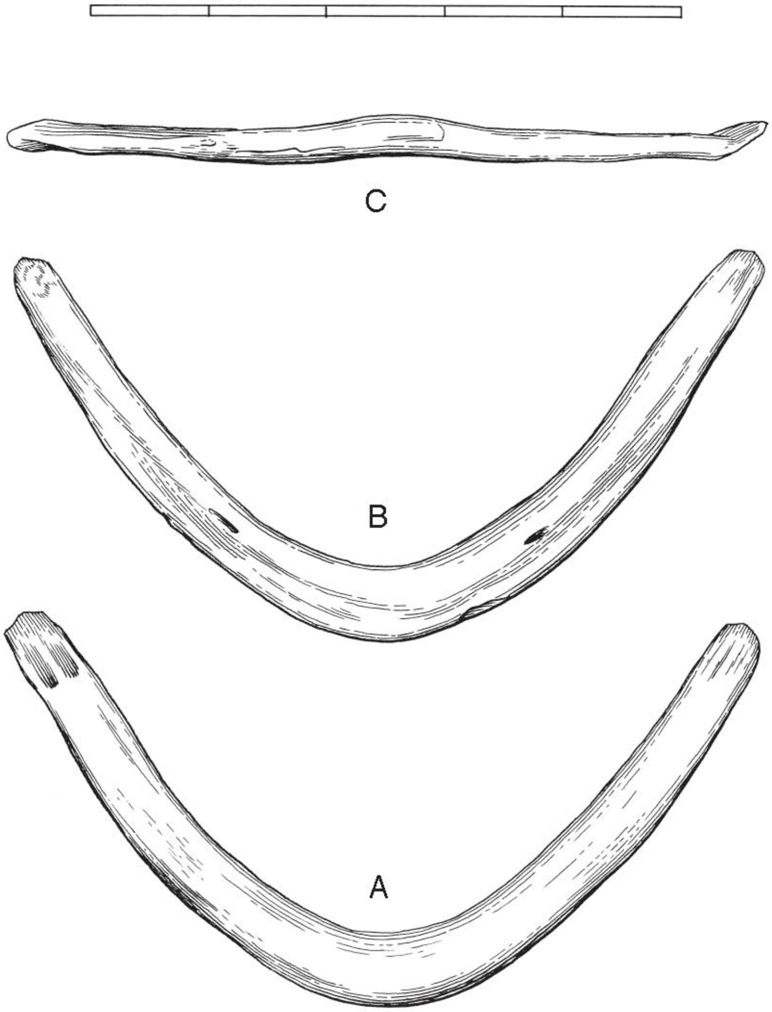


Figure 17. Furcula of *Bambiraptor feinbergi* in anterior (A), posterior (B), and ventral (C) views. Scale bar in cm.

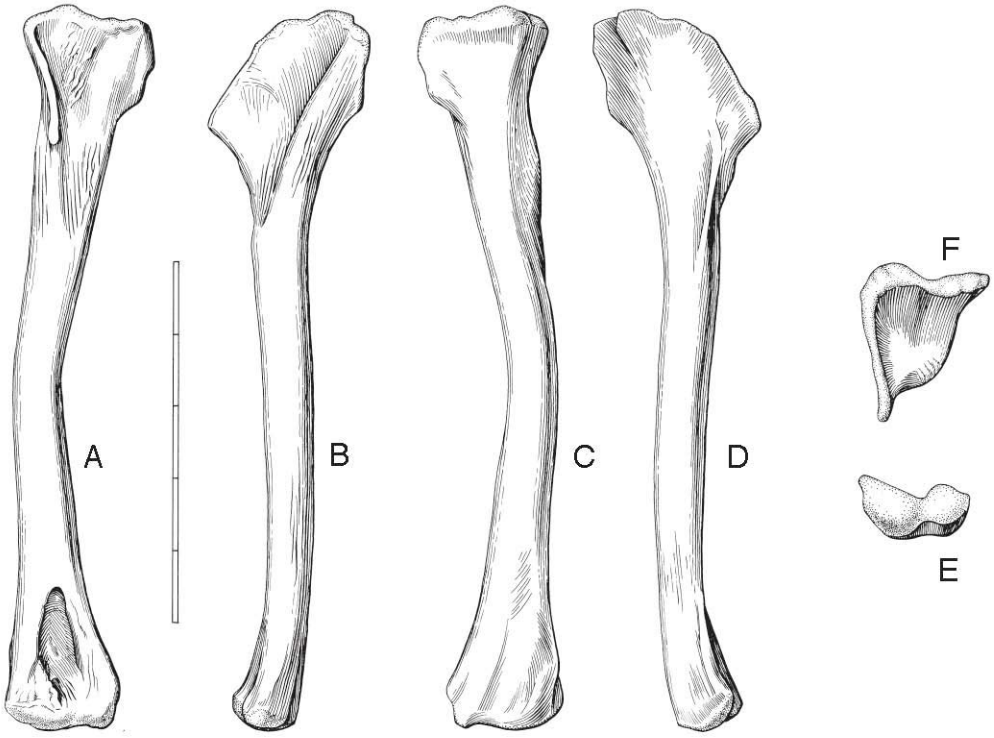


Figure 18. (above) Right humerus of *Bambiraptor feinbergi* in anterior (A), posterior (B), lateral (C), medial (D), distal (E), and proximal (F) views. Scale in cm.

The head of the humerus (fig. 18) is strongly convex, has a smooth articular surface, and is larger than that of *Deinonychus* (Ostrom, 1969). The shaft is relatively long and slender, and supports a well-developed pectoral crest. Distally, the humerus expands into radial (larger) and ulnar condyles separated by a shallow groove. The distal condyles are separated by a depression in the holotype. The slightly concave proximal end of the ulna is triangular in section (fig. 19e). The olecranon forms a strong ulnar ridge on the exterior surface similar to *Velociraptor* (Norell and Makovicky, 1999). The shaft is bowed and flares into a thin, wide distal articular surface (fig. 19f). This condyle turns slightly medially and forms a flange that seems to be absent in *Deinonychus* (Ostrom, 1969). The radius (fig. 20) is a

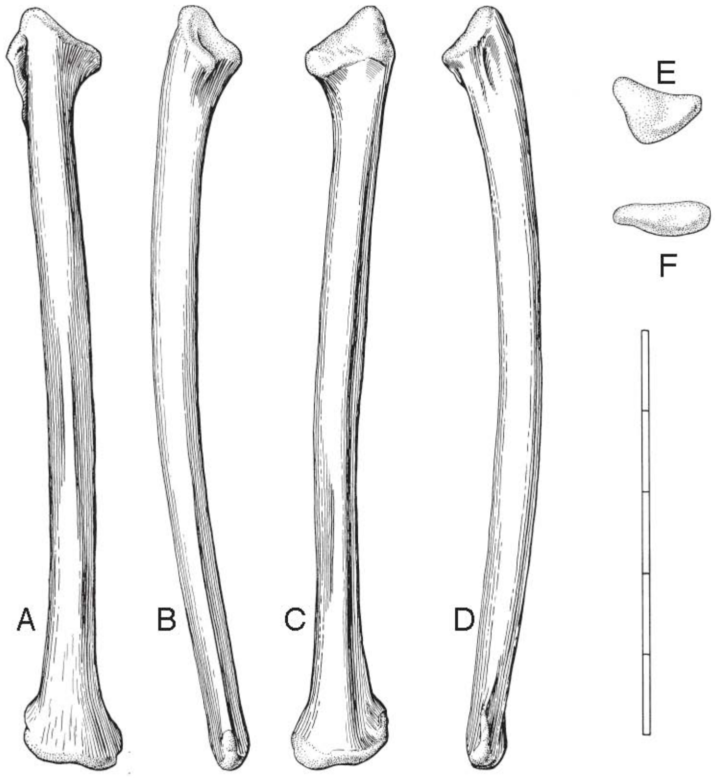


Figure 19. Right ulna of *Bambiraptor feinbergi* in anterior (A), posterior (B), lateral (C), medial (d), distal (E), and proximal (F) views. Scale bar in cm.

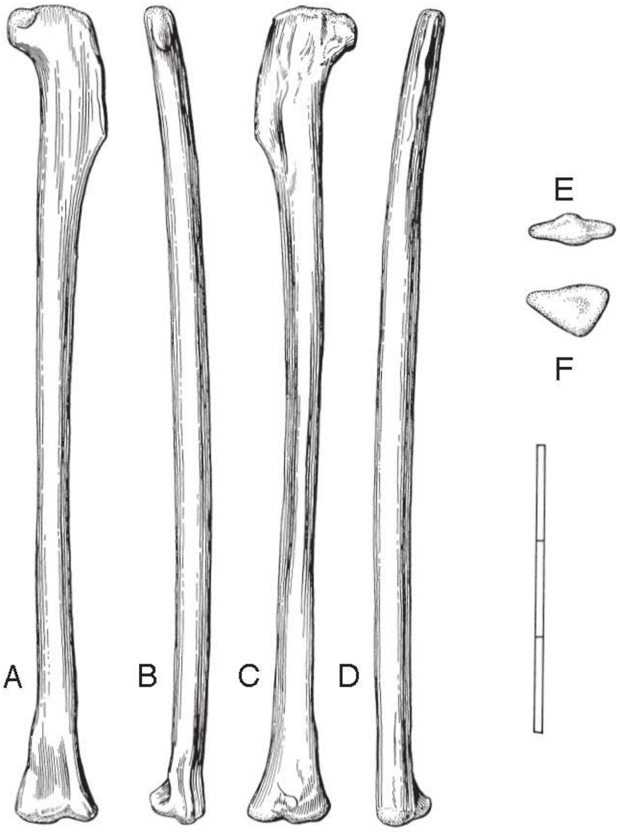


Figure 20. Right radius of *Bambiraptor feinbergi* in anterior (A), posterior (B), lateral (C), medial (D), distal (E), and proximal (F) views. Scale bar in cm.

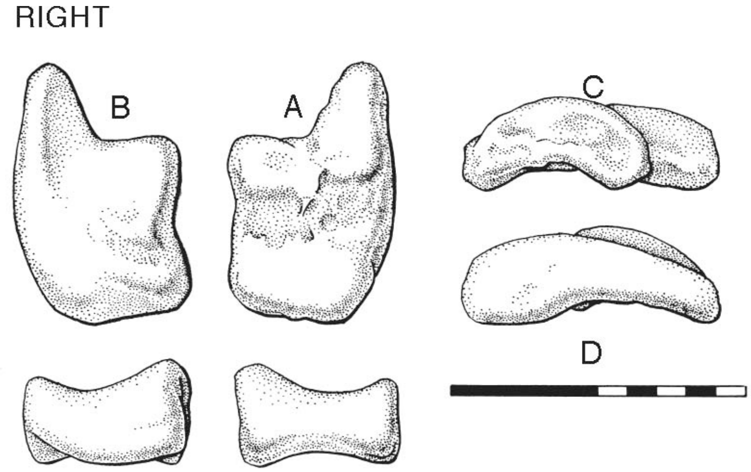
slender, thin-shafted bone that is circular in cross section. A flattened, striated area on the medial surface of the proximal end fits between the proximal tubercles of the ulna.

The hands bear long, curved claws although the manual digits, except for the first digit, are relatively inflexible compared with the pedal digits. The wrist contains two carpal bones (a semilunate bone and radiale) that allow for a folding back of the hand as well as a slight degree of lateral flexure.

Both semilunate bones (radiale of Ostrom, 1969; fused distal carpals 1 and 2 of

Chure 2001 and others) were recovered with the holotype, and another was found with the adult *Bambiraptor* (AMNH 002). The semilunate has a saddle-shaped proximal articular surface (carpal trochlea) that is notched (fig. 21) and articulates mostly with the ulna. Distally, the semilunate caps a portion of metacarpal I and the entire proximal surface of metacarpal II, as in most maniraptoriforms. The second, smaller carpal bone found in the holotype is the radiale (fig. 22). Both the right and left radiale were found near the semilunate carpals. This small, ovoid bone slid along the carpal trochlea of the semilunate.

Metacarpal I is short and robust, and has a ginglymoid distal articulation as in *Deinonychus* and *Velociraptor* (fig. 23). This bone contacts Metacarpal II for most of its length through a relatively flat proximolateral surface.



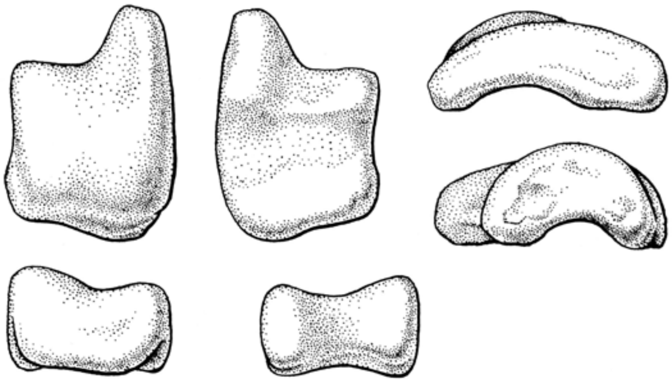


Figure 21. Right and left semi-lunate bones of *Bambiraptor feinbergi* in proximal (A), distal (B), dorsal (C), and ventral (D) views. Scale bar in mm.

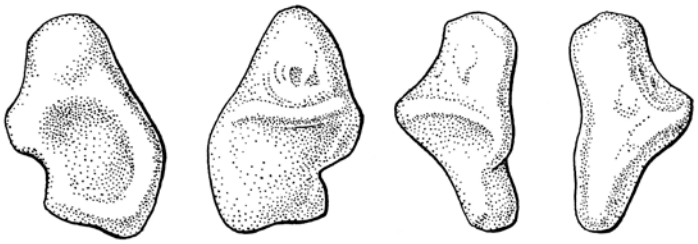


Figure 22. Right radiale of *Bambiraptor feinbergi* in proximal (a), distal (B), dorsal (C), and ventral (D) views. Scale bar in mm.

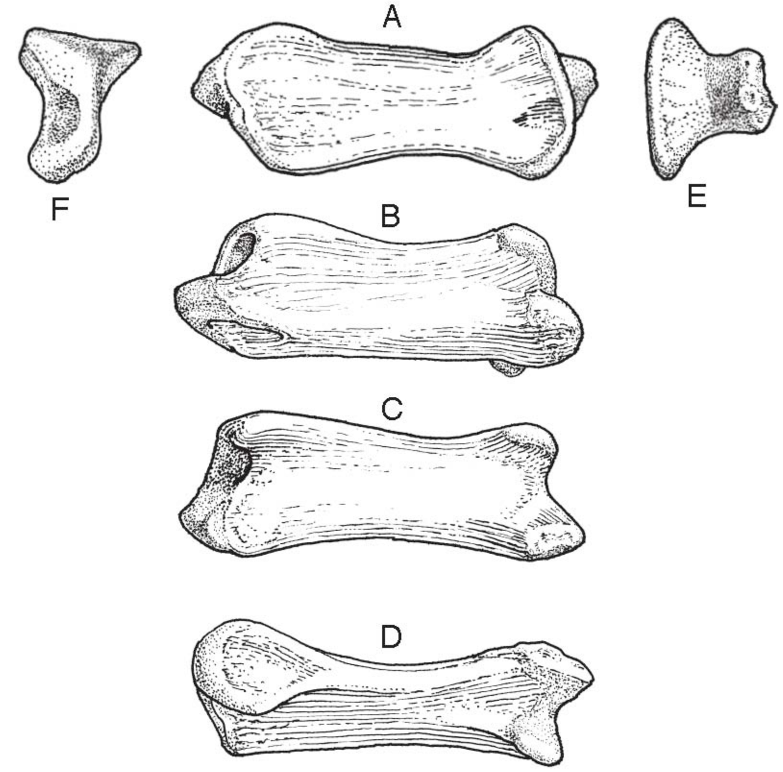


Figure 23. Left metacarpal I of *Bambiraptor feinbergi* in medial (A), dorsal (B), ventral (C), lateral (D), distal (E), and proximal (F) views.

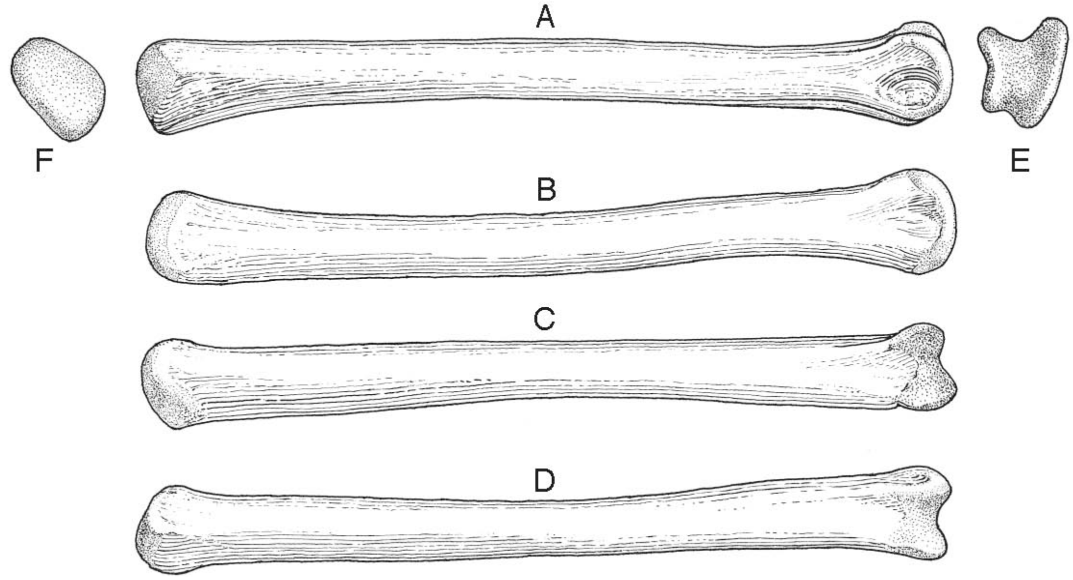


Figure 24. Left metacarpal II of *Bambiraptor feinbergi* in medial (a), lateral (b), ventral (c), dorsal (d), distal (e), and proximal (f) views.

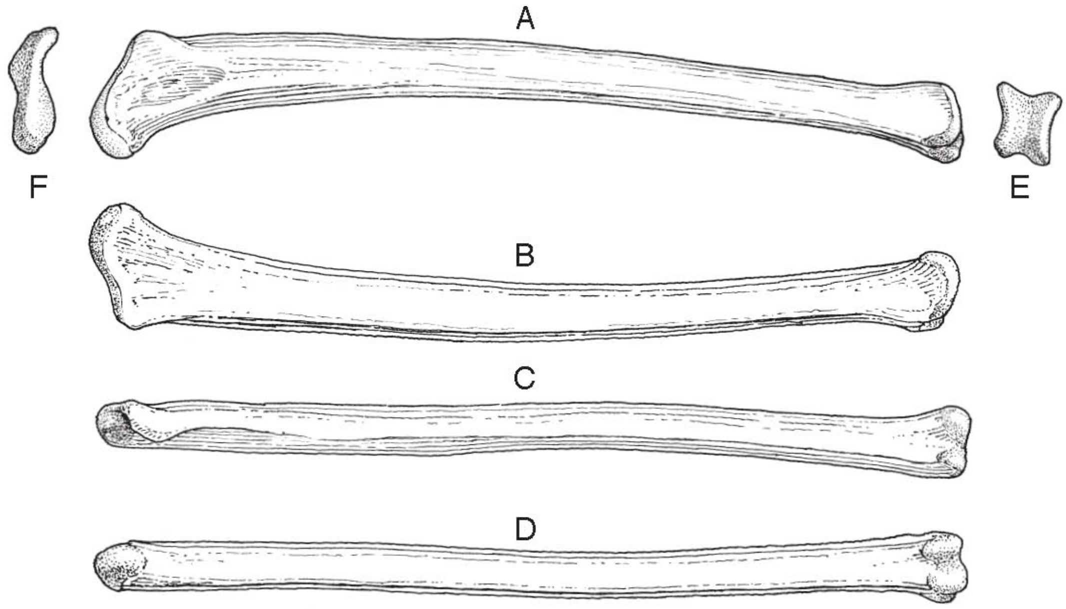


Figure 25. Left metacarpal III of *Bambiraptor feinbergi* in medial (a), lateral (b), ventral (c), dorsal (d), distal (e), and proximal (f) views.

Metacarpal II (fig. 24), the longest of the three, is circular in cross section. Metacarpal III is the thinnest and is slightly bowed (fig. 25).

The three digits are long and gracile. The second is the longest, the third is nearly as long, and the first is the shortest. The phalangeal formula is 2-3-4. Phalanx I-1 is the longest and most robust phalanx of the hand, followed by II-1. Digit I has the largest claw, which has a greater range of flexion/extension than the other two fingers. When the hand closed, the phalanx and claw rotated toward the central axis of the hand. However, it crossed palmar to the other digits, and was not capable of grasping. The articular surfaces of the phalanges of the second digit suggest that this finger was relatively stiff and inflexible. Manual phalanx III-1 is thin and relatively short, but is almost four times the length of III-2. The longest phalanx of the third finger is III-3. The interphalangeal articulations cause this digit to move toward digit II during flexion. The manual unguals are laterally compressed, have prominent flexor tubercles, and are more strongly curved than the unguals of the pes. Digit III is the most gracile finger, and is directed inward when flexed. Other than being from a smaller animal, the manual bones of the *Bambiraptor* holotype are essentially the same as those of *Velociraptor* (Norell and Makovicky, 1999).

Pelvic Girdle and Hindlimb

The pelvis of the holotype of *Bambiraptor* is more or less intact. Dromaeosaurid pelves are known for their high degree of pubic retroversion (Norell and Makovicky, 1997), and *Bambiraptor* as a dromaeosaurid shares this feature. Additionally, the ischia are shorter than the pubis as in most maniraptoran coelurosaurs (Rasskin-Gutman, 1997).

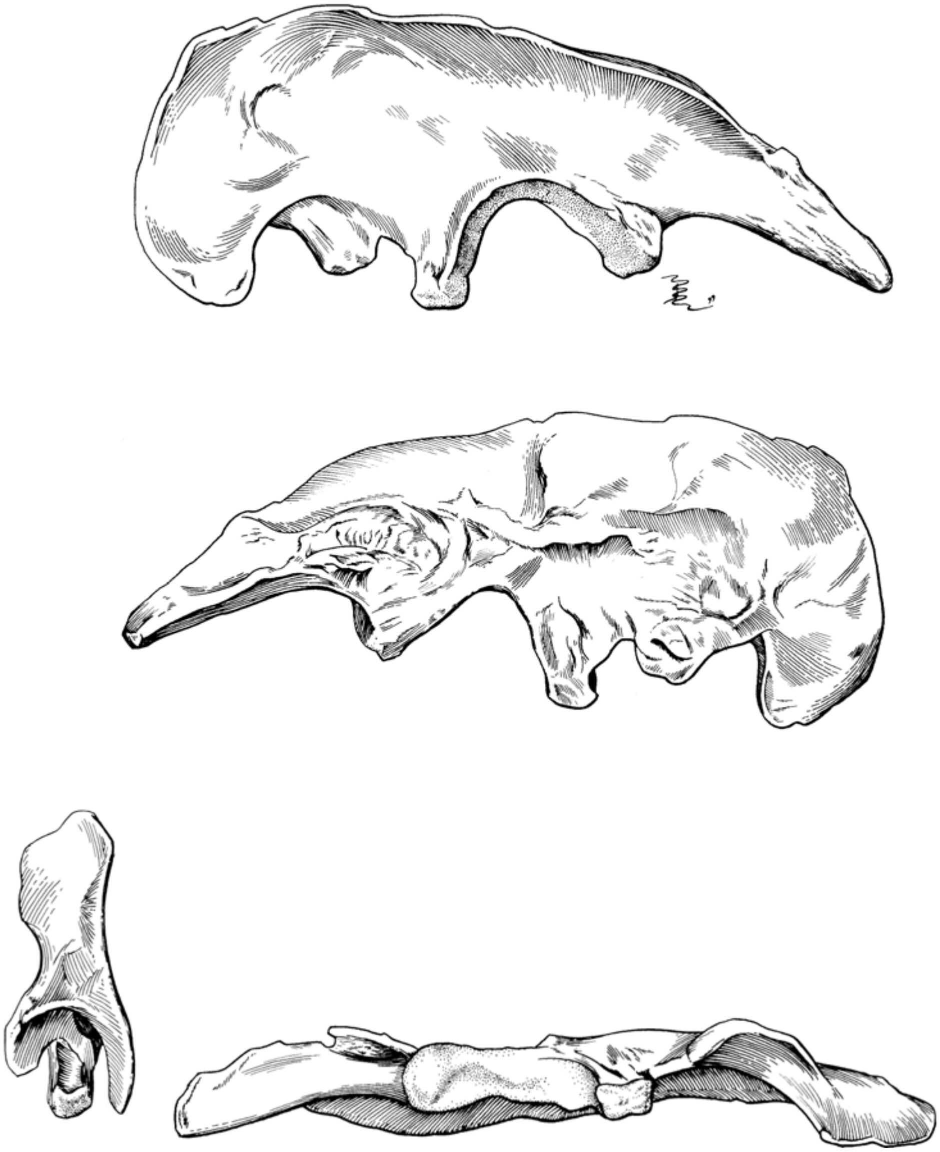


Figure 26. Left ilium of *Bambiraptor feinbergi* in lateral (A), medial (B), distal (C), proximal (D), and ventral views (E).

The postacetabular region of the ilium (fig. 26) is shorter than the preacetabular blade, a condition opposite that of the dromaeosaurid described by Norell and Makovicky (1997). The dorsal margin of the ilium is gently curved, whereas that of the *Velociraptor* is relatively straight. As a consequence, the distal end of the ilium of *Bambiraptor* is more strongly tapered. The pubic peduncle is tall, as is typical of *Deinonychus* and *Velociraptor* (Norell and Makovicky, 1997). The ischial peduncle is sub-triangular and more pronounced than in other dromaeosaurids. The pubis (fig. 27) was oriented posteroventrally as in other dromaeosaurids. It has a sub-triangular ischial peduncle. Proximally, the shaft is oval in section, but in the distal half of the bone extends medially into a pubic apron. There is a large pubic boot, which has no anterior component and tapers posterodorsally to end in a blunt tip.

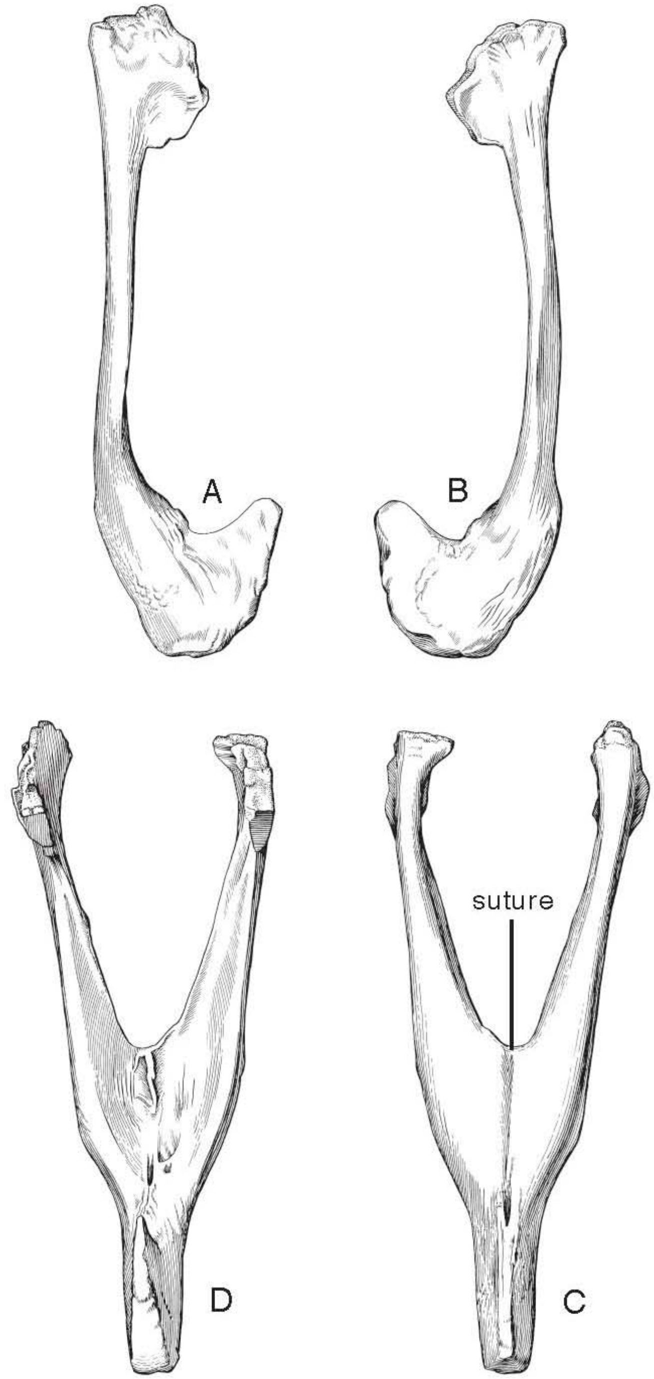


Figure 27. Right and left pubis of *Bambiraptor feinbergi* left lateral (A), right lateral (B), anterior (C), and posterior (D) views. (See table for length).

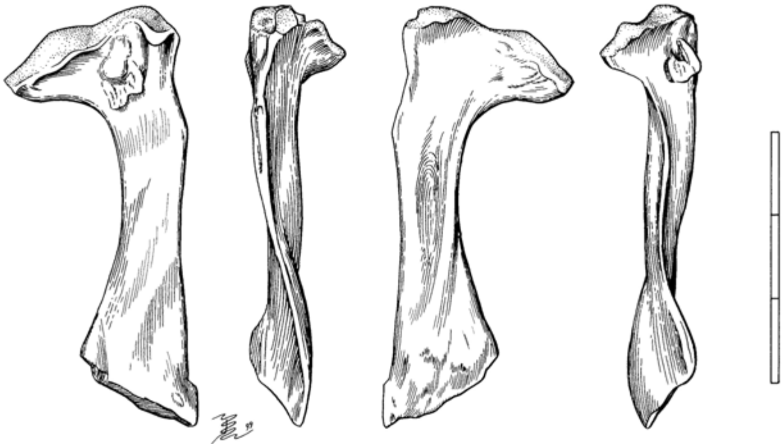


Figure 28. Right and left ischia of *Bambiraptor feinbergi* in lateral (A), medial (B), anterior (C), and posterior (D) views. Scale bar in cm.

The ischium (fig. 28) is similar to those described for *Deinonychus* and other dromaeosaurids (Barsbold, 1983; Norell and Makovicky, 1997). This ischium is only half the length of the pubis as in most maniraptorans. Proximally, the pubic process is longer and narrower than the relatively short, stout iliac process. There is a low posterodorsal process near the proximal end of the flattened shaft of the ischium. This is similar in position to the more pronounced postero-dorsal processes of *Rahonavis* (Forster et al. 1998), *Microraptor, Sinornithosaurus, Unenlagia,* and *Archaeopteryx* (Xu et al. 2000). The distal ends of the ischia contact each other but are not fused. The relatively small obturator process is positioned at the end of the bone, which is presumably a juvenile trait.

There is a distinctive twist to the femoral head, which is also found in some other non-avian theropods (*Troodon*) and birds (*Archaeopteryx, Enantiornis*). The shaft of the femur (fig. 29) is strongly bowed as in many small coelurosaurs and enantiornithine birds (L. D. Martin pers. comm.). There is a prominent posterior trochanter (Ostrom, 1969) near the proximal end of the shaft. A slight rugosity on the shaft may represent the insertion of the M. caudifemoralis brevis. Posterodistally, the popliteal fossa separates the medial and lateral condyles.

The tibia (fig. 30) is longer than the femur. At the level of the fibular crest, the shaft of the tibia is sub-triangular in cross section, and is penetrated by a nutrient foramen as in other theropods. The rod-like shaft of the fibula has a diameter of less than 1 mm. The distal end of the fibula overlaps the anterolateral margin of the astragalus where it contacts the proximal end of the calcaneum. The disc-shaped calcaneum is small relative to the astragalus as it is in all other dromaeosaurids. There is no sign of fusion between the two bones. The ascending process of the astragalus is 30 mm high. It tapers dorsally to a point offset toward the lateral edge of the tibia.

One right (III) and two left (III and IV) distal tarsals were found in association with the metatarsals of the holotype. They are similar to the same elements in *Deinonychus* (Ostrom, 1969), *Velociraptor* (Norell and Makovicky, 1997), and most other theropods that have these bones preserved.

Metatarsal I is a short, proximally tapering bone. The distal end has a single collateral ligament pit, and ends in a nearly ginglymoid articular surface. Metatarsals II, III, and IV were the weight-bearing

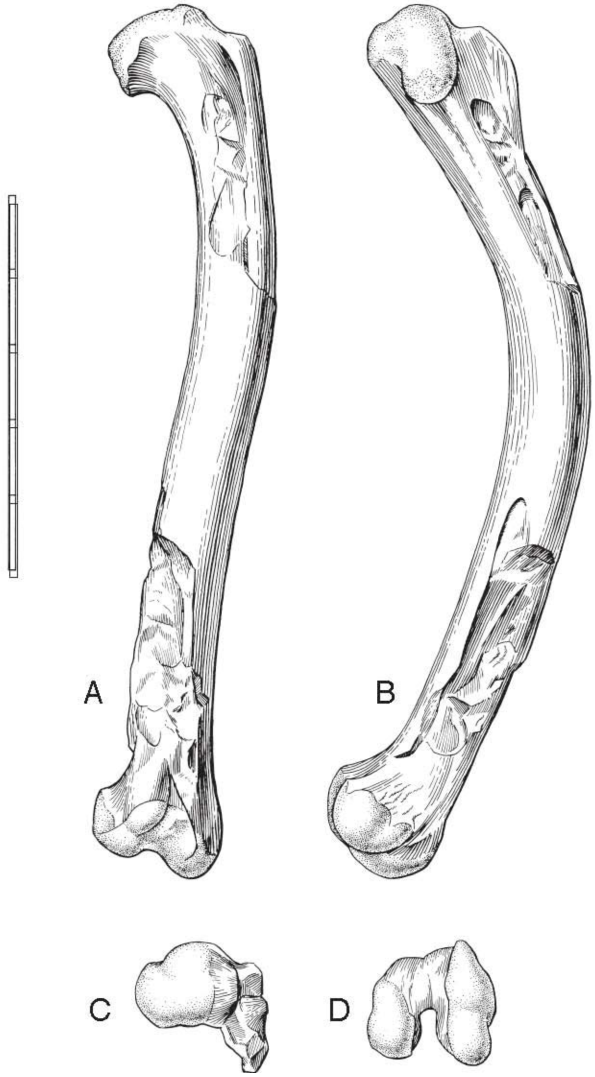


Figure 29. Left femur of *Bambiraptor feinbergi* in lateral (A), medial (B), dorsal (C), and ventral views (D). Scale bar in cm.

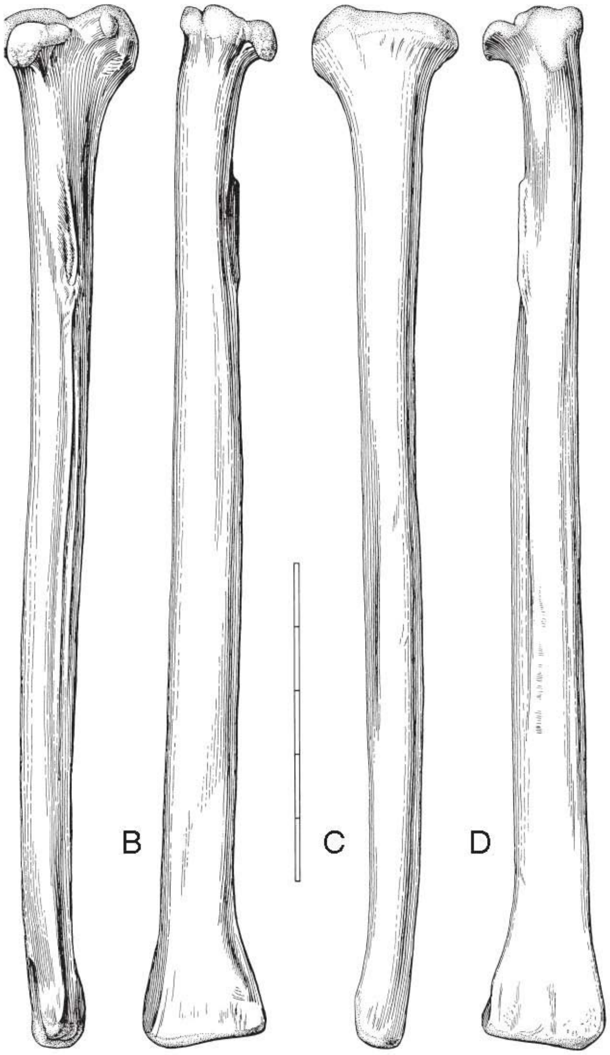


Figure 30. Right tibia of *Bambiraptor feinbergi* in lateral (A), medial (B), anterior (B), and posterior (D) views. Scale bar in cm.

portion of the foot. Metatarsal II is shorter than either the third or fourth metatarsals, and is less robust. Metatarsal III is mediolaterally flattened in cross section, and the proximal end is squeezed between its neighbors. The distal end has a relatively large semicircular articular surface, and characteristic of dromaeosaurids it would have permitted a wider range of parasagittal motion in the third digit than was possible in most other theropods. The rounded, distal articular surface of Metatarsal IV also would have permitted wide excursion of the associated toe. It is not as prominent as the distal end of the third metatarsal.

None of the phalanges were articulated, but were closely associated. Like other dromaeosaurids, the foot of *Bambiraptor* has characteristic phalanges (fig. 31) and the retractable, raptorial claw on the second digit. The other digits have significantly smaller and less strongly curved unguals (figs. 32, 33). The raptorial claw is supported by two robust, specialized phalanges. In spite of the strength and size of the second pedal digit, it is shorter than the third and fourth toes, but has more contact with the metatarsal. Consequently, this toe probably rarely touched the ground. It is quite possible the foot acted as a didactyl unit as described by Ostrom (1969), although no convincing trackway evidence of "two-toed" dinosaurs has been published to date (J. O. Farlow pers. comm. 1999). The proximal and distal articulations of the second phalanx of the second digit (fig. 31) gave the raptorial claw a very specific range of motion. The sickle-shaped claw is laterally compressed, highly recurved, and ends in a sharp tip (fig. 32). Pedal III-1 is the longest phalanx of the foot. Similar to *Rahonavis*, the penultimate phalanges are longer than the antepenultimate ones (table 4). The unguals of the third and fourth digits are shorter and less strongly curved than that of the second digit (fig. 33).

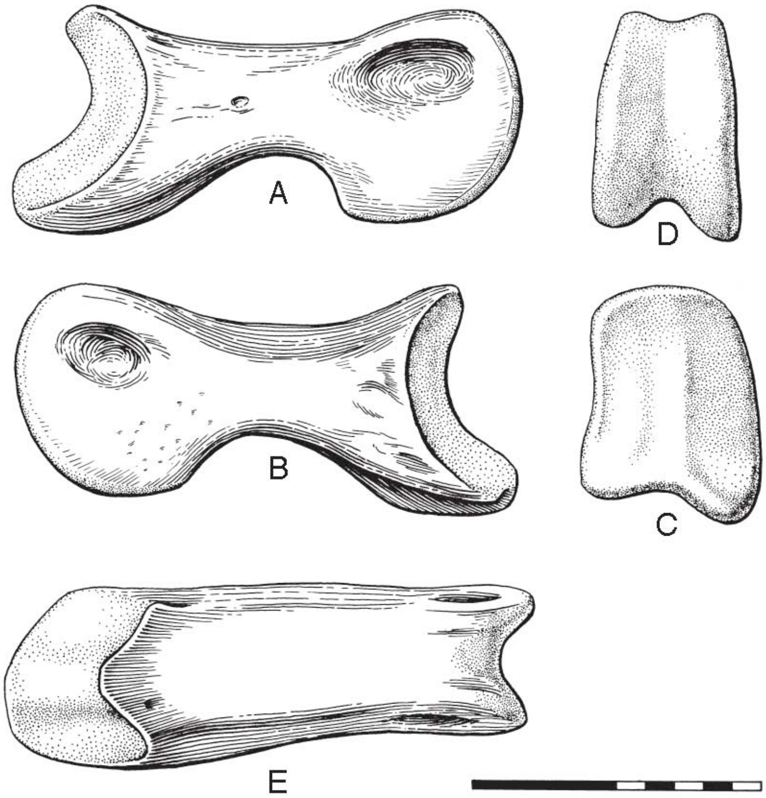


Figure 31. (left) Right pedal phalanx II-2 of *Bambiraptor feinbergi* in lateral (A), medial (B), distal (C), proximal (D), and ventral views (E). Scale bar in mm.

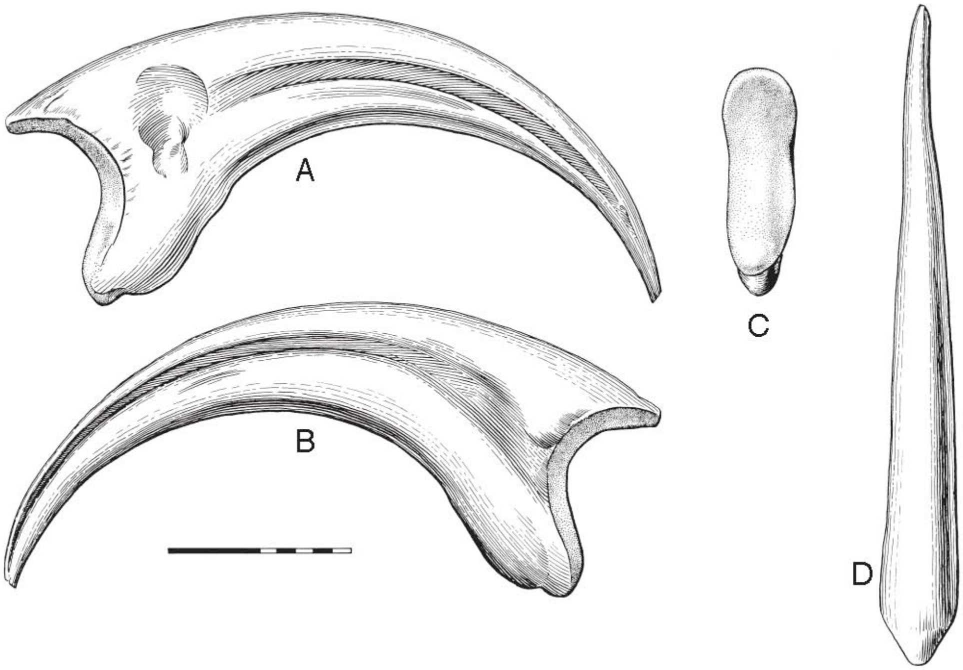


Figure 32. Right pedal ungual phalanx II-2 of *Bambiraptor feinbergi* in lateral (a), medial (B), proximal (C), and dorsal views (D). Scale bar in mm.

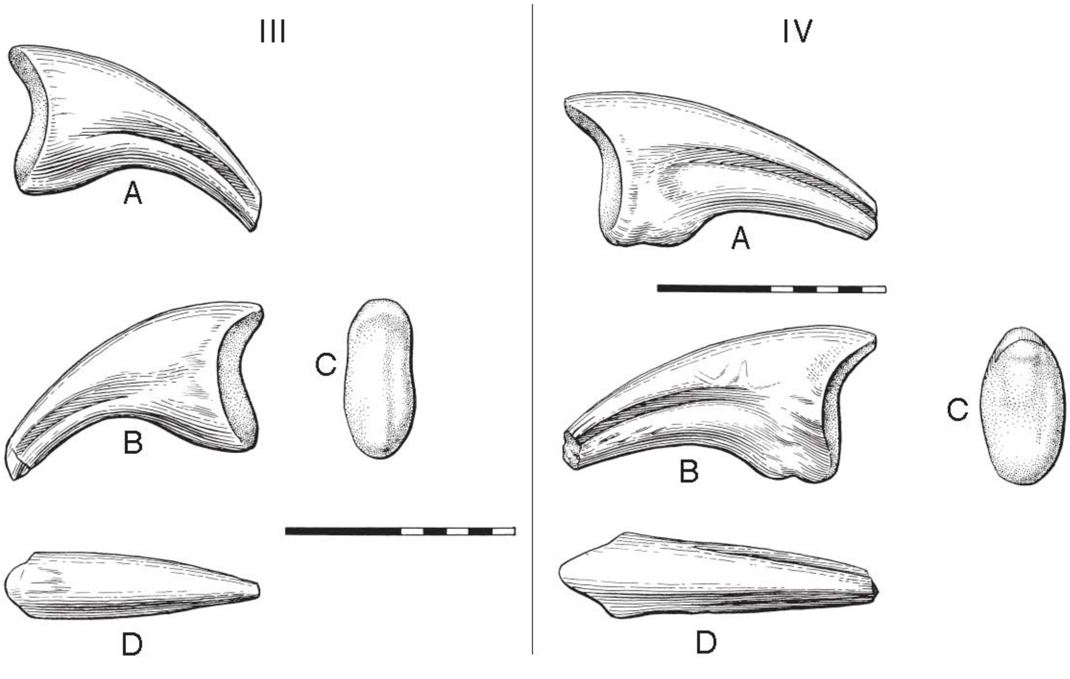


Figure 33. Right pedal unguals III and I of *Bambiraptor feinbergi* in lateral (A),

medial (B), proximal (C), and dorsal (D) views. Scale bar in mm.

TABLE 4. Measurements of appendicular skeletal elements of the holotype, *Bambiraptor feinbergi*.

FORELIMB	LEFT	RIGHT
Humerus	105*	100
Ulna	95	93
Radius	8585	
MANUS	LEFT	RIGHT
Metacarpal I	16.8	16.8
M-I-1	32.5	32.3
M-I-2 ungual	31+	20+
Metacarpal II	47.8	46.5
M-II-1	21.1	21.4
M-II-2	35	35
M-II-3 ungual	—	43
Metacarpal III	44.9	43.8
M-III-1	15.5	16.5
M-III-2	6.3	5.5
M-III-3	23.5	18+
M-III-4 ungual	—	—

PELVIS	LEFT	RIGHT
Ilium	86	78†
Ischium	53	50
Pubis	103	103
HINDLIMB	LEFT	RIGHT
Femur	118	118
Tibia	167	170
Fibula	170†	—
PES	LEFT	RIGHT
Metatarsal I	18.3	11+
P-I-1	—	12.1
Claw	10.6†	14.0
Metatarsal II	70	67.5
P- II-1	14.3	14.0
P- II-2	14.6	14.2
Ungual	46.0	tip only
Metatarsal III	77	81
P-III-1	29.6	27.8
P-III-2	17.6	15.4
P-III-3	—	16.9
Claw	—	24

Metatarsal IV	70	74
P-IV-1	23.6	23.4
P-IV-2	16.6	17.8
P-IV-3	11.6	12.3
P-IV-4	12.3	12.9
Claw	—	22
Metatarsal V	43+	33.2

*Maximum lengths are in millimeters unless otherwise noted. All measurements of phalanges are “inter-condyle” lengths. †Approximate measurement; e.g., distal tip of P-I ungual; distal end of mt V. The right manus is missing M-II claw and M-III claw; the left manus is missing M-III claw. The left pes is missing the following bones: P-I-1, P-III-3, P-III ungual, P-IV ungual; the right pes is missing the proximal portion of the sickle claw P-II-3.

Figure 34. Life restoration of *Bambiraptor feinbergi* in Two Medicine Formation time scenario.

Discussion

In *Bambiraptor,* the enlarged cerebellum suggests agility and higher intelligence than its contemporaries had (Jerison, 1973; Bock, 1985). Large optic lobes, combined with possibly overlapping fields of vision, probably indicate good vision (Allman, 1999), although the small olfactory bulbs suggest its sense of smell was less acute than in tyrannosaurids, *Troodon,* and other theropods. The relatively large brain, overlapping fields of vision, small size, and elongate front limbs might indicate that *Bambiraptor* was arboreal. The complex environment encountered by a tree-dwelling animal may account for the evolution of a large brain (Bock, 1985). An alternative hypothesis is that brain size increased because it was hunting complex prey items (Radinsky, 1974). This may have included lizards and mammals, which have been found in the gut region of *Sinosauropteryx* (Chen et al. 1998). Giffin (1990) also shows that *Coelurus* (3.04), *Deinonychus* (2.63), and *Allosaurus* (2.66) all had large SQs (high neural supply), implying manipulative ability. These values are higher than those of even modern birds that are active fliers (for example the SQ of mallard ducks is 2.33). In the shoulder girdle, the glenoid is oriented laterally, which is similar to the conditions in some other non-avian maniraptorans (including *Unenlagia* and *Deinonychus*) and *Archaeopteryx.* It allowed the long arms a range of motion that was only restricted anteriorly. The scapula has an acromion that projects forward and medially, serving as the primary platform for the attachment of the furcula. The sternal plates are much longer than the coracoids, and form a large, flat ventral surface for the attachment of the pectoral musculature. Each has facets for five pairs of sternal ribs. The humerus moves through a limited range of anterior motion and a wider range of dorsal-ventral movement. It can be folded back against the body, but cannot be brought forward much beyond a vertical plane passing through the glenoid. Furthermore, throughout its range of motion, the deltopectoral crest of the humerus is positioned anterodorsal to the glenoid. The pectoral girdle of *Bambiraptor* does have a sizable origin for the M. supracoracoideus. The humerus has the appropriate posture to allow the range of motion (flexure and longitudinal rotation) found in the flight stroke of modern birds and a potential insertion for the M. supracoracoideus.

In the manus, it is clear that the second and third digits worked in concert most of the time as a functional unit. If they had been separate, the weak construction of digit III would have made it vulnerable to breakage. Not only is the third digit constructed of slender phalanges, but the articular surfaces also forced the digit to fold against the middle digit. When the manus is considered as an operating unit, the first digit is the most robust and has the largest claw, but it was probably not capable of opposing the other fingers.

Bambiraptor is well adapted to a cursorial existence. This is indicated by the similarity in hindlimb proportions between *Bambiraptor* and modern running birds (Coombs, 1978).

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CHAPTER 3

A REVIEW OF THE EARLY CRETACEOUS JEHOL GROUP IN NORTHEASTERN CHINA AND A REVISION CONCERNING THE ORIGIN OF FLIGHT PARADIGM

Chapter Summary

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.

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.

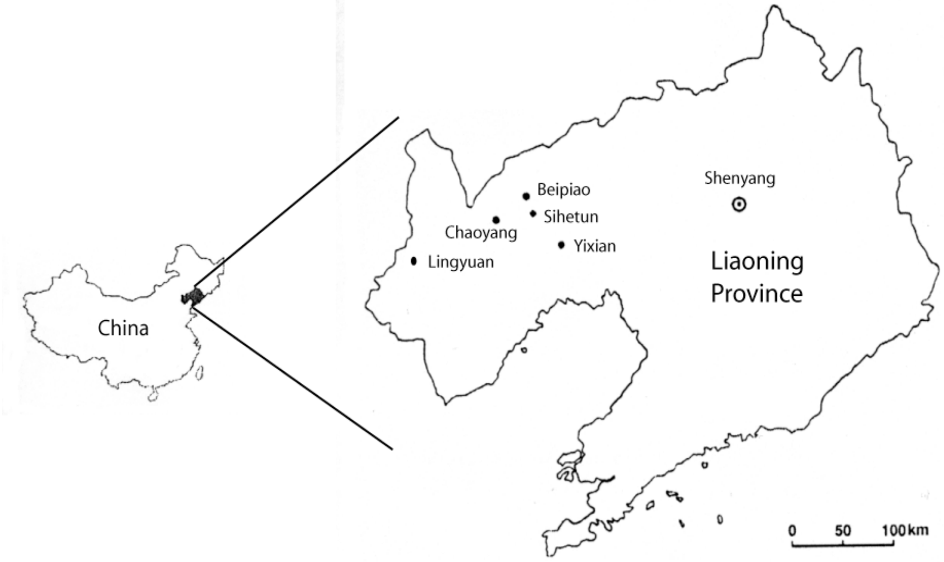

Figure 35. Study area showing fossil localities from the Jehol Group in western Liaoning Province, China (after Hwang et al. 2002).

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 volcaniclastic 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. 35) 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 diagenesis (Davis and 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, volcanigenic 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 volcaniclastics, 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 volcaniclastic sediments after the displacement of the Tancheng-Lujiang fault (Chen, 1992).

The study area (fig. 36), a series of northeast basins, 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 monoclinal and dip to the southeast.

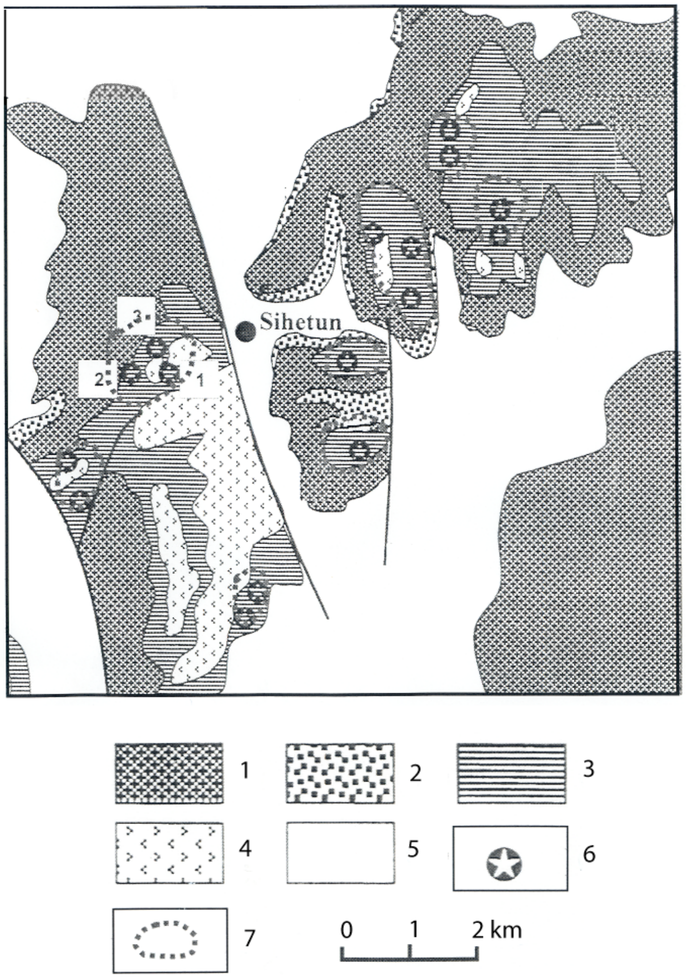

Figure 36. Geologic map of Sihuten area (from Wang et al., 2000; Chang et al., 2003); Dotted lines represent possible maars (Chu, G. 2005 pers. comm.). 1. basalt and andesite (lava); 2. Conglomerate and volcanic breccia; 3. Shale and

tuff; 4. Subvolcanic rock; 5. Tuccongzi Formation; 6. Fossils localities; 7. Maar outline.

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 at 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. 37). But the Jehol Group has been defined poorly and some authors have placed additional formations into the group, both above and below the Yixian 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. 37).

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. 37) (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. 37).

The lower portion of the Jehol Group, the Yixian Formation, consists of four basaltic units [lava] and four sedimentary units (fig. 37). 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. 37).

The Sihuten locality, south of Beipao City, is the type section (figs. 36, 37, 39) 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 Shangeheshou 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. 36, 37, 38) (Chang et al., 2003).

The Lujiatun Beds (I in fig. 37—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 uncomformably Jurassic fluvial deposits dated at 139.4 Ma and underly 128.4 Ma beds (Chang et al., 2003).

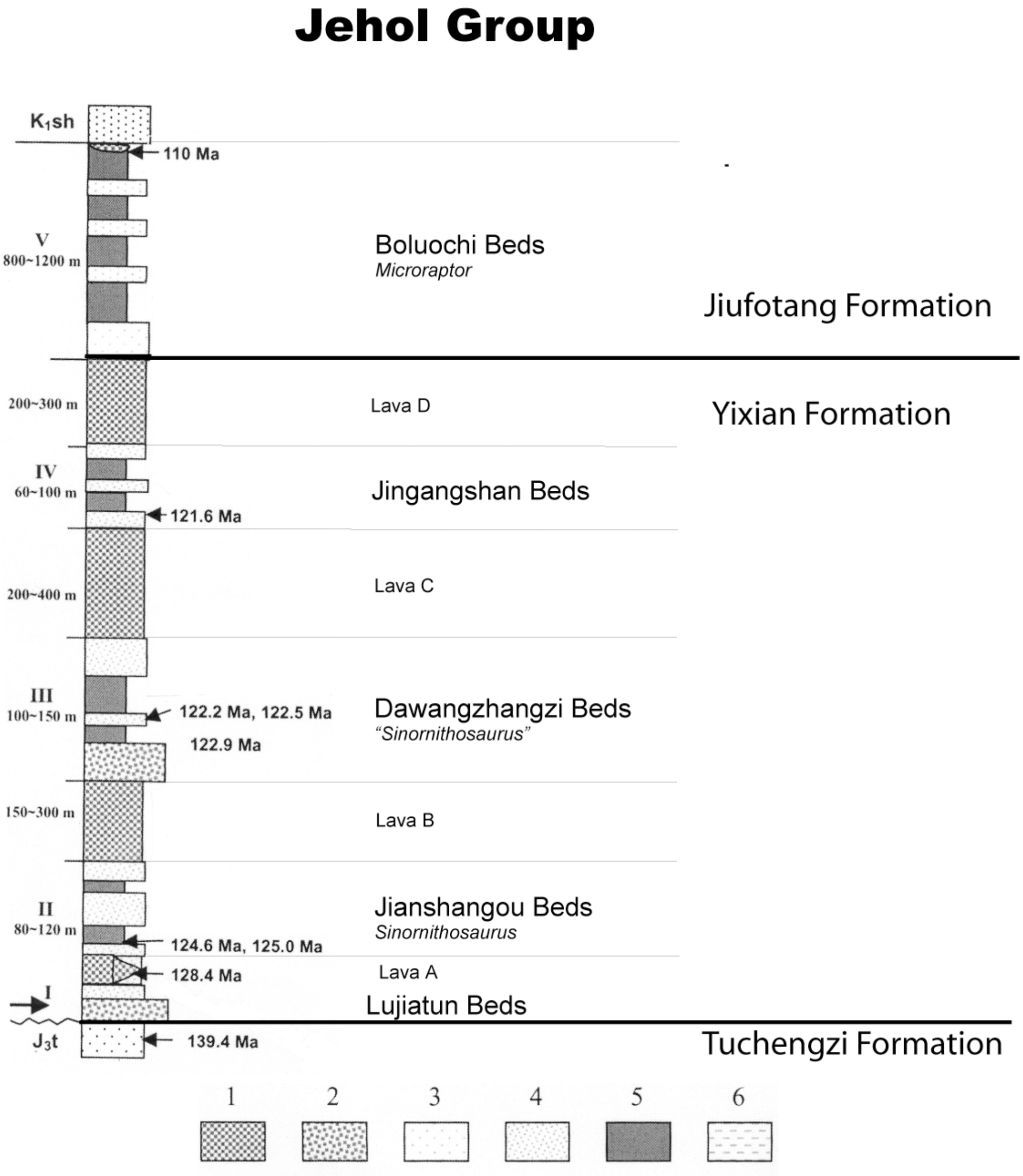

Figure 37. Stratigraphic column of the Jehol Group (modified from Chang et al., 2003). Fossil taxa occurrences are indicated between the lavas A, B, C, D.

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

It is unclear whether the Lujiatun Beds of the Yixian can be correlated to the Daohugou Beds in Inner Mongolia. The Daohuguo 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, *Epidendrosaurus* (Zhang et al., 2002) and Pedopenna (Xu and Zhang, 2005). The Daohuguo Beds overly an ignimbrite with a ^{40}Ar /^{39}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. 37) 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 *Archaefructus* (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.

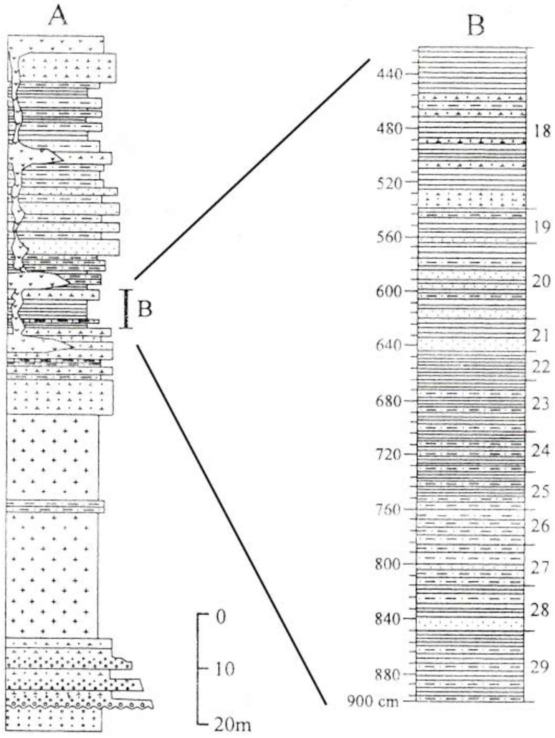

Figure 38. The composite stratigraphic section A and the excavating profile B of the lower Yixian Formation in Sihuten and neighboring area, western Liaoning (from Wang et al., 1998).

At the locality of Sihuten Village, Beipiao City, Wang et al. (1998) numbered 37 quarry layers (fig. 38) in an excavation of the lower part of the Jianshangou Bed

(II in fig. 37) of the Yixian Formation (fig. 37). 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. 39) also found in the excavation profile of the Sihuten 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 al., 2003). An intermediate to basic sub-volcanic dike intrudes bed 6 at the Sihuten 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).

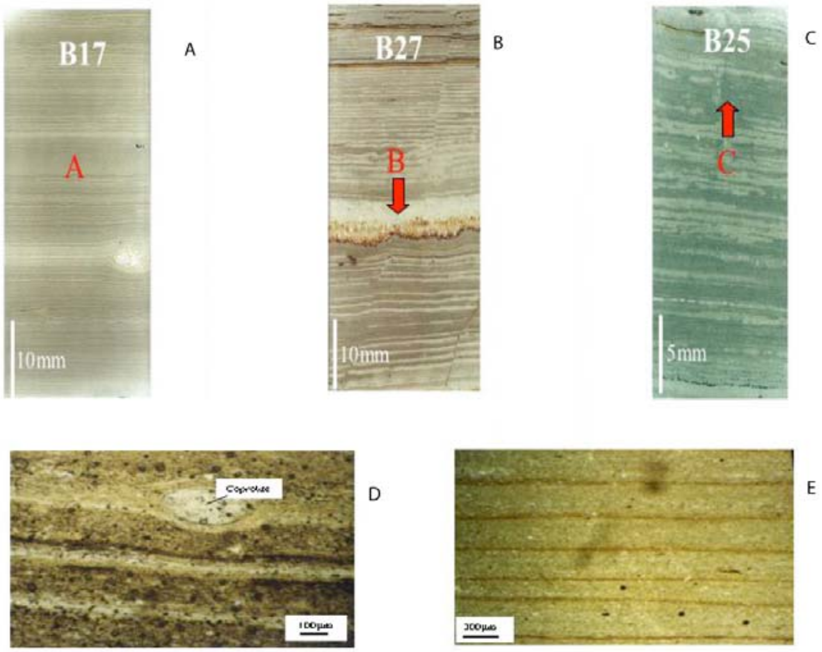

Figure 39. Varves from Sihuten area excavating profile in lower Yixian Formation. (A), coprolite; (B), ash layer; (C), burrow; (D), coprolite; (E), clastic varves. (from Chu, G. 2005 pers. comm.)

The Dawangzhangzi Beds (III in fig. 37) 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. 37**).** The black and gray sandstone, mudstone, and shale are rich in tuff.

The fish *Lycoptera muroii* is the only abundant component of the vertebrate fauna, although birds and pterosaurs are known (Chang et al., 2003).

The Buluochi Beds (V of fig. 37) 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}Ar/^{39}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. 37). 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. 40). 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 be 18 to 38 km, and the volume of fallout ash covered 200 to 320 km^3 (Guo et al., 2003). The distribution area was approximately 5 by 14 km (Chu, G. pers. comm., 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 Sihuten. The pillow lava indicates the volcanic activity was not exclusively subaerial. Guo et al. (2003) suggested alternatively that the Sihuten 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 Sihuten 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. 36). 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^2 to 10 km^2 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 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), asphyxsiation 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. 39**)**. 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 and hydrogen flouride caused deleterious effects on the environment and climate resulting in mass mortalities found in the other layers.

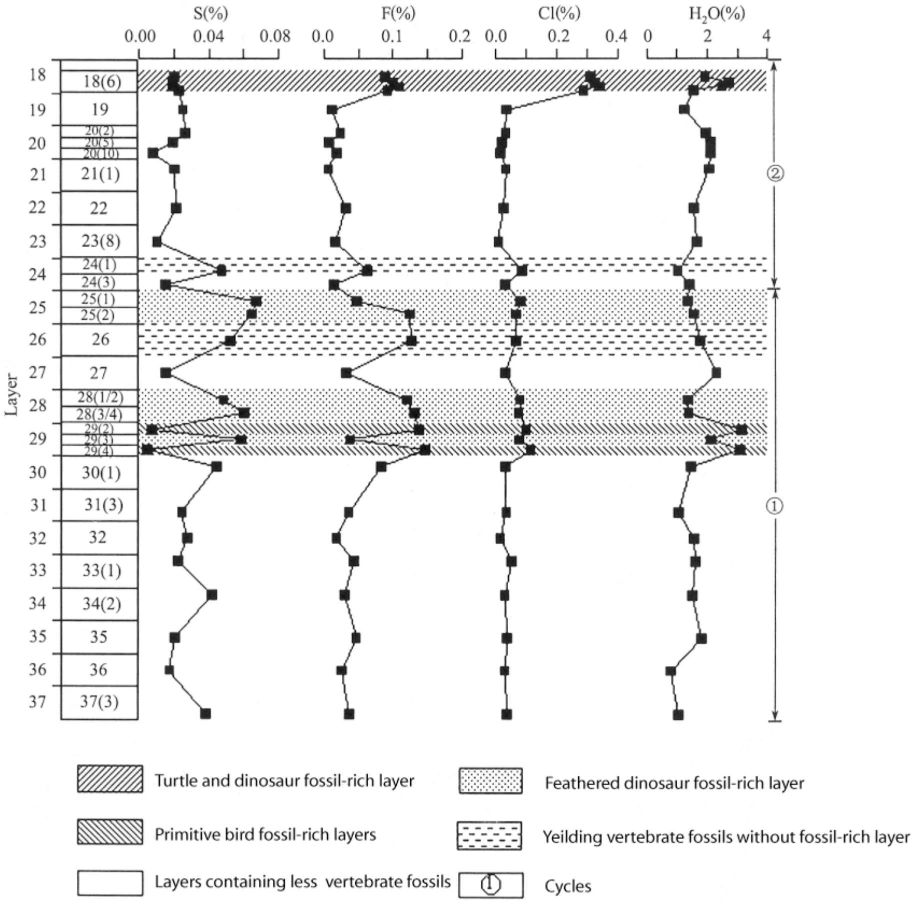

Figure 40. Graph of concentration of volatiles emitted with fossil layers in Sihuten excavating profile (from Guo et al., 2003).

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 C° (Rampino and Ambrose 2000). Such loading of the atmosphere caused a global volcanic winter with more severe local affects 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 Sihuten 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. Secondarily, 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 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 and Briggs, 1991). A low degree of decay prior to 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 petrifaction and permineralization of hard parts (Lucas and 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 and 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 and 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 and 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. 41a, 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 with the *trees down* concept involving an arboreal lifestyle. Nopsca (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 and Chiappe, 1999).

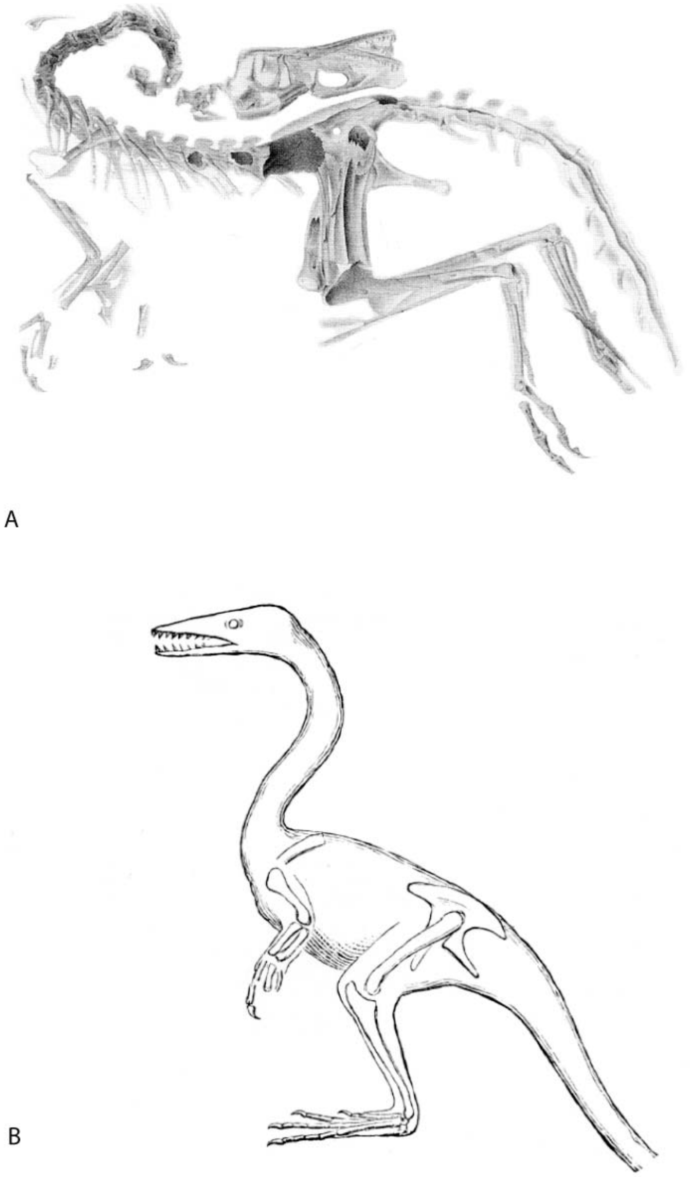

Figure 41. *Compsognathus longipes* (A), fossil skeleton (from Wagner, 1861); (B), birdlike life restoration (from Marsh, 1895).

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

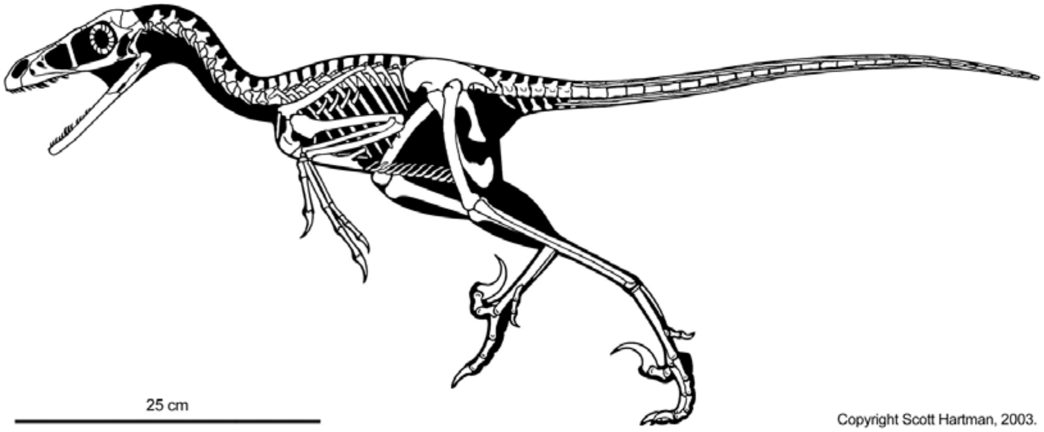

Figure 42. *Bambiraptor feinbergi* reconstructed skeleton (from S. Hartman, 2003).

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. 43) 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 and 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 and Zhou, 2004).

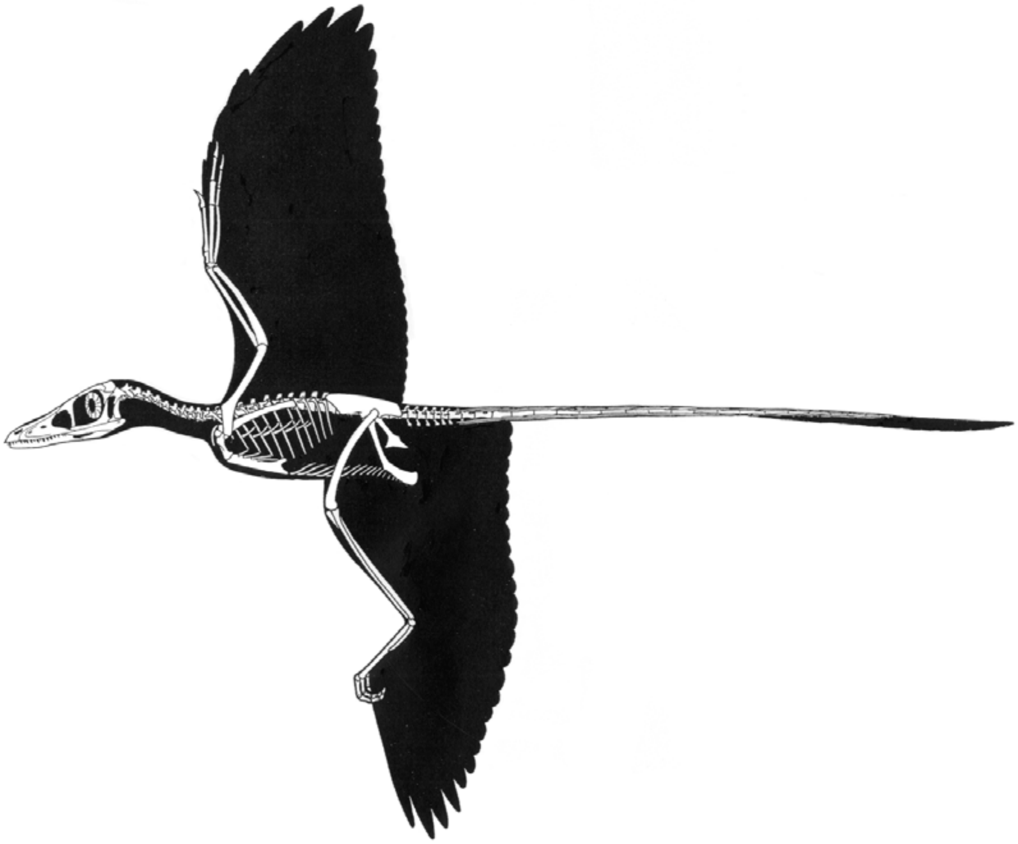

Figure 43. Skeletal reconstruction with wings and body outline of a generalized Jehol microraptorian (courtesy G. Paul, 2005).

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 containing *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 specious, 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 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 prescacral vertebrae have pleurocoels (Burnham, 2004). The rib cage, outlined by the sternum and gastralia on articulated skeletons, is deepest at the 6th or 7th 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 Microraptoria.

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, pers/ comm.., 2005). In *Bambiraptor feinbergi*, the ankle joint is a simple, horizontal hinge (fig. 42).

Metatarsal I's distal displacement is present in *Archaeopteryx* and *Microraptor* and does not occur in an articulated foot of *Velociraptor* (Norell and 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.

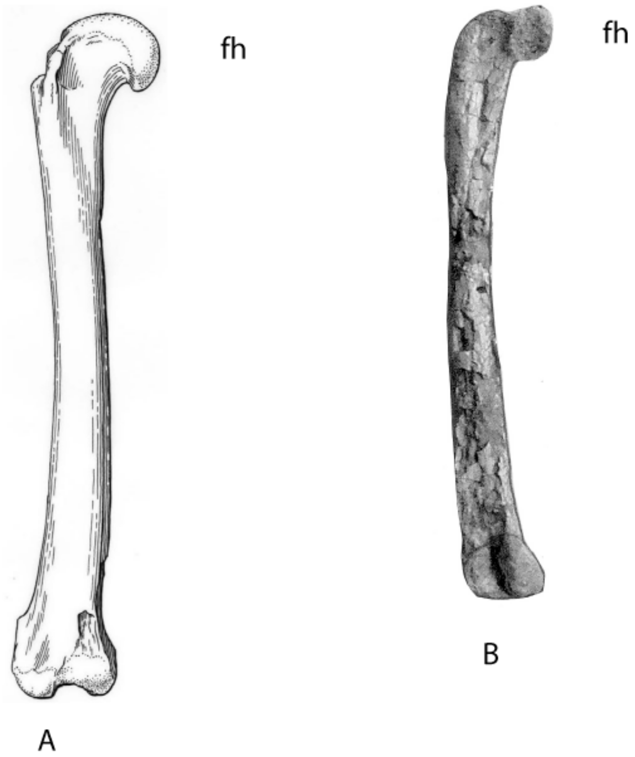

Fig 44. Anterior view of right femora of (A), adult *Bambiraptor* FIP 007; (B), *Microraptor* sp. IVPP V 126662 (fh, femoral head; bones not to scale for comparison).

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 Hellmann's 1926 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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CHAPTER 4

ARCHAEOPTERYX – A RE-EVALUATION SUGGESTING AN ARBOREAL HABITAT AND AN INTERMEDIATE STAGE IN *TREES DOWN* ORIGIN OF FLIGHT

Chapter Summary

The fossil-Lagerstätte of the Upper Jurassic Solnhofen Formation contains the earliest known specimens of *Archaeopteryx*. The paleoecology that was indigenous for these archaeopterygian birds is not well known. The marine Solnhofen Formation also included other such terrestrial fliers as pterosaurs and insects. These volant (i.e., able to fly) taxa along with continental plant material were likely blown over the marine waters by storms some distance from their natural habitat. Paleobotany, paleogeography, and paleoclimate reconstructions of the Late Jurassic indicate that these terrestrial organisms could only have originated from nearby landmasses with freshwater that supported open forests of conifers and other gymnosperms. This habitat was ideal for the skeletal adaptations seen in *Archaeopteryx* in which its climbing ability far outweighed its putative cursorial attributes. Moreover, these archaeopterygian birds were constructed primitively compared to flapping flight mechanisms of recent birds, further suggesting arboreal features in archaeopterygian

birds were indicative of their lifestyle. With a primitive wing beat, *Archaeopteryx* represents an intermediate form between gliders and flapping fliers.

Introduction

This paper re-evaluates the paleoecology of the Upper Jurassic Solnhofen Formation, the functional morphology of *Archaeopteryx*. It also proposes an ecomorphic hypothesis consistent with a *trees down* origin of flight. The origin of flight has been fraught with opposing arguments for over a century. Flight either evolved from the *trees down*, with protobirds being powered by gravity, or from the *ground up*, whereby they launched into the air using their own muscular power. Both arguments were stimulated by two nearly simultaneous discoveries in the Solnhofen Formation – a feathered bird, *Archaeopteryx* and a small, bipedal dinosaur, *Compsognathus*. *Archaeopteryx* is the oldest known fossil bird fossilized with clear impressions of modern feathers (fig. 45). The focus on origin of flight includes *Archaeopteryx* because some of specimens have articulated wings with aerodynamically constructed feathers (Feduccia and Tordoff, 1979; Griffiths, 1996) as well as asymmetrically feathered hindlimbs (Longrich, 2006).

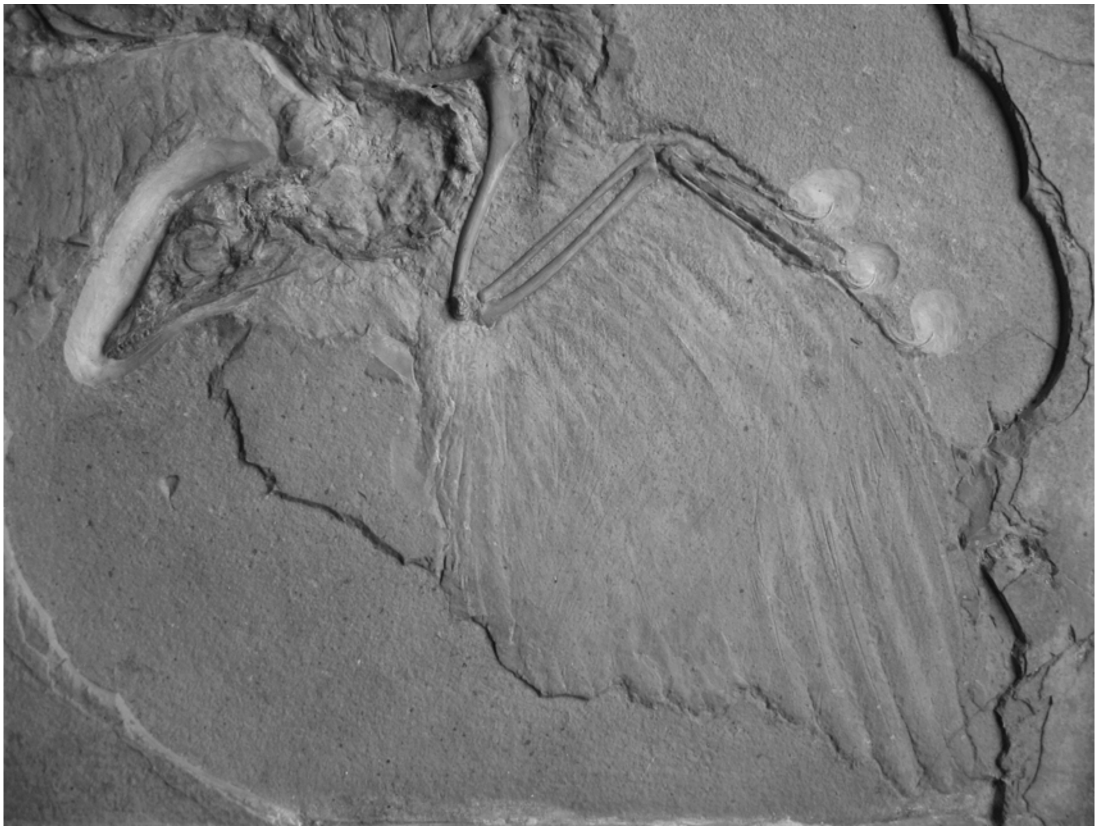

Figure 45. Main slab of the Berlin exemplar of *Archaeopteryx* showing feather impressions in articulation forming a wing (dorsal view of left forelimb).

In light of new discoveries of such four-winged gliders in China as *Microraptor* (fig. 46) with feathered hind wings (Xu et al., 2003), *Archaeopteryx* must be re-evaluated in order to understand how flight may have evolved in this context.

Figure 46. *Microraptor gui* – IVPP V 13352 (holotype – photo permission of X. Xing) showing hindlimb feathers; length of entire animal is approximately 77 cm (Xu et al., 2003).

Hypotheses concerning the origin of flight have been framed within multiple contexts, including the paleoecology of the Solnhofen Formation (Viohl, 1985; Chiappe, 1997; Yalden, 1997; Chatterjee and Templin, 2003) and functional morphology (Martin, 1991; Jenkins,1993). This report refutes previously held notions that *Archaeopteryx* evolved within a habitat of scrubby trees (Viohl, 1984; Barthel et al. 1990; Chiappe, 1997). A forest with a tall, coniferous canopy was probably the habitat for *Archaeopteryx* as for other continental organisms found in the Solnhofen Formation. This study also refutes ground-up flight for *Archaeopteryx* (Ostrom, 1974;

Padian and Chiappe, 1998; Burgers and Chiappe, 1999; Mayr et al., 2006). Archaeopterygian birds almost certainly took flight from the trees down.

Historical context

The perception that the Solnhofen Lagerstätte represents a specific area is partially a historical artifact. Many of the century-old fossil collections lack specific provenance other than simply 'Solnhofen'. In actuality, the fossils are from different outcrops and may be of slightly different ages (see Schweigert, 2007). The term, "Solnhofen fossil", thus, may denote any specimen from the Upper Jurassic limestones of Southern Bavaria, Germany (Kemp, 2001). For the purpose of this study, it is less problematic since the species of organisms in question probably spanned the age of the Solnhofen Formation (Kemp, 2001).

Long-term quarrying in the Solnhofen Formation provided a collection of well-preserved fossils of marine and continental flora and fauna. Many of the specimens show excellent preservation forming a *Konservat-Lagerstätte* (Barthel et al., 1990; Selden and Nudds, 2004).

Solnhofen quarries remain valued sources for building stones, tiles, and sculpture media, whereas some of the finer-grained stones were used as lithographic plates (Barthel et al., 1990; Selden and Nudds, 2004; Koch, 2005). This process is still in use although limited to more esoteric endeavors by artisans using the lithographic presses invented over a century ago. Scientific and commercial quarrying continues to produce significant discoveries. New specimens include another

Archaeopteryx, represented by the Thermopolis exemplar (Mayr et al., 2006, 2007), and a compsognathid dinosaur with scales, described as *Juravenator* (Göhlich and Chiappe, 2006; Göhlich et al., 2006).

Geological context

The Solnhofen Formation is the source of the Solnhofen Lithographic Limestones (Solnhofener Plattenkalke) and was deposited during the latest Kimmeridgian to the Tithonian (Röper, 2005). The area is known as the White Jurassic (Weißer Jura) of Southern Germany, and the name reflects the purity of these marine limestones (Barthel et al. 1990). The Solnhofen Formation is up to 150 m thick, and bedding ranges from paper-thin up to 30 cm thick. The Mörnsheim Formation (Tithonian) overlies the Solnhofen Formation and also includes fossils and localities referred to as Solnhofen Limestone (Kemp, 2001). The Solnhofen Formation is underlain by the Rögling Formation or other coeval formations of late Kimmeridgian age, and also contains specimens referred to as Solnhofen (fig. 47).

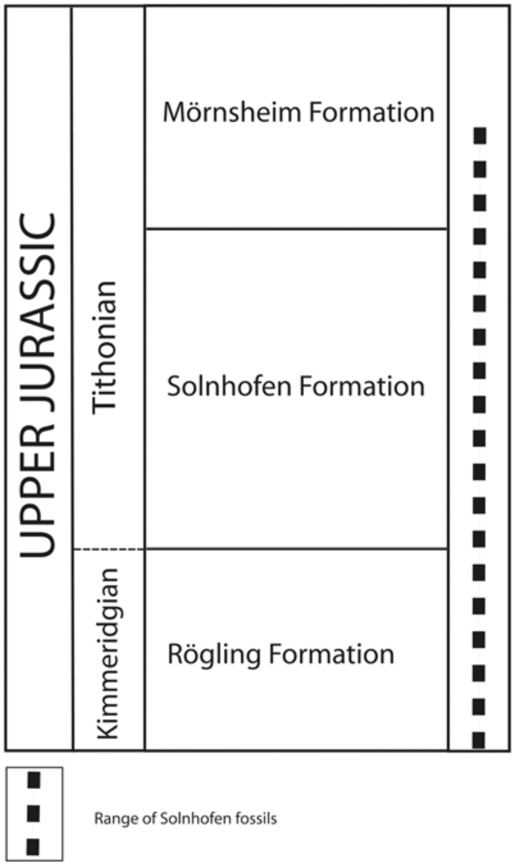

Figure 47. Upper Jurassic Solnhofen Formation of Bavaria, Germany. Dashed line indicates range of fossils historically referred to as Solnhofen.

Solnhofen Formation outcrops are discontinuous, scattered, and limited in extent to an area of approximately 80-100 km by 25-30 km (Viohl, 1998; Röper, 2005). This area includes quarries located near the villages of Solnhofen and the town of Eichstätt in the west of Southern Germany to the vicinity of Regensburg in eastern Bavaria (fig. 48). The region is elevated and rests on an ancient carbonate platform termed the Southern Franconian Alb.

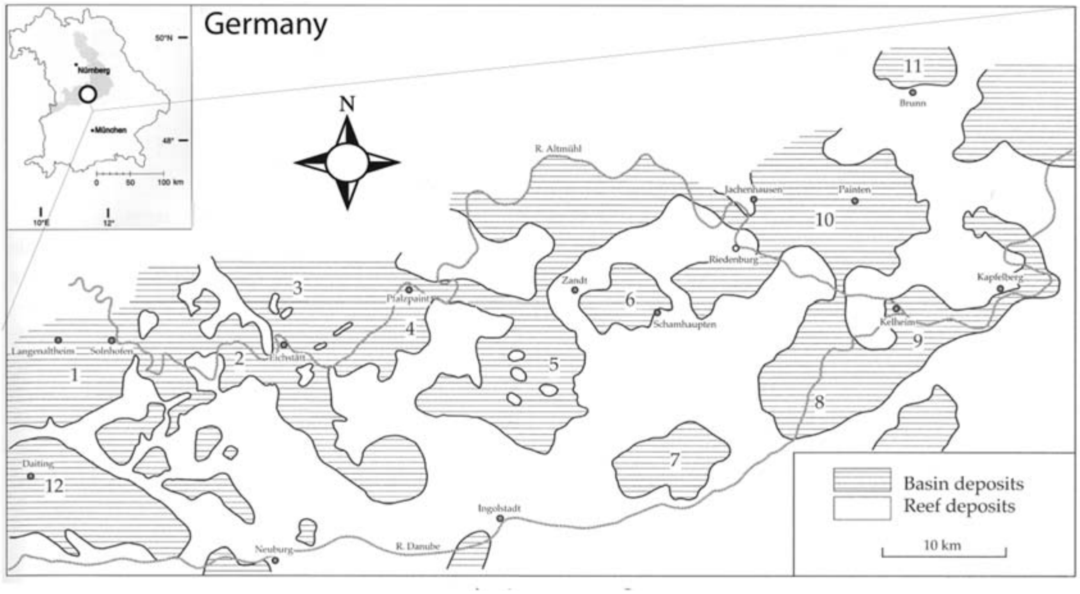

Figure 48. Solnhofen basins and reefs in Bavaria, Germany. The ages of the basins range from late Kimmeridgian (Rögling Formation and time equivalents: Painten, Brunn, Schamhaupten) to early Tithonian (Solnhofen Formation and time equivalents: Solnhofen, Eichstätt, Zandt, Pfalzpaint, Langenaltheim, Hienheim; Mörnsheim Formation: Mörnsheim, Daiting) (modified from Meyer and Schmidt-Kaler, 1989; Röper and Roth, 1998; Selden and Nudds, 2004; inset after Link and Fürsich, 2001).

The Solnhofen Formation resulted from carbonate deposition in an epicontinental sea during the late Jurassic. These deposits overlie biogenic mounds formed mostly by sponges. The topography of the seafloor was interspersed with small depressions or basins draping pre-existing biogenic mounds (Koch, 2005). Intercalated marls and limestones delineate the bottom of these basins today. Exact ages have not been determined for each of the basins (Renesto and Viohl, 1997), but they likely span the late Kimmeridgian to late early Tithonian (Kemp, 2001; Röper, 2005; Schweigert, 2007).

Landmasses referred to as the London Brabant Massif and the Rhenish Massif bordered the Solnhofen basins to the north, and the Bohemian Massif was the landmass to the east (Koch and Weiss, 2005; fig. 1). The Solnhofen basins were separated by coral reefs that lay to the south and east, possibly blocking direct connection to the Tethys Sea. Detrital carbonates found in the Painten lagoon (the present-day Rygol Quarry) are interpreted as storm-induced microturbidites (Link and Fürsich, 2001). The Daiting locality may be nearer the coast, based on an accumulation of aquatic tetrapod taxa (Kemp, 2001). It is not known precisely how close the large landmasses were to these basins (Kemp, 2001). Röper (2005) and others (e.g., Viohl, 1997; Göhlich and Chiappe, 2006) speculate that the Solnhofen Formation represents a Jurassic archipelago that included nearby small islands; however, there are no geologic remnants or direct evidence for any islands. Wings (2000) described a hardground within the upper 5 m of the Solnhofen Formation that contained various *in situ* benthic organisms, including oriented, sessile bivalves and crinoids, cropping out near Langenaltheim.

Paleontology

The Solnhofen Formation includes excellent preservation of many terrestrial and aquatic organisms (e.g., Barthel et al. 1990; Frickhinger 1994, 1999; Viohl, 1998;

Selden and Nudds, 2004; Röper, 2006). It is also the first known deposit where fossil birds and pterosaurs are found together. Fish, crustaceans, cephalopods, and planktic crinoids (*Saccocoma*) are the most abundant macrofossils in the Solnhofen Formation. Nannofossils are also abundant and include coccoliths (Keupp, 1977a). Coccoid spheres interpreted as cyanobacteria are found in the strata and may have formed mats (Keupp, 1977b) covering carcasses, tracks, and trails, as well as acting as a binding agent in the carbonate ooze (Barthel et al. 1990). These mats may be partially responsible for the excellent fossil preservation of the biota (Wilby et al 1996).

The birds, pterosaurs, and insects comprise a major continental component (Viohl, 1985; Barthel et al. 1990). Such nearshore terrestrial vertebrates as lizards, turtles, crocodilians, and dinosaurs are rarely found in the Solnhofen Formation. Faunal and floral elements of terrestrial and freshwater environments must have been transported into the marine environment. Although the Solnhofen Formation has been considered a *Konservat-Lagerstätte* for some time, fossils are actually rare and their excellent preservation has attracted more attention than their contextual information. The excellent state of fossil preservation is due to such lithologic parameters as low porosity, extremely low permeability, pore radii, and inner surface area (Koch, 2005, 2007). Anoxic bottom waters of the basins (Barthel et al. 1990; Viohl, 1998) and cyanobacterial mats blanketing the remains (Barthel et al. 1990; Wilby et al. 1996; Röper, 2005) may have reduced significantly the decaying processes acting on the dead organisms.

The term *Konservat-Lagerstätten* implies preservation of an ecosystem (Shields, 1998) and such is the case in the Solnhofen Formation. Important paleoecological indicators are the plants and insects. Plant fossils are preserved by compression, carbonization, and permineralization (Barthel et al. 1990). The terrestrial flora consists of leaves, cones, scales, seeds, and branches of conifers (*Araucaria, Athrotaxites, Brachyphyllum, Palaeocyparis, Hirmeriella, Cupressinocladus*), gingkophytic trees (*Ginkgo, Furcifolium*), seed ferns (*Cycadopteris*), and Bennettitales (*Sewardia, Bucklandia, Zamites, Sphenozamites, Podozamites*) (Jung, 1995; Viohl, 1998). Some of the specimens must be regarded as form genera, especially *Brachyphyllum* (Taylor and Taylor, 1993). The insects are usually complete and are represented by 12 orders and more than 50 genera (Barthel et al.1990; Frickhinger ,1994; Grimaldi and Engel, 2005). Classification to the species level for many insects is often obscured by lack of fine details preserved.

Insect Paleoecology

The list of fossil insects reported by Barthel et al. (1990) indicates that they originated from a forest community tied to a nearby freshwater source necessary for their lifecycles (Viohl, 1985; Barthel et al. 1990). Additionally, an interesting component of the insect fauna includes large sawflies (or wood wasps). In female sawflies the genitalia or ovipositor includes a sawlike organ from which the animals get their common name. As a consequence of this egg-laying behavior and due to the necessity of boring through bark, the females have a long, needle-like ovipositor so their fossils are readily recognized. The presence of large sawflies implies evidence of trees. Since the Solnhofen sawflies were fairly large, they probably utilized large fallen logs, based on the size and behavior of modern sawflies. The only source of large logs would have been a forested habitat.

Pterosaurs

The first pterosaur fossil was found in the Solnhofen Plattenkalk in 1784 (Wellnhofer,, 1991) and was mistakenly considered an aquatic animal because it was found together with marine organisms (Watson, 1973; Veldmeijer, 2000). Pterosaurs continue to be one of the most significant aspects of the Solnhofen fauna, where they are clearly more abundant than birds (Wellnhofer, 1970; Kellner, 1994; Bennett, 1995; Kellner and Campos, 2000; Chatterjee and Templin 2004). The large number of pterosaurs implies they occupied nearshore marine habitats compared to birds or insects that are not marine. It is also likely, however, that some pterosaur species lived in fully continental settings. For example, *Rhamphorhynchus* specimens or discoveries are biased towards a juvenile population and may have been blown in from inland areas by seasonal storms (Bennett, 1995). Smaller pterosaur taxa including rhamphorhynchoids show arboreal features, with claws adapted for tree climbing (Bennett, 1997). Furthermore, Chatterjee and Templin (2004) have postulated that small pterosaurs probably travelled out to sea no further than 5 or 10 km.

Paleoecology

Arguments supporting dwarf trees and a more or less barren habitat for *Archaeopteryx* result, in part, from a paleobiological framework using a terrestrial fossil record found in marine rock units (Jung, 1974; Viohl ,1985; Chiappe, 1997). The reconstruction of short trees in open areas for the Solnhofen Formation was based on a poorly known fossil flora, hampered further by the lack of complete specimens. For instance, *Brachyphyllum* material from the Solnhofen Formation includes the tips of branches with helically arranged leaves. These branches were assumed to represent xeromorphic conifers only 3 m tall (Jung, 1974; Barthel et al. 1990; Chiappe, 1997). This interpretation, however, can be re-evaluated based on several factors. Although *Brachyphyllum* belongs to the Cheirolepidiaceae, a large Mesozoic family of succulent-like conifers, it was not necessarily a small tree. The reconstruction by Jung (1974) assumed the morphology of the trunk was cactus-like and could not support a tall structure. Recent discoveries of complete Cheirolepidiaceae have now shown these conifers actually had a woody stem or trunk and were capable of growing 20 m tall (Axsmith and Jacobs 2005). Furthermore, the leafy twigs of *Brachyphyllum* have been found with reproductive organs believed to be araucarian (Kendall, 1949), suggesting there were at least two species of these conifers.

Another assumption used to support a lack of trees near the shoreline was the absence of fossil logs (Viohl, 1985). There were no rivers, however, to transport logs to the open sea, as evidenced by lack of fluvial deposits (Viohl, 1985; Barthel et al. 1990). Any large logs that had fallen into the nearshore environment would have become waterlogged and remained nearshore. The lack of logs in the Solnhofen deposits reflects the depositional environment, not the paleoecology. Logs are more rarely found in the marine fossil record and finding them in restricted marine deposits devoid of fluvial sediments would not be expected, even if the surrounding land were forested (e.g., Benton, 1993; Boggs, 2006).

Plant fossils from Solnhofen Formation have been interpreted as originating in a semiarid, occasionally wet, forested environment (Viohl, 1985; Barthel et al. 1990), which included conifers (Frickhinger, 1994, 1999; Jung, 1995; Renesto and Viohl, 1997). Conifers comprise many taxa with tall trees; some modern araucarians grow up to 60 m tall (Taylor and Taylor, 1993). Araucariaceae had a cosmopolitan distribution throughout the Jurassic (Harris, 1979). Undoubtedly, conifers formed part of the vast structured forests covering the landmasses to the north and east of the Solnhofen basins similar to the Yorkshire Jurassic Flora.

Functional Inference from Taphonomical Evidence

Such *Konservat-Lagerstätte* deposits as the Solnhofen Formation are crucial for the study of taphonomy because the quality of preservation is usually coupled with high numbers of organisms. In many instances, these specimens have been photographed or illustrated and are prevalent in the literature due to their significance as well as their aesthetic quality.

Taphonomy of articulated vertebrate skeletons provides information regarding functional morphology (Walker, 1980). Since articulated skeletons infer that they were still held together by connective tissues before final burial, articulated skeletons closely reflect closely the life positions of bony elements. A certain death posture, therefore, implies the living animals' capability to position the limbs accordingly. The death posture closely reflects most ranges of motion allowed by its functional morphology (Weigelt, 1927, 1989; Kielan-Jaworowska and Hurum, 2006).

Certain groups of animals, in particular, appear to exhibit characteristic death poses. For instance, a hindlimb sprawling posture – hindlimbs outward and flexed at the knee – usually found in Mesozoic bird fossils including *Microraptor* from the Early Cretaceous of China (Xu et al. 2000, figs. 1-3; Hwang et al. 2002, fig. 3; Xu et al. 2003, fig. 1c), is also found in *Archaeopteryx* (Mayr et al. 2006, fig. 1; 2007, figs. 1-3). Weigelt (1927) terms this sprawling posture as the passive position. Notably, this pose is almost never found in dinosaurs, a group exemplified by upright posture (Dodson 1973). Articulated, fossilized remains of birds, pterosaurs, dinosaurs, mammals, reptiles, and amphibians show the hindlimb sprawl is not ubiquitous in all these groups (Kielan-Jaworowska and Hurum 2006). A significant number of occurrences of skeletons with sprawling postures are found in animals that, in life, are known to have the range of motion for sprawling locomotion. Other groups, especially dinosaurs and mammals, lack similar sprawling death poses since they were upright walkers, with a few exceptions like psittacosaurs and bats. This departure from classic dinosaurian pose in *Microraptor* may reflect a less derived condition for this group and further enhance *trees down* origin of flight in which a sprawling, arboreal ancestor is fundamental (Burnham, 2006b). Moreover, the sprawled example of *Archaeopteryx* greatly enhances the notion of an arboreal lifestyle for the first bird (fig. 49).

Archaeopteryx is now known from at least ten specimens that provides us with taphonomic information and locality data (fig. 50). There is a distinct bias as to locality, with the best-articulated specimens being found closer to the Eichstätt quarry (Davis, 1996). Intriguingly, the better-preserved insects and plant fossils are also found and not in other Solnhofen basins.

Solnhofen, however, may be considered a taphonomical wastebasket or pathway and there is no evidence to support the idea that *Archaeopteryx* was indigenous to the basinal areas (Kemp, 2001). In fact, most of the terrestrial fauna has been transported. Additionally, there are preservational biases. Quality of preservation and degree of articulation seems to improve near Eichstätt and Solnhofen localities. This indicates length of transport may be a factor whereby these basins may have been closer to the forested landmasses.

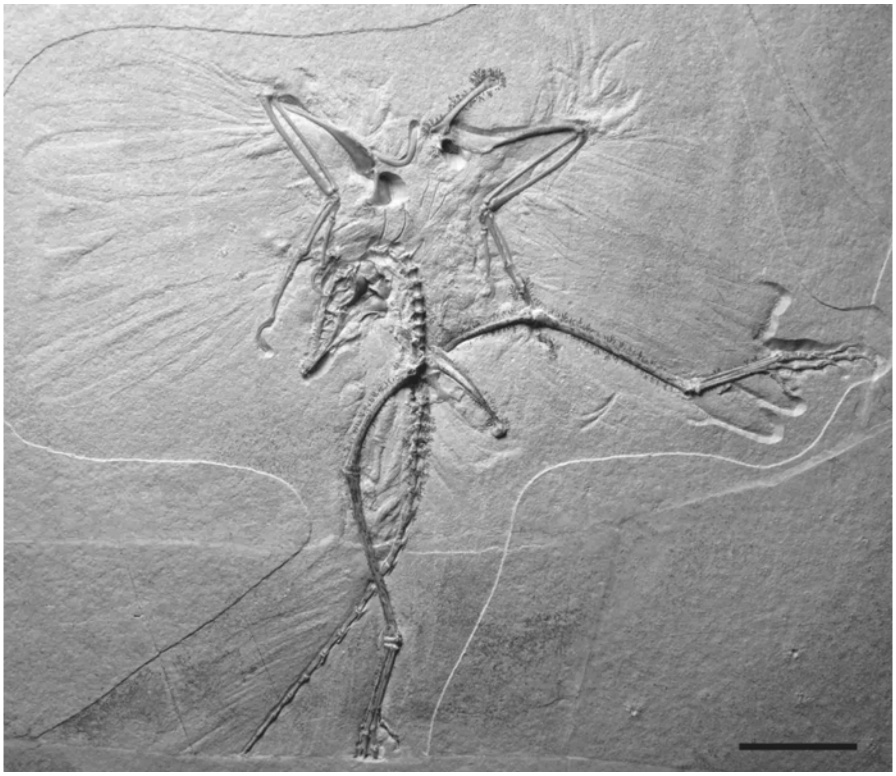

Figure 49. Photograph of Thermopolis *Archaeopteryx* (from Mayr et al., 2006; ©Gerald Mayr/Forschungsinstitut Senckenberg). The hindlimbs are sprawled with the femora nearly perpendicular to the hips.

These and other biases can be found in the avian and dinosaurian record (Davis, 1996), and are reflected in the pterosaur (Bennett, 1995, Wellnhofer, 1991) and insect faunas (Tischlinger, 2001).

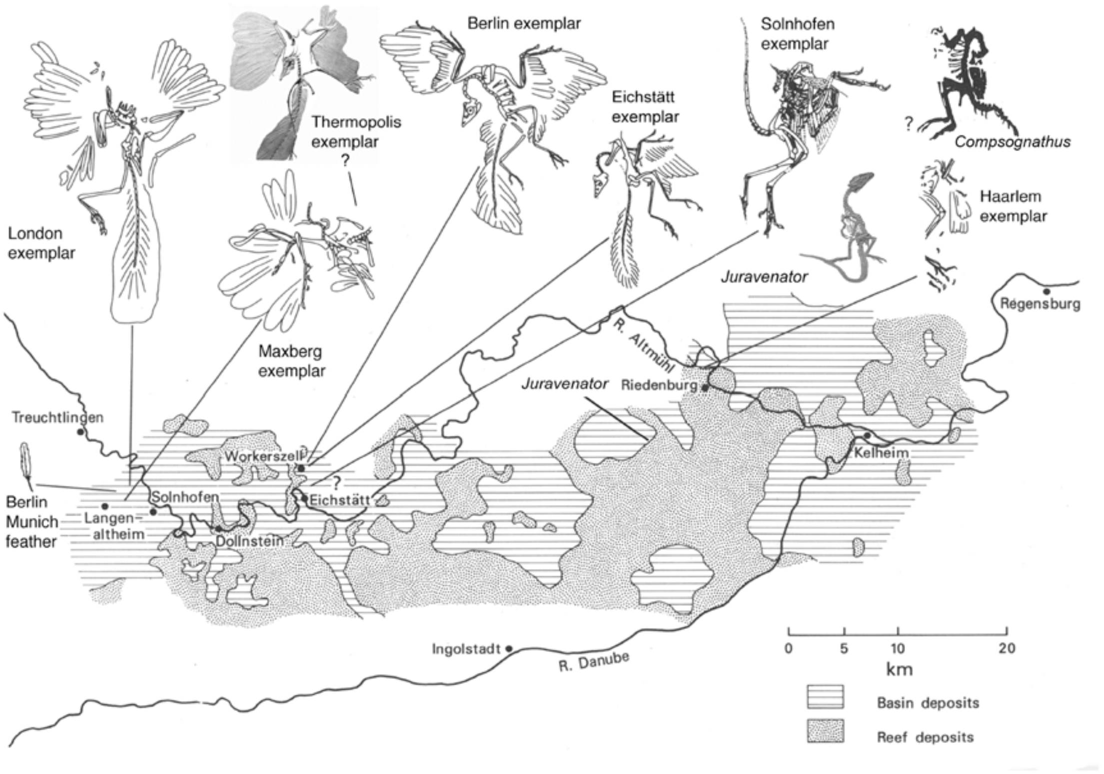

Figure 50. Locality map showing provenance of archaeopterygian birds and compsognathid dinosaurs in the Solnhofen basins (modified from Wellnhofer, 1998; Davis, 1996).

Discussion

Seasonal storms were likely responsible for transport of the aerial components of the flora and fauna (Viohl, 1985). Geologic evidence for such storms can be found in the sedimentary structures in the Painten basin that are interpreted as storm-induced turbidity currents (Link and Fürsich, 2001), and in the alignment of sessile organisms in the Langenaltheim hardground (Wings, 2000) that parallel the East-

North-East to West-South-West Trade Winds prevalent in the Late Jurassic (Barthel et al. 1978). Renesto & Viohl (1997) report that leaves, twigs, and ends of branches are removed from trees during storms commonly and blown out to sea. Moreover, weaker, succulent-like branches of such conifers as *Brachyphyllum* were probably easily broken off from their woody trunks in high winds. This may explain the higher occurrence of these fossils in the Solnhofen Formation. Since most of the insects are winged, the transportation of airborne individuals from the forest out to the sea further from land than they could fly was inevitable. *Archaeopteryx* was also windblown out over the basins and drowned as suggested by the preservational patterns of the articulated skeletons (Davis, 1996). Since *Archaeopteryx* was probably a poor flier (Chatterjee and Templin, 2003; Norberg, 2004) it is doubtful that it regularly flew out that far to sea under its own power. Pterosaurs, especially the rhamphorhynchoids, also suggest a windblown component to explain the occurrence of arboreal forms and the apparent seasonal migration size pattern of smaller individuals (Bennett, 1995).

Conclusions

As a marine unit, the Solnhofen Formation contains a large number of pterosaurs, insects, and birds preserved as accidental fauna – organisms dying and being preserved in places they do not inhabit normally (e.g., Hole 1981; Hasiotis, 2000). Regardless of the reconstruction of the Solnhofen Formation as an archipelago or as a carbonate platform area, it does not necessarily represent the habitat of these animals or their ecosystem (Kemp, 2001). Solnhofen terrestrial flora and fliers were aerially transported from forested landmasses with freshwater sources nearby. This may have been by strong seasonal trade winds, storms, or monsoons (Viohl, 1985; Wings, 2000).

The windblown fossil flora indicates a structured forest with a coniferous canopy of woody gymnosperms (*Araucaria, Palaeocyparis,* and *Brachyphyllum*), Bennettitales in the lower tier with a ground cover of seed ferns (*Cycadopteris*) and fallen logs. The taphonomy and ecology of the insect fauna also supports this forest ecology (Tischlinger, 2001; Kemp, 2001), especially with the presence of large sawflies. It is likely that small, arboreal pterosaurs and such primitive birds as *Archaeopteryx* occupied this forest habitat and were blown out to sea by storms, along with the insects and plant debris. The higher concentration of such intact and articulated fossils as insects and archaeopterygians in the Eichstätt area can be explained reasonably by aerial transport during storms.

A Jurassic landscape with a conifer canopy fits well for *Archaeopteryx* since it was not a great flier and must have required trees and tall plants as launching points. Phugoid gliding, in which animals descend from the canopy to the subcanopy (Stafford et al., 2002), demonstrates a more realistic and energy efficient mode of locomotion for *Archaeopteryx* in a forest ecology and only requires trees of medium height of about 10 m (Chatterjee and Templin, 2003). Furthermore, *Archaeopteryx* possesses no clear adaptation as a runner (Martin, 1983, 1991; Yalden, 1985, 1997); however, it does have anatomical features that suggest tree climbing and a sprawling posture (Martin, 1991; Longrich, 2006) and strongly implies arboreality. The sprawling hindlimbs and tibial feathers of *Archaeopteryx* also reflect that it evolved from a sprawling ancestor that was also a glider. The Jehol avian fauna from China, especially *Microraptor*, further corroborates that hindlimb feathers are primitive (Xu et al., 2003).

In fact, the known cursors represented by the small compsognathid dinosaurs are extremely rare and possibly utilized the patchy, open areas (e.g. shoreline trackway described by Pförringer, 2000) within the forested landmasses further from the shoreline. Since *Archaeopteryx* has feathered hindlimbs (fig. 51) (Beebe, 1915; Christensen and Bonde 2004; Longrich, 2006) and was probably arboreal (Martin, 1983, 1991; Feduccia, 1993; Longrich, 2006), it could not have possibly come from the same niche (Davis, 1996) as compsognathids (*Juravenator, Compsognathus*), which have quite different locomotory adaptations (short arms and robust hindlimbs) and also have scaled integument, some of which is preserved on their tails (Göhlich and Chiappe, 2006; Göhlich et al. 2006; Peyer, 2006), rather than feathers.

Although *Archaeopteryx* feathers and wings are similar to modern birds the shoulder girdle lacked the dorsal wing-flapping range of motion found in modern birds. Jenkins (1993) found that the key aspect that allows dorsal flapping in birds is the shape of the shoulder socket. *Archaeopteryx* lacks an open glenoid, restricting the wing beat to ventral flapping, and thus, had reduced powered flight compared to modern birds. It is possible that *Archaeopteryx* never flapped its wings except to control landings.

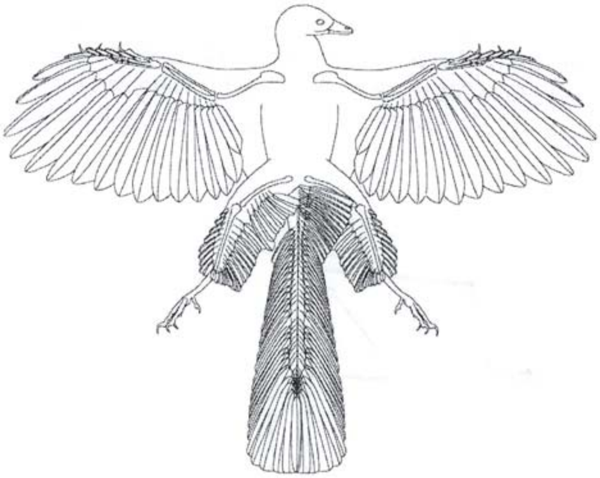

Figure 51. Life reconstruction of *Archaeopteryx* (from Longrich, 2006).

The key question then becomes not how well *Archaeopteryx* could fly, but how was it able to get airborne in order to fly? Within a treeless landscape, it was thought that *Archaeopteryx* must have taken flight from the ground up (Viohl, 1985; Chiappe, 1997) and complicated physical solutions were proposed to accommodate this scenario (Burgers and Chiappe, 1999; Dial, 2003). A forested habitat for *Archaeopteryx* provides a necessary pretext for the arboreal origin of flight –high places (Feduccia 2001; Chatterjee and Templin (2003) rather than *ad hoc* arguments (Chiappe, 1997) needed to account for missing trees and negative evidence (lack of fossil logs) for a terrestrial origin of flight.

Beebe (1915) envisioned a series of stages in the evolution of flight. Each stage represented advancements in flight capabilities. The first stage was a

Tetrapteryx stage – a hypothetical, arboreal glider that had a pelvic wing (e.g. *Microraptor*), followed by the *Archaeopteryx*-like stage with a reduced pelvic wing, and ultimately modern birds. Although modern birds have no pelvic wing, they still retain feather tracts along the hind limb (Lucas and Stettenheim, 1972). Essentially, this idea now seems incontrovertible in light of full pelvic wings on *Microraptor*. Due to its primitive flight ability, *Archaeopteryx* can only be placed at an intermediate stage in the evolution of flight. The caveat is that the evolution of birds is now tied to this new paradigm of flight origin whereby maniraptoran “dinosaurs” (e.g. *Microraptor*) are not only the progenitors of flight, but possess fundamental avian attributes, and therefore, must actually be birds themselves (Martin, 2004; Feduccia et al., 2005).

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CHAPTER 5

"*When the bird and the book disagree, always believe the bird.*"

—John James Audubon

Summary

A summary of the origin of flight and subsequent revisions based on new findings were presented in this dissertation (Chapter 1, 3, 4). These results demonstrate that the origin of flight in birds occurred from the *trees down* early during their evolutionary history. In this dissertation, the origin of flight was considered as a separate issue from the origin of birds, although it is implicit in a *trees down* origin of flight, that the evolutionary divergence of birds from dinosaurs occurred at this time as well. At this juncture, a sprawling proavian ancestor became arboreal during a terrestrial radiation of dinosaurs. Evidence for ecological and morphological adaptations which impacted avian evolutionary history, demonstrating a *trees down* scenario, can be found by examining the fossils of the surrounding biota and evaluating the functional morphology of relevant taxa.

Functional morphological adaptations necessary to evolve flight can be broken down into stages. These stages began with a small, arboreal quadruped and culminated with modern flapping flight in birds. During these stages birds repeatedly evolved secondarily flightless lifestyles and coexisted with theropod dinosaurs on the ground, resulting in convergence on terrestrial adaptations. Although this complicates evolutionary history, in order to unravel origin of flight, as well as phylogenetic relationships, we need to assume ecomorphs occupied similar niches over time (Martin and Meehan, 2005).

For over a century, two predominant theories for the origin of flight have been argued. *Trees-down* origin of flight is thought to have developed from a small, quadrupedal animal which climbed trees, parachuted down or powered gliding using gravity. Evolving feathers and patagia on limbs and tails provided safer landings by decreasing the glide angle. Eventually fluttering the forelimb wing to control landings, evolved into modern wing flapping. A flight stroke that evolved from these adaptive stages, especially climbing and fluttering, supports the *trees-down* origin of flight. A *ground-up* theory implies a terrestrial origin of flight. Small, fast-running, bipedal dinosaurs evolved long arms to capture prey. The proto-feathers covering their bodies for insulation become more birdlike, especially on their arms. As their arms become wings large enough to provide thrust, they developed the ability to take off from the ground while leaping and running. Since this mode of behavior seemed biophysically counterintuitive, *ground-up* theory never garnered serious attention. When modern cladistic methodologies predicted *ground-up* as the only plausible scenario to fit phylogenetic history, elaborate physical arguments accommodated cladistic phylogenies. Most workers then ignored *trees-down* flight origins, but the discovery of feathered four-winged gliders has once again shifted the origin of flight paradigm away from *ground-up*.

Prum (2003) and others (Padian, 2003) suggest a unifying analysis, framed in a cladistic approach, in which the origin of the group, the origin of feathers, and the origin of flight are inseparable. This may not be the case, however, since these are three separate questions framed in a single methodology, thus preventing comprehensive treatment (Love, 2005). Sumida and Brochu (2000) have recognized that "the origin of a group, the origin of a structure, and the origin of a behavior or function are fundamentally different questions, and a cladogram primarily addresses the first." Therefore, cladistic methodology alone is not sufficient for an overall explanation of the origin of flight (Love, 2005). With information from new discoveries (e.g., *Microraptor* and other hindlimb feathered maniraptorans) and concentrating on ecomorphic scenarios rather than cladistic methodology, the origin of flight can be unraveled. The origin of the group and origin of feathers can then be placed in the resulting systematic framework. A phylogenetic context is not a necessary methodology before a morphologic investigation of flight origins is executed (Love, 2005).

Functional morphology helps us understand the evolutionary origin of a morphological feature. Therefore, the significance of a particular character may be paramount (for instance—hindlimb wings). Taphonomy provides additional sources of information concerning form and function as well as preservational biases in the geologic record. Additionally, the paleoecological realm in areas relevant to the origin of flight provide contextual information influencing the evolution of structures.

From the early studies, (Beebe, 1915; Heilman, 1926), we can see that the hypothetical gliding stage in the origin of flight was biophysically logical. Ostrom (1986) also realized this logic was "difficult to refute" (Zhou, 1999). This was substantiated by the recent discovery of four-winged gliders in the Early Cretaceous of China (Xu et al. 2000, 2003) as well as the evolutionary history of primitive birds in China (Zhou, 1999). Even more recently, there has been a report of feathered hindlimbs on other maniraptorans (Xu and Zhang, 2005) as well as leg feathers on primitive enantiornithine birds—*Confuciusornis*, *Longipteryx*, and *Protopteryx* (Zhang and Zhou, 2004; Zhou and Zhang, 2006). These new, primitive maniraptorans and enantiornithurine birds demonstrate that the progenitors of bird flight were small, quadrupedal gliders. This was further enhanced by new information on the Late Jurassic *Archaeopteryx*, showing that it not only exhibits a sprawling posture (Martin, 1991; Longrich, 2006; see also Mayr et al. 2005, fig. 1; 2007, figs. 1,2,3), but had hindlimb feathers as well (Christensen and Bonde, 2004, Longrich, 2006). In fact, many recent birds also have long feathers on the hindlimbs (e.g. red-tailed hawk, owl, pigeon) (Lucas and Stettenheim, 1972).

Since the ancestral arboreal stage was quadrupedal, maniraptorans retained long limbs and the arms became better adapted for tree climbing (flexible wrists and recurved manual claws). In fact, if Heilman (1926) had known of the sprawling posture of the Thermopolis exemplar of *Archaeopteryx*, he probably would not of postulated a bipedal stage for his Proavis model. Heilman (1926) states that his reasoning was based on the limb posture of the only two *Archaeopteryx* exemplars known at the time—the disarticulated London specimen and the Berlin specimen. Although aesthetically beautiful, the Berlin specimen was twisted around its torso by its spreading wings, leaving the hindlimbs to appear parasaggital. We can see from the Berlin exemplar, however, that the femur, although in a parasaggital plane, is actually out of socket with the acetabulum in this position (fig. 52).

Figure 52. Berlin exemplar of *Archaeopteryx lithographica* showing right ilium and femur in lateral view. Note: proximal end of femur is ‘out of socket’ from acetabulum while in parasagittal position (anterior portion of the ilium is facing to top of figure).

As primitive, arboreal proavians evolved into gliders, profound changes occurred in the pelvis, hindlimbs, and pes to function as a gliding airfoil. Indeed this is confirmed by long, asymmetrical flight feathers on the hindlimbs of *Microraptor*. What remains contentious, however, is the position of the hindlimbs during gliding

(Padian and Dial, 2006). Recently, Chatterjee and Templin (2007) reconstructed *Microraptor* as a glider, but the hindlimbs were positioned parasagittally with the pedal feathers forming a biplane wing (Chatterjee and Templin, 2007: fig. 2). Information showing key hindlimb articulations has been enigmatic and specimens published so far do not show femora or pelvis morphology. This led Chatterjee and Templin (2007) to assume a parasagittal pose based on the pelvic girdle and femora of another maniraptoran, *Bambiraptor* (see Chatterjee and Templin 2007: supplemental information, fig. 6). This paper provides new osteological information, based on a recent transfer preparation of a Chinese microraptorine, which exposes a lateral view of the acetabulum. Another unpublished microraptorine specimen, housed at the Institute of Vertebrate Palaeontolgy and Palaeoanthropology (Chapter 3, fig. 43), provides a view of the femoral head. Manipulation of microraptorine pelvic and femoral casts demonstrates the femora could be abducted approximately 65 to 75 degrees to the vertebral column. The femur can be abducted even further (83 degrees) if it is allowed to swing caudally. This position would place the hindlimb wings nearly in the same plane as the forewings and also form a continuous aerodynamic surface with the feathered tail (L. Martin personal communication).

Modern gliders, including the lemur *Galeopterus*, the lizards *Draco* and *Ptychozoon*, and the harlequin tree frog *Rhacophorous* sprawl the hindlimbs during gliding. Taphonomic information on pterosaurs, fossil bats, *Microraptor*, and *Archaeopteryx* demonstrates hindlimb positioning (femoral abduction) in this manner as well. Longrich (2006) reports modern birds with a high range of femoral abduction and reports abduction of 45 to 60 degrees in *Archaeopteryx* would reduce stall speed and turning radius.

Ultimately, the novel anatomical feature of most gliders, as well as *Microraptor* and *Archaeopteryx,* is a dorsally unrestricted acetabulum (fig. 53). Morphology of the ilium shows that both of these taxa, as well as other members of this clade (Longrich, 2006), also lack a significant supra-acetabular crest, but only in *Microraptor* is the acetabulum partially closed and the walls partially inclined (dorso-laterally). With this inclined articular surface comprising the dorsal portion of the acetabulum, this morphology prevents the femoral head from inserting deeply into the hip joint or socket. Thus, with the resulting increased range of motion, the hindlimbs are able to sprawl (abduct) in a ‘spread-eagled posture’ useful to the animal for climbing or gliding.

Contrastingly, there is a horizontal articular surface and a supra acetabular crest comprising the upper rim of the ilium found in Dinosauria (Longrich, 2006, fig. 11). Parasaggital posture, typical of dinosaurs, allows the balancing of a horizontal vertebral column over the hindlimbs for an upright, bipedal posture while their femora are held vertically. With this pose, dinosaur femora are deeply socketed into the pelvis. Although modern birds are bipedal, their femora are held horizontal (contra dinosaurs who have vertical femora), and the femora sprawl around the ribcage. In the bipedal gaits of modern birds, the femora move very little and the tibiae have the greater range of motion. In this way birds are bipedal, but there is no parasaggital gait and the center of balance is not over the hips as in dinosaurs.

Figure 53. Right lateral view of microraptoran pelvis (modified cast).

Examination of the microraptorine femur shows differences in the articular surface of the femoral head and inclination of the head as well (Burnham in press—Chapter 3, fig. 42). Osteologically, *Archaeopteryx* and *Microraptor* are better suited for arboreal rather than cursorial lifestyles but the strongest evidence is hindlimb feathers preserved in the fossils of both taxa. The femoral feather tract (pelvic wing) (Beebe, 1915, Heilman, 1926) has been confirmed in a detailed study of pterylosis by Lucas and Stettenheim, (1972). Furthermore, Lucas and Stettenheim (1972) provide the position and arrangement of crural feather tracts extending down to the metatarsals in Modern birds. Since we are unable to determine the exact insertion points of fossil feather quills, modern analogs can be used to understand the most likely position of the crural feathers on *Archaeopteryx* and *Microraptor*. In *Microraptor*, the tarsal feather tract would extend along the metatarsus on the dorsolateral surface with the longest, asymmetrical feathers on the outside of the wing**.**

The proximal articulations of *Microraptor*'s ankle are angled so the foot swings medially and interpreted herein as both an arboreal feature and a gliding feature (Burnham, in press–Chapter 3). When climbing trees, this would allow the foot to walk up the rounded surface of the tree trunk. Enantiornithine birds also have a similar ankle joint, but there is a well-developed ball and socket to allow this motion. It is unknown if *Microraptor* has developed a ball and socket arrangement since this joint is not easily exposed on the Jehol specimens but the distal surface of the tarsus-metatarsus is slightly concave. Lastly, the metatarsi of modern birds, *Archaeopteryx*, and *Microraptor* have ginglymoid distal articular surfaces (p. 64, fig. 70 of the x-ray of Solnhofener exemplar by Wellnhofer 1989; Hwang et al 2002; Xu et al. 2003, 2003; Burnham, 2006). Ginglymoid articular surfaces allow the pedal digits to curl while perching. This toe-curling function was further adapted for prey dispatch in terrestrial maniraptorans on digit two. It has been proposed that this retractable pedal claw was used as a tree-climbing tool in arboreal forms (Chatterjee and Templin, 2004). The enlarged scythe claw on pedal digit two is found on *Archaeopteryx*, *Microraptor* (Mayr et al. 2005, Xu et al., 2000, 2003; Hwang et al., 2002), and *Bambiraptor* (Burnham et al. 2000).

Conclusions

Archaeopteryx, Microraptor, and *Bambiraptor* were all capable of tree climbing, hence they were arboreal to varying degrees, and this has been demonstrated anatomically and functionally. *Microraptor* represents a primitive stage of flight as a glider. It is nearly impossible to conceive of *Microraptor* spending much time on the ground because of the long feathers on its ankles. Because of its reduced tail (lack of bony rods), *Archaeopteryx* was less derived, but was primarily a glider. Quite possibly, both *Archaeopteryx* and *Microraptor* were capable of some ventral wing flapping as long as they could take off from high places. *Bambiraptor* was more terrestrial (Burnham 2004—Chapter 1; 2007 in press—Chapter 2) and considered secondarily flightless (Paul, 2002). *Bambiraptor*'s small size and large brain (Burnham, 2004) suggests it may have hunted from trees and a reduction of carpal bones in the wrist represents a functional change in the forelimbs from tree-climbing to hunting and grasping.

One of the major issues concerning avian evolution is the timing of bird origins. This issue has been debated using the fossil record and molecular clock interpretations (Benton, 2000, Cracraft, 2001). Paleontological evidence indicates a Late Cretaceous origin for a few Neornithine lineages (Feduccia, 1999), an Early Cretaceous origin for enantiornithines and ornithurines (Zhou, 2004) and a Late Jurassic origin for the oldest bird, *Archaeopteryx* (Chiappe and Dyke, 2002). Molecular data pushes many of the modern lineages of neornithine taxa well into the

Cretaceous (100 mya) or older (Cooper and Penny, 1997, van Tuinen and Hedges 2004). Molecular time estimates seem to coincide with continental breakup in the Mesozoic (Hedges et al. 1996) and the tectonic breakup of Pangea that resulted in the biogeographical distribution of birds, dinosaurs, and mammals.

Fossil evidence shows dinosaurs radiated suddenly in the late Carnian [Triassic] with ornithischians, sauropodamorphs, and small theropods simultaneously appearing and filling herbivorous and carnivorous niches (Benton, 2006). Apparently, there were no insectivorous or arboreal forms within the primitive Dinosauria so early birds would have had little competition for insects usually found in the trees (Zhou and Zhang, 2006).

The paleogeographic position of Solnhofen was farther from larger continents, as Pangea broke apart in the Early Mesozoic. Although *Archaeopteryx* is considered the earliest bird, it would have been preceded by a quadrupedal proavian during the Triassic. Such arboreal ancestors would certainly benefit from vast upland forests that were abundant worldwide during the Triassic (Long and Padian, 1986). Pangea was still intact during the Triassic and such taxa may have been more easily dispersed.

Microraptor is found in the Early Cretaceous in Asia. Maniraptorans were present alongside enantiornithine birds as well as pterosaurs (Chang et al. 2003). There is ample evidence showing a densely forested habitat for these animals in China during the Early Cretaceous (Zhou and Zhang, 2006). Moreover, gliding mammals were present as well (Meng et al. 2006). Jehol apparently supported a rich arboreal fauna.

More importantly, most of the modern ecosystems familiar to us today were developing at this time. It is hard to conceive this was a time for the origin of birds when two separate lineages of early birds had already developed modern flapping flight (Zhou and Zhang, 2006). This would suggest a far more ancient origin to explain this pattern of distribution and development.

Although taxa are defined based on shared, derived features (de Queiroz and Gauthier, 1992), it is important to also examine primitive features for morphologic evidence. Characters are reflective of form and function and thus indicators of how flight may have evolved. With primitive, arboreal maniraptorans as gliders, the origin of flight is consistent with the *trees-down* scenario as well as congruent with ecomorphic data associated with the fossils. Functional morphology demonstrates that gliding, arboreal forms possessed the necessary anatomy and limb mechanics to evolve the flight stroke—a far less complicated biophysical scenario than evolving flight from the *ground up*. Based on the totality of the evidence *trees-down* theory is the only alternative for the origin of flight in birds.

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