Mesozoic Birds of China

by

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Abbreviations for figures

Cranial abbreviations

Ant.f.-Antorbital fenestra

Ang.-Angular

Art.-Articular

Boc.-Basioccipital

Bo.tbr.-Basioccipital tuberosity

Bpt.-Basipterygoid

Bpt.pr.-Basipterygoid process

Bs.-Basisphenoid

Bt.p.-Basitemporal plate

C.-Coronoid

D.-dentary

Ec.-Ectopterygoid

Ep.-Epipterygoid

Epo.-Epiotic

Eu.-Eustachian tubes

Exoc.-Exoccipital

Ex.op.c.-External opthalmic canal

Ext.nar.-Exteranl nares

F.-Frontal

F.m.-Foramen magnum

Gl.-Glenoid

In.n.- Internal nares

Ju.-Jugal

La.-Lacrymal

L.i.c.-Linea internus cranialis

M.p.p.-Maxilla-palatine process

Mx.-Maxilla

Mx.p.- Maxillary process of the premaxilla

Md.-Mandible

N.-Nasal

N.f.-Nutrient foramen

N.p.-Nasal process of premaxilla

O.-Orbital

O.c.-Occipital condyle

Orb.rug.-Orbital rugosity

Op.-Opisthotic

Pa.-Parietal

Par.-Prearticular

Pf.-Postfrontal

Pl.-Palatine

Poc.-Paroccipital

P.o.p.-Postorbital process

Prf.-Prefrontal

Prm.-Premaxilla

Pro.-Prootic

Ps.-Parasphenoid

Ps.r.-Parasphenoid rostrum

Pt.-Pterygoid

Ptd.-M. Pterygoideus

Q.-Quadrate

Qj.-Quadratojugal

Sa.-Surangular

Soc.-Supraoccipital

S.f.-Supratemporal fenestra

Spl.-Splenial

Sq.-Squamosal

T.f.-Temporal fossa

V.-Vomer

Axial abbreviations

A.-Atlas

A.d.v.-Anterior dorsal vertebrae

A.s.c.-Articular surface of centrum

Ax.-Axis

C.-Capitulum

Cd.-Caudal

C.p.-Costal process

Ct.-Centrum

Cv.-Cervical

Di.-Diapophysis

D.f.-Diapophyseal foramen

Do.-Dorsal

Ca.-Capitulum

Di.-Diapophysis

G.r.-Gastric rib

K.-Keel

Lu.-Lumbar vertebrae

N.a.-Neural arch

N.c.-Neural canal

N.s.-Neural spine

Pl.-Pleurocoel

Poz.-Postzygapophysis

Prz.-Prezygapophysis

Pp.-Parapophysis

Py.-Pygostyle

Ri.-Rib

Sc.-Sacral vertebrae

S.c.v.-Synsacral caudal vertebrae

Sp.-Spine

S.t.v.-Synsacral thoracic vertebrae

Apendicular abbreviations

Shoulder girdle and forelimb

A.a.l.-Attachment for anterior articular ligament

A.c.f.-Anterior carpal fossa

A.c.m.-Anterior carinal margin

A.l.d.-Attachment for anterior latissimus dorsi

A.p.-Alula process

B.a.-Bicipital attachment

B.c.-Bicipital crest

B.d.-Brachial depression

B.g.- Bicipital groove

Br.a.-Attachment for brachialis anticus

B.s.- Bicipital surface

B.t.- Bicipital tuberosity

Ca.-Carina

Cap.-Capitulum

C.b.a.-Attachment for coraco-brachialis

C.g.-Capital groove

Cl.-Clavicle

Cmc.-Carpometacarpus

Co.-Coracoid

Co.f.-Coracoid fenestra

Co.fa.-Coracoidal facet

Co.fo.-Coracoid fossa

Co.h.-Coracoid head

Co.s.-Coracoid sulcus

Co.t.-Coracoid tuberosity

C.p.-Costal process

C.t.-Capitular tuberosity

C.t.a.-Ligament attachment of carpal tuberosity

DI-III.-Digit I-III

D1-3.-Facet for digit 1-3

D.c.-Deltopectoral crest

D.p.-Deltoid process

D.l.-Dorsal lip of coracoid groove

D.m.b.-Depression for m. brachialis

Ect.-Ectepicondyle

Ect.p.-Ectepicondylar process

E.p.-Process for extensor

Ent.-Entepicondyle

Ent.p.-Entepicondyle process

F.ar.-Fercular articulation

F.p.-Flexor process

Fu.-Fercula

Gl.-Glenoid

H.c.-Humeral cotyle

H.h.-Humeral head

Hu.-Humerus

H.u.d.-Humero-ulnar depression

I.b.a.-Impression for brachialis anticus

Ic.v.-Intercostal vacuity

Im.v.-Intermetacarpal vacuity.

I.t.-Intermetacarpal tuberosity

I.p.-Intercondylar process

L.a.-Ligament attachment

L.c.-Lateral condyle

L.ct.-Lateral cotyle

L.f.-Ligament furrow

L.p.-Ligamental prominence

L.pr.-Lateral process

L.l.f.-Lateral ligament fossa

L.t.-Lateral tuberosity

L.t.g.-Lateral tricipital groove

M.a.s.-Medial articular surface

McI-V.-Metacarpal I-V

M.d.-Medial dorsal ridge

M.d.a.-Medial distal angle

M.l.f.-Medial ligamental fossa

Ml.p.-Mediolateral process

Mn.-Manubrium

M.p.f.-Medial proximal foramen

M.t.-Medial tuberosity

M.t.g.-Medial tricipital groove

O.-Olecranon

Ol.f.-Olecranon fossa

P.1-4.-Phalanx 1-4

P.a.a.l.-Process for anterior articular ligament

Pec.-Attachment for pectoralis

P.c.r.-Papillae of caudal remiges

P.l.d.-Attachment for posterior latissimus dorsi

Pl.p.-Posterolateral process

Pn.f.-Pneumatic foramen

Pn.fo.-Pneumatic fossa

P.p.-Ligament attachment for pisiform process]

P.r.d.-Proximal radial depression

Proc.-Procoracoid

Prs.-Presternum

P.s.f.-Papillae of secondary feathers

Ps.r.-Parasphenoid rostrum

R.-Radius

R.c.-Radial condyle

R.g.-Rotular groove

R.s.-Radial sulcus

S.c.f.-Supracoracoidal foramen

Sc.-Scapula

Sc.b.-Scapular blade

Sc.f.-Scapular facet

Sc.s.-Scapular shaft

Sc.t.-Scapular tuberosity

S.f.-Sternal facet

S.i.-Sterno-coracoidal impression

S.l.f.-Scapho-lunar facet

Sl.n.-Semilunar notch

S.m.h.-Sulcus for m. humerotricipitis

S.m.s.-Sulcus for m. scopulotricipitis

S.p.-Sternal plate

S.pr.-Sterno-coracoidal process

St.-Sternum

S.t.-Sulcus for tricipital

S.t.l.-Sulcus for the transverse ligament

T.c.-Carpal trochlea

T.d.-Tendinal depression

T.d2.-Trochlea for digit 2

T.g.-Tendinal groove

T.l.c.-Trochlea of lateral condyle

T.m2.-Tuberosity for metacarpal 2

T.m.c.-Trochlea of medial condyle

T.r.-Thoracic ribs

Tr.-Trochlea

Tri.-Tricipital attachment

T.t.-Tibial tuberosity

Tub.-Tuberculum

U.-Ulna

U.c.-Ulnar condyle

U.d.-Ulnar depression

U.f.-Ulnar face

Ul.-Ulnare

Ung.-Ungual

V.l.-Ventral lip of coracoidal groove

V.m.s.-Ventral manubrial spine

X.a.-Xiphial area

Pelvic girdle and hind limb

A.i.c.-Anterior iliac crest

Ac.-Acetabulum

A.i.g.-Anterior intercondylar groove

A.i.l.-Anterior intermuscular line

A.m.g.-Anterior metatarsal groove

A.p.-Ala preacetabularis ilii

At.-Antetrochanter

At.l.-Attachment of anterior articular ligament

C.cr.-Cnemial crest

Cd.-Caudal vertebrae

C.l.f.-Colateral ligament fovea

DII-IV.t.-Trochleae for digits II-IV

DII.t.w.-Wing of trochlea for digit II

D.f.-Distal foramen

F.-Fibula

F.c.-Fibular crest

F.c.l.-Fovea for collateral ligament

Fe.-Femur

F.g.-Fibular groove

F.h.-Femoral head

I.a.-Ischiac angle

Ia.r.-Interarticular region

Icta.-Intercotylar region

I.f.-Intercondylar fossa

I.i.-Iliotrochanteric impression

I.i.f.-Ilio-ischiatic foramen

Il.-Ilium

Il.f.-Iliac facet

I.n.-Intertrochlear notch

Ip.f.-Ischiopubic fenestra

Is.-Ischium

Is.p..-Ischiac peduncle

L.a.-Ligament attachment

L.a.s.-Lateral articular surface

L.c.c.-Lateral cnemial crest

L.co.-Lateral condyle

L.ct.-Lateral cotyle

L.e.g.-Lateral extensor groove

L.l.a.-Lateral ligament attachment

L.l.p.-Lateral ligament prominence

L.tr.-Lesser trochanter

M.a.f.-Medial articular facet

M.co.-Medial condyle

M.c.c.-Medial cnemial crest

M.ct.-Medial cotyle

M.d.r.-Medial dorsal ridge

Md.a.f.-Foramen for medullary artery

MtI-V.-Metatarsal I-V

N.-Neck

N.f.-Nutrient foramen

Ob.-Obturator foramen

Ob.r.-Obturator ridge

P.1-4.-Phalanx1-4

Pa.-Patella

Pb.-Pubis

Pb.b.-Pubic boot

Pb.p.-Pubic peduncle

Pe.p.-Pectineal process

P.f.-Popliteal fossa

P.fo.-Proximal foramen

P.i.c.-Posterior iliac crest

P.i.g.-Posterior intercondylar groove

P.i.l.-Posterior intermuscular line

P.l.a.-Proximal ligament attachment

P.m.f.-Fossa for the parahypotarsalis medialis

Pn.f.-Pneumatic foramen

Pr.c.-Preacetabular crest

Pr.p.-Groove for peroneus profundus

Po.c.-Postacetabular crest

Po.k.-Posterior keel

R.d.-Renal depression

R.l.a.-Attachment for round ligament

R.g.-Rotular groove

S.-Shaft

Sc.-Sacral vertebrae

S.c.v.-Synsacral caudal vertebrae

S.b.-Supratendinal bridge

S.di.-Sacral diapophyses

S.p.f.-Fossa for the supratroch plantaris

Syn.-Synsacrum

T.-Tibia

Tbt.-Tibiotarsus

T.c.-Trochanteric crest

T.ca.-Tendinal canal

Te.f.-Tendinal foramen

T.f.-Trochanteric fossa

T.g.-Tendinal groove

Tmt.-Tarsometatarsus

T.t.a.-Tuberosity for tibialis anticus

Ung.-Ungual

Foreward by Delong Jiang

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June, 1997

The discovery of Mesozoic birds from localities in North China in recent years has disturbed a century of tranquillity in the paleornithological world. In 1984 Professor Lianhai Hou from the Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, described a new avian species named *Gansus yumenensis* produced from Mesozoic terrestrial sediments in Yumen Co., Gansu Province, which differed significantly from specimens derived from marine sediments. Subsequent consecutive discoveries in China were represented by Mesozoic taxa including *Sinornis* and *Cathayornis,* which disturbed the status quo of the realm of Chinese paleontology. In 1990, published research upon *Confuciusornis* and *Liaoningornis* received high approval from the academic world and elevated the influence of Chinese paleontology to a new apex.

Over one hundred years ago, *Archaeopteryx,* the oldest fossil bird ever recovered in the world, was excavated from the Bavarian region of Germany and estimated to be approximately 150 million years old. This taxon displayed characters of retaining a dentition and possessing long flight feathers, leading to many years of research which resulted in a general consensus that Aves is directly descended from the Reptilia. But *Archaeopteryx* is extremely distinct from modern members of Aves, and its morphology causes academic workers to assume that a great many more "intermediate" avian taxa existed within the evolutionary process. It is regrettable that after the discovery of *Archaeopteryx*, there was a 100 year hiatus in which there were no satisfactory intermediate avian forms excavated. The 1994 discovery in China of *Confuciusornis* provided supplementary data that filled the void between *Archaeopteryx* and modern taxa. Although geological research confirmed a younger age for *Confuciusornis*, nevertheless, its edentulous character was considered extremely significant and provoked excitement in workers about the rapid evolution of avian taxa during this time period. Concurrently, there was an extremely abundant contemporaneous fauna produced from *Confuciusornis* deposits in exquisite states of preservation rivaled by no other Mesozoic localities in the world. These specimens represent the epitome of systematic research upon the early evolutionary history of Aves.

The volume *Mesozoic Birds of China* is the painstaking crystallization of ten years of applied research upon archaic birds conducted by Professor Lianhai Hou, from the Institute of Vertebrate Paleontology and Paleoanthropology. Documented within the volume are two classes, seven orders, nine families, thirteen genera, and sixteen species of Mesozoic birds excavated from China. An extremely complete description of each species is provided and are associated with skeletal reconstructions, measurements, discussion of taxonomy and phylogeny, and a comparison of the Mesozoic taxa to modern forms, *Archaeopteryx,* and archaic reptiles. The text and figures are exquisite and represent a supplementary reference for every facet of biological study in addition to providing a reference for specialists in the paleontological realm. The volume is of genuine academic value, worthy of publication, and will act as an incentive to all who preserve and study the avifauna of China. And not to forget, the Taiwan region may also constitute a rich repository for Mesozoic or archaic avian fossils, as it is only a matter of time before research and excavation are initiated. This volume, although restricted in its availability, is recommended for the enjoyment of all.

Foreword by Guangmei Zheng

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July, 1996

In the past several years, a great quantity of Mesozoic bird specimens have been excavated and studied in China, creating a global sensation recognized as "one of the most significant discoveries in vertebrate paleontology this century," and fundamental toward a reevaluation of avian origins and evolutionary history.

Over a century has passed since the first documentation of an of an archaic bird feather impression (Meyer, 1861) to the seventh specimen of *Archaeopteryx* documented by Wellnhofer (1988). But all these specimens are derived from the Late Jurassic (~145 Ma) lithographic limestones in the Solnhofen district of Bavaria, Germany, and possess numerous transitional characters lying between archaic reptiles and extant birds. These specimens instill a fascination among workers and are the source of numerous hypotheses concerning the origin and evolution of Aves. Despite the incongruities among these hypotheses, there is a generally consistent published consensus that *Archaeopteryx* represents the most primitive Aves and that it represents a stem group from which Aves was derived. The documentation of *Protoavis* by Chatterjee (1991) from the Late Triassic terrestrial sediments of North America predates *Archaeopteryx* by 75 million years, and although the cerebral hemisphere of the American specimen is more derived than that of *Archaeopteryx,* its postcranial characters differ from other members of Aves, such that if this specimen is substantiated as an early member of the class it will indeed provoke phylogenetic problems. The questions, however, still remain: Is *Archaeopteryx* the direct ancestor and does it represent the stem group of Aves? What is the nature of taxa more primitive than *Archaeopteryx*? And what were the adaptive radiations of Aves in the Mesozoic? Moreover, the probability that this class of animals would be preserved in the geologic record at all is close to nil due to its aerial mode of locamotion and thinly walled pneumaticised skeletal elements. To date, the entire global quantity of fossil bird localities and specimens is extremely limited. This is the enigma facing ornithologists.

The treatise *Mesozoic Birds of China* by Professor Lianhai Hou is one answer from the paleontologists of China to this global problem. The entire volume is a documentation of the excavation and research upon the subclasses Archaeornithes and fossil Neornithes, the former of which contains three orders, five families, nine genera, and eleven species while the latter contains three orders, four families, four genera and four species. A portion of this treatise concerns abundant specimens of archaeornithines and neornithines derived from four stratigraphic units spanning the Late Jurassic to Early Cretaceous from provinces in China located between North latitudes 35° and 45° including Shandong, Hebei, Liaoning, Inner Mongolia, Ningxia, and Gansu. This extensive distribution and occurrences in multiple stratigraphic horizons holds a primary status in the academic community today. Furthermore, the archaic ages and the conspicuous regional characteristics of the specimens constitute rare data that provide evidence for the origin and adaptive radiation of the class Aves.

The author, Lianhai Hou, conducts comparative research between primitive avian forms represented by *Confuciusornis* and relatively more derived avian taxa represented by *Liaoningornis* and *Chaoyangia.* It is initially proposed that within the evolutionary process in the Late Jurassic and Early Cretaceous adaptation for "natural saltation" occurred twice. Avian radiation initiated in the Late Jurassic through both anagenesis and cladogenesis which represents a new concept in traditional evolutionary discourse. The author further advances hypotheses of extensive geologic activity between the Late Jurassic and Early Cretaceous which sufficiently influenced biotic development. He notes that the origin of Aves should be traced back to the Late Triassic and suggests that *Archaeopteryx* is not a direct ancestor but represents an independent lineage with specialized adaptations. This leaves *Confuciusornis* as the representative for the conventional aeronautic lineage. These extremely abundant specimens comprise the foundation for research and reinterpretation that undoubtedly provokes dissent toward traditional evolutionary theory. Thus, the fossil birds of China constitute a major contribution to avian research globally.

The abundant discoveries of archaeornithine and neornithine specimens have now turned the focus of attention from Germany and the United States to China. Those following with interest concentrate upon the research of the notable North China Rehe Fauna. Also due to systematic research in China is the initial recognition of fossil birds as index fossils for the age of the fauna, leading to significant biostratigraphic applications. With the initiation of the Dongtang geologic event in the Late Jurassic, cladogenesis occurred combined with extinction of the existing fauna and flora which led to the genesis of the Rehe fauna.

This monograph provides numerous original hypotheses regarding the origin and adaptive radiations of Aves in addition to provocative ideas. We look forward to results of even more prolific research in the future.

Foreword by Alan Feduccia

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June, 1996

No field of paleontology has undergone more of a dramatic revolution during the past two decades than has paleornithology, especially with respect to Mesozoic birds. Beginning in the early 1970's and continuing to the present, there has been a dramatic increase in the number of studies on bird origins; yet, in reality, little new evidence has been brought to bear on the subject. On the other hand, our knowledge of Mesozoic landbirds has been dramatically increased not by speculation, but by the addition of new material, especially from China. At the time of their initial discovery, a little known paper by Cyril Walker in 1981 first introduced to the world a new group of archaic Mesozoic landbirds which he called the "opposite birds" or enantiornithines, described from material collected during the 1970's from the Upper Cretaceous Argentinian Lecho Formation by Jose Bonaparte. Given the incompleteness of the skeletons and the lack of skulls, little was made of this revelation at the time, and it was only later realized that *Gobipteryx* , collected from the Late Cretaceous of Mongolia during the 1970's, as well as a host of other previously described fossils belonged to this newly revealed group. Others included the members of the Avisauridae, initially described as a new family of theropod dinosaurs, and birds from the Lower Cretaceous of Spain, and now from fossils found on practically every continent, including Australia.

However, by far the most dramatic discoveries have come from the work of Professor Hou Lianhai and his colleagues, especially Zhou Zhonghe, who is now studying at the University of Kansas. The first early Cretaceous bird discovered from China was not an enantiornithine, but the ornithurine *Gansus yumenensis*, recovered from Gansu Province, northwestern China, in 1981, and described by Hou and Liu in 1984. However, a new era in our understanding of bird evolution was ushered in during September of 1990, when Zhou Zhonghe discovered two small, articulated bird fossils excavating paddlefish (*Polyodon*) fossils from lacustrine shales of the Jiufotang Formation. The first of these birds was described as *Cathayornis*, and since that time literally dozens of specimens of Lower Cretaceous enantiornithines have been recovered, adding greatly to our knowledge of early landbirds. Then, several years ago, specimens of late Jurassic birds began to appear from lacustrine deposits. These important fossils, the first described as the urvogel *Confuciusornis sanctus*, is now known from a dozen or so specimens, and more recently a bird approaching ornithurine morphology, *Liaoningornis*, has been recovered from the same deposits, thus confirming the early dichotomy of modern type, or ornithurine birds, and the sauriurine, or archaic Mesozoic birds. The importance of these Chinese birds discovered by Professor Hou and his colleagues at the Institute of Vertebrate Paleontology and Paleoanthropology at Beijing's Chinese Academy of Sciences, cannot be overstated. Indeed, these discoveries will form the basis of our new understanding of the early evolution of birds. Hou's book on the Mesozoic birds of China is an exciting event and will be much anticipated.

Foreword by Larry D. Martin

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June, 1996

When I first began to work on birds from the Age of Dinosaurs (Mesozoic) in 1963 there were only two Jurassic bird skeletons known. the London and Berlin *Archaeopteryx* specimens. John Ostrom quite reasonably reflected this fact when he stated that those two specimens were the most important and valuable fossils ever found. The record from the Early Cretaceous was even worse with a couple of fragmentary specimens that were lost in World War II and some forty isolated bones of the primitive hesperornithiform, *Enaliornis* from the Early Cretaceous (Aptian) of England. Except for *Archaeopteryx*, marine birds dominated the record with the most important specimens coming from the Late Cretaceous of Kansas in North America.

The discovery of additional specimens of *Archaeopteryx* and the Early Cretaceous birds in Spain increased our knowledge during the next three decades, but the real revolution in our knowledge of early bird evolution came about in the last five years in China. Prof. Hou had already reported Mesozoic birds from China, but new and more important sources of such materials were found in fish bearing beds some 500 kilometers north and east of Beijing. There a rich flora and fauna including fish, reptiles and mammals began to include entire bird skeletons including the fossils of their feathers. Intensive work has shown that these are among the most prolific fossil bird horizons in the world. More importantly, they were deposited in deep tectonic lakes containing about 1500 meters of sediment. These lakes were freshwater and surrounded by forests. Deposition took place during one of the most important moments in earth history. This was the time at the Jurassic-Cretaceous transition when much of the modern world was born. Flowering plants, therian (modern) mammals, and birds all undergo their first radiation during this critical period.

All of this transition was wondrously preserved in the fine sediments of the Mesozoic lakes. Flying insects, leaves, mammals with impressions of hair, and birds with feathers are abundant. The oldest levels produce many specimens of the Late Jurassic-Cretaceous bird *Confuciusornis*, indicating some sort of communal existence for this *Archaeopteryx*-like bird that climbed trees and had limited powers of flight. These same levels also contain the oldest modern bird. All of these discoveries center around the work of Prof. Hou and Zhonghe Zhou. Between them they have made discoveries that have rewritten avian evolution. Hou made the first description of Mesozoic birds in China. He has been there for all subsequent discoveries and is the best qualified person to describe this exciting world of new discovery.

Preface

Research upon Mesozoic birds in China initiated in the 1980's, followed by the 1984 publication in *Scientia Sinica* of "The Early Cretaceous birds of Gansu Province and early avian evolution" (Hou and Liu, 1984) which, at that time, aroused the attention of the academic world. For over one hundred years since the 1861 publication of *Archaeopteryx* and the 1880 publication of *Ichthyornis,* there has been no further discovery of a relatively complete archaic avian specimen. The recently excavated Chinese fossils shatter this long period of quiescence and represent the first discovery of Mesozoic birds from terrestrial sediments in the world. Because their morphology differs from any Mesozoic avian form known, these specimens are erected within the new order, the Gansuiformes, as the new family Gansuidae. The genus *Gansus* differs from *Archaeopteryx* by representing the earliest avian form adapted to aquatic or riparian environments. Its discovery represents a discontinuous avian lineage although it provides a significant evolutionary link to shorebirds, but its morphological characters continue to be controversial focal points of discussion among ornithologists.

The *Gansus* specimens were initially discovered during the process of Mesozoic fish research being undertaken by the paleoichthyologists Fengzhen Ma and Zhicheng Liu. Henceforth, when excavating of Mesozoic fishes, workers paid particular attention to the possibility of recovering avian specimens.

In September 1989, the young ichthyologist Zhonghe Zhou was conducting excavations for acipenserid fish in the light gray shales of the Early Cretaceous Jiufotang Fm. in the Boluochi vicinity of Chaoyang Co., Liaoning Province, where he excavated three different avian specimens associated with fish. This prompted a contingent of four personnel from The Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), composed of Fan Jin, Jiangyong Zhang, Zhonghe Zhou, and Lianhai Hou to conduct further excavations in the Chaoyang region where they collected another three specimens. Since that time, research and excavations have been conducted annually with the assistance of Yucai Gu from the Liaoning Institute of Archaeology; Yutie Sun from the Chaoyang County Institute of Culture; and a large contingent from IVPP including Jinfeng Hou, Keqin Gao, Yuanqing Wang, Yueming Hu, Jie Jang, Huaquan Shou, Qiuyuan Wang, Wenhua Du, Wei Gao, Ping Wang, and Hilu You. To date, over thirty avian specimens have been recovered from this locality. The smallest specimen was described by Zhou, Jin, and Zhang (1992) as *Cathayornis* and assigned to the family Sauriurae. The largest of the specimens was described by Hou and Zhang (1993) as *Chaoyangia* and assigned to the subclass Neornithes. Another incomplete specimen was described by Zhou (1995) as the Enantiornithine *Boluochia,* while the remaining specimens are still under study.

Concurrent with the publication of *Cathayornis* was a *Science* paper by Sereno and Rao (1992) describing the Early Cretaceous *Sinornis* from Meileyingzi, Chaoyang Co. This specimen was discovered by one of the local farmers and transmitted to Chenggang Rao of the Beijing Museum of Natural History for study and preservation. The locality of Meleyingzi was revisited on numerous occasions by IVPP personnel but another specimen has not been recovered.

Coincidentally, during the exhilarating process of amassing the large Early Cretaceous collection of birds from Chaoyang Co., auspicious news arrived from the eminent geologist Professor Pai Li of the Geological Institute of Hebei Province, who reported to Lianhai Hou that avian fossils had also been recovered from Fengning Co., Hebei Province, which elicited a great amount of excitement. Hou's intense interest made it impossible not to expand his research to all regions with Late Jurassic to Early Cretaceous terrestrial sediments of North China that produced a "Rehe Fauna." The actual investigation and documentation of avian specimens has now become extremely extensive, indicating that not only is China a major source for the genesis of archaic Aves, but that the adaptive radiation and speciation of the class occurred earlier than currently recognized. An evaluation of sites in Fengning Co. was subsequently undertaken by Pai Li, Zhonghe Zhou, and Lianhai Hou. They visited the locality of Linjitu, which is located approximately 100 km north of the municipality of Fengning in the upper reaches of the Luanhe River. Upon reaching the locality the contingent was met by a local farmer who presented them with a complete avian specimen. At first glance of the specimen, Hou was so excited he was rendered speechless. Preliminary analysis of the Fengning specimen indicated that it was more primitive than *Sinornis* and *Cathayornis* and its stratigraphic position was mapped as being lower. Fan Jin from IVPP regarded the stratigraphic position of this site at Linjitu to be within the Late Jurassic Yixian Fm. This specimen was thereupon regarded as a significant transition phase between *Archaeopteryx* and *Sinornis-Cathayornis.*

Following the discoveries of Mesozoic birds from Hebei and Liaoning provinces, IVPP launched expeditions on a massive scale including excursions in the east to Shandong Province and west to Gansu, Ningxia, and Inner Mongolia. The paleoentomologist Professor Junfeng Zhang from the Shandong Natural History Museum obtained a feather from the Late Jurassic to Early Cretaceous Laiyang Fm., prompting a 1993 evaluation of the locality by Lianhai Hou and Zhonghe Zhou together with Professor Zhang at Nanligezhuang Village, near the town of Tuanwangxiang, within the municipality of Laiyangshi. The reason there was only a single feather recovered was due to the destruction of the fossiliferous deposit by individuals with commercial interests. Another isolated feather was also collected by Zhonghe Zhou in Ningxia Autonomous Region.

In 1990, the Sino-Canadian Dinosaur expedition collected an incomplete avian specimen from the Taostu River in the Ordos Basin of Inner Mongolia which shows relatively poor adaptation for flight. Zhiming Dong (1993) made a preliminary report on the specimen and then transmitted it to Hou, who after a detailed study, erected it as *Otogornis genghisi* (Hou, 1994).

Research on the massive collection of Chinese archaic birds has been recognized by paleontologists globally and work is currently being intensified. In the fall of 1993 Hou and Zhou received a specimen from a local farmer named Yushan Yang in Yixian Co., Liaoning, which possessed characters related to *Archaeopteryx.* Nearly simultaneously, another specimen resembling *Archaeopteryx* consisting of cranium and forearm was given to Hou by He Zhang, curator of the Jinzhou Municipal Paleontological Repository. This specimen was collected from Jianshangou near the village of Shangyuan, Beipiao Co, Liaoning. The sediments producing the specimen consist of gray banded calcareous shales at the base of the section determined to be the Late Jurassic Yixian Fm. In addition, a local elementary school teacher provided Hou with a specimen of a hindlimb. The basic morphology of these three specimens resembles *Archaeopteryx* but there are also conspicuously distinct characters such as an edentulous beak, the appearance of the earliest coracoid, the particularly well developed humeral head, and the derived pneumatic foramina. A combined effort to study the specimens was undertaken by Hou, Zhou, Yucai Gu, and He Zhang concluding with the publication by Hou (1995) which erected *Confuciusornis sanctus* as the first Jurassic bird from China.

Up until 1995, the collection of Chinese Mesozoic birds had been prolific, extensive in geographic range, and derived from numerous stratigraphic levels, representing a globally unique occurrence. Just the Chaoyang region itself could be regarded as an Early Cretaceous bird repository. In the past several years nearly ten papers have been published both endemically and in foreign journals although the majority of these papers concern individual specimens while a monograph on systematic research has been in continuous preparation. In 1994 Zhongwei Yan, the ornithologist from the Taizhong Natural History Museum of Taiwan visited Lianhai Hou at IVPP to view some of the archaic bird specimens, after which Hou raised the topic of publication. Professor Yan modestly suggested that after returning to Taiwan he would enquire about assistance from a suitable press. He subsequently approached Chairman Dong, director of the Taiwan Provincial Foundation for Avian Conservation, Culture, and Education while simultaneously obtaining fervent support from Delong Jiang, Director of the Phoenix Valley Provincial Aviary of Taiwan to produce this volume at the earliest possible date. Professor Yan also assisted in other aspects of publication such as the typesetting and proofreading of the volume, and as such the author hereby avails himself the opportunity to express his gratitude to both Zhongwei Yan and Delong Jiang.

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Lianhai Hou

Chapter 1

Historical and geographic synopsis

This volume describes and discusses Mesozoic avian skeletons or feather impressions from seven localities representing at least five stratigraphic levels from the provinces of Gansu, Inner Mongolia, Hebei, Liaoning, and Shandong. The sites initiate at the eastern sea coast near the town of Laiyang, Shandong Province. The next site lies westward toward the interior of China at Senjitu, Fengning, Shenqu, Yanshan Co., Hebei Province. Continuing to the northwest to western Liaoning Province there are three sites including Chaoyang, Beipiao, and Lingyuan; then to Chabu Sumu which is the original site of *Otogornis genghisi* on the Ordos Plateau of Inner Mongolia; and finally furthest west to the renowned petroleum producing region of Yumen, Gansu Province, where the first Mesozoic specimen of *Gansus* dwelled by what is now a small mountain village called Chenjiawan in the Changma region of Qunshan. The distribution of localities that produced the Chinese avian specimens is predominantly concentrated in the southern portion of northeast China and the eastern portion of north and west China. Most specimens are excavated from fluviolacustrine sediments, a portion of which are interbedded with volcanics. An introduction to the geography and history of each locality is provided below.

1. Nanligezhuang.

This site is located in the southern Laiyang Basin approximately 21 km south and slightly west of Laiyang county seat (now known as Laiyangshi) at an altitude of approximately 200 meters. Geographic coordinates of the site are north latitude 36° 70' and east longitude 120° 31' in the hill country of the Shandong Peninsula. The topography is composed of Late Jurassic to Early Cretaceous terrestrial sediments recognized as the Laiyang Fm. A fossil feather was recovered from gray-brown shales of the third member of this formation, associated with abundant specimens of fish and insects. In his publication "A Late Mesozoic insect fauna and its paleoecological characters from Laiyang, Shandong," Junfeng Zhang (1992) records the collection of that single bird feather. This specimen was subsequently transmitted to Lianhou Hai at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) and will be described later in this volume.

Laiyang is a noted county capital on the Shandong peninsula which must be traversed when traveling from the provincial capital of Jinan to the port cities of Yantai or Weihai. It also represents a medial stopping point linking the two major harbors of Qingdao and Yantai. Produce from Laiyang is extremely abundant, and its fruit, such as the pears grown there, are world renowned. Autumn is the best season to conduct field work in this region and the regional paleontological sites represent one of the nation's rich repositories for dinosaurs. *Tsintaosaurus spinorhinus* is produced from Jingangkou in Laiyang Co., *Tanius sinensis* and *Psittacosaurus youngi* are produced from Jiangyunding, and dinosaur eggs are also recorded from the region.

2. Senjitu:

This site is situated in northern Fengning Co., Hebei Province, and is approximately 90 km from Fengning county seat, at the northern margin of the northern mountains of the province and separated from Inner Mongolia merely by a single mountain in the upper reaches of the Luanhe River at the foot of the Yanshan Mountain Range. Its coordinates are 116° 40' east longitude and nearly 40° north latitude. The avian locality lies on the north slope of a promontory at Dongtuyao nearly two km south of Senjitu, where local villagers excavate fossil fish for commercial interests. Avian specimens occur in the same deposits with lycopteriform and acipenseriform fish. The Hebei Provincial Survey Corps has conducted numerous regional geological investigations as has

Professor Si'en Wang from the Chinese Academy of Geology. The specimens are produced from calcareous shales of the fourth member of the Yixian Fm. (Huajiying Fm.) (Fan Jin, pers. comm).

The transportation system of Fengning Co. is predominantly based on the public roads. The itinerary for expeditions to this region is to initiate at Beijing, pass through the city of Shunyi, then Huairou and Changshaoying at Tanghekou. It is then approximately another 60 km north to the city of Fengning, which is located on the eastern side of the Zhangbei Plateau. One then travels north from Fengning to enter the mountain region of northern Hebei Province, where the high peaks and deep ravines constitute a terrain of difficult access. The village of Senjitu is located at the foot of a high mountain on the bank of the Luanhe River, where the natural landscape is exceptionally picturesque. The locality lies in an intermontane basin where the crystal clear river reflects light as a mirror, fish frolic in the water, and sandy beaches line the banks. The region is exceptionally pristine and may be considered a genuine vacation resort awaiting development. Fengning Co. is a Manchurian Autonomous Region of Hebei Province. It is reputed to have been a strategic site for barracking troops during the Qing Dynasty, due to its close proximity to both Chengde to the east and Gubeikou to the south. Currently the nomenclature of the local hamlets and villages reflect Inner Mongolian administrative regions or military encampments, and thus the name Gubeikou (Ancient Northern Mountain Pass) implies a strategic pass of difficult access which penetrates the mountain ranges and river valleys of northern Hebei Province. Gubeikou is currently an important transportation and communication center near Beijing, serving northern and eastern Hebei Province.

3. Boluochi

This site is located in the hill-country of western Liaoning Province, which is a transition zone between the Inner Mongolian Plateau and Liaohe River plain 50 km west of Chaoyang. Coordinates are 120° east longitude and 41°45' north latitude. The fossil locality itself consists of a low mound approximately two km west of the town of Boluochi. Six excavations have been conducted here, initiating in 1989 and yielding over thirty avian specimens in addition to fish, invertebrates, and plants. Provincial authorities have officially designated the site the Chaoyang Paleornithological Preserve. It lies in the lower portion of the Early Cretaceous Jiufotang Fm.

Chaoyang is located in the western hill region of Liaoning Province, between longitude 118° 50' - 121° 17' and north latitude 40° 25' - 42°22', and is the administrative capital os the region. The region spans an elevation of 600 to 1800 m with peaks rising one upon another and chains of undulating hills interspersed with mountain valleys cut length and breadth by arroyos. In this region, the Nuluerhushan mountain range lies north of the Dalinghe River, and south of the river is the Songlingshan Range, both of which constitute northeast-southwest trending ranges.

Chaoyang is an ancient city with a long history of cultural occupation that extends back 150,000 years with the "Gezidongren" Paleolithic site on the bank of the Dalinghe River. Even more noteworthy are the abundant chapters of multi-tribal history in the Chaoyang region including the lithic industry, Gezidongren, and even further back to several Peking Man related sites at one-half million years. There are over 40 cultural and human occupation excavations, known as the Hongshan Cultural Sites of Chaoyang, with its main excavations represented by the Neolithic Niuheliang sites including those of Jishizhong and Nushendian, and the large constructions and altars of Jinzitashi, all of which reflect over a thousand years of Chinese civilization and provide significant evidence for the origins of the Chinese race and the genesis of agriculture, culture, and religion. Genuinely worthy of interest is that these significant cultural sites of China are only just over 20 km west of the Boluochi avian quarries.

Historical documents record this city as the capital Longcheng during the period of the Sixteen Kingdoms (also known as Former Yan [341 AD], the Later Yan, and Northern Yan). During the Northern Wei, Sui, and Tang dynasties (386-905 AD), its name was changed to

Xingzhongfu (prefecture). Subsequently, during the Liao, Jin, and Yuan dynasties (907-1333 AD) it was regarded as a significant metropolis, governed by successive feudal dynasties, that represented a vital communications link in the northeast central plateau region. It was also a central plateau cultural center, a center for cultural exchange between the northern and northeastern nationalities, and a strategic military outpost. The name Chaoyang was given to the city during the 14th year of the Emperor Qianlong of the Qing Dynasty (1749). The city is currently the administrative center of three municipalities: the Chaoyang municipality (local division), Beipiao municipality (county division), and Lingyuan municipality (county division) as well as the administrative center of three counties (Chaoyang Co., Jianping Co., and the Harqin Zuoyi Mongolian Autonomous region), and two districts (the Shuangta District [county division] and Longcheng District [county division]).

Chaoyang is known as a “cultural metropolis” in Liaoning Province with artifacts excavated from the region on display in over 20 nations and other regions of China. Numerous international scholars visit the city to conduct research. There are eight localities of interest at Chaoyang: the Baotajinyan Pagoda, Kobeichangcun, Linxiuyongyun, Fengshanmuji, Nanqiaojingdu, Dongyuqiaoge, Xilingshantai, and Lingheyuzhang. There are also over 100 ancient pagodas in the region, two of which are notable and within the city limits, named the Nanta and Beita pagodas. Beita is a Tang Dynasty brick pagoda. Its foundation was laid during the Northern Wei Dynasty when it was known as the Siyanfotu Pagoda and during the Sui Dynasty was named the Baoansita Pagoda as part of the Baoan Temple. A large set of valuable cultural relics has been excavated from the pagoda’s chambers. The Youshunsi Buddhist Monastery lies within the city limits and ancient tombs are scattered about from the Warring States Period, in addition to the Western Han, Sui, Tang, Liao, and Jin dynasties. This is genuinely a place of value for both conducting research and viewing cultural artifacts at one’s leisure.

4. Meileyingzi.

This site is located approximately 20 km southeast of Boluochi, Liaoning, described previously. Traveling from Buolochi one crosses the Dalinghe River which is lined by small sand dunes that create some difficulty in driving. The locality is on the northern slope of a deep innermontane ravine in sediments equivalent to those at Buolochi, the light gray shales of the Jiufotang Fm.

5. Jianshangou.

The site is located on the southeast municipal boundary of the city of Beipiao, Liaoning, and under the jurisdiction of the town of Shangyuan. The distance from Shangyan to Beipiao is 30 km and the towns are linked by public road and railway. Jianshangou is approximately 18 km west of Shangyuan and is the type locality of *Confuciusornis*. The site is located in the basal calcareous shales of the Yixian Fm., where the sediments are interbedded with volcanics.

Beipiao is known as the coal production capital of western Liaoning Province. The history of coal mining here can be traced back to the reign of the Emperor Guangxu of the Qing Dynasty (1875) and by 1920 large-scale mining operations were initiated. Beipiao Co. is located northeast of Chaoyang at 120°16’-121°20’ east longitude and 41°20’-42°30’ north latitude. Its eastern neighbor is the city of Fuxin, very close to the southwest is Chaoyang, the south and southeastern borders contact Jinxian and Yixian counties, and to the north and west is Inner Mongolia. In addition to coal production at Beipiao, gold and iron is also mined, constituting one of the two gold-producing counties in China.

Numerous physical attractions occur within the confines of Beipiao, the primary site which is Mt. Daheishan (Great Black Mountain) which borders the Inner Mongolian Aohanzu tribal zone with its imposing perilous peaks and luxuriant dark green verdant forests from which the mountain derives its name. Its principle peak is a planar surface with an elevation of 1,074 m upon which are ruins of a Liao Dynasty sentry post (907-1101 AD) associated with a well, remnants of a vegetable garden, housing structures, and other cultural features. Littering the peak are cultural artifacts including ceramic fragments, arrowheads, and copper coins. At the base of the mountain is a continuously flowing low temperature mineral spring with an average temperature of 18° C, which would be an ideal location for convalescence. The forest trees here are towering, birds and beasts flit about sporadically, there are pastures with deer grazing, and generally the area is a famous scenic spot for travelers.

Approximately 20 km north of Beipiao is an Inner Mongolian encampment where there is an ancient willow tree over 400 years old that has enveloped elms and which has been provided the name “Yimu bao ernu” (a mother embracing two daughters). This tree’s trunk diameter is 179 cm and has become hollow. Of interest is that within the hollow are growing two prominent “sister trees,” one being an approximately 100 year old 16 m tall elm and the other being an approximately 90 year old 16 m tall elm. This scene reminds the local villagers of a mother embracing two daughters, interdependent for survival, and sharing immeasurable love.

Just over 20 km southwest of the city of Beipiao at the town of Taohuatu stands a “weather tree.” This tree, the willow *Chosenia macrolepis,* is able to forecast rain. The morphology of its branches resembles a willow but its leaves resemble the Russian thistle *Salsola collina.* In the spring, summer, and fall this tree does not bud until rain approaches, whereupon red buds blossom into pink flowers. After it ceases raining the flowers then immediately and completely drop from the tree. In this manner, if the branches are laden with densely packed flowers, one knows that a heavy storm is approaching and if the buds are absent from the tree then it will be a clear day. This tree has thereupon become a meteorological station for the local populace and has attracted innumerable curiosity seekers and travelers.

Vertebrate fossils in the Jianshangou region of Beipiao are produced from the calcareous shales of the Yixian Fm. In addition to a large quantity of primitive birds being entombed here, there are also primitive mammals, reptiles, amphibians, and fishes. Furthermore, specimens of primitive angiosperm seeds are also recovered which represent a breakthrough in evolutionary biology.

The road log to the most prominent fossil locality from Beijing consists of two routes: The eastern route initiates from Beijing and passes through the Hebei Province counties of Yutian, Fengrun, Wuning, Qinhuangdao, and exits the province at Shanhaiguan. One enters Liaoning Province and traverses the towns of Suizhong, Xingcheng, Jinxi, Jinzhou, and finally, a little over 20 km northwest of Yixian, Jianshangou. The western route leaves Beijing to pass through Shunyi, Huairou, and Miyun to enter Hebei Province and traverse the town of Xinglong, enter the mountain summer resort town of Chengde, then from Pingyang to Liaoning Province, beginning with the towns of Kazuo, Lingyuan, Jianping, passing the Early Cretaceous bird locality of Boluochi to reach Chaoyang, and from there only a little over 30 km to Jianshangou.

The eastern route is longer by more than 600 km and principally traverses the coastal tourist region, including the convalescent town of Beizaihe, the first gate of the Great Wall on the coast, Shanhaiguan, the ocean port Qinhuangdao, and the important strategic city of Jinzhou in Liaoning. The western route is comparatively shorter: the distance from Beijing to Chaoyang is 518 km, or a day’s travel. The sites of interest along this route include the resort mountain town of Chengde, the extremely significant Liaoning Neolithic site of Niuheliang, and the Early Cretaceous bird locality of Boluochi.

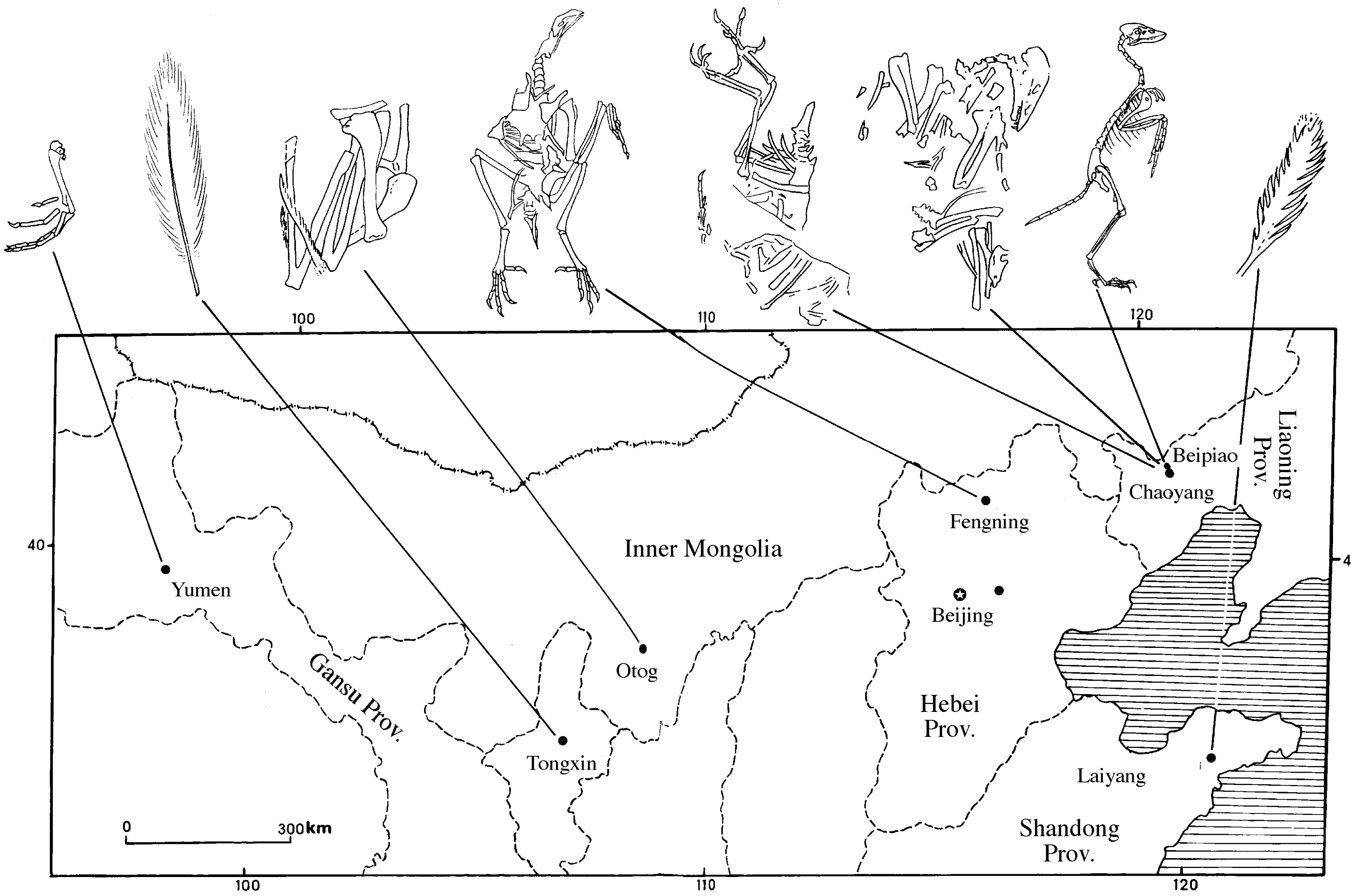

Figure 12. The distribution of Chinese Mesozoic bird localities.

6. Chabu Sumu.

Bird skeletons are produced from an Inner Mongolian site approximately 60 km southwest of Otog Qi, in a river valley of the expansive Maowusu Desert on the south bank of the Yausitu River approximately 10 km east of the prominent temple of Chabu Sumu. Coordinates are east longitude 108° and north latitude 38°50'. The city of Otog Qi is approximately 200 km southwest of Dongsheng, the capital of the Yikezhaoming Tribe.

Two routes are available from Beijing to the Chabu Sumu locality. The northern route begins in Beijing at Changping and exits the Great Wall at Badaling to first arrive at the town of Xuanhua. One then passes through Zhangjiakou (Kalgan) and continues north to the Inner Mongolian metropolis of Jining, which constitutes an important Inner Mongolian and international railway transfer station. From Jining one then travels west approximately 200 km to the provincial capital of Hohhot, then west upon the alluvial plain that bounds the southern margin of the Daqingshan Mountains (a portion of the Yinshan Range). After just over 200 km one arrives at the city of Baotou, which is a steel producer on the grassy plain of the Gobi. One then continues west to the western Inner Mongolian metropolis of Linhe in the great bend of the Yellow River. Continuing southwest one then arrives at the abundant coal-producing capital of Wuhai, then turns southeast for approximately 160 km to arrive at the city of Otog Qi.

To take the southern route one departs Beijing through Zhangjiakou, then through the city of Yanggao in Shanxi Province to Inner Mongolia through the great gate at the city of Fenzhen along the Great Wall. One then travels to Hohhot and from there travels south to Dongsheng crossing a portion of the desert region to arrive at Otog Qi. This route is relatively shorter, although it still requires three days to reach the fossil locality.

The locality of Chabu Sumu is within the desert on the Ordos Plain, so accessibility is difficult regardless of whether one takes the northern or southern route. Moreover, on the road it is possible to appreciate the local scenery and landscape. Scenic and cultural attractions include the Baijiezhaojunmu Tombs around Hohhot, and other places of historic interest. In the city of Baotou one may tour Wudangzhao, which is the largest sacred Buddhist site in Inner Mongolia. And in the city of Dongsheng one will certainly want to visit the Chengjisiganling Mausoleum where not only magnificent architecture is presented but the surrounding grassy plain is exceptionally beautiful. Furthermore, on the road to Chabu Sumu from Dongsheng, if one encounters a wind storm it is possible to witness migrating sand dunes, which are particularly imposing.

7. Changmachenjiawan:

This locality is approximately 120 km southwest of Yumen, Gansu Province at coordinates of nearly 97° east longitude and 40° north latitude on the northern margin of the Qilianshan Mountains. The site lies in a portion of the Jiuquan Basin in Late Jurassic to Early Cretaceous terrestrial sediments. The avian specimens are produced from gray-brown mudstones in the middle of the Early Cretaceous Xiagou Fm.

From Beijing it takes a minimum of five days to reach this locality and it is evident from a map that regardless of taking a northern or southern route, it is necessary to traverse several provinces and numerous sites of interest.

It is necessary to explain thatsince this manuscript was written, more Mesozoic bird localities may have been discovered.

History of research

Prior to the discovery of Mesozoic birds in China, the early evolutionary history of birds was not as well understood as those of other vertebrates, although the subject of avian origins has become a focus of attention among paleontologists and biologists since the first description of *Archaeopteryx* in 1861. But for a hundred years now, there have been no specimens excavated which predate *Archaopteryx* (the 1991 description of the Late Triassic *Protoavis* has not been generally recognized by ornithologists) and no additional contemporaneous avian specimens have been recovered from any other region. There is a plethora of literature discussing this archaic bird, and persistent controversy surrounds the origin of the class due mainly to the lack of fossil data in the geologic record. Many morphological characters of *Archaeopteryx* are shared with the Reptilia, whereas those uniting the genus to Aves are fewer. Currently, a majority of workers consider *Archaeopteryx* as representing a side branch and not a stem group in the evolution of the class. Conversely, the reason *Archaeopteryx* stimulates such keen interest and high regard in the academic world is because it has both reptilian and avian characters, indicating that Aves indeed evolved from a reptilian lineage.

Numerous reptilian characters in addition to several avian characters are present in *Archaeopteryx* providing an exceptional transition form between the two classes. Its discovery strongly supports Darwin’s theory of evolution. Reptilian characters in *Archaeopteryx* include the following: (1) an extended tail composed of numerous caudal vertebrae; (2) vertebral centra are amphicoelous and not anemocoelous; (3) sacral vertebral count is few, being only six; (4) skeletal elements are not pneumatized and lack pleurocoels; (5) upper and lower jaws bear numerous acute teeth; (6) metacarpals have not been formed into a carpometacarpus; (7) forelimb digits are separated into three clawed digits; (8) tibia and fibula are equivalent in length; (9) tarsals are unfused and do not compose a tarsometatarsus; and (10) ribs are gracile and do not bear uncinate processes.

Characters in *Archaeopteryx* that relate it to Aves include: (1) the presence of feathers, including primary and secondary flight feathers, and tail feathers; (2) a furcula composed of fused clavicles; (3) the posteriorly elongated pubis and ischium and compressed preacetabular region of the pelvis; (4) four digits on pes with the hallux in opposition to the other digits; and (5) the third metacarpal fused to the carpals.

To date, seven *Archaeopteryx* specimens have been recovered from the marine and lagoonal sediments of the Solnhofen region of Bavaria, Germany, and after numerous years of study, two species are now recognized: *A. lithographica* and *A. bavarica.* Currently, there is intense interest in the skeletal morphology of the genus, and prolific hypotheses regarding avian origins. Mudge (1879) proposed that the ancestor of Aves was an underived reptile, or a member of the thecodont reptiles in the stem group Archosauria. Fossil evidence for this hypothesis was provided by Broom (1913) in his descriptions of the small Early Triassic South African pseudosuchian *Euparkeria* and also by Heilmann (1913, 1926) in his descriptions of the South African Triassic *Sphenosuchus*. *Euparkaria* is bipedal, gracile in morphology with a delicate skeleton, and a portion of its skeleton is pneumatized. Its skull is also gracile and has large temporal and antorbital fenestrae. Broom, however, not only recognized *Euparkaria* as the ancestor to birds but also to all the major reptiles. *Sphenosuchus* may represent a primitive arboreal crocodilomorph.

Feduccia and Wild (1993) described the bird-like archosauromorph *Megalancosaurus* from the Late Triassic of Italy, providing more evidence for the archosaur-bird hypothesis. Its beak resembles *Archaeopteryx* with numerous teeth; there are large avian-like orbits, and a pair of large antorbital fenestrae. Further characters resembling Aves include its relatively long cervical series, and a narrow and long scimitar-shaped scapula.

Several workers have promoted hypotheses uniting Crocodylia and Aves as sister groups based upon comparative skeletal morphology. These characters include the double articulation of the pneumatized quadrate, presence of a mandibular fenestra, similar position of the internal acoustic meatus, the cerebral branch of the carotid artery being surrounded by two pneumatocoels, thecodont dentition with short, conical, and bluntly rounded crowns which bear a constriction between the crown and tooth root; and pneumatized internal cranium.

Martin (1979) stated that *Hesperornis* and the Crocodylia shared derived cranial cavities that were absent in dinosaurs and as such the Crocodylia were the closest living amniotes to Aves. Walker (1981) concurred that Crocodylia and Aves shared an intimate sister group relationship within the Archosauria.

Sereno and Arcucci (1991) studied articulations of the tibiotarsus and noted that *Euparkeria* may have shared a simple condylar articulation with Aves. This provided new impetus and further confirmed that Aves and Crocodylia shared a common ancestor.

The pneumatized skeleton of *Compsognathus* is produced from the same strata as *Archaeopteryx*, and has a body size equivalent to a chicken and cranial, hindlimb, and caudal morphology similar to that of *Archaeopteryx*. This provoked Huxley (1864, 1867) to propose a dinosaurian origin of Aves which was supported by reknowned comparative anatomists of the time including Cope (1867), Parker (1864), Darwin (1872), Schmidt (1872), Marsh (1877), Gegenbaur (1878), Williston (1879), Parker (1882), and Baur (1883, 1886). The skeletal morphology of birds and small theropod dinosaurs shares numerous synapomorphies which include gracile and pneumatized skeletal elements, elongated cervical vertebrae, derived forelimbs with similar digital proportions, similar humerus and ulna morphology, scapula becoming elongate and narrow, sacral vertebra exceeding three in count, and tibia being light, gracile, with a proximolateral facet for the fibula. The most recognized authority on paleornithology, J. H. Ostrom (1974), supported the dinosaur origin theory and repeatedly states that Aves was derived from small theropod dinosaurs and that the ancestor of *Archaeopteryx* would share numerous synapomorphies with theropod dinosaurs, or that perhaps these would be due to convergence with one lineage developing into *Coelophysis* and the other into Aves. These synapomorphies and contemporaneous occurrences make the predominant hypotheses that of a common ancestor between dinosaurs and birds.

Among the various theories of avian origins, it is important to recognize which hypotheses are testable or documented. In the past, the most significant obstacle to understanding avian origins lay in the extreme absence of specimens in the fossil record, which greatly restricted anatomical research and understanding of archaic bird morphology, particularly relating to the comprehension of functional anatomy. In recent years, a large collection of Late Jurassic to Early Cretaceous birds has been excavated in China which provides the most current and valuable data in the origin and developmental radiation of Aves.

Mesozoic birds in China are distributed in the northern regions of the country. The sediments in which these specimens are deposited predominantly represent terrestrial deposits that containi what is known as the Jehol Fauna. These sediments are abundant in paleontological data and attract the attention of both Chinese and foreign paleontologists and geologists.

In the Late Jurassic to Early Cretaceous, Northern China was principally constructed as a series of fluviolacustrine basins, particularly in the western Liaoning region. The geological sequence indicates a regional series of northeast to north-northeast trending basins which basically represent intermontane fault or graben basins which were allegedly the result of the subduction of the Pacific plate beneath Eastern China. The consequent surface topography is therefore expressed as disjointed topographic relief. During this time period, and particularly in the Late Jurassic, there was frequent and intense volcanic activity which geologists refer to as one of the expressions of the

Yanshan Movement. During this period, igneous activity was intense, and the climate was correspondingly mesic and warm with abundant aquatic systems within the basins that supported a diverse biota, while the riparian and mountain slope habitats maintained a taxonomically diverse flora. As volcanic activity gradually decreased, there developed extremely well developed fluvial, lacustrine, and paludal facies in the Early Cretaceous, while pyroclastic facies waned, and the flora became exceptionally luxuriant.

Based upon lithologic and faunal characteristics, several geologists and paleontologists have concluded that the climate in the Late Jurassic to Early Cretaceous associated with the fossil birds was temperate and semi-mesic. But other data suggest a semi-tropical to warm mesic climate, as expressed by the sedimentary regime of predominantly gray and gray-green sandstones and mudstones containing a flora completely dominated by gymnosperms, particularly conifers, with the additional presence of *Ginkgo*. Ferns are dominated by *Selaginella* and secondarily by the Schizaeaceae. Insect faunas are represented by genera such as *Ephemeropsis*.

The fauna coexisting with the avian specimens is relatively complex and because it is supported by the relatively beneficial ecological conditions of the time, both the flora and fauna are extremely profuse and taxonomically diverse. Simplified faunal lists are provided below:

Vertebrates

Vertebrates include mammals, reptiles, amphibians, and fishes, which are the most prolific group and reflect the extensive aquatic systems of the time. To date there are at least eleven genera recorded. Most faunas are dominated by a *Peipiaosteus-Lyxoptera-Jinanichthys* complex (Jin, 1995) which consists of: *Peipiaosteus pani, Propsephurus liui, Liasteus hangi, Sinamia zdanskyi, Lycoptera davidi, L. muroii, L. sinensis, L. sankeyushuensis, Jinanichthys longicephalus, Huashia, Nieerkunia,* and *Longdeichthys luojiaxiaensis.*

The fish fauna coexisting with the avian genus *Gansus* represents a significant assemblage that is slightly younger than that of the Jiufotang Fm. and is regarded as the *Jiuquanichthys-Cocolepis-Qilianichthys* complex (Ma, 1993). It consists of *Coccolepis yumenensis, Qilianichthys huaxiaensis, Q. changmaensis, Changma shenjiawanensis,* a primitive teleost (indet.), and a small quantity of Amiiformes. The Jiuquan fish fauna is predominantly distributed where there are many specimens of *Jiuquanichthys liai, Ikechaoamia orientalis,* and *Sinamia.*

In 1994 during an expedition to western Liaoning, in the government offices of the town of Shanyuanzhen, in Beipiao, the author was shown two reptile specimens, one representing an anuran and the other a squamate. At that time he thought he would borrow them for study but the civic authorities would not permit it. In 1995, when he returned to conduct further research, these specimens had corroded into an unrecognizable state. This was indeed regrettable and the deteriorated condition really should not have occurred. These specimens represented the oldest documentation of these forms in China and the anuran represented a specimen rarely documented globally. Additional Reptilia in the fauna include *Manchurochelys manchouensis, Yabienosaurus tenuis, Monjurosuchus splendens, Chaoyoungosaurus liaoxiensis, Teilhardosaurus carbonarius,* and *Psittacosaurus meileyingensis.*

In 1994, at the same locality that produced *Confuciusornis* at Jianshangou, a complete skeleton of a symmetrodont mammal was discovered and is currently being described. It may represent a unique taxon and is significant in the study of mammalian evolution and radiation.

Invertebrates

Invertebrate specimens are both more plentiful and taxonomically diverse. Particularly prolific are the insects, which are represented by approximately 300 specimens representing 18 orders, including the Diptera, Coleoptera, Odonata, Orthoptera, and Neuroptera. Two branchiopod faunas are also represented: the *Jibeilimuadia-Keratestheria* complex and the *Eosestheria* complex. Eastern branchiopod complexes are exceptionally abundant in the Yixian and Jiufotang formations where they are found at all locations and are further supportive evidence for abundant aquatic systems. Ostracods are also recovered with avian specimens, occur diachronously, are represented by different complexes, and represent one of the most abundant biotic forms in the sediments.

Botany

Floral data indicate that after a Middle Jurassic arid and semiarid period on the continent, the botanical record becomes reduced, but by the Late Jurassic to Early Cretaceous, particularly in northern China, the climate became warm and mesic with a completely revitalized and well developed biota of abundant taxa. This flora is represented by several profuse and particularly robust gymnosperms such as *Ginkgo* and conifers. Five floral types are recognized in approximately 50 genera and 90 species: the Equisetinae, true ferns, cycads, *Ginkgo*, and conifers.

Chapter 2. Taxonomic descriptions

Class Aves Linnaeus, 1758

There has been no consensus regarding the taxonomy and phylogeny of the class Aves in the past 200 years. Haeckel (1866) erected the subclass Sauriurae based upon the morphological characters of *Archaeopteryx* and placed the remaining extant avian taxa in the subclass Ornithurae. Subsequently, Stejneger (1885) erected the subclass Odontoholcae based primarily upon Marsh’s (1872) description of *Hesperornis.* This phylogeny has persisted for nearly a century.

The subject of avian origin and evolution deepened from 1950’s to 1980’s following the taxonomic and morphologic descriptions of extant forms in addition to the increase of paleontological specimens. This was particularly due to extensive global discoveries of avian specimens from the Cretaceous. Wetmore (1940) and Walker (1981) each proposed their own phylogenies: the latter erected a new subclass Enantiornithes based upon autapomorphies of the Late Cretaceous *Enantiornis leali* from Argentina. Zheng (1982) subsequently recognized two subclasses: the Archaeornithes and the Neornithes. Later, Cracraft (1986, 1988) conducted detailed analyses of the major lineages of Aves and concluded that *Archaeopteryx* was the sister taxon to the entire class, whereas *Hesperornis* and *Ichthyornis* were the sister taxa to modern Aves. He also believed that *Enantiornis* shared an intimate relationship with the Carinatae but was not significant in the analysis of archaic avian relationships, and he further questioned the legitimacy of the subclass Enantiornithes. Martin (1991) conducted another detailed analysis and comparison of *Archaeopteryx* and concluded that Mesozoic birds should be divided into two subgroups, Sauriurae and Ornithurae; the former contains the infraclasses Archaeornithes and Enantiornithes, and the latter containes the infraclasses Odontoholcae and Carinata. However, Brodkorb (1963-1971) retained the taxonomy erected in the previous century. Needless to say, a plethora of accounts regarding avian systematic relationships exist, including Ostrom (1976), Sereno and Rao (1992), Norell et al., (1995), and Fastovsky and Weishampel (1996).

The discovery of abundant Mesozoic bird specimens in China supplements hypotheses and fills vacancies in avian systematics. Not only are these specimens numerous but they also manifest a variety of morphologies, reflecting various degrees of evolutionary states, while their diversity assists in the interpretion of the paleoenvironment. At one locality specimens are extremely morphologically distinct and exhibit different evolutionary phases. This is particularly significant toward understanding Late Jurassic and Early Cretaceous avian phylogeny.

Numerous workers have conducted research upon the diagnosis of avian characteristics including Walker (1981), Cracraft (1988), and Kurochkin (1995). These characters include: the presence of feathers and furcula, completely fused astragalus and calcaneum, elongated premaxilla, reduced maxillary process of the premaxilla, absence of a quadrate-squamosal contact, absence of a postorbital, squamosal and occipital are completely fused, proximal metatarsals are fused, caudals are not in excess of 25, forelimb is rotated with incipient folding upon the lateral side of the skeleton, digit I is in opposition to remaining digits, and the pelvic girdle is posteriorly inclined to a moderate degree.

Sauriurae Haeckel 1866

This long established subfamily contains a single order, a single family, and a single genus (*Archaeopteryx)*. A second species *A. bavarica* was erected by Wellnhofer (1993), based upon a new specimen that possessed characters including the increased spacing of a serrated mandibular dentition. This specimen also documented the first description of a sternum. The continuous discoveries of Chinese Late Jurassic primitive birds will undoubtedly provide substantial supplementary members to this subfamily.

Because so few specimens represent this subfamily, there is controversy regarding its precise diagnostic characters. Principally recognized are: quadrate-quadratojugal are in contact, dentary is long and slender, cervical vertebrae are not heterocoelous, carpals are not fused, digits IV and V are reduced, scapula is conically shaped, coracoid is narrow, pubis is long and posteriorly oblique, sacrum bears six centra, tarsals have become lost, tarsometatarsus is basically fused, proximal tarsometatarsus is anteroposteriorly compressed, and lateral longitudinal grooves are present on ungual phalanges.

Order Confuciusornithiformes Hou, Zhou, Gu, and Zhang, 1995

Family Confuciusornithidae Hou, Zhou, Gu, and Zhang, 1995

Genus *Confuciusornis* Hou, Zhou, Gu, and Zhang, 1995

Species *Confuciusornis sanctus* Hou, Zhou, Gu, and Zhang, 1995

Specimens: In the initial publications (Hou et al. 1995A, 1995B, Hou et al. 1995) three Jurassic specimens with complete feather impressions were erected as the species (IVPP specimen numbers V10918, V10919, and V10895). However, subsequent observations of the incomplete hindlimb of specimen 10919 indicated rather significant distinctions from the type. Most recently a relatively complete *Confuciusornis* skeleton has been recovered that displays a hindlimb resembling that on V10895 and confirms the distinct discrepancies of the V10919 specimen. Therefore, this specimen will hereby be recognized as a distinct species with a description provided later in the text.

Stratigraphic position and age: Interbedded calcareous shales of the Late Jurassic basal Yixian Fm.

Locality: Jianshangou by the village of Shangyuanzhen, Beipiao Municipality (Beipiaoshi), Liaoning Province.

Ammended diagnosis: The size of the Eichstaff *Archaeopteryx* specimen. Edentulous but with regularly patterned grooves in the jaws indicating the presence of a keratinous beak. Orbit is large and antorbital fenestra is circular. Proximal end of humerus is expanded with a pneumatoceoel present. Ungual phalanx of the first digit is long and robust, manus phalanges are slender and unreduces, and carpals are unfused with metacarpals. Ischium is robust with a slightly expanded sital end and a dorsal process near its proximal end. A fifth metatarsal is present. Pes talons are large and recurved.

Summary description: Morphological studies of *Archaeopteryx* have been conducted for over 100 years and in the past 20 years numerous monographs and other works have been published upon it. Obviously, due to deficiencies in preservation, the interpretations of several morphological characters are inconsistent. Due to the absence of a complete squamosal, the precise configuration of the jaw articulation is in doubt. An additional ongoing debate concerns the nature of the pectoral girdle and the effective strength for flight. *Confuciusornis* postdates *Archaeopteryx* but due to its autapomorphic characters and the characters it shares with *Archaeopteryx*, is a new member of the Sauriurae represented by abundant specimens of Late Jurassic primitive birds which provide data for the comprehension of Jurassic avian evolution and diversity. They also provide insights into the origin of Aves.

In this study, documentation of the morphology of *Archaeopteryx* was based upon two casts provided to IVPP by the British Museum of Natural History and the Berlin Museum. In addition, reference is made to a restoration of the skeleton by Martin (1991). Additional documentation was derived from the paleornithological literature.

1. Occipital region.

Several occipital elements enclose the foramen magnum and form the posterior cranial wall. The foramen magnum on both *Confuciusornis* and *Archaeopteryx* are identical, being situated posteriorly and resembling the configuration of their reptilian ancestors. Only recently has the occipital region of *Confuciusornis* been prepared sufficiently for description. The left side is poorly preserved but the right side including the foramen magnum is well represented. Dorsal to the foramen magnum is a relatively substantial supraoccipital which, in posterior perspective, has a trapezoidal posterior wall. On its dorsal section a posteriorly extended crest surpasses the occipital plane and becomes confluent with the dorsal supraoccipital-parietal crest to represent the highest point on the cranium. Exoccipitals form the lateral walls of the foramen magnum, are larger than the supraoccipital, are transversely expanded, and constitute the largest pair of elements on the posterior wall of the cranium. Their most prominent characteristic is the formation of an exoccipital tympanic bulla, which is homologous to the exoccipital tympanic wing on extant avian taxa. At the lateral side of the tympanic bulla is a large and broad paroccipital process. Upon the anterodorsal margin of this process is the foramen for the hypoglossal cranial nerve (XII). Ventral to the foramen magnum is a relatively small basioccipital, although its morphology and that of the occipital condyle are obscured due to compressional distortion.

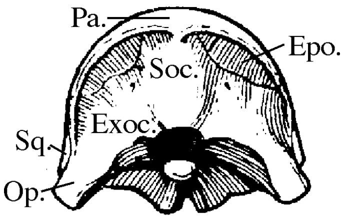

Figure 1. Occipital view of *Confuciusornis.*

2. Auditory region.

The auditory region is composed of three tympanic elements which bear an intimate relationship to the elements on the occipital region. The epiotic is a long, linear, and oblique element located on the lateral supraoccipital and dorsomedial margin of the exoccipital and contacts the ventral parietal. The opisthotic is posterolateral to the epiotic and is isolated from it posteriorly by the exoccipital process. It is a lamelliform element that is rather similar to that described for *Archaeopteryx* by Martin (1991). The prootic is difficult to distinguish due to being subjected to compressional distortion, but it should lie anterior to the epiotic and medial to the squamosal with the exoccipital lying posteroventral to it.

In the general design of the vertebrate skull, the squamosal is considered a portion of the zygomatic region, but during the course of avian evolution it has become a pair of elements that have undergone extensive modification, and are located on the dorsal angle of the cranium close to the auditory region. On *Confuciusornis* each is well developed and lies posteroventral to the frontal and ventrolateral to the parietal to compose the posterior wall of the neurocranium; it represents a principal component of the temporal fossa. In morphology, it is a trapezoid plate with a ventral margin that contributes to the articular surface in combination with the quadrate. This is in distinct contrast to that of *Archaeopteryx.*

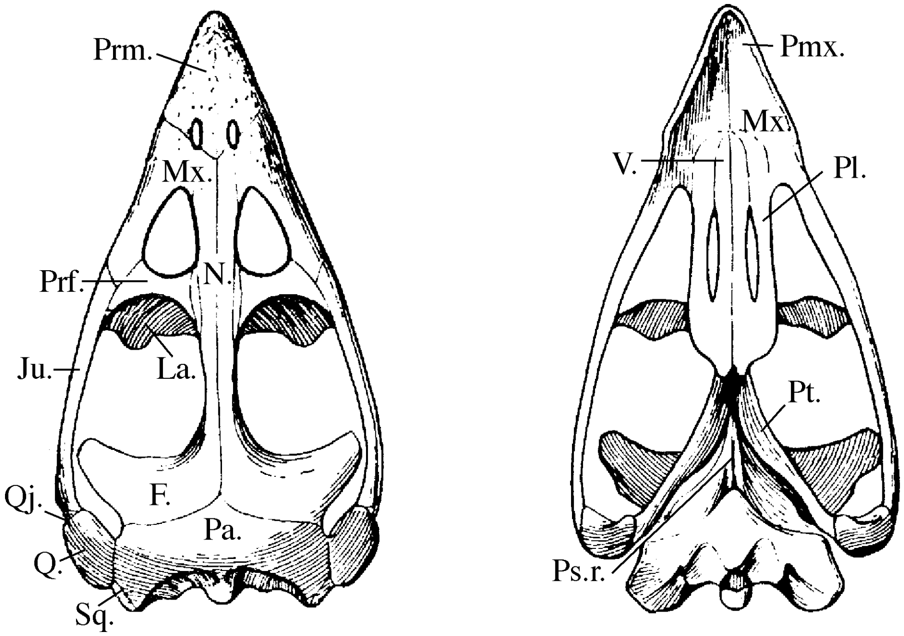

Figure 2. Diagrammatic restoration of *Confuciusornis sanctus* skull (from Hou, 1995).

3. Basal plate.

The basal plate of the avian neurocranium is composed of the basisphenoid with its associated processes and the rostral process of the parasphenoid. However, the most posteroventral wall of the neurocranium on true birds and on *Confuciusornis* consists of the horizontal plate of the basioccipital. The *Confuciusornis* basisphenoid and basioccipital have been somewhat displaced in position. The basisphenoid is relatively short, and the pair of anterior basipterygoid processes are extremely small. Anterior to the basisphenoid, the rostral process of the parasphenoid is well developed as being relatively long. Absent, however, is the typical pituitary fossa (sella turcica) between the basisphenoid and the rostral process of the parasphenoid, but an interorbital septum is extremely well developed.

4. Mid-parietal region.

The dorsal midportion of the neurocranium, or the parietal region of the skull, is composed of the parietal and frontal. On *Confuciusornis* these elements resemble those of *Archaeopteryx* and are not fused. The parietals are the principal posterodorsal elements of the cranium and are represented by two lateral elements but are incompletely preserved due to compressional distortion. The anterior parietal is thinly lamelliform, forms the dorsal surface of the neurocranium, and contacts the frontal with a broad suture line. The posterior portion of the parietal forms the posterior crest of the skull and increases in thickness to form a V-shaped laterally extended crest in the occipital region. The lateral margin of this crest contacts the posterior margin of the squamosal.

The frontals of *Confuciusornis* are narrow and elongated anteriorly but broad posteriorly, which differs from *Archaeopteryx* but is rather similar to the frontals described for *Protoavis* from the Late Triassic of the US, which has yet to be acknowledged as a legitimate member of the class Aves. Only the base of the frontal is not preserved. On the right side it is relatively well preserved and is overlain by the parietal. A large portion of the lateral frontal constitutes the medial wall of the orbit. The anterior frontal process extends along the interorbital region to the ventral nasal and forms the thin and narrow posterodorsal wall of the nares. The length of the anterior process greatly exceeds that of the base and there is a conspicuous unfused boundary line between the two frontal processes.

5. Orbitosphenoid.

This region is composed of the circumorbital and palatal series of elements. The circumorbital consists of the prefrontal and lacrimal, the former of which is represented by a pair of irregular triradial elements (only the left is visible on the type) located lateral to the anterior process of the frontal and posterior to the lacrimal. Two of its branches extend to the lateral side of the frontal, are short, thick, and form the anteromedial wall of the orbit. The branch that extends anteroventrally, or toward the ventral lacrimal, is relatively large and elongated with a terminus that fuses to the main body of the posteroventral lacrimal and forms a portion of the anterior wall of the orbit.

The long, broad lacrimal forms the anterior wall of the orbit and is the single element that separates the antorbital fenestra from the orbit. At the long and broad anterior margin of this element a crest extends from the margin of the frontal anteroventrally and distinctly defines the anterior orbital outline. The posterior edge of this crest is sharp, thin, expansive, and lamelliform.

The palatal complex consists of paired palatines, vomers, and pterygoids. The palatine has been compressionally distorted, obscuring its morphology, but it is located posterior to the palatal process of the maxilla. Expansively broadened at its base, it becomes a slender and elongated maxillary process. Its anterior margin contacts the palatal process of the maxilla with a tight suture line and posteriorly it is in contact with the pterygoid. The medial margins of the left and right basal portions extend anteromedioventrally to form a pair of short medial sections. The dorsal basal portions constitute the rostral process of the parasphenoid.

The vomer is the longest element at the midpoint of the anteroventral cranium. This narrow and long horizontal plate is posterior to the midline of the palatal process of the maxilla. Lateral to it lies the maxillary process of the palatine. Dorsal to the vomer is the olfactory canal. The internal nares should lie at its posterior terminus and medial margins of the palatine, although this cannot be documented due to the affects of compressional distortion.

The pterygoid constitutes a major element of the medioventral neurocranium and tightly unifies the anterior and posterior portions of the skull. It is shaped as a curved rod with three contact surfaces or individual processes. The anterior process contacts the posteromedial margin of the palatine. The second process lies posterior to the anterior process and anteromedial margin of the pterygoid where it contacts the basipterygoid process. The third process ascends from the pterygoid to contact the quadrate. At the anterior branch of the quadrate there is a suture line (distinct on the left side) that very possibly represents a contact with the quadrate process of the pterygoid.

6. Ethmoid.

A pair of nasals is visible at the anterodorsal portion of the cranium as a pair of elongated rectangular plates that are aligned along the midline of the rostrum and compose the majority of the dorsal olfactory canal. Their anterior margin contacs the short nasal process of the maxilla, laterally they contact the expansive medial margin of the maxilla, posterolaterally they fuse to the prefrontal, and posteriorly they terminate at the anterodorsal frontal.

7. Visceral cranium.

This region is composed of the mandibular arch and hyoid arch, but because of the preservational conditions of the specimens only a portion of the mandibular arch is recognizable.

The *Confuciusornis* quadrate has been affected by compressional distortion but still appears extremely robust and extremely irregular in morphology; it has several radiating branches, and crosses a basicranial articulation toward its contact with the neurocranium. Posterodorsally, it is in contact with the squamosal (or the opisthotic process) and anterodorsally it contacts the pterygoid. Dorsally, it is still only a single ascending branch with two surfaces and it is not discernible whether there are anterior and posterior branches here. The posterolateroventral section fuses with the terminus of the quadratojugal and jugal. The main body of the quadrate is expansive to facilitate the mandibular musculature; there are several attachment surfaces and thickened inflations. On the London specimen of *Archaeopteryx* the right quadrate is relatively well preserved and resembles that of *Confuciusornis*, although its posterodorsal contact appears to be inconsistent.

The quadratojugal of *Confuciusornis* resembles that of *Archaeopteryx* in being a relatively small triangular plate that is ventrolateral to the jugal. Its horizontal surface is relatively spacious and is fused dorsomedially to the jugal. Its vertical surface is relatively thin, slender, and extends posterodorsally; its distal end is configured as an acute and thin plate that fuses to the ventrolateral surface of the quadrate. The posterior quadratojugal and jugal form the posteroventral portion of the orbit.

The jugal is an elongated plate that forms the ventral margin of the orbit. Its anterior portion is relatively broad and becomes confluent with the maxilla. Just dorsal to the maxillary contact it is in contact with the ventral margin of the lacrimal. Posteriorly it attenuates to form an acute terminus that curves dorsally and fuses to the lateral quadrate. At its horizontal portion its ventrolateral side is in contact with the quadratojugal. In later species of Aves the postorbital process facilitates the musculature with the dorsal jugal.

The maxilla composes the principal region of the rostrum and consists of a pair of large elongated and expansive anterior cranial elements with a complex morphology. Its four components are the maxillary body, nasal process, jugal process, and palatal process. From dorsal perspective, the anterior maxillary body is expanded and the posterior portion is narrow. Anterolaterally there are two nutrient foramina. There are shallow striations approaching the midline which confirm the presence of a keratinous beak. The posteromedial margin extends posteriorly toward the dorsal midline to compose a narrow nasal process. Its posterolateral portion extends posterodorsolaterally to form the jugal process. The anterolateral side of the main body of the maxilla curves ventrally to form the lateral margin of the dental trough. The ventral palatal process is visible as an expansive and flattened plate with its anterior margin in contact with the palatal process of the premaxilla, its anteromedial end in contact with the vomer, and its posterior portion in contact with the palatine.

The premaxilla is irregular in shape and shaped much like an arrowhead. Its components are the main body, the dental trough process, and the nasal process. Its most characteristic feature is the systematically grooved ornamentation along the dorsal midline of the main body in addition to the presence of small lateral striations. This is further evidence that *Confuciusornis* possessed the first, although extremely short, bird beak. The anteroventral premaxilla is composed of a short dental trough process, but whether or not it bore dentition is unknown due to breakage (most recent specimens excavated confirm that the dentition is completely lost). The palatal process is broad and spacious with a posterior margin in contact with the anterior margin of the palatal process of the maxilla. The nasal process is the longest process of the element and forms an ascending branch which runs dorsally along the midline to form the separation of the external nares. The terminus is inlaid with the nasals.

Table 1. Cranial measurements of *Confuciusornis sanctus* (mm).

Length of skull	50.0
Breadth of skull	27.0
Orbital length	16.0
Orbital breadth	14.0
Antorbital fenestra length	9.0
Antorbital fenestra breadth	5.5
Antorbital fenestra to anterior rostrum	14.0
Premaxilla length	9.0

The postcranial skeleton of *Confuciusornis* is not as completely preserved as that of *Archaeopteryx.* Portions of the vertebral column are missing, the pectoral girdle is not preserved, and the forelimb is incomplete. Elements of the forelimb that are represented include the proximal humerus, which is extremely inflated and transversely expanded and has a head that is large and crescentic at its apex. The breadth of the proximal humerus exceeds half the humeral length, and has medial and lateral processes that are bluntly conical. At the midsection of the proximal end is a relatively large pneumatocoel which represents the oldest documentation of this character in the class. Its precise function is enigmatic although obviously it is related to facilitating flight and is a modification for weight reduction. The humeral shaft is relatively gracile and straight. In *Archaeopteryx* not only are there no adaptations for weight reduction, but the proximal humerus is narrow and long with an extremely small head. Clearly, these two are distinct because the latter genus lacks any complex derived morphological features for the adaptation for flight as in later avian genera.

Another significant character of the *Confuciusornis* forelimb is the particularly well developed ungual on digit I: its length exceeds that of the proximal phalanx, however its curvature is not as intense as in *Archaeopteryx.* The data and conclusions provided by Feduccia (1993) indicate that both *Archaeopteryx* and *Confuciusornis* had maintained manual and pedal ungual phalanges that were equivalent in their range of functional ability for perching and climbing. It is obvious on the *Confuciusornis* specimen block that there was a keratinous sheath covering the ungual that extended its length by approximately one-third.

Neither distal ulna nor radius bear multifaceted articular surfaces as noted on other genera of Aves and instead they bear condyles like ancestral reptiles for articulation with carpals. There are at least three relatively well preserved carpals. Three metacarpals are present: metacarpal I is short and broad. Metacarpal II is particularly robust and has a large articular facet for digit II. Metacarpal three is gracile and long, being the thinnest in the series, with a diameter less than half that of McII although its terminus is expanded. The first phalanx of digit I is the longest among all the individual phalanges. Digit II is equivalent in length to McII and is the largest among all digits. Digit three is the smallest and weakest among the digits but bears three phalanges, more than the other digits. Its first phalanx is particularly short and small.

Only a single relatively well preserved specimen of the pelvic girdle is represented (V10895). It lacks only its anterior portion and in general morphology resembles *Archaeopteryx* in comprising three unfused elements. The ilium is the largest of the elements; it has an expansively broad lateral surface that forms the majority of the acetabulum. Its dorsal margin is slightly crescentic with low pre- and postacetabular processes. In *Archaeopteryx* the dorsal margin is basically flat and straight, its preacetabular process is high and its postacetabular process is low and acute.

The ischium is relatively robust with a smooth and glossy surface. Proximoventrally a low crest extends posteriorly to the posteroventral terminus. At the proximodorsal margin posterior to the acetabulum, a dorsal process with an apex that contacts the ventral margin of the postacetabular process of the ilium and forms an acetabular-ischial fenestra. There is a thick inflation at the terminus of the dorsal margin to facilitate contact of the abdominal musculature. This thick inflation is shorter than the terminus of the ventral angle. Consequently, the terminus of the ischium lies on a dorsoventral oblique plane with a concave surface ventral to the thick inflation. There are at least two discrepancies from the London specimen of *Archaeopteryx,* the first of which is the bifurcated terminus of its ischium. Secondly, the dorsal process on *Confuciusornis* is quite distinct from all specimens of the former. Furthermore, many Early Cretaceous specimens have been recovered, but none of them bear this feature, and as such this is a taxonomic character worthy of note.

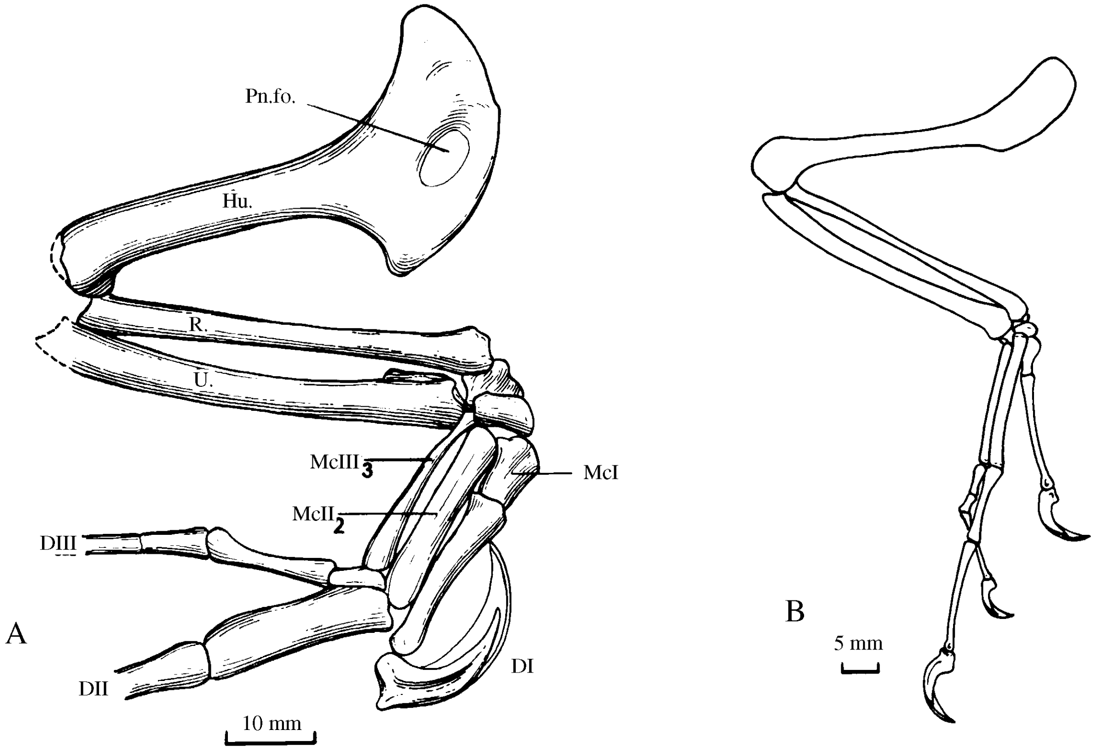

Figure 3. Comparison of *Confuciusornis sanctus* (Left) and *Archaeopteryx lithographica* (Right) forelimbs.

The pubis is incompletely preserved on V10895 as the distal end is missing, but a complete and distinct impression of the element is preserved in the matrix. The proximal end is relatively broad and spacious. Proximolaterally there is a small pubic process, the anteromedial margin of which composes the anteroventral wall of the acetabulum. The posterior pubis is thin and posteriorly oblique. The distal end is rounded but not expanded, nor is it fused with its distal counterpart. This is quite distinct from *Archaeopteryx* which has fused distal pubes that are expanded to form a boot.

Only a single left femur is preserved on V10895 that has been shifted somewhat in position. This is an extremely stout element, and although the head has suffered some damage, the rest of its proximal region and remaining element are well preserved. The proximal region is extremely flattened, broad, and spacious. The shaft is very slightly anteroposteriorly compressed and has a small amount of curvature but not to the degree as noted on *Archaeopteryx*. The two distal condyles are more well developed than in *Archaeopteryx* and project conspicuously anteriorly with a distinct intercondylar fossae.

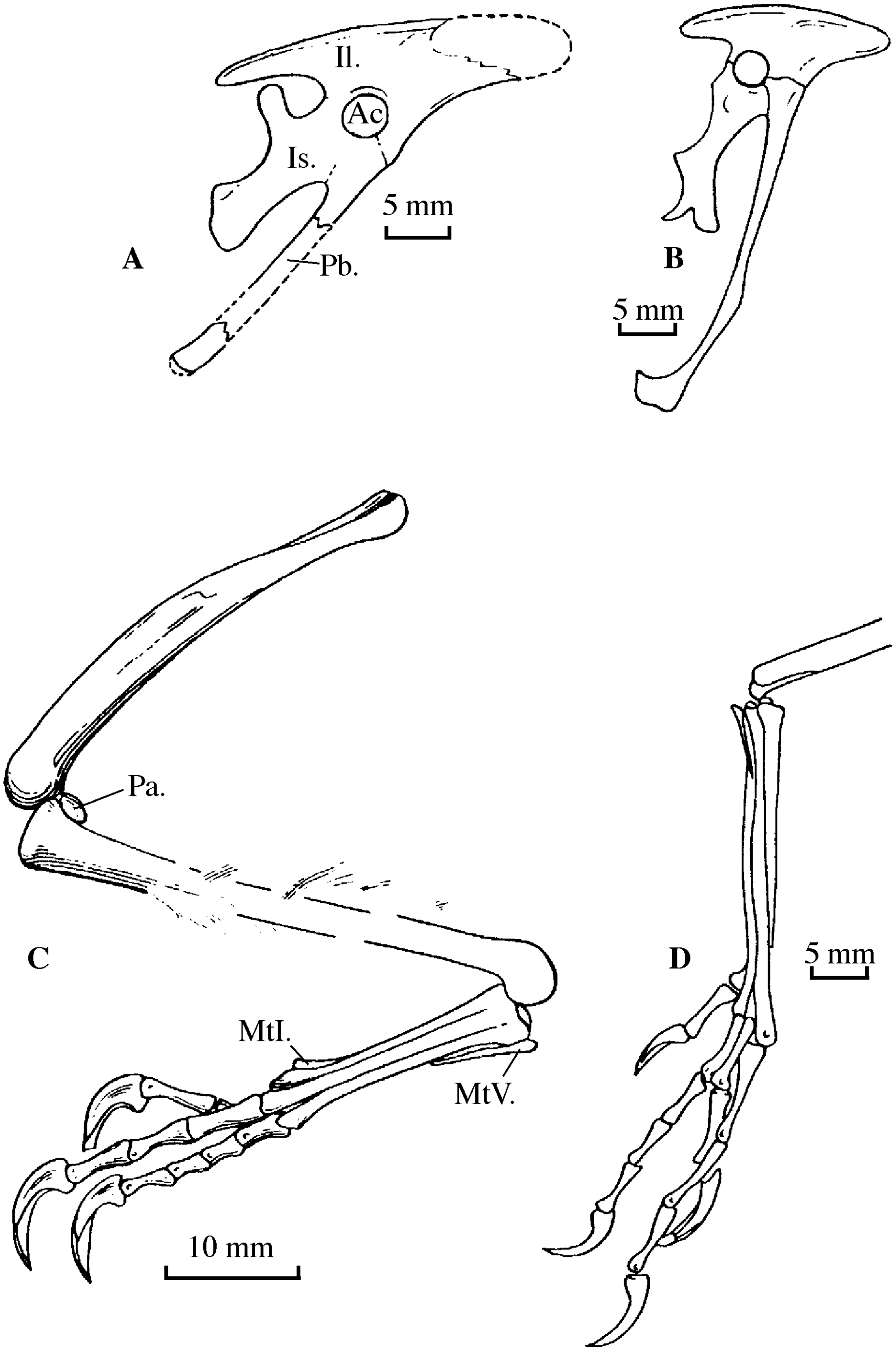

Figure 4. Comparison of *Confuciusornis sanctus* (A & C) and *Archaeopteryx lithographica* (B & D) pelvic girdle and hindlimbs.

On the hindlimb of V10895 there is an elliptical, flat, and smooth patella preserved between the tibia and femur. This is an extremely interesting phenomenon in avian evolution. This element acts as a buffer of equilibrium during the articulation of the femur and tibia and strengthens the flexion of the hindlimb, particularly during climbing and during active feeding, or a long period of flexion as in the process of brooding of young or roosting. Despite the absence of a noticeable posterodistal patellar groove, *Confuciusornis* may be compared to *Archaeopteryx* as having a relatively strong power of flexion due to the presence of a patella. A patella is not documented on any Early Cretaceous birds in China, which may be due to its being highly autapomorphic and thereupon lost.

The tibiotarsus is the longest and most robust skeletal element in *Confuciusornis*. Its termini are both slightly expanded, the shaft is straight, and laterally there are feather impressions upon it. As it is preserved in lateral perspective, the complete morphology of the condyles is obscured, but from lateral perspective the proximal articular surface appears to be slightly convex, unlike other archaic avian taxa in which there are two differentially sized concave articular facets. The proximal end is also slightly more expanded than the shaft. The ventral margins of the distal condyles are rounded, do not expand posteriorly, and are slightly anteriorly projected. From an anterior perspective it is difficult to discern whether or nor the condyles are triangular in morphology, and thus these features can not be compared to *Archaeopteryx*.

Only a single tarsal is preserved on V10895 and it is not entirely distinct. *Archaeopteryx* retains three reduced tarsals, which again indicates that *Confuciusornis* is more derived. The tarsometatarsus of *Confuciusornis* resembles that of *Archaeopteryx* in its length being only slightly longer than half the length of the tibiotarsus. Moreover, metatarsal V is retained and only the proximal tarsometatarsus is completely fused. The tarsometatarsus is relatively broad; metatarsal I is extremely short and slender and is only in contact with the distomedial side of MtII, which is also relatively slender. MtIII is the most robust and longest of the metatarsals, MtIV is slightly thinner than MtIII but more robust than MtII. MtII is the longest of the metatarsals.

Four digits are present on the foot which has a phalangeal formula of 1-2-3-4. Digit III is the longest with the third phalanx as a relatively long and hooked ungual that has a relatively well developed flexor tuberosity at its ventral base and flexor grooves laterally that run to the terminus of the ungual, indicating that *Confuciusornis* was well adapted for relatively strong claw flexion.

Comparison and discussion: Both *Archaeopteryx* and *Confuciusornis* are assigned to the Sauriurae (Hou et al., 1995) and share numerous characters. Both genera are recognized as primitive terrestrial birds despite the fact that *Archaeopteryx* is preserved in marine lagoonal deposits while *Confuciusornis* is derived from fluvio-lacustrine sediments. The two genera are also recognized as generally contemporaneous.

If one considers *Archaeopteryx* to possess numerous autapomorphic or derived characters, then *Confuciusornis* possesses even more. The seven specimens of *Archaeopteryx* represent the most primitive species of Aves and to date are regarded as the only data representing the origin of the class. The discovery of *Confuciusornis* destroys the notion that Jurassic birds are rare. Concurrent with the discovery of *Confuciusornis* is another report from Korea of a new discovery of *Archaeopteryx* from Jurassic sediments, which reportedly consists of a forelimb. Strict attention will be provided to the results of research upon this new material, particularly with regard to its relationships to *Archaeopteryx*.

Both *Confuciusornis* and *Archaeopteryx* share plesiomorphic characters for Aves, including the presence of feathers, absence of a postorbital, pelvic girdle rather conspicuously posteriorly oblique (moderately), and a fused proximal tarsometatarsus (Cracraft, 1988). However, both still retain numerous reptilian plesiomorphies, including unfused cranial elements on mature individuals, foramen magnum positioned posteriorly on the occiput, retention of three

Table 2. Postcranial measurements of *Confuciusornis sanctus* (mm).

Humerus	Preserved length	51.0
	Proximal breadth	28.0
	Longitudinal diameter of pneumatic foramen	7.0
	Breadth at midshaft	7.0
	Distal breadth	8.5
Ulna	Preserved length	42.0
	Proximal breadth	6.2
	Breadth at midshaft	4.0
	Distal breadth	5.3
Radius	Preserved length	45.0
	Proximal breadth	3.5
	Breadth at midshaft	3.0
	Distal breadth	5.0
McI	Length	9.0
	Breadth	3.5
McII	Length	22.5
	Breadth	3.5
McIII	Length	19.0
	Proximal breadth	2.0
	Breadth at midshaft	1.1
	Distal breadth	3.0
Manus digit I	Length	20.5
	Proximal breadth	4.5
	Length of ungual and sheath	20.0
Manus digit II	Phalanx 1 length	21.0
	Phalanx 1 breadth	6.0
	Phalanx 2 preserved length	10.5
Manus digit III	Phalanx 1 length	5.0
	Phalanx 2 length	14.0
	Phalanx 3 length (preserved)	13.0
Femur	Length	33.0
	Proximal anteroposterior breadth	5.0
	Anteroposterior breadth at midshaft	3.5
	Approximate distal breadth	3.3
Tibiotarsus	Length	41.0
	Proximal anteroposterior breadth	4.2
	Breadth at midshaft	3.1
	Distal anteroposterior breadth	4.2
Tarsometatarsus	Length	20.0
	Proximal breadth	5.0
	Distal breadth	4.5
	MtV length	8.0
Pes digit I	Approximate length of phalanx 1	5.0
	Ungual length	5.5
Pes digit II	Phalanx 1 length	7.0
	Phalanx 2 length	5.2
	Ungual length	6.5

Table 2. cont.

Pes digit III	Phalanx 1 length	6.0
	Phalanx 2 length	5.0
	Phalanx 3 length	5.0
	Ungual length	8.0
Pes digit IV	Phalanx 1 length	4.0
	Phalanx 2 length	3.0
	Phalanx 3 length	3.0
	Phalanx 4 length	4.5
	Ungual length	7.0
Ilium	Length	2.3
	Breadth at midsection	5.2
	Acetabulum anteroposterior breadth	4.0
Ischium	Length	13.3
	Proximal breadth	5.4
	Distal breadth	5.0
	Dorsal process height	3.0
Pubis	Length	22.0
	Proximal breadth	3.0
	Distal breadth	2.3

individually clawed manus digits, unfused metacarpals, and hindlimb with unfused tarsals. The position of these two genera in the origin and evolution of birds is quite evident, and although both are biogeographically distinct and their remains have been subjected to different taphonomic processes, they share noticeable morphological characters that indicate that after birds diverged from their reptilian ancestors, their evolution occurred at a modest rate in the Late Jurassic. This is particularly noticeable in the large quantity of specimens excavated from the Early Cretaceous of China (Hou and Liu, 1984; Hou and Zhang, 1993; Hou, 1994; Hou, 1995; Hou et al., 1995).

Although the evolutionary level of *Archaeopteryx* and *Confuciusornis* is extremely basal, they are distinct from each other in numerous characters as enumerated below:

1. *Archaeopteryx* bears numerous acute maxillary and dentary teeth while *Confuciusornis* is basically edentulous with the exception of an extremely small amount of premaxillary teeth.

2. The rostral region of *Archaeopteryx* possesses an abundant dentition and lacks grooving or striations that would indicate a keratinous beak. On *Confuciusornis* the premaxilla and anterior maxilla are grooved and striated, which distinctly indicate a keratinous beak. Supplemental dentition is absent. Thus, *Confuciusornis* represents the most archaic beaked bird.

3. The anterior frontal on *Archaeopteryx* is relatively broad, whereas on *Confuciusornis* it is extremely narrow and expands only posterodorsal to the orbit.

4. Controversy exists regarding the nature of the squamosal on *Archaeopteryx* but on *Confuciusornis* the squamosal is well developed with a distinct quadrate-squamosal contact.

5. *Confuciusornis* possesses a distinct prefrontal but the presence of this element on *Archaeopteryx* is controversial.

6. The posterior parietal crest of *Archaeopteryx* is not as high and broad as that of *Confuciusornis.*

7. On *Confuciusornis*, a long process extends posteriorly from the apex of the supraoccipital and is fused to the ventromedial crest of the parietal. This construction is distinct from *Archaeopteryx*.

8. *Confuciusornis* possesses a large exoccipital tympanic bulla which may represent one of the fully pneumaticized neurocranial chambers. This is absent on *Archaeopteryx*.

9. The lacrimal of *Archaeopteryx* has a well developed anterior branch but on *Confuciusornis* the lacrimal has a well developed posteriorly oblique branch.

10. The proximal humerus of *Archaeopteryx* is narrow and long but in *Confuciusornis* is broad and transversely expanded; its breadth is more than half the length of the shaft and a distinct pneumatic foramen is present.

11. On the *Confuciusornis* manus, the first digit's ungual phalanx is extremely long and exceeds the length of the first phalanx, but on *Archaeopteryx* this same element does not exceed the length of the first phalanx.

12. The distal ischium on *Archaeopteryx* is bifurcated but in *Confuciusornis* it is not bifurcated and lies at an oblique angle.

13. The distal pubes of *Archaeopteryx* are broad, spacious, booted, and fused to each other but on *Confuciusornis* the distal pubes are not expanded, the termini are rounded, and not fused.

14. *Archaeopteryx* has a straight dorsal margin of the ilium but on *Confuciusornis* this margin is crescentic.

15. *Archaeopteryx* lacks a patella but *Confuciusornis* possess an elliptical patella.

16. *Archaeopteryx* retains three distinct tarsals but *Confuciusornis* retains only one which is fused neither to the tibiotarsus nor tarsometatarsus.

18. Although there are a number of *Archaeopteryx* specimens only flight feathers are represented and torso feathers are extremely rare. *Confuciusornis* not only preserves flight feathers, but also abundant torso feathers, including down feathers.

A complete list of discrepant characters is not provided above although the characters enumerated are sufficient to justify the extreme distinctions between the two genera. The derived characters of *Confuciusornis* include the presence of a keratinous beak, absence of dentition, and presence of a pneumatic foramen on the humerus. A beaked primitive bird in the Late Jurassic is extremely noteworthy, because it represents the most archaic beaked bird, it indicates that the presence of a keratinous beak is a significant character in the early evolution of birds, and that it is a necessary implement in avian feeding. The reduction or loss of dentition corresponds to the presence of a beak. Following the presence of the keratinous beak and loss of the dentition, the digestive system of birds probably began modification, including the specialization of the stomach and the ingestion of gastroliths for grinding foodstuffs. This would replace the function of the dentition.

The specialization of the humerus in *Confuciusornis* indicates a correspondingly adaptive pectoral girdle. The presence of the pneumatic foramen is related to the proximal transverse expansion and represents an attempt to decrease skeletal weight while increasing the ability for flight, thereupon increasing the strength of the humerus and modifying the pectoral girdle.

The presence of flight feathers and secondary torso feathers (including down) completes the distribution of feathers on the avian torso in the Late Jurassic. The absence of these feathers on *Archaeopteryx* may be related to the depositional environment.

Comparison of these two genera leads to the following conclusions: There are noticeable distinctions between the two genera although fundamentally they are morphologically similar. The two genera are biogeographically distinct, but together with the documentation of an *Archaeopteryx* forelimb in Korea, indicate that there are at least three localities that produce Late Jurassic avian data. In the Late Jurassic the rate of avian evolution is quite distinct from that of the Early Cretaceous.

The current archaic avian data at hand is restricted, such that additional better preserved specimens are required to advance the comparative analysis of Jurassic and Cretaceous birds, confirm avian evolutionary patterns, allow further comprehension of biogeographical distribution in the Jurassic, assist in the comprehension of avian evolution and diversification, and provide better data for determining the origin of the class Aves. Current data implies that there was a tendency for avian lineages to radiate in the Jurassic.

New data on *Confuciusornis*

In the fall of 1995, Yueming Hu and others traveled to the Jianshangou region of Beipiao, Liaoning, to initiate investigations into Mesozoic vertebrates. He obtained a fossil bird specimen from one of the local residents of the small village of Sihetun near Jianshangou, on the western Chaoyang-Beipiao thoroughfare, and thereupon immediately telephoned the author of this monograph. Hou immediately traveled to the village to find three households which had collected a total of four *Confuciusornis* specimens, in addition to an exceptionally valuable different and smaller specimen which was excavated from the same stratigraphic horizon as *Confuciusornis.* The locals then provided Hou with a tour of the fossil producing locality for stratigraphic clarification, where he was astonished to find a large contingent of local inhabitants in the process of excavating fossils along a single productive layer. As a scientist, Hou had no authority to interfere in the activities of the local populace and as such found it best to notify the appropriate office of the local authorities about the presence of a paleontological heritage site.

The several specimens of *Confuciusornis* excavated in 1994 were incompletely preserved and were derived from different localities. The new specimens are relatively well preserved and consist of three specimens (including a single feather) produced from equivalent stratigraphic units which produced the skull and forelimb that represent the type. These sediments of mudstones and marls are consistent with those of the type locality.

After the initial publication that erected the genus *Confuciusornis,* there was extensive interest and strong reactions from paleontologists within and outside of China. These new specimens allow a more complete and supplemental description of the morphology of *Confuciusornis,* particularly in the postcrania and torso feathers, in addition to allowing a more complete comprehension and comparison to *Archaeopteryx,* and increasing the understanding of early avian radiation. These new specimens indicate that the genesis of the class Aves was neither in the Late Jurassic nor was this time period the first phase of avian evolution. The new specimens indicate a specialization of forelimb claws and the presence of a large sternum, and confirm the large proximal pneumatic foramen on the humerus, indicating that *Confuciusornis* was on the main path toward active flight. The presence of *Confuciusornis* supplants the traditionally recognized position of *Archaeopteryx* as the sole representative of the archaic condition. Its morphology forces workers to renew their opinions about primitive birds, avian origins, and developmental directions. A description of the new specimens is provided below.

Confuciusornis sanctus Hou, Zhou, Gu, and Zhang, 1995

Specimens: A single individual lacking its right forelimb, hindlimb, and tail (V110304).

Locality and stratigraphic position: Basal light gray mudstones of the Late Jurassic Yixian Fm., Sihetun Village, near the town of Shangyuanzhen, Beipiao (Beipiaoshih) Municipality, Liaoning Province.

Description: The skull has been subjected to dorsoventral and slight left lateral compressional distortion. The anterior left side is overlain by the right side and a large portion of the posterior frontal has been crushed such that suture lines are difficult to distinguish. However, clearly preserved on the right side are elements including the mandible, orbital elements, premaxilla, and nasals, which are all morphologically consistent with those of the type and clarify several details.

The premaxilla is relatively large with conspicuous, regularly patterned, relatively deep striations associated with relatively thick grooves on its margin. The anterior end of the premaxilla is not very acute and the nasal process of the premaxilla is not elongated, which are characters consistent with the type, and represent plesiomorphic characters for the genus. The premaxillary ramus is relatively long and high and its posterior margin contacts the maxilla with a long and oblique suture line. The small external nares are bounded anterolaterally by the premaxilla and posteriorly by the anterolateral portion of the nasals. The small size of these nares is in distinct contrast to the large and elongated external nares of *Archaeopteryx*. The anterior maxilla is high and its vertical posterior margin forms the anterior wall of the antorbital fenestra. The posteriorly extended ramus of the maxilla becomes narrow and forms the ventral wall of the antorbital fenestra. Striations on the maxilla are not as conspicuous as on the premaxilla and grooving is also light. The terminus of the maxillary ramus is in contact with the jugal. Further observations are not possible due to compression from the mandible.

Here, it is noteworthy to document a triangular element that forms the anterior wall of the antorbital fenestra between the posterolateral margin of the premaxillary nasal process and the posterior margin of the longitudinal branch of the maxilla. The presence of this element is confirmed on the type and hypodigm and it is determined to be a septomaxilla, an element that is located in various positions on the skulls of diapsids, including “thecodonts,” the Mesosauria, and therapsids. On *Confuciusornis* this element more closely resembles its homologs on the thecodonts. If this element is indeed a septomaxilla, its presence would be exceptionally significant in determining which clade of reptile gave rise to Aves and would lend credence to the theory that Aves originated from the thecodont reptiles.

The nasals are completely preserved and are consistent with those of the type, being a pair of linear plates that are not transversely expanded. Surficially, they are smooth, glossy, and lack any conspicuous pitting ornamentation. Posterolaterally, the nasals contact two small triangular postorbitals and anteriorly they contact the premaxilla, where there are a few short striations. The interorbital region, where the posterior nasals contact the anterior frontal, is extremely narrow. The nasals form the medial wall of the extremely large, elliptical antorbital fenestrae and occupy the medial surface of the palate, being isolated from the orbit only by the relatively large descending branch of the lacrimal. The lacrimal is an oblique, elongated, and triangular element. Further description of it is impossible due to being compressed against the sclerotic ring. The sclerotic ring is poorly preserved on the type but is completely preserved on the new specimen. It is surprising to note the thickness of the individual plates as opposed to the thin plates on extant taxa. Moreover, some of the plates are relatively large, providing extremely good protection for the eye. This specimen is comparable to the Eichstatt *Archaeopteryx* specimen, which also possesses a relatively well preserved sclerotic ring.

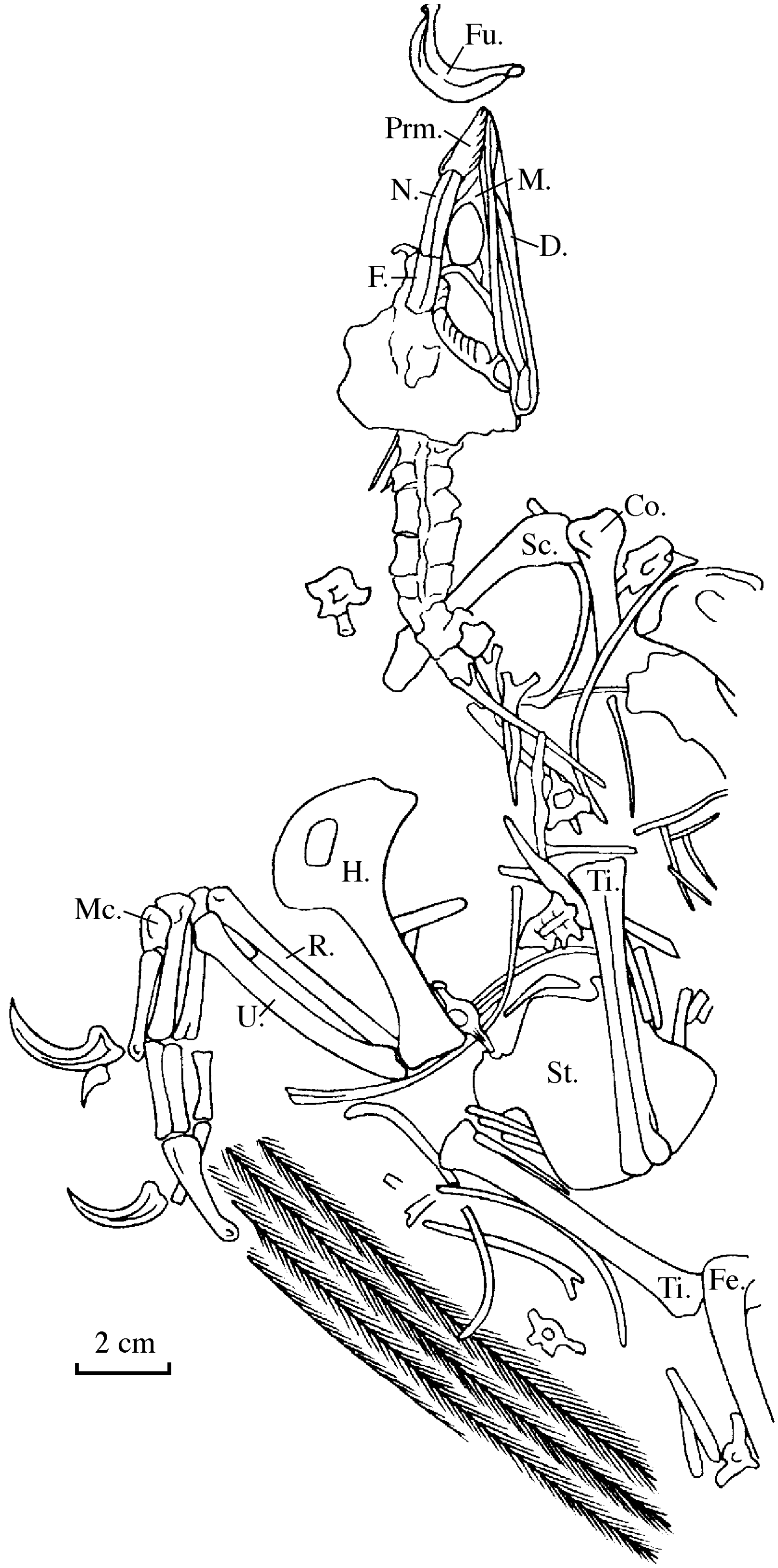

Figure 5. Drawing of *Confuciusornis sanctus* specimen V110304.

The cranium posterior to the posterior frontal is completely crushed and suture lines are indistinct, although the frontal appears to be consistent with the type; its anterior interorbital portion is extremely narrow and expands abruptly at the posterior wall of the orbit. Its posterior contact with the parietal is indistinct because the parietal is also extremely damaged. Cranial contact with the atlas is tight.

In lateral perspective, the main body of the quadrate is extremely distinct and is in articulation with the mandible. Its posterior margin is medially depressed and its posterodorsal process projects to contact the squamosal, although it has become displaced. The squamosal extends posterolaterally with its medial side overlapping the quadrate process. As on the type specimen, the squamosal is relatively well developed.

Most recently, Elzanowski and Wellnhofer (1996) reevaluated the skull of *Archaeopteryx*, confirming that the squamosal is a thickened plate, which is quite distinct from *Confuciusornis* on which it is a rather expanded cranial element. The anterior quadrate has a folded surface. Its anterior process has been compressed upon and interlocks with the pterygoid. The contact of the anteroventral angle of the quadrate with the quadratojugal has also been displaced and the gracile quadratojugal is exposed ventral to the posterior end of the mandible.

The right mandible on the new specimen is extremely well preserved. Fusion is incomplete at the symphysis as a suture line is still quite conspicuous. A well developed mandibular fenestra is present posteriorly. The retroarticular process does not extend posteriorly and instead is directly vertical, has a relatively flat ventral margin, and its anterodorsal margin ascends extensively to form a convex arc, resembling a design for intensive food aquisition. Anterolaterally, the mandible is striated but posteriorly it is relatively smooth and glossy. The dentary forms the lateral wall of the mandible, with its anterodorsal margin as a convex arc and the lingual surface being concave. In medial perspective, the angular extends anteriorly to become tightly fused to the lateral side of the prearticular and on the medial side of the dentary extends posteriorly to the posterior mandibular fenestra to contact the medial margin of the articular. The surangular is robust, long, and represents the second largest element on the mandible next to the dentary. It forms the posteroventral margin of the mandible and extends directly anteriorly to the anterior portion of the dentary, while posteriorly it extends to the posterior end of the mandible to contact the dorsomedial margin of the articular. The prearticular lies between the angular and surangular as an elongated plate, forms the ventral margin of the mandibular fenestra, and its posterior margin contacts the anterolateral side of the articular. The articular is relatively compressed, but tall and thick, and represents the most posterior element on the mandible. The glenoid is shallow with distinct lateral pitting, in distinct contrast to *Archaeopteryx*. A short and small vertical element, identified as the coronoid, is present at the anterior mandibular fenestra, although it does not project dorsally to surpass the surangular and form a process. At the medial midsection of the mandible there is a large splenial which lies medial to the surangular as an extremely thin plate that extends directly anteriorly. It is distinct from the splenial of *Archaeopteryx* which is triangular, whereas on this specimen it is an elongated crescent.

The vertebral column of the new specimen is incomplete although it preserves more elements than on the type specimen, including cervicals, a single thoracic, and caudal vertebrae. The cervicals are basically complete, the first (atlas) being the most distinctive of the vertebrae and covering the occipital condyle. Posterior to the second cervical, the neural arches have become separated from the centra to form a single groove running down probably eight to nine vertebrae. Neural spines are all relatively low, a ventral keel is present on the centra which are rather short and are not heterocoelous, the neural canal is relatively large, and diapophyses unite to form a haemal canal, although posterior cervicals lack this structure. Bicapitate and robust cervical ribs are rather conspicuous, initiate on the fourth cervical and elongate posteriorly along the column. There is a single anterior thoracic vertebra with relatively large diapophyses, a relatively long ventral keel, and its neural canal is also relatively large. A single caudal vertebra is associated with the distal end of the tarsometatarsus, with a circular centrum, extremely well developed diapophyses, and an extremely low neural spine.

Only the left scapula and coracoid are missing on the pectoral girdle; the remaining elements therefore provide reliable data toward a unilateral comparison to *Archaeopteryx*. The furcula is completely represented on this specimen and although it has been shifted in position, where it lies at the rostral region of the skull, it is completely undamaged. Its size and morphology are consistent with that of *Archaeopteryx,* with the exception of the clavicle branches which are distinctly short, thick and flatly broadened. At the proximal end of each branch there is an oblique and elongated depression and at the termini there are coarsened articular condyles. At the proximal articular condyles, the clavicle branch is reduced to become slender. The distance between the clavicle termini is 27 mm, which is 5 mm shorter than the London *Archaeopteryx* specimen.

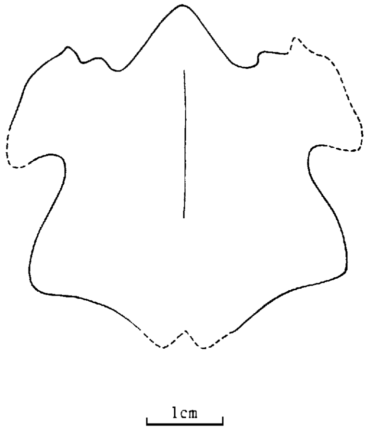

Figure 30. Schematic drawing of the *Confuciusornis* sternum.

The right scapula and coracoid are preserved in natural configuration which is extremely benneficial toward the comprehension of the pectoral girdle. The preservation on *Archaeopteryx* is similar in that on the vast majority of specimens the scapula and coracoid are also preserved in articulation. These elements on both genera are basically similar. The contact of the scapula and coracoid is medial, there is a large rounded glenoid fossa, and the scapula is long and plate-shaped with a reduced distal end. The proximal coracoid is large and expansive with a concave dorsal surface and lateral surface that is expanded to form a crescentic-shaped process that extends distally to become extremely thin. Its posterior side has a groove for contact with the sternum and its terminus is concave. The coracoid morphology of *Confuciusornis* is quite distinct from all those on the Early Cretaceous specimens and more closely approaches the morphology of its reptilian ancestors.

On the type a sternum is absent, but on the new specimen, the sternum is completely preserved. Its morphology is unexpected, being particularly autapomorphic. It is much more well developed than that of *Archaeopteryx* and is also distinct from the Early Cretaceous specimens. Both a carina and posterior process are absent; its anterior end is rounded and descends at its sides while laterally becoming expansive and spacious. On each side there extends a short and relatively expansive “anterior process.” The terminus of this process does not protrude to form a vertical notched line and at the posterior portion of the lateral process it is very slightly expanded. The midline of the sternum is slightly posteriorly projected, thereupon making the terminus a blunt triangle. Although a fully formed carina is absent, there is still a very slight projection upon the midline of the body and at each anterior and posterior end there is a circular depression which may facilitate an incipient increase of sternal musculature. The right side of this specimen is overlain by the right tibiotarsus prohibiting a complete description. The morphology of this primitive bird’s carina is unique.

Ribs are relatively well preserved. Cervicals, thoracic, and gastric ribs are preserved randomly on the block. Cervical ribs gradually elongate posteriorly along the column. In general morphology the proximal ends are rather expanded and distinctly bicapitate. Thoracic ribs are distinctly elongated, gracile, and slightly curved with more narrow and constricted proximal ends. Gastric ribs are slender and rounded with slightly thickened proximal ends and extremely thin distal ends. They are systematically aligned and intersect each other to compose a latticed yoke configuration.

The forearm digits are incomplete on the type specimen, but on the new specimen the left forearm is well preserved with a large amount of feathers, allowing a reconstruction of the forearm and a comprehension of the flight feather configuration. On the right side only the proximal humerus is preserved. The left humerus is complete with a robust but relatively short shaft and an elliptical proximal pneumatic foramen which is surrounded by extremely thin bone which gradually thickens laterally as does the shaft. Thus the proximal end is expansive and extremely thickened, with a large and pronounced medial tuberosity, a feature that is obscured on the type. Its counterpart, the lateral tuberosity, is relatively small and positioned more distally, with a thickened posterior wall. There is a low trough at the lateral side of the pneumatic foramen such that the most depressed region of the pneumatic foramen is at its proximal end, clearly developing the structure of pneumatization. The proximomedial side of the pneumatization has a projected beam that extends directly to the medial tuberosity and then posteriorly fuses to the shaft. The shaft is extremely straight and lacks the curvature found in later avian taxa. Approaching the distal end, the shaft expands slightly. The medial condyle is large but its condylar process is small, whereas the lateral condylar process is large.

The radius and ulna are slightly shorter than the humerus. The ulna is consistent with the type, displaying a slight degree of curvature, its proximal end is not very large, and there is only a shallow olecranon fossa for articulation with the medial condyle of the humerus. Distally there is a shallow carpal articular facet, as in *Archaeopteryx* but not in later avian taxa, which have a large trochlea for the carpometacarpus. The radius is slightly thinner than the ulna and has a straight shaft and a humeral cotyle on its proximal end. Its distal end is expanded with a carpal articular facet.

On extant avian taxa, the articulation of the humerus with the radius-ulna is quite distinct from that of archaic taxa, for on the former the proximal ulna has a medial and lateral cotyle for articulation with the humeral condyles, and on the radius the proximal humeral cotyle combines with the lateral cotyle of the ulna to articulate with the lateral condyle of the humerus. In *Confuciusornis* and *Archaeopteryx* the proximal ulna lacks medial and lateral cotyles and as such articulation occurs solely with the medial condyle of the humerus. This feature is a plesiomorphic character reflecting an inability to fly, and although the ulna maintains secondary flight feathers upon it, the humerus still retains the articular relationship derived from reptilian ancestors which lacked adequate force for propulsion.

Carpal definitions are more distinct on the new specimen than on the type. The type maintains a large and irregularly shaped carpal on the ulnar side of the manus, while on the radial side there is a single columnar shaped carpal. One side is rounded and smooth while the other side is relatively compressed. A third small carpal lies between these two which, on the type, is a thickened plate but on the new specimen the third carpal more closely resembles an ellipse located at the proximolateral side of the second metacarpal.

In summary, *Confuciusornis* and *Archaeopteryx* are consistent in the presence of three carpals. The metacarpals on the new specimen are morphologically consistent with the type. McI is not elongated but is particularly broadened with a thick lateral margin but approaching the margin of McII it becomes extremely thin. A large concave surface lies on the midshaft, the morphology of the entire element is slightly irregular, a distal facet is present for articulation with digit I, and the lateral side retains a muscular-tendinal depression. Metacarpal II is the most robust and longest in the series, has an expanded proximal end with a convex articular surface, a broad and flattened shaft, and an extremely large articular surface for digit II. Metacarpal III is more slender than McII but of equivalent length, its proximal end is not expanded and instead is constricted.

Although the first manus digit has only one phalanx aside from the ungual, it is relatively long, possesses lateral ligament fossae, and articulates with the large and scimitar-shaped ungual with a well developed broad articular facet. Proximally, the articular facet for McI is expanded with a relatively large articular facet. The ungual claw of the first digit is the largest among the three. Its keratinous sheath is well preserved and 12 mm longer than the ungual. A bony cushion lies at the base of the ungual associated with a deep concave facet for articulation with the first phalanx, lateral grooves are present that extend nearly to the apex of the claw, and its curvature is nearly 90°.

The first phalanx on manus digit II is as extremely broadened as McII, both sides of the shaft are thick, and at its midsection there is a longitudinally elongated depression which matches the condition of McII. Both these characters are incipient adaptations for flight. On *Archaeopteryx,* the second metacarpal and digit II are the most robust elements on the manus but do not exhibit the same conspicuous modifications for flight as in *Confuciusornis.* The second phalanx of digit II in *Confuciusornis* is longer than the first phalanx, is not as broad, and gradually becomes slender distally. The ungual of digit II has shifted to a position approaching the ungual of digit I. It is short, small, robust, has only a slight amount of curvature, and is obviously evolving into a phase of gradual reduction, being directly related to strengthening the ability for flight. In *Archaeopteryx,* the ungual on digit II is extremely large and on some specimens is larger, stronger, and more curved than the ungual on digit I. Generally in *Archaeopteryx,* the unguals on digits I and II are equivalent in size and the ungual on digit III is the smallest. This is in distinct contrast to the condition in *Confuciusornis* and confirms that the second digit on *Archaeopteryx,* although being capable in assisting in flight, has not been modified distinctly from its morphology for scaling trees and has not become distinctly adapted for flight. Therefore, it is concluded that *Archaeopteryx* fundamentally did not possess the ability for flight, and although it possessed feathers, its behavior lay in the mode of scaling trees with the use of its claws and gliding between the foliage. There is a large amount of data that confirms that *Archaeopteryx* was a terminal side branch of Aves.

Digit III of *Confuciusornis* has three phalanges, all of which are relatively short and slender. Its ungual phalanx is much larger than that on digit II and resembles the ungual on digit I, also has an approximate 90° curvature, and laterally there are even broader lateral ligament grooves. This indicates that when *Confuciusornis* was scaling a tree, it principally utilized digits I and III for a handhold as these claws were obviously strengthened, which alleviated digit II for facilitating the entire function of flight, and increased the ability for gliding between trees. On the new specimen the second phalanx of digit II has slight curvature. This is also confirmed by observations of several other specimens and is also recognized as a modification for the adaptability of flight.

When the author and his colleagues were in the process of amassing the large collection of Jurassic primitive avian specimens, a large amount of feathers were recovered both attached to individual skeletons, as individual specimens, or in an aligned series. These specimens represent torso feathers, primary feathers, down feathers, and flight feathers. There is still no adequate microscopic analytical technique for the study of fossil feather impressions and thus detailed observations on the microstructure of various types of feathers cannot be conducted. This is extremely regrettable because the microstructure of the feather is directly related to the ability to fly. If it were possible to study the feathers of *Confuciusornis* microscopically, it would then be possible to conduct comparisons with the feathers of both extant taxa in addition to *Archaeopteryx,* which would lead to the recognition of the evolutionary phases of feathers in addition to determining the genesis of genuine flight feathers. Currently, from the perspective of general morphology, it may only be confirmed that *Archaeopteryx* and *Confuciusornis* feathers have extremely short barbs, and thus the entire feather is distinctly narrow and long, unlike those on extant taxa which are broad and thick. It is possible that both *Archaeopteryx* and *Confuciusornis* lacked the complex interlocking construction present in extant taxa and this is the primary reason why they did not possess a true ability to fly.

Among the hindlimb elements is a pair of tibiotarsi lying posterior to the sternum. The tibiotarsus is thin and long, its shaft is straight, and the proximal articular surface is convex. The distal condyles are slightly anteriorly projected; the distal end resembles the proximal end in having a convex articular surface, and an intercondylar groove is extremely narrow. At the distal end of the left tibiotarsus there is an incomplete femur overlying the proximal end of the tarsometatarsus. The femur is more robust than the tarsometatarsus, its proximal end is greatly inflated, but its head is missing as are the distal condyles. A right fibula is preserved which is extremely long, has a well developed proximal end, and a shaft which gradually attenuates to become extremely slender at its distal end. Only the proximal end of the tarsometatarsus is preserved overlain by the femur, which prohibits the description of its morphology, but in cross-sectional view it appears to have been composed of three unfused tarsals.

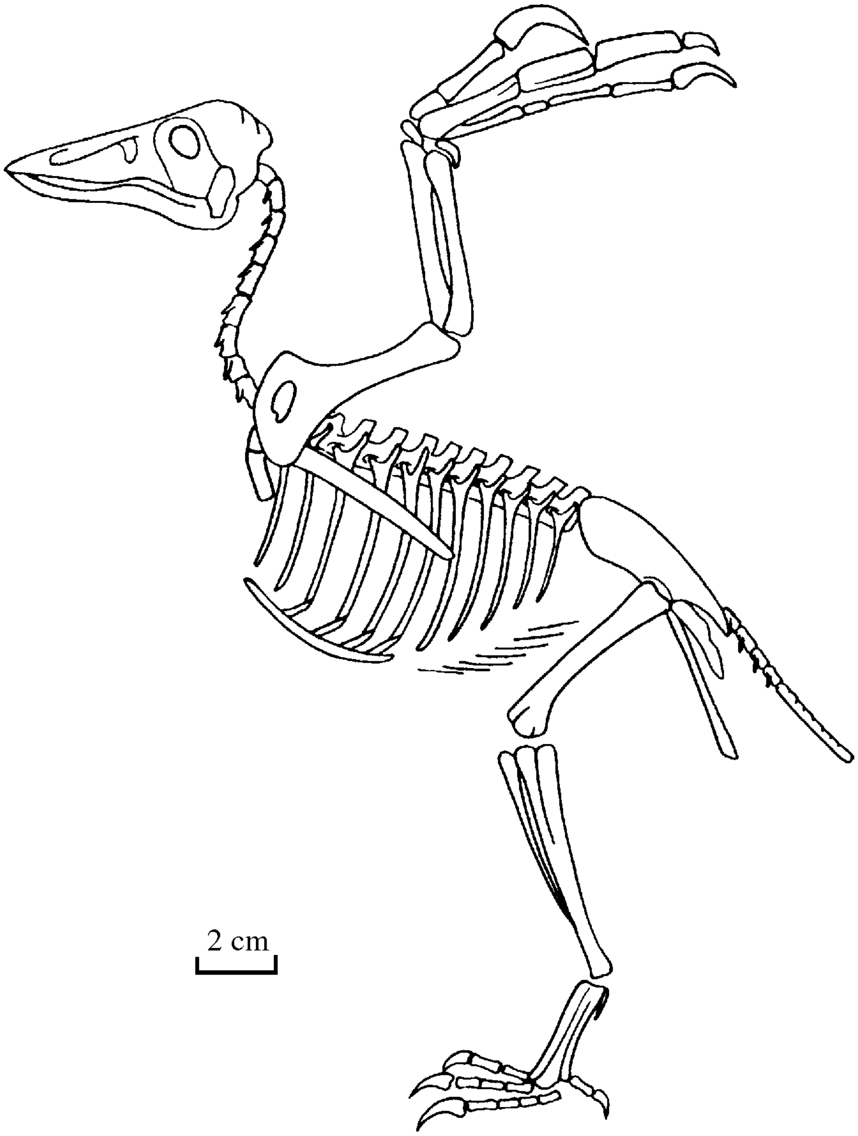

Figure 31. Schematic reconstruction of *Confuciusornis.*

Table 3. Skeletal measurements of the new specimen of *Confuciusornis* (mm).

Cranial length	73.0
Greatest posterior breadth of cranium	40.0
Antorbital fenestra length	6.5
Antorbital fenestra breadth	11.0
Mandible length	62.0
Preserved cervicals length	60.0
Scapula length	52.0
Coracoid length	28.0
Humerus length	61.0
Proximal humerus breadth	31.0
Pneumatic foramen length	11.0
Distal humerus breadth	15.5
Ulna length	55.0
Radius length	52.0
Metacarpal I length	11.0
Metacarpal I breadth	6.5
Digit I length	19.0
Digit I ungual length	16.5
Metacarpal II length	32.5
Metacarpal II breadth	6.0
Digit II length	46.0
Digit II ungual length	8.0
Metacarpal III length	31.0
Digit III length	33.0
Digit III ungual length	21.0
Furcula length	21.0
Furcula shaft breadth	6.0
Furcula breadth at suture	5.5
Sternum length	45.0
Sternum anterior process breadth	41.0
Sternum distal breadth	42.0
Tibiotarsus length	66.0
Tibiotarsus proximal breadth	10.0
Tibiotarsus distal breadth	9.0
Fibula length	35.0
Fibula proximal breadth	6.0
Femur preserved length	43.0

Discussion: The new specimen not only supplements significant morphological characters of *Confuciusornis,* but also allows a more comprehensive understanding of the nature of the genus, and provides more substantial characters to compare with *Archaeopteryx.* Its scapula is extremely similar to the latter, its furcula appears to be a little more primitive, and its clavicle branches are extremely short, all of which restrict *Confuciusornis* to a streamlined, rather short torso. The scapula-coracoid morphology is extremely close to that of *Archaeopteryx;* both elements are tightly articulated, and resemble the morphology associated with the Reptilia. Although the coracoid morphology of *Confuciusornis* is distinct from that of reptiles, it is always associated with the scapula, which is a plesiomorphic condition derived from the most recent ancestor of *Confuciusornis* and *Archaeopteryx*. The coracoid morphology of both archaic genera is vastly distinct from those of modern avian taxa.

The new specimen displays a complete forearm associated with primary feather impressions. Combined with the particular modifications of the second metacarpal, digit II, and ungual of digit II, it provides comprehension of specific modifications for the origin of flight, as prior to the discovery of this specimen only vague hypotheses were formulated regarding feather development and forelimb modifications. Currently, the degree of development of *Confuciusornis* elements allows a comprehension of feather construction in its archaic stages. The developmental modifications of individual elements advances the understanding of morphological succession in systematic evolution. They also support the premises derived from the large amount of other Jurassic and Early Cretaceous specimens, and promote the formulation of theories on the origin of flight and evolutionary trends.

The new *Confuciusornis* specimen provides additional comprehension in the morphology of its extremely well developed sternum. Despite the conservative or archaic condition of the pectoral girdle, the anterior branches and the sternum imply that there is a distinct trend toward the development for flight. This sternum is completely distinct from that of *Archaeopteryx* because the well developed anterolateral processes not only strengthen the contacts for the ribs by their elongation, they also facilitate contacts for the pectoral girdle; its anterior margin is modified into a medial process and which also facilitates lateral and distal contacts with the coracoid. It is surprising that the sternum lacks a furcula process although at the midpoint of each side there are particularly coarsened surfaces for attachment of pectoral musculature. This is further verification that *Confuciusornis* had an incipient ability to fly and that *Archaeopteryx*, although contemporaneous, does not share these adaptations.

The modifications on the new specimen indicate that archaic birds shared characters with reptilian ancestors, modified various organs toward an avian morphology at a differential rate, and that the avian evolutionary sequence progressed along distinct radiations. It is hypothesized that initial avian development flourished out of the reptilian stock in the Late Triassic to Early Jurassic with specialized protective scales that became feathers. Despite the incomplete distribution of feathers on the torso, from the perspective of various forms of confrontational and predatory reptiles, the initial avian ancestor differed from the other taxa by being the object of pursuit and predation. The data confirms that the initial appearance of birds occurred with a relatively large body, unlike the appearance of primitive mammals, and that the primitive avian skeleton was constructed for agility and evasion of reptilian predators. Therefore, it appears the selection for avian morphology was based upon rapid running and fleeing into trees to avoid predators. It may also be hypothesized that when primitive birds scaled trees, the presence of feathers assisted in propulsion particularly by fanning the forelimbs, to the point where it would even lift the animal airborne. When these animals were dwelling in trees, and particularly when foraging for fruit in trees, they could mobilize their body by spreading their forelimbs and could safely glide from one tree to another, providing them with the ability of traversing open space to find new habitats. Thus, the feathers were not only used for homeothermy but also served higher functions. There may be a six to seven million year interval from the initial origin of the class Aves to the time period represented by *Archaeopteryx* and *Confuciusornis*. The well developed unguals on the first and third digits of *Confuciusornis* indicate that it may have predominantly behaved by gliding between trees. *Confuciusornis* differs from *Archaeopteryx* in representing a lineage that continued to modify its skeleton with conspicuous characters leading directly toward the evolution of flight.

Archaeopteryx has modified its features to occupy a new habitat, the aerial realm. One of these organs is the modification of feathers on the forelimb for the ability to fly. A second adjustment for facilitating flight is the modification of the sternum for propulsion. A third modification lies in its style of feeding. In *Confuciusornis*, the primary modifications are as follows: First, *Confuciusornis* is edentulous and represents the first bird with a keratinous beak replacing the dentition. Second, on the forelimb, its proximal humerus is pneumaticized for the reduction of weight, metacarpal II and digit II are expanded and elongated for the facilitation of feathers, and the ungual is gradually reduced. However, as a defensive mechanism, the unguals on digits I and III are strengthened for the ability to climb. Thirdly, concurrent with the increased strengthening of the forelimb is the enhancement of the pectoral musculature providing the ability for flight. Other organs that are indirectly related to the evolution of flight became modified at a slower pace, such as the pelvic girdle and hindlimb.

At the initial stages of of organ modification, several developments were not coordinated and were basically repressed in their phase of biotic evolution. These so-called uncoordinated modifications are represented by various contrasting recently modified and morphologically primitive organs, which thereby represents objective evolution, and which is determined by developmental morphology. This phenomenon is represented in *Confuciusornis* by the uncoordinated development of the pectoral girdle and the sternum as well as between the cranium and vertebral column.

These characters provide further confirmation of the traditional concepts of evolution. However, from the perspective of the large amount of Late Jurassic and Early Cretaceous bird specimens, it appears that both gradualism and punctuated equilibrium occurred synchronously. Biological appearance and development are conducted within complex phases in systematic evolution. Following the consistent increase in data, some theories will be provided with a reevaluated perspective or supplemented confirmation, forcing more parsimonious and objective development, and guiding the study of paleontology toward a more stringent direction of authoritative advancement.

Confuciusornis chuonzhous **sp. nov.**[*]

Type: Part and counterpart of a distal portion of a left hindlimb including the distal tibiotarsus, complete tarsometatarsus, and ungual phalanges (V10919).

Age and stratigraphic position: Late Jurassic interbedded gray-green argillaceous sandstones of the basal Yixian Fm.

Locality: Huangbanjigou, near the village of Shangyuanzhen, municipality of Beipiaoshi, Liaoning Province.

Etymology: For the former name of the city of Beipiao, “Chuanzhou.” This city name was established in 951 AD, resurrected in the Yuan Dynasty under the Khan Tartars, but abandoned in the Ming Dynasy. The specimen was excavated from within the political jurisdiction of Beipiao.

Diagnosis: A relatively large and robust primitive bird with a robust tibia that bears feather impressions laterally; anteroposteriorly it is relatively thick, and the distal end is unexpanded. Both an unfused astragalus and calcaneum are present, a metatarsal V is present and is isolated, except for its articulated proximal end. Ungual phalanx on digit I is exceptionally small and its degree of curvature is more than in any other Jurassic bird.

Description: In the introduction to *C. sanctus* it was mentioned that initially this specimen was identified as belonging to that species; however, reevaluation of specimens for the

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[*] Translator’s note: The English summary in the original text erects the nomenclatuure “meidus” for this specimen but the Chinese text designates the species “chuonzhous”which in itself is published as a typographical error. The correct Pinyin romanization should read “chuanzhous.” Thus *C. meidus* should be regarded a nomen nudum and *C. chuonzhous* regarded the legitimate nomenclature.

composition of this manuscript noted distinct discrepancies between this specimen and the type, justifying the erection of a new species. The fossil locality for this specimen, Huangbanjigou, is located less than one km directly north of the type locality for the genus, Jianshangou, and although there is some slight discrepancy in its lithological character, Huangbanjigou is still considered stratigraphically equivalent to the type locality.

The preserved length of the tibia is 28 mm, its maximum breadth is 4 mm, and feather impressions lie laterally although precise feather impression boundaries are obscured due to taphonomic processes. Tibia pneumatization is high, walls are relatively thick, its distal end resembles the condition on *Archaeopteryx,* being unexpanded laterally, and distinct condyles are absent, resembling the primitive reptilian condition by articulating with an independent astragalus and calcaneum.

The metatarsals are also relatively robust with lengths in excess of 30 mm; their proximal ends have begun to fuse, and there is some lateral expansion. It is difficult to assess whether or not independent tarsals are present due to compressional distortion, but based upon the primitive morphology of this specimen, it is assumed that the tarsals were not fused to the metatarsals and perhaps were not preserved. The most characteristic feature of the metatarsals is the presence of a relatively robust MtV that is isolated except at its proximal end, which is still not fused but in articulation with the other metatarsals. MtI is at least 8 mm shorter than the other metatarsals. MtIII is extremely long. The first phalanx of digit I is less than half the length of the other phalanges. There appears to be three phalanges on the first digit, with the medial phalanx being extremely short and in articulation with the clawed ungual phalanx. If this interpretation is correct, then it would be exceptionally autapomorphic, as there are no reptilian ancestors with a first pedal digit with three phalanges and it is therefore possible that this condition represents an aberration. The ungual on the first digit is extremely short and thick with a slightly curved terminus and is less than half the length of the other unguals. Remaining phalanges are also exceptionally preserved, with only digit III partially obscured by digit II, and its proximal phalanx is vague. The two proximal phalanges of digit II are quite distinct, the second digit is longer than digit I, and its ungual is broader (higher) than all the others. Only the most proximal and distal phalanx is visible on digit III, with the proximal end of the first phalanx relatively long and the distal end of the second to last phalanx relatively weak. The ungual of digit III is long, exceeding 15 mm in length; its proximal end is slightly damaged, and like the ungual of digit II it has a low degree of curvature. Five phalanges are present on digit IV, the first four are relatively short, and the length of the ungual approaches that on digit III with a similar degree of curvature.

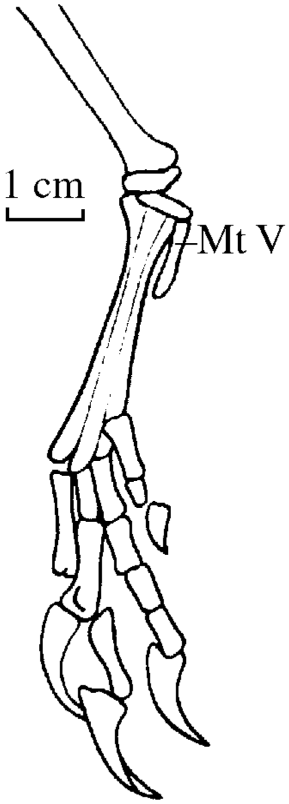

Figure 32. Schematic drawing of *Confuciusornis chuonzhous* sp. nov. right hindlimb (V10919).

Comparison and discussion: To date, there are only two genera and three species of Jurassic birds known globally: *Archaeopteryx lithographica, A. bavarica,* and *Confuciusornis sanctus.* This text hereby records a fourth species that was initially assigned to *C. sanctus* but is now erected as a new species based upon the characters of the hindlimb.

With regard to tibia metatarsal proportions, the tibia is incompletely preserved on *C. chuonzhous*, but on *C. sanctus* the metatarsals are slightly longer than half the length of the tibia, which is 41 mm in length and 2.5 mm in breadth, whereas metatarsal length is 22 mm, and MtV length is 7 mm, being extremely slender and fused to MtIV. The breadth of the *C. chuonzhous* tibia is 4 mm, metatarsal length is 33 mm, MtV length is 10 mm; it is robust and isolated from the other metatarsals. The tibia-metatarsal proportions described above indicate the clear distinctions between the two species. *C. sanctus* retains only a single tarsal whereas *C. chuonzhous* probably possessed at least two. On *C. sanctus* the distal tibial condyles are conspicuous and anteriorly projected but on the new species the distal tibia is in a more primitive condition.

In extant taxa the morphology of the ungual phalanges determines the defining taxonomic characters for the orders Cursores, Natatores, Grallatores, Raptatores, Scansores, Columbiformes, and the genus *Coturnix* (Zheng, 1982). Feduccia (1993) compiled statistics on the claw curvature of extant avian taxa and concluded that curvature of less then 100° indicated cursorial behavior, a vast majority of taxa with curvature between 80°-140° are perching forms, and those with curvature exceeding 120° are adapted to climbing. Based upon this data, he determined that *Archaeopteryx* was a perching form and not a cursorial predator. The curvature of the pes claws on *Confuciusornis sanctus* is equivalent to those of *Archaeopteryx.* Moreover, the ungual on digit I is particularly elongated, indicating that the forelimb functioned as a stabilizing mechanism for the body and was a stronger element for assisting in climbing than on *Archaeopteryx*, being further evidence that *C. sanctus* was an arboreal dweller. The ungual curvature of *C. chuonzhous* exceeds the parameters for perching forms and the tibia and metatarsals are more robust. Consequently, this species is assigned to the cursorial group.

The fifth metatarsal of *C. chuonzhous* is longer than in a vast majority of the specimens of *Archaeopteryx* and longer than that of *A. bavarica.* The remaining metatarsals are all shorter than those of *A. bavarica.* This reflects the primitive nature of *C. chuonzhous* and in combination with its robust and strengthened unguals, is a further indication that it is adapted to cursorial behaviour.

Tibia morphology of *C. chuonzhous* resembles that of *Archaeopteryx* with indistinct medial and lateral condyles and an articulation with the calcaneum, which itself is associated with unfused tarsals that are reduced in number and articulate distally with metatarsals. This morphology is completely adequate for habitats in trees, cliffs, or on the ground. The *Confuciusornis* forelimb is completely modified for flight but still requires a relatively long phase of evolutionary development to match the mophology of extant taxa. Therefore, primitive birds contemporaneous with *C. sanctus* are considered to possess forelimbs with three independent digits for support, stability, and equilibrium of the torso.

Furthermore, the primitive condition of Jurassic birds is expressed in the smaller and weaker ungual of pedal digit I, which is in contrast to the condition of later taxa and particularly extant forms. The primitive first digit unguals are smaller than the rest in the pedal sequence, prohibiting the use of the hindlimbs from acquiring prey or scaling trees. On extant species the first pedal digit is in opposition to the other three, and is large and acute. The first ungual on arboreal dwelling taxa is the largest and most recurved. Predaceous claws, including the largest digit I ungual when seizing prey, are capable of penetrating flesh. Therefore, the function of the ungual on the first digit is regarded as extremely significant in the adaptation to a perching mode, predation, or a defensive mechanism. However, this important character has yet to be discussed by workers in the field of paleornithology, and therefore a preliminary discussion will be conducted based upon the several specimens of *Archaeopteryx,* two *Confuciusornis* specimens, and a large quantity of Early Cretaceous avian specimens.

In general, the hindlimb of archaic reptiles possessed five digits and the hindlimb claws, particularly the ungual of digit I, were not well developed. Among the Dinosauria, and particularly the ornithomimids, which basically had omnivorous feeding patterns, the first digit has been lost. In carnivorous dinosaurs, digit I has also been reduced or lost. The digital formula of

Archaeopteryx is completely distinct from that of the Dinosauria, because the first ungual in *Archaeopteryx* and *Confuciusornis* has become extremely weak, although its associated phalanx shows no appreciable reduction. In contrast, the first phalanx is elongated, not shortened as on the other digits, and lies in opposition to them.

After the initial radiation of Aves from the Reptilia, in order to flee the surface of the ground to avoid predatory enemies and develop the ability to scale trees, the ancestral bird modified its reptilian extremities, particularly the first pedal digit, which was modified from an anterior placement to a posterior position to lie in opposition to the other digits for the function of scaling trees and perching on branches. Extant lacertilians with the capability of scaling trees and walls include forms such as the African *Chamaeleo* and *Gekko*, although one these taxa relies on friction of the digital skin pads, while the other relies on the inflation of the digital scales and not their digital morphology.

Obviously, the preliminary evolutionary modification of avian forms included the contemporaneous changes in the fore- and hindlimbs. A discussion of forelimb modification and the evolution of flight will be provided later in the text. Here we turn to avian digital modification, noting that fore- and hindlimb modifications were coordinated. After the completion of the posterior rotation of digit I in the most archaic avian lineage (which required a relatively long period of time), there was continuous evolution of the adaptation to the aerial realm and particularly for the ability to fly between arboreal habitats, which required the evolution of pedal digit I. The presence of *Archaeopteryx* and *Confuciusornis* in the Jurassic suggests that perhaps the majority of primitive arboreal birds did not deviate from utilizing their forelimb unguals, and thus the forelimbs, manus, and digits of these taxa were unfused with the presence of three digits bearing acute clawed unguals. The first manus ungual on *Confuciusornis* is extremely large and intensely recurved, which is an indication of its strength. However, evolutionary modification is not in equilibrium because there are more derived avian forms that are contemporaneous with *Archaeopteryx* and *Confuciusornis*. This condition is similar in extant avian taxa, which contain birds that are adapted for highly specialized habitats in addition to birds that are morphologically relatively primitive. Extinct families were unable to adapt to habitats.

On the latest avian specimen excavated from the Jurassic of Fengning Co., Hebei Province, there is a large, relatively well developed, and acute pedal ungual on digit I, and although it is slightly smaller than the other unguals it is quite distinct. Its modification is associated with additional derived characters, including the absence of a fifth metatarsal; tarsals have all been lost, and caudal vertebrae have become fused to compose a pygostyle. Within the large collection of Early Cretaceous avian specimens from Chaoyang, Liaoning, the first pedal ungual has become distinctly modified to match the morphology of extant forms; its size and degree of acuity is in complete contrast to those of the other unguals, which indicates that the facility for grasping with the pes has been advanced, and that it has become modified for adaptation to a new habitat.

The modification of the first pedal ungual accompanied the appearance and modification of characteristic digit musculature and ligaments. The hallux particularly displays several significant well developed muscles and tendons. First, the long hallucal flexor muscle initiates with a tendon on the fibular side of the femoral popliteal area, where it is unified with the long digital flexor for the extension of digits; it concurrently facilitates extension and lateral rotation of the foot. Additionally, the transverse metatarsal ligament initiates on the first metatarsal at the base of the first digit, intimately connecting the first digit to the other three digits. The rectal hallical ligament and oblique hallucal ligament are directly connected to the phalanx to strengthen the hallux (digit I) and other digits for the ability to grasp. Another muscular complex for strengthening pedal mobility is the perforate digital flexor (flexor digitorum perforans), which on modern birds traverses muscular and tendinal complexes to directly contact the termini of each of the digits. Surficially, it has extremely specialized digital fibrous sheaths (vagina fibrosa) within which musculature is mobilized and thus the tendons and sheaths are closely interconnected. In this manner, the muscles are allowed to relax while retaining pedal immobility and perching with a firm grasp. This avian autapomorphy is extremely significant behaviorly, as it allows birds to pass the night sleeping while perched in a tree, facilitates laying eggs into the nest, and use as defense against daily predators. With this capability, although the individual is in a tree, it expends no energy, and there is no fatigue, allowing extensive periods of relaxation.

There is still an enormous amount of functional development associated with the avian foot, such that here it is only possible to raise several aspects of it. Descriptions of muscle complexes including the short digit flexors, digital extensors, dorsal complexes, and posterior complexes will not be reiterated here.

Archaeopteryx and *Confuciusornis* probably only possessed rudimentary pedal musculature for true avian functions. Their feet were in an evolutionary phase that is extremely distant from extant avian pedal morphology, which allow a free range of avian mobility.

Confuciusornis suniae[*] sp. nov.

Type: A complete skeleton provisionally housed at the Institute of Vertebrate Paleontology and Paleoanthropology under catalog #V11308. The specimen was provided for study by Mr. Shikuan Liang of the Chaoyang Municipal Paleontological Repository, Liaoning province.

Locality and stratigraphic position: Stratigraphically, the specimen occurs slightly higher than *C. sanctus,* being derived from the Late Jurassic white mudstones of the basal Yixian Fm. at the village of Sihetuncun, Chaoyang Co., Liaoning Province.

Etymology: “Sun” being pinyin romanization for the surname of the wife of the private collector, Mr. Shikuan Liang, who provided the specimen to IVPP for study. The nomenclature is in dedication of her virtuous character. The author stands in complete admiration of the couple’s sincere, faithful, and loving relationship, and concurs with colleagues that this new species of *Confuciusornis* should commemorate Ms. Sun through her family name.

Diagnosis: The rostral end of the premaxilla has a particularly open vacuity, the nasal process is elongated, external nares are large, frontals are short, and parietals are well developed. Cervical vertebrae are particularly flattened and broadened with small pleurocoels laterally; neural spines are narrow and extremely low anteroposteriorly. Thoracic vertebrae are long and thin with deep and long grooves within the pleurocoels. Lumbar diapophyses are fused. The posterior most three lumbar diapophyses are fused, sacral diapophyses are fused to the medial wall of the ilia, sacral neural spines are fused, and caudal vertebrae are basically fused. . Sternal body is narrow and long with deep elongated lateral recesses.

Description: This specimen is in an exceptional state of preservation due to the attention provided to it by Mr. Liang, who sent the specimen still embedded in its matrix to IVPP where it underwent an extended period of meticulous preparation on its dorsal side by Mr. Yutong Li. Detailed scrutiny of this specimen indicates that the merchant who sold it to Mr. Liang made some modifications to the right forelimb. It is evident that a portion representing the ungual of the first digit to the first metacarpal does not belong to this specimen. This is determined by its coloration in addition to indications that there is a duplicated section of first metacarpal. The left forelimb, however, is completely preserved and indicates that the reconstructed first digit is basically consistent and will have no effect on interpretation of the specimen. At the time of burial, the cranial bones were disarticulated and shifted in position and the cervical vertebrae had also been

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[*] Translator’s note: On page 220 of the English summary in original text this species is erroneously listed as *shuzhi* which should therefore be regared a nomen nudum.

shifted. An obvious feature is the poor degree of feather preservation; only few impressions are present. These are the only blemishes on an otherwise perfect specimen.

Skull: At the most anterior end of the premaxilla there is an extremely conspicuous V-shaped embayment, a feature that is not documented on any other specimen of *Confuciusornis*. It is obviously not an ontogenetic feature because the posterior margin of the embayment is completely fused and a medial suture line is unobservable. This character is also absent on all extant and other fossil species as well. There are relatively large grooves with additional delicate and short striations on each of the posterodorsolateral sides of the embayment. Ventral to the larger grooves the bone is flat, narrow, and smooth, lacking any further ornamentation. The nasal process of the premaxilla differs from that of *Confuciusornis sanctus* by being longer and extending posteriorly from the midpoint, with its posterior section being unfused. The lateral premaxilla forms the anteroventral wall of the external nares. The maxilla is anteriorly oblique, with its ventral portion overlying the posterolateral premaxilla.

The maxilla is a low triangular element with abundant irregular surficial pitting. Its anterior contact is with the premaxilla and posteriorly it gradually attenuates to become thin and narrow, to contact only a portion of the jugal and form the ventral wall of the external nares.

A triangular septomaxilla forms the anterior wall of the external nares and lies between the base of the nasal process of the premaxilla and the anterior margin of the maxilla. Although this element is interpreted to be present on the new specimen of *Confuciusornis,* its verification requires additional specimens. In the Crocodylia and synapsids, the septomaxilla is present at the posterior margin of external nares, and it is only on the phytosaurs, such as *Machaeroprosopus,* that it has migrated to the anterior region of the external nares. Obviously, this single character can not justify a close relationship between phytosaurs and birds, as a synthesis of numerous morphological characters is required.

The nasals and frontals are in contact but have been shifted in position. Lateral to the nasals are a pair of relatively large lacrimals which, although also displaced, display a distinct irregular morphology. The frontal is extremely avian in morphology with a broad and thick semicircular orbital rim which extends from the medial margin directly to the posterior margin of the orbit. The sclerotic ring has also been displaced with a portion of it being overlain by the nasal process of the premaxilla but the majority of it is well preserved, being nearly quadrate in morphology. The anterior wing of the frontal extends directly to the midpoint of the nasals. Posterior to the orbit it is broad and spacious with two mound-shaped processes projecting from both sides of the midline that unite with the parietal suture to form a V-shaped configuration. The parietals are also well preserved, being completely fused at their midpoint with a small process projecting posteriorly and anterior portion being in contact with the frontal through an upside-down V-shaped depression. The parietal contacts the occipital with a crest or ridge. With the exception of the occipital, the remaining occipital cranial elements have all been displaced, particularly the lateral acoustic process, which is exceptionally projected on the occipital region. The squamosal is compressed against the posterior cranium but is still quite distinct, overlying and compressing the quadrate on the left side. On the right side it is obscured by cranial elements such as the pterygoid. The foramen magnum is posteriorly positioned and has suffered dorsoventral compressional distortion. The occipital condyle is rather laterally expanded.

Although the specimen is prepared in dorsal perspective, a number of the palatal elements are exposed due to the disarticulation of the skull. A relatively acute and thin anterior end of the vomer is exposed on the right side of the lacrimal. A portion of the palatine is exposed between the premaxilla and the maxilla although its complete configuration is unclear. A pair of pterygoids is extremely well preserved with a slightly curved basal region which becomes thin as it extends directly laterally. The left posterior maxilla has been compressed upon the anterior portion of the mandible and the posterior portions of both mandibles lie lateral to two cervical vertebrae. These two posterior mandibles appear to represent a single side which is probably due to post burial deformation; otherwise they represent two distinct elements. The lateral side of the articular has a dorsally projected process and its terminus represents one of the three elements of the glenoid fossa. The prearticular extends anteriorly to the medioventral surangular. An angular is well developed and extends directly anteriorly but becomes obscured by the premaxilla at its anterior end; thus only a portion of it is visible between the nasal process of the maxilla and the sclerotic ring. The right dentary has been displaced to lie posteromedial to the right maxilla where anteriorly it is acute and long and posteriorly it is narrow. The splenial is located quite distinctly at the center of the dentary.

Vertebrae: The entire vertebral column is preserved, and with the exception of the displacement of several cervicals, the sequence has not undergone much deformation. The first several anterior cervicals have been crushed together with the scattered cranial elements and thus it is regrettable that the atlas and axis cannot be described. There are at least nine extremely derived cervicals. The centra are amphicoelous and extremely broad and low, with an extremely broadened neural arch which is laterally high and medially concave. The neural spine is low and narrow. Prezygapophyses are large with their articular facets placed anteriorly and projected laterally. An elongated trough lies laterally on each side of the neural arch and diapophyseal foramena are present. Postzygapophyses are extremely short and centra articular facets are extremely narrow.

The thoracic vertebrae are large and circular, slightly flattened ventrally, are medially concave, neural arch is high, neural canal is circular, diapophyses extend anteriorly, and there are relatively deep and complex pleurocoels. Neural spines are extremely high, the anterior centrum articular face is large and expansive, and posterior articular facet is slightly smaller. There are approximately ten thoracic vertebrae and worthy of note is that three in the lumbar region are fused in their neural spines and diapophyses. They have a relationship with the ilium, although they are still separated from it. The lumbars are also basically fused with the termini of the sacral diapophyses, four sacrals are also fused and there is a relatively large interval between the sacrals and lumbars, allowing a distinct recognition of the two series. Distal termini of the sacral diapophyses contact the medial wall of the ilium and neural spines are fused together with the lumbars. This fusion is more derived and well developed than noted on the Early Cretaceous *Sinornis* or *Cathayornis* species. In the caudal region on this new species of *Confuciusornis* there are approximately 25 vertebrae with at least ten anterior caudals being unfused, or in natural articulation, and morphologically they resemble the thoracic vertebrae, although the centra are slightly smaller. Posterior to these are approximately 15 fused caudals which represent the first documentation of a pygostyle. Caudal diapophyses are narrow transverse plates, and neural spines are fused to form a single, high, linear medial crest that gradually becomes lower anteroposteriorly. Boundary lines delineating the centra are still quite conspicuous and perforations are still present between the neural spines. This caudal fusion is distinct and differs somewhat from the general condition of the other Early Cretaceous species.

Ribs: Almost none of the cervical ribs are preserved, because there is only a single right proximal end of a posterior rib present which displays a relatively short capitulum and relatively long tuberculum. Sternal ribs are extremely elongated, basically elliptical in cross-section and maintain a relatively long and shallow groove on their posterior side that extends from the proximal to distal end. There is no appreciable distinction between the morphology of a sternal and dorsal rib. On the right side there are four relatively short and thick rib segments but these are clearly not gastral ribs and it is difficult to accurately diagnose whether or not they are sternal ribs. Gastric ribs are distinct and randomly scattered on the block anterior to the fused lumbar vertebrae and lateral to the thoracic vertebrae. They are extremely slender and not as long as the sternal ribs.

Pectoral girdle: The pectoral girdle is extremely well preserved but the only element that may be completely described is the scapula. Only the right proximal end of the coracoid is visible, as the rest is overlain by the humerus. The left coracoid is completely obscured. The furcula is represented only by the two termini of the clavicle branches exposed at the lateral sides of the scapulae. The scapula is exposed dorsally as being completely fused with the coracoid, its relatively deep glenoid is situated at its proximoventral end, its proximodorsal margin is crescentic and relatively broadened, and slightly distal to the proximal end the scapular shaft is its narrowest. The dorsal margin of the scapula (the side approaching the vertebrae) is relatively rounded and from this point posteriorly the blade gradually decreases in thickness. The posterior blade of the scapula is thin and slightly expanded with a reduced terminus. On the dorsal surface of the proximal shaft there is a shallow groove that runs posteriorly past the midsection where it then attenuates. The ventral margin of the scapula is also relatively rounded from its proximal end to the scapular blade but at the distal end it becomes thin. Consequently, the entire element is elongated with a thick proximal end and thin distal end.

The coracoid basically resembles the morphology of *C. sanctus,* having an extremely expanded and thick proximal end and an extremely thick dorsal margin where it contacts the scapula and composes the anterior margin of the glenoid fossa. There is an expansive surface for articulation with the clavicle, the lateral margin is projected, and from the proximal point of its fusion with the scapula it forms a 90° curvature extending posteriorly and becoming thin. Its distal end is overlain by the humerus, obscuring its morphology. The clavicle branches of the furcula are extremely robust and its termini articulate with the large clavicle articular facets. The clavicle is the most robust element on the pectoral girdle.

Sternum: Morphology of this element is vague due to being obscured by the scapula, thoracic vertebrae, and ribs. But its right side appears to be planar, heart-shaped, relatively elongated with a rather acute terminus, and a lateral process is absent.

Forelimb: Compared to *C. sanctus,* the proximal pneumatic foramen on the humerus is smaller, indicating that it is gradually becoming lost, and therefore the depressed region surrounding the foramen has become more shallow and the proximolateral wall has become thin. In addition, the lateral tuberosity is extremely inconspicuous, and the medial tuberosity is not as well developed as on *C. sanctus,* although a medial crest is still present which extends from the proximal end to the humeral shaft. The shaft is straight, short, slightly laterally compressed, expands laterally toward the distal end, and there is a distinct lateral ectepicondylar process in the shape of a longitudinal prominence distal to which is a low and concave ectepicondyle. These latter features are absent in *C. sanctus.* At the distal end of the humerus the medial margin of the entepicondyar process curves toward the midsection of the shaft but an actual entepicondyle is indistinct. Although there is no true olecranon fossa, there is a small depressed region. Distolaterally, there is a distinct autapomorphic ulnar condylar groove which is undocumented on any other fossil bird, although extant taxa possess a similar groove which is extremely shallow.

The radius and ulna are relatively robust, and the straight-shafted radius being slightly thinner than the ulna. The proximal ulna is slightly laterally oblique and is expanded with a large humeral articular facet that is slightly concave at its midsection. A large spaceous cavity is present proximodorsally that extends as a distal groove and gradually narrows, but upon reaching the distal end it again broadens and finally, at the terminus of the ulna, again forms into a relatively deep cavity. At the distoventral ulna there is a projected and laterally expanded angle in addition to an irregularly shaped ulnare in articulation. The radius contacts the ulna with a proximal process, its proximal end is small, has an extremely narrow articular facet for the humerus, and a shallow groove is present proximally which extends and disappears by the midportion of the shaft. The cross-section of the shaft distal to the midportion is nearly circular but at its distal end it expands into a boot where it articulates with what appears to be a radiale. There has been no displacement of the carpal elements, which is a rare condition.

The carpal sequence is extremely well preserved and their morphology is distinct. The ulnare is irregular in shape and rather spherical with a large articular facet for the ulna but smaller articular facets for the other carpals and metacarpals. It predominantly articulates with MtIII. The radiale is large, boot-shaped, maintains a flat and elongated articular facet for the radius, and a large, deep, and concave facet for MtII. Between the ulnare and radiale are an additional two small spherical carpals.

The metacarpals are slightly distinct from those on *C. sanctus*. This is predominantly displayed in the more robust nature of MtII and the nature of its articulation with the carpals, as its dominant proximal articular facet is large and crescentic. The first metacarpal is slightly smaller and has been displaced distally. MtIII is laterally compressed to become thin and weak in addition to being slightly reduced. Its shaft is slightly curved approaching MtII, proximal articular facet is extremely small, and although the distal articular facet for the phalanges is slightly inflated, it is not expanded. MtI is ladle-shaped with a relatively thin distal end that maintains a relatively large and concave articular facet for the first phalanx. The thin lateral edges of MtI are nearly as thin as those on MtII and it is in tight contact with the latter with the medial margin becoming thicker. This metacarpal's proximal articular surface is extremely narrow, is not on the same plane as the proximal surface of MtII, and has actually lost an articular facet for the carpals. MtII is the most robust of these elements with a proximal surface as a large crescentically shaped trochlea, rather resembling the laterally surfaced morphology of extant taxa in which carpal articulation occurs proximolaterally. The lateral margins of the trochlea are expanded with a relatively deep medial depression that appears to represent a medial ligamental fossa. The shaft is robust with a short groove at its proximal end. Distally, the articular facet for the first phalanx of digit two is large with a process that extends to articulate with the expansive facet on the phalanx. The articular surface at the proximal end of the first phalanx of digit I is convex and maintains a process that extends to facilitate a better articulation with the metacarpal trochlea. The ungual of digit I is the largest and most recurved in the series, resembling the condition of *C. sanctus*. Digit II has three phalanges the first of which is short and broad with a large proximal articular facet. The second phalanx is larger with a more robust proximal end and a distal end that gradually thins to articulate with an extremely small ungual. Digit III has five phalanges which are all short, with the exception of the ungual. The first and second phalanges of digit III are particularly short. Digit III is the most slender and weakest in addition to being slightly shorter than digit II, and ts ungual is relatively large and hooked.

Pelvic girdle: In dorsal perspective, the pelvic girdle is extremely well preserved with all three elements in natural articulation. The iliac body is elongated as is the preacetabular region which is also expanded with a relatively thick dorsal margin, an extremely thin ventral margin, and rather rounded anterior margin. The acetabular region is thickened, its anterior margin is projected to form a process, although it is unlike that on extant taxa, where there is a dorsal antitrochanter, and as such the position of the *C. suniae* process differs. Worthy of note is that dorsal to the acetabulum on the ilium there is a posterior, obliquely directed, long, and deep groove that nearly reaches the end of the ilium. The ilium posterior to the acetabulum is much shorter than the anterior portion and is narrow and rounded, with a slightly acute terminus.

The ischium is extremely autapomorphic as there are three processes extending off the main body: The first is relatively short, broad, and forms the posterior wall of the acetabulum. The second process is plate-shaped, extends, and expands obliquely dorsally from the distomedial side of the ilium to the vertebral column, appearing as though it encircles the most posterior portion of the synsacral vertebrae. The third and largest process is one which extends posteriorly to the distal end. As previously stated, this morphology it is extremely autapomorphic with both ischia projecting to form broad and spacious arms that laterally encircle the unfused synsacral caudal vertebrae. They become broad and expansive at the terminus of the ilium and have a reflected angle at their distal ends that are medially constricted and a dorsal margin that is relatively thick. The ventral margin is linear with a terminus that extends directly to the ventral side of the synsacral caudal vertebrae. Whether the distal ends are fused or not is unclear as they are overlain completely by the caudals.

The pubis is still the longest element of the three sacral elements but is more conservative and simple in morphology compared to the well developed anterior ilium and autapomorphic ischium posterior to it. It is present as a narrow, elongated, and thickened plate with its anterodorsal margin composing the ventral wall of the acetabulum. The dorsal section extends anteroventrally to surpass the anterior margin of the acetabulum, which represents the origin of the "pectineal process" of extant avian forms. The pubes extend posteriorly and at the lateral side of the ischium extend directly to the most posterior fused caudal centra but they do not expand. There is a very slightly projected, low dorsal ridge and the terminus is rounded.

Hindlimb: On the right hindlimb elements distal to the right tarsometatarsus are missing but the left side is exceptionally complete. This limb is extremely robust with a very slightly curved, relatively long, and robust femur. Although its head is rather enlarged, it nevertheless lacks a neck, resembling the morphology of its reptilian ancestors. Distinctive morphology of the femur includes the particularly well developed fourth trochanteric ridge proximally, which is larger than on many archaic reptiles. The fourth trochanter on the extant *Alligator sinensis* is relatively well developed and projects laterally but it is positioned relatively low on the shaft. The shaft of *C. suniae* is very slightly anteroposteriorly curved and the posterodistal end has an elongated and broadened trough initiating at the lower half of the shaft, and the lateral margins are thinned. The distal end maintains a deep trough, the position of which corresponds to the popliteal region on extant birds and thus it probably represents the attachment for Popliteus musculature. Distomedial and distolateral condyles are well developed, the intercondylar groove is narrow, a short process extends posteriorly off the lateral condyle, while another process on the fibular side facilitates the Flexor musculature. Between these processes there is a deep depression. The medial condyle is relatively broad and large with a particularly noticeable depression dorsal to it. There is a small triangular bone which has been modified from tendon situated lateral to the distomedial condyle that should represent a patella.

The fibula is extremely slender and exceeds the length of the tibiotarsus by three-quarters. Its proximal end is relatively broad with a convex articular surface. On the medial side of the shaft there is a ridge to facilitate the tibiotarsus. The tibiotarsus is robust and is slightly longer than the femur. Both termini are not very expanded, the proximal articular facet is extremely planar and articulates principally with the medial condyle of the femur. From an anterior perspective, the proximal end appears to maintain a lateral cnemial crest which resembles extant Aves by being a relatively large semi-circular structure. On the posterolateral shaft there is a relatively long fibular crest. Extant Aves possess a proximomedial cnemial crest but on this specimen it is represented only by a small process. The shaft is slightly compressed anteroposteriorly. Distally, genuine medial and lateral condyles are absent and instead there are two differentially sized articular facets, the medial of which is relatively long and broad while the lateral facet is relatively short. There is a depression dorsal to these articular facets which represents the location for the subsequent development of the supratendinal bridge. On the lateral side of the distolateral articular surface, there is a relatively pronounced bulge, suggesting the presence of an ectepicondylar depression. Whether or not a depression is present on the entepicondylar region is still unknown due to lack of specimen preparation.

The tarsometatarsus is the shortest element on the hindlimb, being relatively broad. and exposed on its posterior side. Its proximal end is the only portion of it that is fused, which is distinct from other specimens, but resembles the Early Cretaceous birds from Western Liaoning Province. MtIII and MtIV are nearly equivalent in length, MtV is only visible in proximal cross section as the majority of it, including the proximal articular surface, is missing, but in lateral perspective it appears to be relatively flat. In cross-section, the shaft of MtIII appears to be hollow. MtI is located posterodistal to MtII with the two being in tight association. The distal trochleas on all the metatarsals are relatively broad with that of MtIII being the largest. There is an extremely narrow groove on the posterior MTIV which becomes deeper and broader approaching its distal end. In posterior perspective the proximal ends of MtII and MtIII are spaciously broad,

Table 4. *Confuciusornis suniae* measurements (mm).

Premaxilla length	39.0
Premaxilla to anterior margin of nares	12.0
Preserved maxilla length	26.0
Maximum breadth of preserved parietal	26.0
Pterygoid length	24.0
Breadth of mandible articulation	7.0
Breadth of cervical 6	9.0
Length of cervical 6	8.0
Length of cervical 6 neural spine	2.5
Scapula length	42.5
Proximal breadth of coracoid	7.5
Distance between clavicle termini	21.0
Sternum length	43.0
Approximate breadth of sternum	24.0
Approximate length of sternal rib	49.0
Approximate breadth of sternal rib	1.7
Humerus length	51.0
Approximate breadth of proximal humerus	28.0
Length of proximal humeral pneumatic foramen	6.0
Humerus breadth at midshaft	10.5
Breadth of distal humerus	1.05
Ulna length	46.0
Ulna breadth at midshaft	4.5
Radius length	44.0
Radius breadth at midshaft	3.0
Radiale length	6.5
Ulnare length	5.5
Metacarpal I length	8.0
Metacarpal I breadth	5.5
Metacarpal II length	25.5
Metacarpal II proximal breadth	7.5
Metacarpal II midshaft breadth	4.0
Metacarpal III length	18.0
Phalanx of manus digit I length	19.0
Ungual of manus digit I length (including sheath)	20.0
First phalanx of manus digit II length	18.5
First phalanx of manus digit II breadth	6.0
Second phalanx of manus digit II length	20.0
Ungual of manus digit II length	8.0
First phalanx of manus digit III length	5.0
Third phalanx of manus digit III approximate length	14.0
Fourth phalanx of manus digit III length	15.0
Ungual of manus digit III length	16.0
Length of thoracic 8	5.0
Breadth of thoracic 8 anterior articular surface	4.0
Synsacral lumbar vertebrae approximate length	13.0
Synsacral lumbar vertebrae diapophyseal breadth	11.0

Table 4 cont.

Synsacral sacral vertebrae length	18.0
Synsacral sacral diapophyseal breadth	14.0
Synsacral caudal vertebrae length	32.0
Synsacral caudal vertebrae breadth	8.0
Ilium length	33.5
Ilium preacetabular length	23.0
Anterior ilium approximate breadth	8.0
Preserved length of ischium	22.5
Transverse process of ischium length	10.0
Pubis length	47.0
Pubis terminal fusion breadth	2.0
Femur length	45.0
Femur proximal breadth	10.0
Femur distal breadth	7.0
Tibiotarsus length	55.0
Tibiotarsus proximal breadth	8.0
Tibiotarsus distal breadth	7.0
Fibula approximate breadth	41.0
Fibula proximal breadth	4.5
Tarsometatarsus length	26.0
Tarsometatarsus proximal breadth	6.0
Tarsometatarsus distal breadth	7.0
Pes digit I length including ungual	15.0
Pes digit II length including ungual	22.5
Pes digit III approximate length without ungual	18.0
Pes digit III ungual length	10.0
Pes digit IV length without ungual	19.0
Pes digit IV ungual length	12.0

MtIV is only visible at the lateral margin, and only toward the distal end is its shaft noted to also expand and constitute a major portion of the tarsometatarsus. Distally MtIII and MtIV are equivalent in length and MtII is the shortest with its trochlea situated proximal to that of MtIII.

Phalanges and unguals: The manus and pes digits are all relatively short but the unguals are all relatively large and recurved. Pedal digit I is extremely short but the articular surface for its ungual is extremely broad and thus from a ventral perspective, the distal end is broader than the proximal end and the ventral surface of the shaft is slightly concave. The ungual on pes digit I is the smallest in the series. Digit II has two phalanges, each of which are longer than the pes digit I phalanx, the articular surfaces at each end are expanded, the ventral surface is relatively concave and there is a longitudinal groove present. Lateral grooves on the ungual are particularly well developed. Digit III has three phalanges, the first two of which are relatively long and robust and the third phalanx is relatively short although its proximal end is expanded. The ungual of digit III is equivalent in size to the ungual on digit II. Digit IV has four relatively short and thick phalanges although its length is nearly equivalent to digit III and its ungual morphology is also nearly equivalent to that of digit III. The last phalanx is the longest in the sequence.

Comparison and discussion

This new Late Jurassic primitive avian specimen should be assigned to the genus *Confuciusornis* based upon following characters: the jaws are edentulous; and have grooved surficial ornamentation and a keratinous beak, the proximal humerus maintains a pneumatocoel, the ungual on digit I is particularly enlarged, the ungual on digit 2 is particularly small, and the sternum is extremely well developed. Justification for the erection of the new species *C. suniae* is based upon characters distinct from the other known species of *Confuciusornis* including the autapomorphic "V" shaped vacuity on the premaxilla, elongated nasal process of the premaxilla, transversely expanded cervical vertebrae, extremely small neural spines, sternum heart-shaped and lacking lateral processes, fusion of the lumbar and synsacral vertebrae, and fusion of the posterior caudals.

C. suniae corresponds to the size of *C. sanctus* and as described above, differs from the latter in its extremely distinct "V" shaped surface of the premaxilla, the function of which is still not determined. If, as in the extant family Anseriformes, it is an adaptation for aquatic habitats, then the rostrum would be spaciously expanded and not have a bifurcated orifice. Therefore, the autapomorphic character of the beak causes one to also consider the corresponding morphology of the hindlimb, in which the fourth digit is as long as the third digit and maintains the largest ungual among the series. Metatarsals III and IV are also similar in length indicating that at very least the species is adapted to riparian habitats and possibly to fully aquatic habitats. Other significant autapomorphies include the arcuate orbital region with an expanded and thickened margin which reinforces the frontal and provides it with an angled edge, which is a rarely documented feature on primitive birds. Whether it represents a conservative function, facilitates a cranial crest, or perhaps represents a combination of the two is unknown. Extant migratory birds have more substantial orbital regions compared to predators, song birds, or ground dwelling birds. And although wading birds have particularly thickened and broadened orbital regions their morphology is unlike that of *C. suniae.*

On the new specimens of *C. sanctus,* cervical vertebrae are poorly preserved but it is possible the centra are relatively broad. The cervicals of *C. suniae,* however are unexpectedly distinct. Firstly, the diapophyses are broadened and there is a lateral projection. Secondly, the centra are thin and expanded. Thirdly, the neural spine is low and small. Fourthly, the anterior diapophyseal articular facets are positioned anterolateral to the centrum articulation and project anteriorly, which implies increased mobility between the cervicals, unlike the simplified general condition of the postzygapophyes being posteriorly compressed upon the prezygapophyses of its counterpart. Moreover, the anterior and posterior articulations are multiple, complex, and not in tight articulation. This may possibly be a function of supplementing articulation because the centra are not sufficiently modified (saddle shaped) and would thus provide more flexibility in the cervical region as opposed to the inflexible and rigid mode of its reptilian ancestors. This specimen's dorsal vertebrae still retain primitive characters such that individual dorsal vertebrae recovered in the field would be diagnosed as belonging to a small member of the Reptilia and not Aves. The fusion of the lumbar and sacral vertebrae is another apomorphic character for this species and to date is the first documentation of this character in a specimen from the Early Cretaceous of Western Liaoning. Its occurrence here indicates that not only is this character contemporaneous with the other members of the fauna, but also that the degree of evolutionary development differed between taxa. That is to say that the environment was selecting for this phenomenon.

The pneumatocoel in the proximal humerus is conspicuously more reduced than in *C. sanctus*, which is regarded as an apomorphic character. It was previously predicted that *Confuciusornis* would possess pneumatocoels independent from the hollow limb shaft, representing a character for flight adaptation. *C. suniae* slightly postdates *C. sanctus* and as such the documentation of a conspicuously smaller humeral pneumatocoel contradicts the concept of reducing skeletal weight to adapt to flight, unless the organism is capable of making the pneumatocoels confluent in order to attain the same objective. A comparison of these two species indicates that both have apomorphic forelimb morphology in which the third metacarpal is fused to the second metacarpal, particularly at their proximal ends, the shafts have become more slender and slightly curved, and there is a tendency to fuse the carpals. Some of the carpals have become fused with the proximal second metacarpal while the proximal end of the second metacarpal has developed a relatively large trochlea, which distinctly resembles later avian forms. Obviously, the forelimb of *Confuciusornis* is still not a well developed wing and its flight stroke is determined to be very weak because the basic characters determining a wing morphology lie in the reduction and incipient fusion of the carpals while digits become reduced or approach fusion in addition to the extreme reduction in ungual phalanges by the retention of only one or two. Additionally, the length of the humerus still slightly exceeds that of the radius and ulna, further indicating a weak power stroke.

An autapomorphic character of *C. suniae* lies in the relatively robust long bones of the forelimb and hindlimb. This is particularly noticeable in the hindlimb where there is hardly any distinction of robusticity between the femur, tibiotarsus, and the tarsometatarsus. The tibiotarsus is only slightly longer than the femur and the tarsometatarsus does not attain one-half the length of the tibiotarsus. The short tarsometatarsus is a symplesiomorphic character among primitive birds and is perhaps due to the organisms being not fully adapted to their habitats. However the degree of habitat adaptation may be more fully reflected in the measurement index of the pedal elements. The hindlimb of *C. suniae* has one additional prominent plesiomorphic character: the fourth trochanter is extremely well developed for facilitating the attachment of the Caudofemoralis and laterally the Caudofemoralis brevis.

But there is an extremely well developed fibular groove on the distolateral femoral condyle which is not documented on any other Late Jurassic bird. Another apomorphic character of the hindlimb lies in the well developed fibular crest on the lateral side of the tibiotarsus, which is not documented on *C. sanctus* or *Archaeopteryx.* The remaining characters of the hindlimb, however, are all relatively primitive.

In general, this new specimen of *Confuciusornis* is in many respects more derived than other specimens. Undoubtedly, this is due to its occurrence in a higher stratigraphic level and also because it has a greater adaptation for flight, which evolved relatively rapidly and involved the morphological modification of several organs. The degree of modification on this specimen exceeds that for intraspecific variation. Within the evolutionary process, after the appearance of *Confuciusornis* in western Liaoning, there occurs regional speciation, particularly between different habitats, such that appropriate conditions in isolated habitats would lead to the genesis of species while within a single geographic region, and stimulated by a number of factors (environmental fluctuation for instance), the inheritance of modified fundamental genetic codes would also provide speciation.

C. chuonzhous has a particularly small ungual on the first digit of the pes and the remaining pedal unguals are not very curved, differing distinctly from *C. suniae*.

In 1995, global interest was stimulated after the publications in *Nature* and *Chinese Science Bulletin* regarding the discovery of *C. sanctus* within the Late Jurassic basal mudstones of the Yixian Fm. in the Shangyuan region of Beipiaoshi, western Liaoning. This was followed by subsequent discoveries of numerous specimens, some of which were in pristine condition. The attention provided to *Confuciusornis* was primarily due to three factors: First, this was the first well preserved specimen of a primitive bird discovered in over a hundred years, since the excavations of *Archaeopteryx* in Germany, and it was contemporaneous with the latter. Second, despite the numerous characters shared with *Archaeopteryx*, the Chinese genus is edentulous, representing the oldest member of Aves with a keratinous beak replacing the dentition. Moreover, the humerus possesses the autapomorphic character of a pneumatocoel and the sternum is relatively well developed, differing widely from that of *Archaeopteryx*. Third, the autapomorphic nature of abundant new *Confuciusornis* specimens provokes workers into renewed debate regarding the origin of Aves.

Both genera possess plesiomorphic characters for the class Aves, including the presence of feathers, absence of a postorbital, large orbit, a large antorbital fenestra, and a well developed sternum. Furthermore, both maintain cranial elements that are relatively thick and not fully pneumaticized, the nasal process of premaxilla is extremely short, carpals are unfused, digits are separated, there are three large and acute unguals, vertebral centra are amphicoelous, and the hallux is in opposition to the other metacarpals. Both genera share fundamental plesiomorphic characters in addition to distinctly derived characters. That is to say, the two are noticeably distinct by the presence of full dentition on one and the earliest occurrence of a keratinous beak replacing the dentition on the other. In addition to the dentition, the crania of the two genera are also distinct in many characters: The margins of the premaxilla, maxilla, and mandible of *Confuciusornis* are ornamented with long longitudinal striations between which are troughs, a condition which is absent on *Archaeopteryx,* and may be interpreted as the genesis of the keratinous beak. Also, after the divergence from its reptilian ancestors, *Confuciusornis* inhabited ecological niches that differed from *Archaeopteryx* and its ancestors. However, there is still an extremely primitive character retained on both taxa, represented by the presence of the extremely short process of the premaxilla, which is a character inherited from reptilian ancestors. In addition, the two genera share apomorphic characters, indicating that they lay within the same evolutionary phase (or level). The nasal process of the premaxilla only attains the anterior margin of the external nares, a condition also documented in numerous archosaurs such as the Pseudosuchia, Crocodylia, and several members of the Dinosauria. An additional shared character includes the presence of an exceptionally large splenial, the only difference between the two lies in its slightly more elongated and acutely triangular morphology on *Archaeopteryx* whereas on *Confuciusornis* it is long, thin, and plate-shaped with a rounded terminus. Despite the relatively short premaxilla on *Confuciusornis,* the nasals and anterior frontals are narrow and long, indicating a more narrow and elongate rostral region than on *Archaeopteryx,* which has a more broadened anterior frontal.

The quadrate morphology on *Confuciusornis* is basically similar to that of *Archaeopteryx* although on the latter the quadrate contact with the braincase is a matter of significance as its contact is posterodorsal and because of the absence of the squamosal there is controversy regarding its veracity. The quadrate-squamosal contact in *Confuciusornis* is distinct. On the ancestral reptilian forms there is an intimate relationship between the quadrate and quadratojugal and on the majority of archosaurs the mandible articulates with both these elements, but it is only in the ornithischian dinosaurs and other related diapsids that the quadratojugal has become reduced and migrated anteriorly to become a portion of the jugal and isolated from contact with the mandible. On extant Aves the quadratojugal and jugal are completely fused and it is only on juvenile specimens that the quadratojugal is independent and in contact with the anteroventral portion of the quadrate. On both *Confuciusornis* and *Archaeopteryx* the quadratojugal is still independent and is basically present as a triangular element that is in contact with the posterolateral side of the jugal and fused with the ventrolateral side of the quadrate, but still does not compose part of the jaw articulation.

The posterior portion of the *Confuciusornis* skull differs from *Archaeopteryx* as the former is not constricted or narrow and instead is relatively broad. It also differs from the vast majority of coelurosaurian dinosaurs and is more similar to the Crocodiliformes.

Postcranially, *Confuciusornis* is extremely distinct from *Archaeopteryx*, primarily in its vertebral morphology. To date, there has been no specialized study of *Archaeopteryx* vertebrae, but current data indicates that the cervical centra are elongated and a ventral keel is absent, whereas in *Confuciusornis* the centra are relatively short, the neural arch is particularly enlarged, and there is a relatively well developed ventral keel which are characters shared with several thecodonts and Crocodylians. The sternum of *Confuciusornis* also differs by the presence of a long and relatively deep elliptical groove on its lateral side (it is reported that several small theropods also possess this character) which may represent a character for weight reduction, and also slightly resembles the morphology on Crocodiliformes. *Confuciusornis* caudal vertebrae are also distinct from *Archaeopteryx* by having reduced centra with rather elongated diapophyses and displaying a general developmental direction of the gradual and complete loss of the tail, whereas on *Archaeopteryx* the caudal centra are extremely elongated and nearly all the centra lack diapophyses, with the exception of several centra proximal to the sacrum. Not only is there an absence of the trend toward tail reduction, but conversely, the tail appears to be functional.

The forelimb of *Confuciusornis* is most characteristic: its proximal humerus is extremely inflated, particularly transversely expanded, and maintainins a pneumatocoel. This morphology is absolutely autapomorphic, although it does resemble the humerus on some Crocodiliformes even to the extent of sharing several characters with extant crocodiles such as *Alligator sinensis.* The humerus of *Sphenosuchus* from the Late Triassic-Early Jurassic of South Africa is also particularly broadened with an extremely thickened proximal margin and extremely well developed deltoid process. Obviously, the pneumatocoel on the *Confuciusornis* humerus is for the reduction of weight and thereby the facilitation of flight. On *Archaeopteryx*, the proximal humerus is only slightly expanded, resembles a thin rectangular plate, and its humeral head is extremely small and inconspicuous. On the anconal aspect of the *Confuciusornis* proximal humerus lateral to the pneumatocoel, there is a relatively long conspicuous crest for facilitating the Posterior latissimus dorsi, which is nearly absent in *Archaeopteryx* and the coelurosaurs, but is relatively well developed on the Crocodiliformes, where it also facilitates the attachment of the Teres major. The expansion of the proximal humerus on *Confuciusornis* facilitates the further development of the Biceps which in turn is intimately related to a more flexible pectoral girdle.

Additional forelimb distinction lies in the large unguals on its first and third digits, particularly on digit I which is extremely large and recurved, while the ungual on the second digit is reduced. These are functional adaptations and extremely significant as the second digit phalanges are extremely robust, representing the primary element for facilitating flight as opposed to the grasping of branches or tree trunks. Thus the facility for grasping lay in the first and third digits. Contrary to this, the manus on *Archaeopteryx* is constructed with the ungual on the third digit being the smallest and the ungual on the second digit retained as an implement for grasping, crawling, and climbing, despite the second digit being more robust as the primary flight mechanism.

The caudal regime on both taxa are not modified for flight and it appears as though the feathers functioned only for ornamentation.

There are extensive distinctions between sternum morphology of the two genera. Previously, *Archaeopteryx* specimens either did not preserve a sternum or it was poorly preserved, until the description of *A. bavarica* (Wellnhofer, 1993), which describes the element as a transversely expanded plate with a slightly crescentic terminus. The sternum on *Confuciusornis* is rather well developed with a projected arcuate anterior margin in addition to two well developed anterior processes and a relatively expanded distal end with a slightly acute and small process at its midpoint. Both have obviously yet to develop a carina and are unlike the morphology of later birds; instead the sternum resembles more closely the condition in the Crocodylia and several squamates. Thus, it is extremely significant that the pectoral girdles of these two genera are very similar, such that if one were to consider the morphology of the pectoral girdle as the sole criterion, then both genera appear to be similar enough to represent a single generic rank. This also indicates the two actually share the same basic plesiomorphic condition of primitive members of Aves.

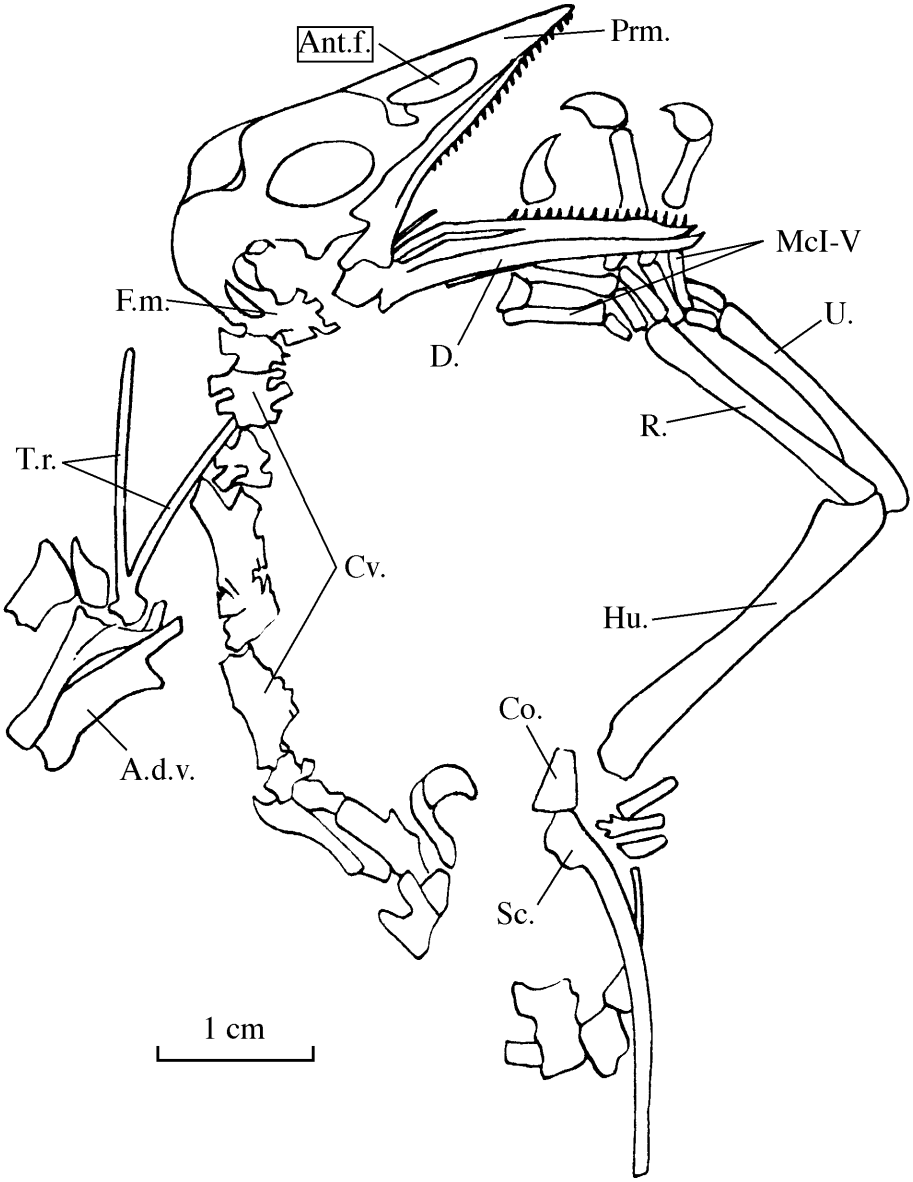

Figure 8. Schematic drawing of *Megalancosaurus* (from Fedducia, 1993).

Another significant character shared between the two genera is the fusion of the distal pubes, which on *Confuciusornis* is not inflated but on *Archaeopteryx* is inflated to form a pubic boot. But despite their morphological distinction, their derived nature is equivalent, although they have yet to initiate the process of developing the genuine avian "open" pelvic girdle. The fused termini of the *Confuciusornis* pubes have a suture line represented by a shallow groove. This is quite distinct from the Early Cretaceous avian specimens that have separated pubi.

The description of *Confuciusornis* morphological characters, its resemblance to, and distinction from *Archaeopteryx,* indicate that these two most primitive birds in the world are extremely distinct from each other, but that they also share numerous plesiomorphic characters which reflect their chronology and also imply that they shared a common reptilian ancestor. The morphology of *Confuciusornis* indicates that the avian ancestors were not dinosaurs, as is currently fashionable to believe. This hypothesis is substantiated by the following two points: The avian forelimb (wing) was derived from the Reptilia and transformed into a flight aparatus through adaptive modification and without undergoing reduction. On the contrary, in order to facilitate flight, the radius, ulna, and carpals have become elongated. Thus the reptilian ancestors could not have been those with short forelimbs. The early members of Dinosauria, and particularly the coelurosaurs, all had particularly short forelimbs. Secondly, the avian fusion of the metatarsals differs completely from the dinosaurian mode which is principally represented by the second and fourth metatarsals whereas on birds the principle metatarsal is MtIII.

Furthermore, it may be inferred from the morphology of *Confuciusornis* that more archaic and primitive forms should be present in Middle to Early Jurassic sediments of China and that extensive exposures of Triassic terrestrial sediments should produce genuine avian ancestors. The Italian genus *Megalancosaurus* should be subject of more extensive study as its extremely well developed braincase, large orbits, acute rostrum, elongated external nares, and a scapula that resembles the avian condition provoke extreme interest. Perhaps its extremely elongated cervical region was also an adaptation toward an avian mode of life and it is very possible that it represents an avian ancestor. But prior to its formal recognition as such, there is still much more research required. For instance, several workers have suggested that a clavicle and sternum are absent on this genus. This small archosaur has relatively elongated forelimbs; humerus, radius, and ulna are nearly equivalent in length, are gracile, and distinctly rather dexterous. Within the Reptilia this is the only taxon with morphology approaching the avian condition and its age is appropriate for the genesis of the class. If a similar archosaur can be recovered from the Triassic sediments of China then the longstanding controversies regarding the origin of the class Aves will be solved.

4. *Jibeinia luanhera* from the Late Jurassic of Hebei Province and its comparison to *Confuciusornis*.

After large collections were made from the Early Cretaceous of Liaoning, at the beginning of summer 1993, Mr. Pai Li, an engineer from the Hebei Provincial Office of Geology, received word of a Mesozoic bird specimen at Fengning Co.. Together with Lianhai Hou and Zhonghe Zhou, an investigation was thereby conducted. Upon the day of arrival at the village of Linjituxiang, a relatively complete avian specimen was presented to the group by one of the local farmers. The next day the fossil locality at the Dongtuyao brick factory was evaluated, where the mudstones of the Yixian Fm. were identified interbedded between limestones. Co-occurring paleontological data include plants and fish taxa including *Lycoptera*, *Yanosteus longidorsalis,* and *Peipiaosteus,* indicating that the stratigraphic position should be slightly higher than the sediments that produce *Confuciusornis.* The specimen from this locality is more derived than *Confuciusornis* but more primitive than the Early Cretaceous *Sinornis* and *Cathayornis* and thereby represents an intermediate form and significant evolutionary link.

Etymology: *Jibeinia luanhera* is produced from Fengning Co. which is located in Northern Hebei Province and is known by the appellation the Jibei Region. The Chinese character Ji represents one of the nine geographical divisions of ancient China which embraces parts of Manchuria, Jilin, Shanxi, and part of Henan Province. Bei is Chinese for north. Species etymology is derived from the Luanhe River.

Diagnosis: The maxilla contains numerous acute but unserrated teeth, the sternum is large and broad, the xiphoid process (medial column) is long, lateral processes are not well developed, carpals are unfused but are in tight association, digit III is reduced, cervical centra are extremely concave, distal pubes are fused but not expanded, proximal metatarsals are incompletely fused, distal metatarsals are completely independent, and MtII is shorter than MtIII and MtIV.

Locality and age: The specimen is derived from the gray Late Jurassic interbedded mudstones of the Yixian Fm. at the Dongtuyao brick factory near the village of Senjitu, Fengning Co., Hebei Province.

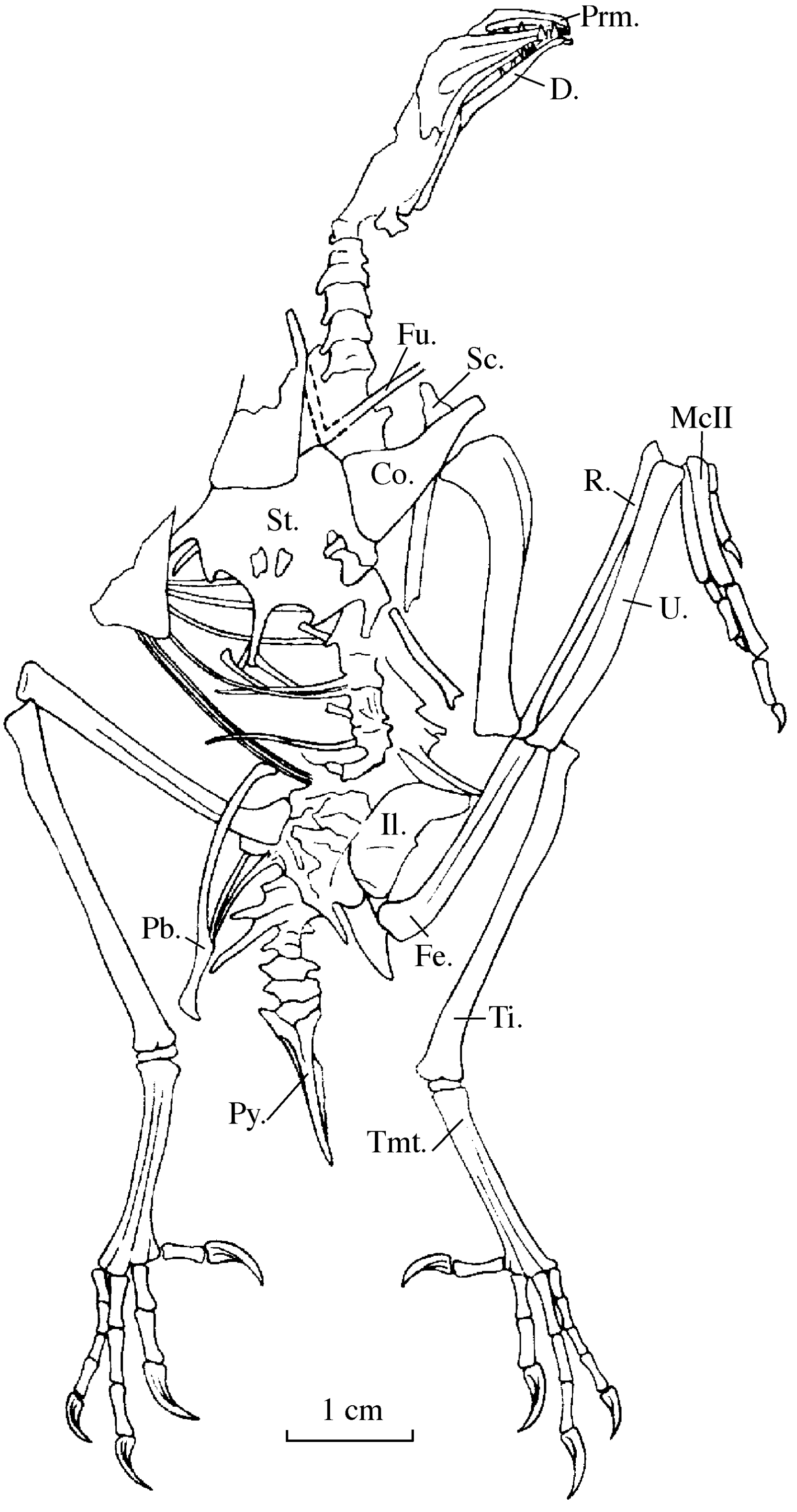

Figure 9. Drawing of the *Jibeinia luanhera* specimen.

Description: The specimen approaches *Cathayornis* in size, consisting of a relatively complete skeleton with an incomplete skull. The postcrania are exposed dorsally and ventrally and the cranium is only exposed ventrally, but this allows a clear description of the mandible.

Posterior to the frontals the cranium is missing. The postcrania are predominantly represented only by impressions. Ilium and ischium are obscure due to compressional distortion.

The nasal process of the premaxilla is slender and long, there are one to four teeth present on the rostrum, and only a portion of the maxilla bearing dentition is visible because the rest is obscured by the mandible. Six widely spaced teeth are visible and alveoli for replacement dentition are absent. Dental morphology is nearly completely consistent with the London specimen of *Archaeopteryx*, noted by Martin (1991), in which he describes a constricted neck between the lengthy tooth crown and expansive tooth root. But on *Jibeinia* the apex of the crown is longer, more acute, and is posteriorly curved. This dental morphology differs from theropods and more closely resembles that of the Crocodylia.

The mandible is relatively well preserved with the left ramus being basically complete. In lateral perspective the mandible is slightly dorsally curved with an arched ventral margin, the dentary is relatively dorsoventrally slender and is relatively long. The posterior elements have been subjected to compressional distortion and thus only the articular is recognized as being extremely well developed with its terminus dorsally oblique. A well developed dentition is present in tight association anteriorly, but posteriorly it resembles that of the maxilla by becoming widely spaced. The individual teeth are relatively large and morphologically resemble those of the maxilla. The longest tooth in the series is 10 mm.

Only the anterior portion of the frontal and parietal’s interior lamina are preserved. There is a short vomer inlaid between two expansive palatines but posterior to it, the morphology and placement of the pterygoids are vague.

The cervical series is short, with only six amphicoelous centra visible. The anterior centra are small but gradually enlarge posteriorly. Lateral pleurocoels are present and neural spines are relatively low and broad. Lengths of the robust cervical ribs are unclear. Dorsal vertebral count is also vague because the majority is obscured, but five amphicoelous anterior lumbars are visible with centra morphologically similar to, but larger than the cervicals, a ventral keel is absent, several rib heads are still in articulation on the left side, and intervertebral plates are present between the centra. There are a minimum of eight sacral vertebra based upon diapophyseal count; the diapophyses are relatively short, and centra are not fused. The caudal vertebrae are fused but not completely, and approximately 10-12 vacuities perforate the diapophyses. Thus the caudals are basically fused to form a conical pygostyle. Neural spines are also fused to form an undulating dorsal ridge. The most anterior caudals are anteroposteriorly compressed and transversely expanded, ventrally there are distinct processes, and diapophyses are particularly elongated.

The coracoid is the best preserved element in the pectoral girdle. Terminal articulations of the furcula are missing, and only the right scapula is present. The coracoid is not elongated, its proximal end is extremely thin with a small rounded head dorsally while distally its contact with the scapula is extremely broad and thick, and as such its has a general morphology of an acutely robust triangular plate. The scapula is an elongated and thickened element and its proximal end overlies the coracoid. The scapular crest is extremely elongated and laterally projected. The clavicle branches are laterally compressed and relatively broad; their proximal ends are acute processes, but do not completely form a well developed articulation with the coracoids.

The sternum is the largest element on the skeleton with a multifaceted morphology. Its transverse breadth is 18 mm which barely exceeds its 17 mm anteroposterior length, a character shared with *A. bavarica*. Morphologically it is more similar to that of *Cathayornis*, but differs in having an extremely short lateral process and a xiphoid process which is the longest on the element. On each side of the posterior xiphoid process there is a small medially hooked projection. Ventrally on the sternum a carina is absent, although the ventral surface is relatively convex, particularly approaching both sides of the midline. It is also convex at the midpoint of the midline, which may represent an incipient carina. There are also relatively distinct, regular ventrolateral grooves which may represent attachment points facilitating pectoral musculature.

Rib morphology is simple: bicapitate, slender, and long. Several ribs are still articulated to the thoracic and lumbar centra. Gastral ribs are rare but conspicuous. It is quite evident that rib morphology closely resembles that of *Chaoyangia* from the Early Cretaceous Lofotang Fm., only more primitive.

Although the left forelimb is basically missing, the right forelimb is completely preserved. Termini of the relatively robust humerus are present but the shaft is represented by a distinct impression. The proximal end is medially curved with a small but distinct head that is associated with a medial and lateral tuberosity. All three processes project distinctly from the proximal surface. Although the deltoid process is not well developed, it still projects laterally. A small depression distal to the medial tuberosity may represent an incipient pneumatocoel. The distal humerus is simple in morphology with a slight lateral expansion. Genuine medial and lateral condyles are not yet formed, and as such the distal end is represented by a slightly depressed planar surface.

The ulna is predominantly represented by a depression in the matrix. Its shaft is straight, the proximal end is slightly curved but not expanded, an olecranon process is absent, and the distal end is laterally expanded with a concave terminus. The radius is more slender than the ulna and is extremely straight; its proximal end is not expanded for contact with the ulna, its distal end is laterally expanded to form a cone that approaches the distal end of the ulna, and its terminus is a small rounded facet that surpasses the distal end of the ulna.

There are still two independent carpals which differ from the condition of the Early Cretaceous birds. These elements overlap slightly with the one on the ulnar side being relatively large but the one on the radial side being relatively small. The three metacarpals are unfused, resembling the condition of *Confuciusornis* and *Archaeopteryx.* McI is short and in close association with the carpals. McII is the largest in the series. McIII expands from its midshaft to its distal end and its breadth is equivalent to McII, a condition resembling *Confuciusornis* but differing from *Archaeopteryx.* Digit I is elongated and greatly surpasses the lengths of McII and McIII, implying a strong flight stroke. The independent first digit gradually becomes reduced although its phalanx and ungual are more well developed than in the Early Cretaceous *Sinornis* or *Cathayornis,* and thus represents a transitional phase in the evolution of flight. Digit II resembles *Confuciusornis* by being the most robust in the series and being composed of two phalanges, the distal of which is relatively small. The size of the ungual is equivalent to that on digit I but has more curvature. The impression of digit III also resembles *Confuciusornis* and *Archaeopteryx* by being composed of three phalanges and an ungual, but it differs in its most distal phalanx being the shortest, the digit is independent, and has been shifted medially.

The pelvic girdle and sacrum have been subjected to compressional distortion, prohibiting a description of the ilium. As such it is only recognized in the right hindlimb region as being a robust element. Only the left side of the ischium is visible, indicating that it is relatively short with a slender slightly curved distal end. The pubis is the longest element in the pelvic girdle with fused and unexpanded termini. These three pelvic elements are unfused, the ischium and pubis are posteriorly oblique, and appear relatively primitive.

The hindlimb is the best preserved element on the specimen with the elements being basically complete. The femur is relatively thin, straight, and weak, with a small head that lacks a neck, still preserving the morphology of its reptilian ancestors, and resembling the condition in *Confuciusornis* and *Archaeopteryx.* Distal condyles are not well developed and the terminus is gently concave. The tibiotarsus is long but not robust. Its proximal end is slightly inflated with a rather planar facet, and lacks medial and lateral articular surfaces in addition to a cnemial crest. Its distal end is also slightly expanded but a trochlea between the medial and lateral condyles is absent and there is only a very slight concave facet. There are at least three independent tarsals retained represented by the astragalus, calcaneum, and centrale. The tarsometatarsus is the shortest element on the hindlimb. Among the metatarsals, MtV has been lost, MtII, III, and IV are not completely fused, MtIII is the longest, MtII is shorter than its two counterparts, and as in the general avian condition, MtIV is the shortest in the sequence and in opposition. The length of the digit I ungual exceeds its phalanx, while the length of the digit II ungual is only slightly shorter than its two associated phalanges. The ungual on digit III is slightly small, and digit IV is the shortest in the sequence.

Table 5. *Jibeinia* measurements (mm).

Approximate cranial length	26.0
Preserved length of nasal process of premaxilla	8.0
External nares length	4.0
Mandible length	20.0
Scapula length	20.0
Scapula breadth	1.5
Coracoid length	11.5
Coracoid distal breadth	7.2
Furcula branch length	10.5
Sternum length	17.0
Sternum breadth	18.0
Humerus length	23.3
Humerus proximal breadth	6.0
Humerus distal breadth	4. 0
Ulna length	24.0
Radius length	24.2
MtI length	2.0
Manus digit I length	4.0
Manus digit I ungual length	2.5
MtII length	9.3
First phalanx of manus digit II length	6.0
Second phalanx of manus digit II length	3.7
Digit II ungual length	2.1
First phalanx of manus digit III length	3.2
Second phalanx of manus digit III length	1.1
Femur length	22.2
Distal femur breadth	2.5
Proximal femur breadth	3.0
Tibiotarsus length	28.0
Tibiotarsus proximal breadth	3.5
Tibiotarsus distal breadth	3.2
Tarsometatarsus length	16.3
Tarsometatarsus proximal breadth	3.0
Tarsometatarsus distal breadth	3.2
Pes digit I ungual length	7.5
Pes digit II ungual length	13.0
Pes digit III ungual length	18.0
Pes digit IV ungual length	14.0

Comparison: The general morphology of this Late Jurassic bird is more derived than both *Confuciusornis* or *Archaeopteryx* and it possesses characters attributed to extant taxa, particularly in the absence of an elongated tail. However, it should still be retained in the sub-class Sauriurae containing *Confuciusornis* and *Archaeopteryx* based upon the presence of a dentition, unfused metacarpals, three independent manus digits, the presence of gastral ribs, and the primitive morphology of the hindlimb. As previously stated, this taxon is a transitional form lying between the Late Jurassic and later Early Cretaceous taxa as further documented below.

The posterior skull of *Jibeinia* is not preserved although its basic morphology is discernable through an impression in the matrix, indicating that it is relatively short with a relatively large cranium, thus being more well developed than in both *Confuciusornis* and *Archaeopteryx.* The posterior portion of the *Jibeinia* mandible is obliquely inclined posteroventrally, which also differs distinctly from the relatively linear ventral mandible on the other two genera. The skull compares more closely to the Early Cretaceous *Cathayornis* and *Sinornis;* however, as indicated in the description above, the dental morphology is more consistent with that of *Archaeopteryx*, although there are some slight distinctions. On the Berlin specimen, the *Archaeopteryx* dentition is relatively robust with the apices posteriorly curved, whereas in the Eichstatt specimen the dentition is slender and long (Howgate, 1984) although in general morphology they are consistent by the presence of a constricted neck between the tooth root and crown. The *Jibeinia* dentition is slightly more acute and there are two pairs of teeth on the premaxilla, in contrast to *Archaeopteryx* which has three pairs. Dentition on the maxilla and mandible of *Archaeopteryx* is relatively abundant and has been studied by numerous workers (Martin and Stewart, 1977, 1980; Martin, 1991; Dames, 1888; Petronievics, 1925; Wellnhofer, 1974; Ostrom, 1976; Brodkorb,1971). After their study of the London specimen, Martin et al. (1980) suggested that the dentition of *Archaeopteryx* resembled that of the Crocodylia. On none of the specimens is there evidence of lateral tooth replacement.

In *Jibeinia* and *Archaeopteryx* specimens, tooth replacement occurs from beneath the tooth. Although there is no actual documentation of a Crocodylian mode of tooth replacement in the available specimens, a medial cavity of the root for facilitating replacement dentition is quite distinct on both genera (Fig. 40a). The dentition of *Jibeinia* is comparable to those of the Early Cretaceous taxa in its morphology but the dental battery is increased. The *Cathayornis* dentition is clearly in a phase of reduction, with the mandible only possessing two teeth, whereas the maxilla is edentulous and the premaxilla bears four small teeth. The dentitions of *Icthyornis* and *Hesperornis,* however, are comparable. Because a vast majority of Early Cretaceous specimens is only preserved as impressions in the matrix and the Early Cretaceous specimens from Spain and Russia lack cranial material, further comparisons cannot be conducted.

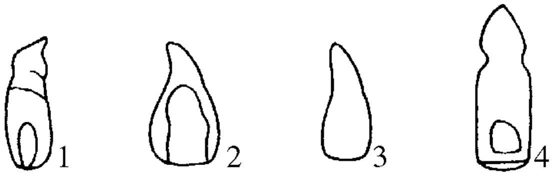

Figure 10. Comparison of early avian and Crocodylian teeth. 1. *Archaeopteryx,* 2. *Jibeinia,* 3. *Songlingornis,* 4. Crocodylia.

Plesiomorphic characters of the *Jibeinia* forelimb include a humerus that is simple in morphology and lacks a pneumatocoel; carpals, tarsals, and phalanges are all unfused; MtI is present; and digit III is still composed of three phalanges, which are all characters consistent with *Archaeopteryx* and *Confuciusornis.* Distinct from these two genera, however, are the relatively distinct medial and lateral tuberosities of the proximal humerus, the length of the digit I ungual is equivalent to MtII and MtIII, digits are tightly associated, and unguals have been reduced. These characters represent a development toward functional flight, are more derived than the morphology of *Archaeopteryx* or *Confuciusornis*, and there is a trend toward fusion of the carpals and phalanges in preparation for independent aerial locomotion. However, *Jibeinia* is more primitive than *Sinornis, Cathayornis,* and the specimens from Spain, as the latter have incipient pneumatocoels; McI has become lost; fusion of Mc2 and Mc3 has begun; and only two phalanges remain on digit III. The Early Cretaceous flight mechanism is relatively dexterous, powerful, and much more advanced toward the functionality of modern forms.

The pectoral girdle is more derived than on *Confuciusornis* and *Archaeopteryx,* most noticeably expressed in the modification of the coracoid, in which its proximal end has become thin or modified for a more dexterous articulation, whereas on the former two genera the coracoid is a short and broadened plate with its proximal end unreduced or more closely preserving the basic morphology of their reptilian ancestors. Because the origin of flight lies in the propulsive mechanism of the pectoral musculature, the morphology of the avian sternum directly influences the functional strength associated with the flight stroke, thus the evolutionary phase of the sternum reflects the functional ability for flight. The *Jibeinia* sternum is much more derived than the older genera, although its breadth still exceeds its length but its configuration is relatively complex. On the two former genera the sternum is small and shaped as a short transversely broadened plate. This is a primary reason some workers believe there is an inability for flight in *Archaeopteryx.* However, it is important here to note that on the *Archaeopteryx* specimens at hand, it is only the *A. bavarica* specimen that preserves a sternum. The *Confuciusornis* sternum is still simple in morphology, lacking a xiphoid or posterolateral processes.

Compared to Early Cretaceous genera, the pectoral girdle of *Jibeinia* is distinctly primitive and cumbersome. The *Cathayornis* coracoid is not only elongated and compressed, the proximal end maintains an articular surface for the scapula and humerus, the scapula is basically thin, narrow, and scimitar-shaped, while the sternum maintains two elongated posterolateral processes, a shorter xiphoid process, and anteriorly there appears an incipient carina. However, on both *Jibeinia* and the Early Cretaceous forms the general morphology of the sternum is broad and circular, unlike that on the much younger *Ichthyornis* in which there is a well developed sternum with a carina.

The hindlimb of *Jibeinia* is in a transitional phase between the Late Jurassic and Early Cretaceous forms, as noted in the unfused proximal metatarsals. However, initial proximal fusion of the metatarsals is inconsistent between *Archaeopteryx, Confuciusornis,* and the Early Cretaceous taxa, and thus this character is autapomorphic on *Jibeinia* and slightly resembles the derived condition on the domestic chicken *Gallus.* During ontogeny of the *Gallus* tarsometatarsus, preliminary fusion occurs distally prior to gradual proximal fusion. Based upon this, one may speculate that *Jibeinia* was the direct ancestor to extant Aves. It must also be noted that the second metatarsal on *Jibeinia* is the shortest, which also differs from all known Mesozoic taxa.

The discussion conducted above illustrates the transitional phase between the Jurassic and Cretaceous that *Jibeinia* represents and provides genuine evidence for the continuity of biotic evolution. Concurrently, this specimen confirms evolutionary phases developing from primitive to derived states. The significance of the discovery of this specimen is self evident, as it indicates a relatively continuous systematic development in the early evolution of Aves.

Jibeinia represents one of two specimens produced from the Yixian Fm. of Hebei Province. The second specimen is produced from a higher stratigraphic level and is morphologically more derived. It is quite evident that although *Jibeinia* and *Confuciusornis* are both produced from the Yixian Fm., the latter is more primitive and the former displays more autapomorphic characters, but not to the extent of possessing a derived sternum with a distinct carina as noted on *Liaoningornis*. Morphologically, *Jibeinia* approaches taxa from the Early Cretaceous Jiufotang Fm. including *Sinornis* and *Cathayornis* but it is still more primitive and as such, as a transitional taxon, represents geologic evidence further substantiating evolutionary theory.

Although the cranium of *Jibeinia* is incomplete, characters documented include the relatively short rostrum, nasal process of the premaxilla is not as well developed, and the premaxilla is not as fused as on *Cathayornis. Confuciusornis,* however, is also relatively derived in its edentulous premaxilla. Thus, it is significant that within early avian evolution, the presence or absence of a dentition does not necessarily represent a primitive or derived character state but only a distinction in inherited genetic coding. This is further illustrated in a comparison of *Cathayornis* to the Late Cretaceous *Ichthyornis* and *Hesperornis* which are several tens of millions of years younger but bear a much more complete dentition. The dental morphology of *Jibeinia* thus resembles that on *Archaeopteryx, Cathayornis, Hesperornis, Ichthyornis,* and other birds with a dentition.

After Aves diverged from the Reptilia, its first major modification lay in the forelimb. The discovery of *Archaeopteryx* not only stimulated workers to consider the origin of Aves but the origin of flight itself, resulting in multidisciplinary research which produced various contradictory hypotheses that persist into the present. In general, there are four groups in the animal kingdom with the capability of flight: The most prominent group is also the most abundant and is represented by the insects, which rely predominantly on keratinous membrane for this function. The other three groups are vertebrates including Aves, the Chiroptera, and the extinct Pterosauria, each bearing individual flight mechanisms. Although the pterosaurs and bats rely on dermal membrane, though flight mechanisms are mutually exclusive. The fossil record of pterosaurs predates that for Aves with the first documentation of the group from the Early Jurassic as opposed to the Late Jurassic record of Aves. Consequently, in the Early and Middle Mesozoic the vertebrates with flight capability were dominated by the Reptilia, mirroring the predominance of reptiles in terrestrial habitats.

In the Early and Middle Jurassic the Pterosauria were extensively distributed as carnivores. Currently, there are no specimens of birds that predate the Late Jurassic and thus the question arises as to whether this is related to the domination of the Pterosauria which perhaps represented the natural enemies of early birds and thus kept avian population to an absolute minimum through predation.

Flight mechanism of the pterosaurs relied completely on the extremely extended fourth digit and thus conjecture interprets wing folding to be an impossibility. Padian (1983) determined the wing membrane of pterosaurs to be composed predominantly of supporting fibers. In contrast, the wing membrane of the Chiroptera is composed of elastic fibers which are supported between the hallux and the other digits, and thus all the phalanges are elongated allowing flexibility of the wing membrane to conform to the configuration of the digits, representing the most derived condition. But as in the pterosaurs, there is functional limitation to this design, as opposed to that of Aves which is represented by a complex of overlapping integumentary structures, and which represents the most efficient mechanism for flight currently found in vertebrates.

In recent years, in addition to the discovery of reptiles such as *Megalancosaurus,* with limb elements sharing characters with Aves (Feduccia, 1993), there are additional reptilian specimens such as the small pseudosuchian, *Longisquama,* from the Early Triassic of the former Soviet Union (Sharov, 1970) that appears to share a common ancestor with Aves in its possession of elongated scale-like structures on its torso. Others question its relationship to both Aves or even the Reptilia (Olshevsky, 1991).

Currently, there are two major hypotheses regarding the origin of flight. The theory of an arboreal genesis, or from gliding, was earliest proposed by Marsh (1880, 1881) with modern analogues represented by flying squirrels, flying reptiles, and the Malaysian “flying frog”

Rhacophorus. Under this scenario, the earliest avian members leaped between trees as precocious feathered forms with underdeveloped forelimbs. After a long period of natural selection in which the distance between arboreal habitats increased, gliding was elevated to a higher degree resulting in continuous modification to the forelimb, particularly in the development of feathers upon digit II and the ulna. This theory is still quite popular and receives support from a multitude of workers.

The second theory as proposed by Bock (1984, 1986), states that avian ancestors were ground dwelling reptiles that underwent an extensive period of natural selection to become functionally bipedal as primitive tenacious ground dwelling birds with the capacity for tree climbing. Terrestrial and arboreal saltation gradually extended in distance and thus resulted in early stages of gliding combined with gradual gliding between differential tree heights and slowly developing the initial power stroke which ultimately strengthened the functional ability for flight. This theory requires numerous modifications upon well-known avian taxa prior to a final extended phase of completion. It also implies an intermediate ancestral reptilian form which had an independent ability to inhabit the atmospheric realm through gradual transition phases. The current most primitive specimens, represented by *Archaeopteryx* and *Confuciusornis,* provide strong support for this theory in their presence of forelimb digits and recurved claws for grasping in arboreal realms. This is particularly noticeable in the mobility of the digit I and III unguals in *Confuciusornis*. Concurrently, the pes of *Confuciusornis*, with its pollex in opposition to the other three digits, insures the ability for stable perching.

The second theory relating to the origin of flight has gained prominent support rapidly (Balda et al., 1985). It was initially proposed by Williston (1879), who recognized that within the process of cursoriality, the forelimbs of the bipedal dinosaurs would be used for assistance in stability and would gradually transform into a feathered wing. He hypothesized that in the Triassic, avian ancestors probably maintained elongated lateral digits to increase functional cursoriality accompanied by the gradual expansion of scales into feathers. Nopsca (1907) concurred and further asserted that the origin of Aves lay in rapid bipedal reptiles with elongated tails. Therefore, the primitive avian forelimb (proto-wing) would have been an apparatus for assisting propulsion and strengthening the motivating force of the hindlimb. Within the past ten years, support for this theory has been gaining, particularly among those such as Balda et al. (1985) who reevaluated the skeleton of *Archaeopteryx* and elucidated the plausibility of the theory by clarifying that the hindlimb of *Archaeopteryx* is extremely well developed with an elongated tibia and a femur and tarsometatarsus length index slightly larger than two to one. This is consistent with extremely rapid cursoriality. Secondly, the hallux ungual is not elongated, the other digit unguals are not strongly recurved or acute, and flexor processes are small, which are characters that approach extant ground dwelling birds in the order Galliformes. In the large quantity of *Confuciusornis* specimens, the general condition of the pes unguals are not as large or recurved as the manus unguals, although a relatively large and recurved pes ungual is present. Thus the hindlimb of this taxon primarily functioned for the grasping of arboreal branches or trunks. The significance of the opposable hallux on the first birds reflects the ability for the rapid departure from the terrestrial surface, which was beneficial toward the development of the forelimb wing in addition to perching in arboreal habitats. The enhancement of digits I and III on the *Confuciusornis* forelimb facilitated ability to grasp branches or trunks upon gliding or flying through arboreal habitats.

Compared to extant members of Aves, the wing morphology of *Archaeopteryx* and *Confuciusornis* do not represent actual legitimate wings despite the presence of flight feathers. This is due to the presence of diverged metacarpals, three unmodified digits, the presence of well developed ungual phalanges, principle forelimb elements being simple in morphology and lacking pneumatocoels, in addition to sharing numerous forelimb characters with several reptiles. The forelimb of *Jibeinia,* however, is much more derived. Although the humerus is simple in morphology, it maintains a sinuous curvature, and the differential degree of robusticity between the radius and ulna is increased. Furthermore, McI is reduced and MtII and III have become more

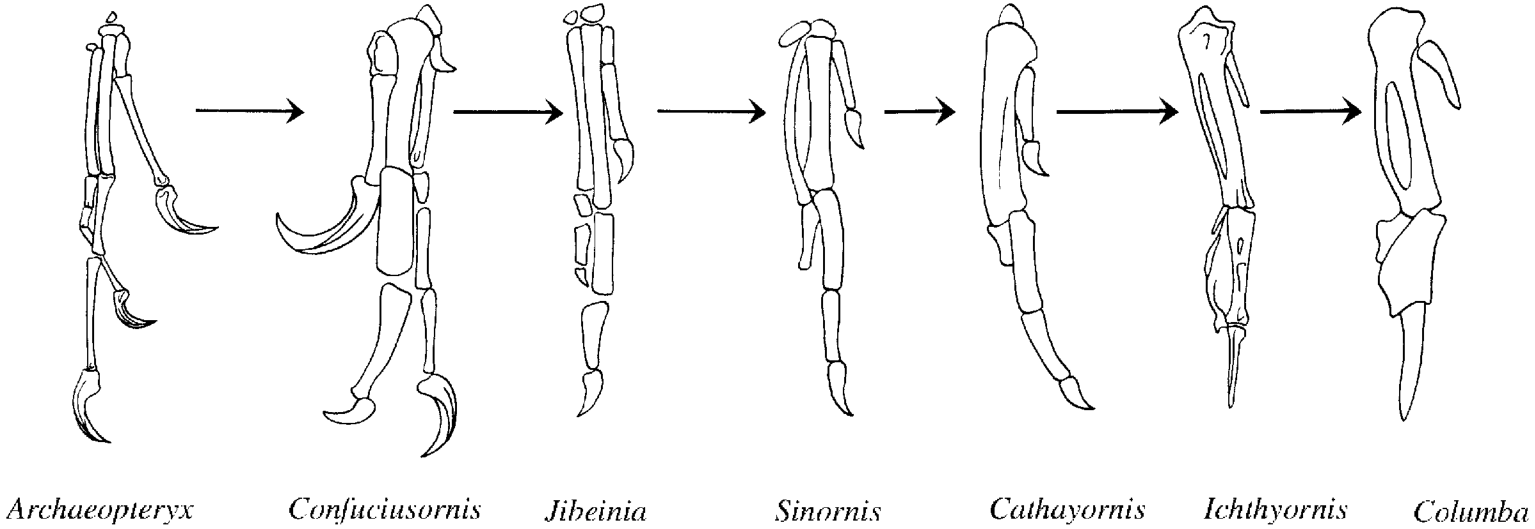

Figure 11. Evolution of the avian forelimb.

closely associated, initiating fusion at their termini. Digits have also begun to facilitate preliminary stages of flight with digit II being more well developed, feathered, elongated, and robust, while digits I and III have become reduced. Unguals have become smaller with that on digit III trending toward becoming lost. *Jibeinia* certainly had the ability to fly, although its wing is still noticeably primitive compared to the Early Cretaceous forms which have undergone even more substantial modifications including characters such as the loss of McI, complete proximal fusion of McII and III, retention of only two phalanges on digit III, humerus with a pneumatocoel, and sternum with a low carina, providing a more substantial ability for flight. In contrast, the sternum of *Jibeinia* is broad in morphology and lacks a carina. The hindlimb of *Jibeinia* lies in a transition phase between *Confuciusornis* and Early Cretaceous taxa with its most conspicuous character being the unfused proximal metatarsals, which differs from the fused condition on *Confuciusornis* and the Early Cretaceous forms, and is consistent with extant taxa. Perhaps then, *Jibeinia* is the direct ancestor to several extant taxa, although this hypothesis is a subject for a different and more detailed study.

Sinornithiformes Ord. nov.

Sinornithidae Fam. nov.

Sinornis Sereno and Rao, 1992

Diagnosis: Skull is relatively short, in cross-section the breadth of manus digit II and the ulna are twice that of digit I and the radius, manus digit I is reduced, both digits I and II maintain small and curved talons, proximal metatarsals are fused, and pygostyle is present.

Sinornis santensis Sereno and Rao, 1992

Ammended diagnosis: As for genus. Moderate in size, extremely short rostral region, gastral ribs present, dentition and pelvic girdle resembles *Archaeopteryx*.

Type: An incomplete skeleton preserving a portion of the skull, a portion of the pectoral girdle and forelimb, complete hindlimb, pelvic girdle and caudal series with pygostyle. Type specimen is housed in the Beijing Museum of Natural History.

Locality and age: Produced from the gray mudstones of the Jiufortang Fm., at Meigeyingzi, in the town of Shenglixiang, Chaoyang Co., Liaoning Province.

Summary: In addition to the description of *Gansus*, *Sinornis santensis* constitutes one the first records of Mesozoic birds in China. It was excavated from Chaoyang, Co. Liaoning Province and described in 1992, the same year as *Cathayornis*. The localities producing the latter two genera lie in the same sedimentary basin only 20 kilometers apart within the Jiufotang Fm.. Actually, *Sinornis* constitutes the first Mesozoic bird specimen found in China but its description was delayed. In 1989, when Lianhai Hou visited this region, he had an audience with the ameteur fossil collector Mr. Zhiyou Yan, one of the local villagers who had an extraordinary affinity for collecting vertebrate fossils. He informed Hou that among the abundant specimens he collected, the *Sinornis* specimen was actually collected in the 1970's. After its discovery, he wrote numerous letters to dinosaur workers in Beijing but none replied until 1980 when Chenggang Rao from the Beijing Museum of Natural History finally responded. Rao then conducted a study with Paul Sereno and published the description in 1992. Consequently, due to regrettable human factors, this valuable avian specimen incurred a delay of nearly 20 years prior to being announced to the world.

Sinornis most closely resembles *Jibeinia* in morphology though it is slightly larger. Characters shared between the two include the relatively short skull, metacarpal and digit lengths are equivalent to radius-ulna, digit II is relatively large and thick, and a pygostyle is present. These two genera not only share apomorphies, but also share plesiomorphies including cervicals not being anemocoelous, humerus relatively primitive in morphology, metacarpals are unfused, and gastric ribs are present.

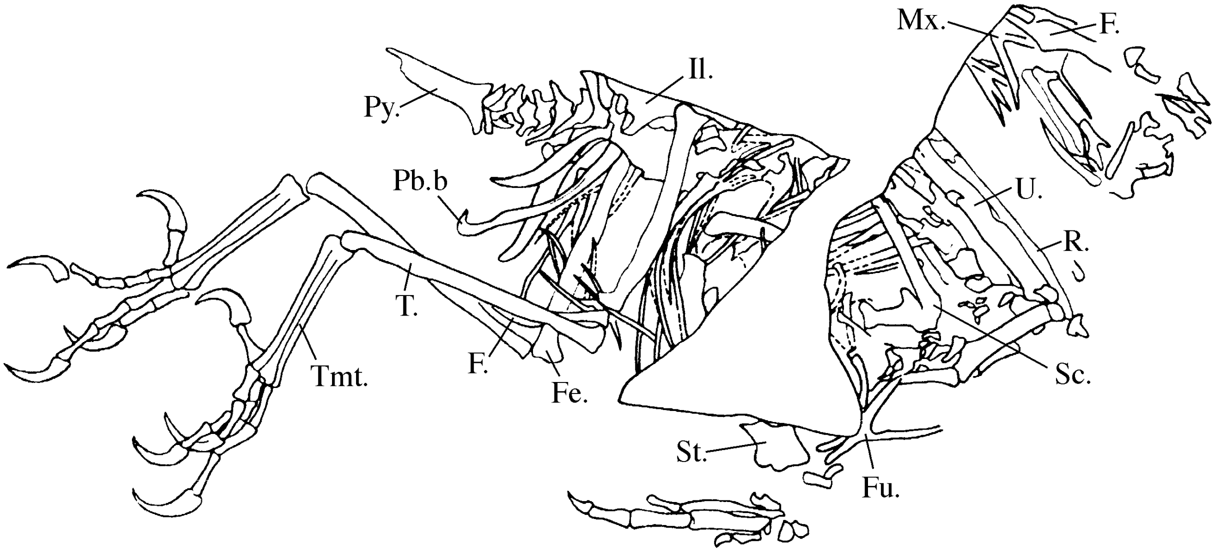

Figure 12. Illustration of *Sinornis santensis* (after Sereno and Rao, 1992)

Not only are *Sinornis* and *Jibeinia* chronologically distinct, they are also distinct morphologically. Crania on both genera are incompletely preserved, although *Jibeinia* is preserved a little better. The rostrum on *Sinornis* is short and robust whereas on *Jibeinia* there is less modification such that the rostrum is more slender. There is a single frontal preserved on the type of *Sinornis* that appears to be extremely expanded. On *Jibeinia*, although the frontal is fragmentary, from the perspective of general cranial morphology, it appears not to be as expanded. Because they both exhibit relatively strong capacity for flight, they display modifications toward derived birds and therefore their cranial morphology should also be more consistent in construction, becoming modified from the low and elongated reptilian design to one more active and dexterous, or becoming shortened and high. This is particularly noticeable in *Sinornis,* in which the rostrum is relatively short, resembling the condition of extant raptors, and as such *Sinornis* may represent the earliest modification for this mode of behavior. The original description and illustrations of Sereno and Rao (1992) indicate a full dental battery such as seen on *Archaeopteryx* and which is also documented on *Jibeinia.* Among the multitude of Early Cretaceous specimens recovered from the Jiufotang Fm. in recent years, specimens bearing a dentition are relatively rare as most are edentulous or retain a minimum amount of teeth only on the premaxilla and anterior dentary. Teeth are unobservable on the type specimen, yet its reconstruction is provided with a full dentition. Consequently, the dental reconstruction is hereby regarded suspect and it should more closely resemble the dentition of *Cathayornis* with a tendency of dental reduction.

The *Jibeinia* forelimb is more completely preserved than that on *Sinornis*. The humerus on the *Sinornis* type is indiscernible but partial ulna, radius, and manus digits are recognizable, allowing a comparison. Both species have gracile radii and ulnae but are rather morphologically distinct. Digit I and digit II have the same transverse diameter index of over 1:2, indicating that digit II facilitated primary flight feather attachment while the ulna facilitated secondary flight feather attachment, providing an increased capability for the flight stroke. Skeletal elements that support feathers have been fortified and thus their ability for flight greatly exceeds that for *Archaeopteryx* or *Confuciusornis.* Another manifestation of their derived condition lies in the digits being shorter than the humerus, radius, and ulna, resembling the condition of much later birds and contrary to the condition of their older counterparts, in which the digits are longer than the humerus, radius, and ulna. This is also an adaptation for strengthening wing mobility. Although claws are still present on *Sinornis* the unguals are even more reduced confirming the tendency toward loss andattesting to the theory that the loss of unguals is necessary for the completion of a totally functional aerodynamic wing.

Regardless of the numerous characters shared, the two genera lie on different evolutionary levels as they are produced from diachronous sediments. Character distinctions on *Sinornis* include the retention of only a single phalanx on digit III while on *Jibeinia* three phalanges are retained in addition to an ungual. *Sinornis* has lost metacarpal I which is still present in *Jibeinia.* The first digit ungual on *Sinornis* is smaller than its counterpart on digit II and is nearly atrophied, but on *Jibeinia* the ungual on digit I is larger than on digit II indicating the retentional function for grasping. Therefore, the forelimb of *Jibeinia* is in a transition phase toward a more complete wing and it lies at a lower evolutionary level than *Sinornis,* although it is obviously much more derived than *Confuciusornis* or *Archaeopteryx.* The forelimb of *Sinornis* is considered more flexible due to the articular relationship of the humeral head to the glenoid fossa, which allows wing excursion to a much greater extent. Furthermore, it provides greater capacity of downward force against the anterior vertebral column. *Confuciusornis* and *Archaeopteryx* were merely capable of dorsal-ventral forelimb excursion. Finally, because the range of humeral excursion was extended, there also followed increased flexibility between the radius-ulna and carpals, providing the capability for lateral wing folding such that the internal angle between the digits and forearm was smaller than 90°, in contrast to *Archaeopteryx* which was only capable of a greater than 90° contraction. Based upon the humeral head morphology and condition of the radius, ulna, and digits, *Jibeinia* much more resembles *Sinornis* than its earlier counterparts.

Sinornis only preserves fragmentary vertebrae in the cervical to dorsal range. Sereno and Rao (1992) interpreted the torso to be short based upon a comparison to *Iberomesornis* from the Early Cretaceous of Spain. It was inferred that dorsals did not exceed eleven centra and that there were eight unfused pre-pygostyle caudals due to the extremely short tail. Based upon this, they determined that the midpoint of the torso had migrated anteriorly as in extant forms, allowing further development of the pectoral musculature and the sternum. This in effect produced a mechanism sufficient for sustained flight.

The most significant applications pertaining to avian flight lies in the pectoral girdle and particularly the functional mechanism delivered by the forelimb digits. The coracoids represent a pair of strong and robust elements that support the humerus at one extremity and the sternum at the other with a kinetic contact. In addition, the Supracoracoideus, which is responsible for lift-off, attaches to the sternum firmly beneath the pectoral musculature, extends as a tendon to traverse the coracoid, and then becomes implanted on the dorsal surface at the base of the humerus. In this manner the coracoid and furcula act as an application of energy transfer. In Aves, the distal fusion of the clavicles composes the characteristic furcula and acts in functional application as a cross-beam to resist the contraction of the coracoids from the force of the forelimbs. The scapula maintains independent activity above the ribs while firmly supporting the humerus. The *Sinornis* furcula is completely consistent with *Cathayornis* in being V-shaped. Furthermore, both clavicles are relatively slender, approaching the morphology of later avian forms. It is only proximally, toward the glenoid fossa where it is not preserved. Consequently, this is more derived than the robust arcuate clavicles noted on both *Confuciusornis* and *Archaeopteryx.* The distal scapula is incompletely preserved but is unlike the scimitar-shaped morphology of extant forms and instead is linear, long, expanded, and not curved. The distal end lies distant from the proximal end but not as much so as on extant forms. On *Jibeinia,* the furcula is more primitive than on *Sinornis,* a furcular process is not preserved, and clavicle branches are relatively broad and thick. Its scapula is also broader and thicker than on *Sinornis*.

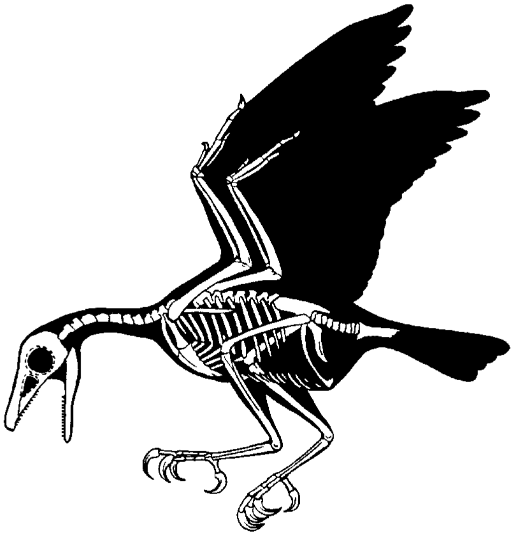

Figure 13. Restoratrion of *Sinornis santensis* (after Sereno and Rao, 1992).

The strength of functional flight lies in the sternum. Its morphological variation is one of the indications of the stage of avian evolution, as it elucidates the degree of development of the pectoral musculature, which in turn reflects the actual strength or weakness of functional flight. The sternum is incompletely preserved on *Sinornis* but those preserved on other taxa from the same stratigraphic position appear to be relatively well developed and thus by correlation, one may assume that the condition was similar on *Sinornis*. Therefore, as on *Cathayornis*, it is assumed that there should be a relatively low carina posteriorly in addition to a relatively well developed counterpart anteriorly.

The pelvic girdle is relatively well preserved and is fundamentally consistent with the vast majority of Early Cretaceous taxa. Sit is rather primitive and resembles *Archaeopteryx*, particularly in the pubis which is extremely elongated, posteriorly oblique, and maintains a booted distal end. The *Sinornis* ischium differs from those of other Early Cretaceous avian forms by being a little longer with a thin and acute terminus. Observations on avian pelves indicate that between the Late Jurassic *Archaeopteryx* and the abundant, extensively distributed, and relatively taxonomically diverse Early Cretaceous taxa, there was no major modification to the pelvic design, which appears to be rather inconsistent with the strong modifications made to the forelimb. The complexity of natural organismic evolution is still poorly understood, but avian taxa are consistent with other living forms in this respect. Avian origins and evolution, in one aspect, are restricted by the primitive characters inherited from their reptilian ancestors, while in another respect, modification is influenced by environmental conditions. Consequently, within the process of organismic evolution, morphological developmental processes and distribution patterns constitute a long and arduous period of systematic engineering. Naturally, the range of avian morphologic evolution is also affected by the directional control of the organism itself. The selected direction of avian evolution lies most notably in the isolation of the forelimb function from the hindlimb function. Within the vertebrates then, Aves constitutes the only organism with differential apparatus, or locomotor modules (Gatesy and Middleton, 1997). With this concept as a basis, the isolation and evolution of those modules primarily facilitated development and modification of forelimb function. The comprehension of the process of this systematic development can only be observed through paleontological data. It is not possible to conduct direct developmental observations to confirm hypotheses, as is done by embryologists. Therefore paleontologists can only diligently persevere and to the best of their ability, develop their data systematically.

Sereno and Rao (1992) provided only a cursory summary of the hindlimb, describing the hallux as being in opposition, unguals being relatively large with morphology for perching and climbing, and the loss of Mt V. This is consistent with the other Early Cretaceous taxa. However, reevaluation of the type specimen indicates additional significant characters: The femur is relatively long, the shaft is robust, and distal condyles are relatively distinct. On later taxa of volant birds, the femur is generally relatively short and the tibiotarsus is relatively long in order to promote rapid cursoriality. Although the distal femoral condyles are relatively well developed, the lengths of the tibiotarsus and femur are nearly equivalent, being rather primitive in character, as its reptilian ancestors maintained a femur that was longer than the tibia. This condition is equivalent in *Archaeopteryx*, where the femur is relatively robust, the tibiotarsus is more slender, distal medial and lateral condyles are well developed and project anteriorly beyond the shaft. Whether or not an supratendinal bridge is present is unknown because all the specimens are preserved in lateral perspective.

Sinornis preserves a fibula with a relatively large proximal end, which differs greatly from the vast majority of specimens excavated from Boluo, Chaoyang Co. and other regions; in these specimens a fibula is not preserved. The tarsometatarsus is one of the most characteristic long bones on *Sinornis* because its proximal end is fused, the shaft is extremely broadened, particularly near the midshaft, and the distal end is slightly expanded with the trochleae for digits II, III, and IV lying on one plane. These tarsometatarsus characters are extremely close to extant raptors and in association with the extremely short rostrum and other cranial characters, it is suspected that *Sinornis* may represent an Early Cretaceous carnivorous bird that is developing into raptor behavior.

The unguals are large, acute, and recurved. The length of the digit I ungual is 18.5 mm or nearly twice the length of the digit I first phalanx and it is in opposition to the remaining digits. It is also evident that its curvature exceeds 90°, indicating that in one respect it is typically adapted to perching while in another respect it displays extreme strength for grasping and thereby again resembles extant raptors. The unguals on digits II, III, and IV are all extremely large, acute, recurved, and well coordinated with the opposable digit I. A supplemental point regarding the pes is that length of digit III greatly exceeds the length of the tarsometatarsus, which is also a characteristic feature for extant raptors. On *Jibeinia* the digits differ by being nearly equivalent in length.

In summary, *Sinornis* is closer in morphology to the Late Jurassic *Jibeinia* than it is to any Early Cretaceous taxa. Character analysis indicates that it represents a facet of a multilateral radiating lineage developing into a raptor lifestyle. It is either the earliest representative of the raptorial lifestyle or the ancestor to all raptors.

Boluochia **Zhou, 1995**

Boluochia zhengi **Zhou, 1995**

Diagnosis: Presence of an acute and hooked beak, sternum with slender elongated lateral process with slight distal expansion, carina undeveloped as a low crest, torso noticeably reduced posterior to the acetabulum, proximal ischium with dorsal process, pubis distinctly posteriorly extended with a strong curvature and distal end booted, distal tibiotarsus intercondylar vacuity extremely compressed and in distal perspective the anterior margin of the medial condyle is relatively flattened. Only the proximal end of the tarsometatarsus is fused, the midsection is distinctly narrow, MtIV is relatively slender and weak, trochleae of the other three metatarsals lie nearly on the same plane, the pes unguals are longer than the phalanges and are strongly recurved with acute termini, and the pygostyle is elongated.

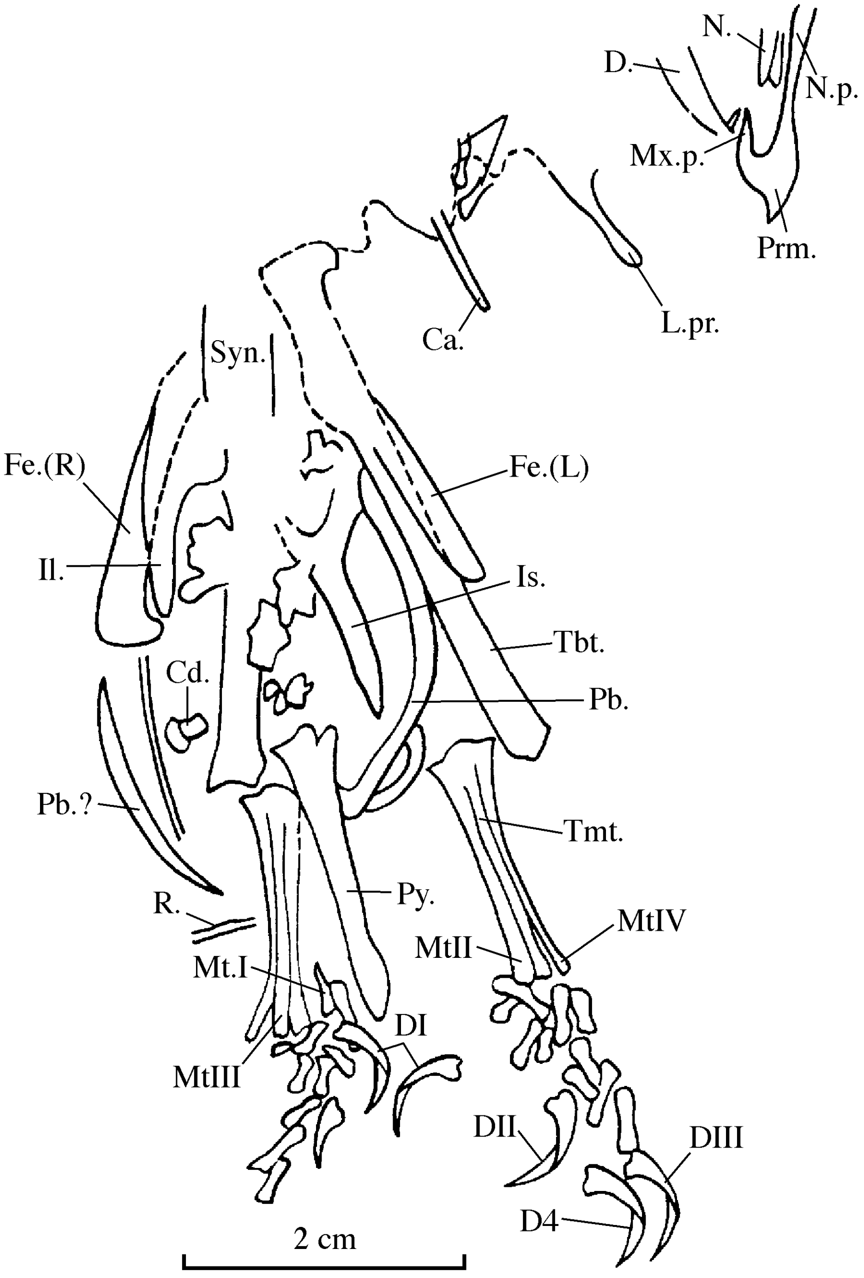

Figure 14. Drawing of V9770 *Boluochia zhengi* (after Zhou, 1995).

Type specimen: An incomplete skeleton that preserves the hindlimb, pelvic girdle, pygostyle, anterior skull, a portion of the sternum, and vertebrae. Specimen number IVPP V9770 is currently housed at the Institute of Vertebrate Paleontology and Paleoanthropology.

Locality and stratigraphic position: Light gray mudstones of the Early Cretaceous Luofotang Fm at the village of Boluochi, Chaoyang Co., Liaoning Province.

Summary: The taxonomic status of *Boluochia* was initially uncertain but after more in depth study and comparison it is regarded as a member of the Sinornithiformes. The main body of the premaxilla is dorsally projected with the anterior end forming an acute hooked process (Zhou, 1995). Thus the short and high morphology resembles *Sinornis*, only this genus is a little more autapomorphic. The femur is robust and although incomplete on the type it is determined to have a transverse diameter larger than the tibiotarsus, which is also consistent with *Sinornis*. The tarsometatarsus is also similar to that of *Sinornis*, being rather expanded at its midsection and the trochlea for the three digits lie nearly on the same plane.

A counterpart for this specimen was not recovered, prohibiting a complete comprehension of its morphology, but the premaxilla is relatively complete with a thin, flat, and linear nasal process. The rostral process of the premaxilla is dorsally projected and its anterior end curves ventrally to compose an acute hook. These characters approach those of extant raptors. Also visible on the type is a rather moderate sized embayment located between the nasal process and the main body of the premaxilla. The maxillary process of the premaxilla is relatively short and gradually thins as it extends posteriorly. Worthy of note is that the premaxilla is edentulous, which differs not only from the reconstruction of *Sinornis,* but from all other avian forms produced from the same locality which, in general, bear four premaxillary teeth.

Table 6. Skeletal measurements of *Boluochia zhengi* (mm) (from Zhou, 1995).

Pygostyle length	21.5
Pygostyle proximal breadth	4.7
Pygostyle distal breadth	4.0
Femur shaft breadth	3.0
Tibiotarsus length	37.0
Tibiotarsus shaft breadth	2.5
Tibiotarsus distal breadth	3.5
Tarsometatarsus length	17.5
Tarsometatarsus proximal breadth	4.0
Tarsometatarsus minimum breadth	1.8

The sternum of *Boluochia* is incomplete but slightly better preserved than in *Sinornis* due to the presence of its posterior portion, although the main body is missing. The carina is sill extremely undeveloped as a low crest. The posterior process is shorter than the lateral process, which is slightly expanded at its terminus.

The pelvic girdle is relatively well preserved although dorsal and ventral portions are obscured; as such, only the posterior acetabulum is visible. It has a relatively flat and straight dorsal margin that is distinctly reduced. The left ischium is characteristic in possessing a proximodorsal process. Posteriorly the ischium gradually attenuates and is unlike the condition of *Sinornis,* which is scimitar-shaped. The pubis resembles that on *Sinornis* with a distal boot. The state of fusion of the three pelvic elements is unclear, although the other Early Cretaceous taxa described generally have unfused pelvic elements.

The forelimb and pectoral girdle of *Boluochia* are not preserved but the hindlimb is extremely well preserved. The femur is incomplete but appears to have been relatively long, distinctly robust, and very possibly similar to that of *Sinornis.* In lateral perspective, the distal condyles are distinctly posteriorly projected to surpass the margin of the shaft. The tibiotarsus is more slender than the femur, the cnemial crest is not well developed, and the distal medial and lateral condyles do not noticeably project anteriorly, but there is a distinctly developed medial ligamental prominence. Among the foot bones, the relatively short tarsometatarsus is the best preserved; it has a fused proximal end that is not laterally expanded. From the proximal end to the midsection the shaft is extremely broad, resembling that on *Sinornis.* From the midsection distally, the shaft conspicuously constricts until the distal end, whereupon it again expands. The distal fourth metatarsal is distinctly separated from MtIII by a fissure and the trochleae of MtII, III, and IV lie nearly on the same plane. Although the phalanges are disarticulated and scattered within the matrix, they can nevertheless be identified. The unguals are large, curved, and are longer than the phalanges.

The pygostyle is particularly noteworthy in two respects. It is particularly long, or longer than the tarsometatarsus, and it has a narrow, elongated, longitudinal dorsal crest that is composed of the fused caudal neural spines. This latter character is shared with *Jibeinia.*

There is an intimate phylogenetic relationship between *Boluochia* and *Sinornis.* Both appear to have edentulous premaxillae, although the premaxilla on *Boluochia* possesses a distinct hooked beak, which may be interpreted in two ways. Primarily, it may represent a further adaptation toward carnivorous behavior, providing further capability for prey capture, because it more closely approaches the morphology of extant raptors. Secondly, it may be interpreted as an assistance for perching, correlated with the gradual loss of dentition, or like the behavior of parrots (Psittaciformes). In this manner, the short, thick, and curved beak would also facilitate ingestion of hard-shelled food items in addition to assisting pedal arrangement for perching. However, parrots have a modified pes with digits I and IV placed posteriorly and in opposition to the anterior digits II and III. *Boluochia* has yet to modify its pes to adapt to its environment to this extent. Regardless of which evolutionary direction *Boluochia* has taken, it still represents a neomorphic condition. And although it maintains a hooked beak, its premaxilla is still relatively low and the anterior process is extremely small. From the perspective of general morphology it resembles *Sinornis* and appears to be evolving in the direction of predatory behavior. Therefore, a continuous evolutionary trend is represented from *Sinornis* to *Boluochia.*

The hindlimb is well preserved on both genera and is beneficial toward interpreting environmental adaptations. The femur is relatively robust on both genera and tibiotarsus is more slender and longer than the femur. But on *Boluochia* the distal condyles of the tibiotarsus do not conspicuously project anteriorly, which is in contrast to *Sinornis.* The tarsometatarsus is also distinct in its constriction ventral to the midshaft, which is also not present on *Sinornis.* Moreover, the distal fourth metatarsal on *Boluochia* is more isolated and the trochlea for the digits more closely approach the morphology of extant raptors, as expressed by the enlarged and broadened trochlea for digit II and the relatively slender and weak trochlea for digit four, which is also closer to extant raptors than is *Sinornis.* However, the trochlea on *Boluochia* are still not perfected, because the articular surfaces are still not extremely well developed and are far from achieving the adaptive morphology of extant taxa. Furthermore, the unguals on both genera are similar, being large, acute, and strongly recurved, but they still do not constitutute fully efficient talons. Both genera lack flexor tuberositys on their unguals, which are fundamental for both effective perching and predation. The well developed ungual morphology but absence of tuberositys is directly related to the development of ungual flexure musculature for support and the genesis of related tendons. Flexure musculature is related to the fortification of the foot for the ability of grasping with the talons which in turn is related to the alleviation of the expense of energy. Consequently, the ungual morphology indicates that each genus lies within a differential evolutionary phase of predatory behavior with *Boluochia* being more derived.

Cathayornithiformes Zhou, Jin and Zhang, 1992

Cathayornithidae Zhou, Jin and Zhang, 1992

Cathayornis Zhou, Jin and Zhang, 1992

Ammended diagnosis: A small genus, skull is small with a minimum amount of fusion, rostrum is relatively long and low, foramen magnum is positioned ventrally, and a relatively full dentition is present on premaxilla and dentary. Scapula is straight and slender with an oblique acromion process. Coracoid has an expansive contact with the sternum, and proximal end becomes narrow. Ventral surface of the sternum is projected, carina is low, and lateral processes are well developed with termini that are expanded as oblique triangles. Humerus and ulna are equivalent in length, humeral head is small or undeveloped, medial and lateral tuberosities are distinct, and there is a small pneumatocoel. Ulna is robust, slightly curved, and possesses a small olecranon process. Radius is slender with an expanded proximal end. Proximal carpals are fused and there is a carpal trochlea. Reduced unguals are present on the first and second digits. Pelvic girdle is unfused. Fibula is long, conical, and is not fused with the tibiotarsus. Pes talons are not extremely curved. Pygostyle is present.

Cathayornis yandica Zhou, Jin and Zhang, 1992

The morphology and paleoecology of *Cathayornis* is relatively well understood (Zhou et al., 1992; Zhou, 1995), as the majority of specimens excavated from Boluochi, Chaoyang Co, Liaoning Province, belong to this genus. It is recognized as a small taxon with little individual variation and resembles the extant Passeriformes, a family which is adapted to a variety of habitats and displays a large range of morphological variation. The summary below reiterates the work of Zhou in addition to supplementing this work by more recent reevaluation.

Specimen: A nearly complete skeleton lacking tarsometatarsus and pes is incomplete. Specimen 9169A and B (positive and negative) is housed at the Institute of Vertebrate Paleontology and Paleoanthropology.

Ammended species diagnosis: A small species within the genus with a transverse groove between the frontal and parietal. A minumum of three teeth are present on the dentary. Sternum possesses a manubrium. Tarsometatarsus is longer than half the length of the tibiotarsus. Caudal vertebrae are shortened, and are not fused with the pygostyle.

Locality and stratigraphic position: Light gray mudstones of the Early Cretaceous Jiufotang Fm., at the village of Boluochi, Chaoyang Co., Liaoning Province.

Summary: Among the known Early Cretaceous Aves, *Cathayornis* represents a small genus that is well preserved, particularly in the cranium, forelimb, and sternum. Many hind limb haracters are still uncertain as the tarsometatarsus is not preserved, although several phalanges and pes unguals are present, allowing interpretation of some adaptive characteristics.

The skull is preserved in lateral perspective, it is relatively long and low with basically unfused cranial elements. The premaxilla is not elongated, does not form a hooked beak, and possesses a minimum of four short and conical teeth that have a slight constriction at their base, resembling *Archaeopteryx* and *Jibeinia.* The nasal process of the premaxilla is slender and long, causing the rostral region to be relatively elongated. External nares are large elongated ellipses and constitute the most conspicuous character of the skull, being a result of the low and planar anterior rostrum, although this bill is still not as pronounced as on the Anseriformes. The maxilla is nearly triangular with a minimum of four teeth. Frontals are elongated, transversely expanded, and constitute the vast majority of the cranium.

The position of the foramen magnum is one of the significant characters in determining the evolutionary level of the avian condition. The preservation of the cervical vertebrae in relation to the skull indicates that the *Cathayornis* foramen magnum is neither posteriorly located nor has it migrated to become completely ventral as in extant taxa. Zhou et al. (1992) stated that “the foramen magnum probably occupies a posteroventral position on the skull.” Therefore, it occupies a phase between *Jibeinia* and later avian taxa.

The anterior mandible is slender and posteriorly broad, the ventral margin is straight, but a precise tooth count is obscured by compressional distortion, although at least three teeth are visible.

The cervical series of *Cathayornis* is relatively long, with perhaps over 8-10 centra. The specimen is preserved with the neck and cranium dorsally retracted and thus cervical articulation is considered relatively flexible. However, detailed observation indicates that the centra are still not heterocoelous or saddle-shaped, but are procoelous, retaining the morphology of its reptilian ancestors. The dorsal vertebrae are not fused, further indicating its primitive condition. There are a minimum of eight fused sacral centra; the diapophyses on the posterior two centra are fused but retain fenestra. Posterior to the sacrals and anterior to the pygostyle are several flexible caudal centra, the precise count of which is unclear. The pygostyle is not well developed and is relatively elongated with an acute terminus, being a little more derived than on *Jibeinia* or *Sinornis.*

The term “wing” is applied for the first time in the description of *Cathayornis,* which is significant in two respects. The forelimb of this genus has entered into the fundamental morphology of the true avian wing: the humerus bears a pneumatocoel, the proximal carpometacarpus is fused, and a carpal trochlea is present (Zhou, 1992). This indicates increased mobility between the carpometacarpus and radius to supplement primary flight, such that not only is original dorsal-ventral mobility possible, but an extensive range of forelimb excursion is now possible, approaching that of extant Aves. Secondly, the forelimb morphology has developed into the fundamental model of a wing: the articular relationship between the distal humerus and the proximal ulna has become more complex because the ulna has a small olecranon process and the humerus has a shallow opposing sulcus to facilitate it. Thus, the *Cathayornis* forelimb can execute the function of a true wing despite the presence of vestigial talons on the digits.

The humerus of *Cathayornis* is more derived than those of *Jibeinia* and other older taxa, as expressed by the presence of a pneumatocoel despite its small size, a relatively large deltoid process, and the relatively well developed distal medial and lateral condyles. Therefore, the determination of a shallow olecranon fossa as described by Zhou (1992) is hereby regarded as credible. However, he also noted the presence of an ectepicondylar process which, in this text, cannot be corroborated.

The ulna is robust with a slightly curved proximal end, a short olecranon process associated with a cotyle, and relatively distinct distal medial and lateral condyles but which are not noticeably laterally expanded. The transverse diameter of the ulna is twice that of the radius. The radius has an extremely straight shaft with a relatively well developed capital tuberosity, a laterally expanded and compressed distal end, and a tendinal groove that is present at the medial side of the distal expansion.

Two independent carpals are present. The ulnare is nearly saddle-shaped and the radiale is relatively small and irregular in morphology. The remaining carpals have become reduced and fused with McII and McIII to form the carpometacarpus. Although in *Cathayornis* this element is fused, it is still primitive because only a well developed carpal trochlea represents an apomorphy.

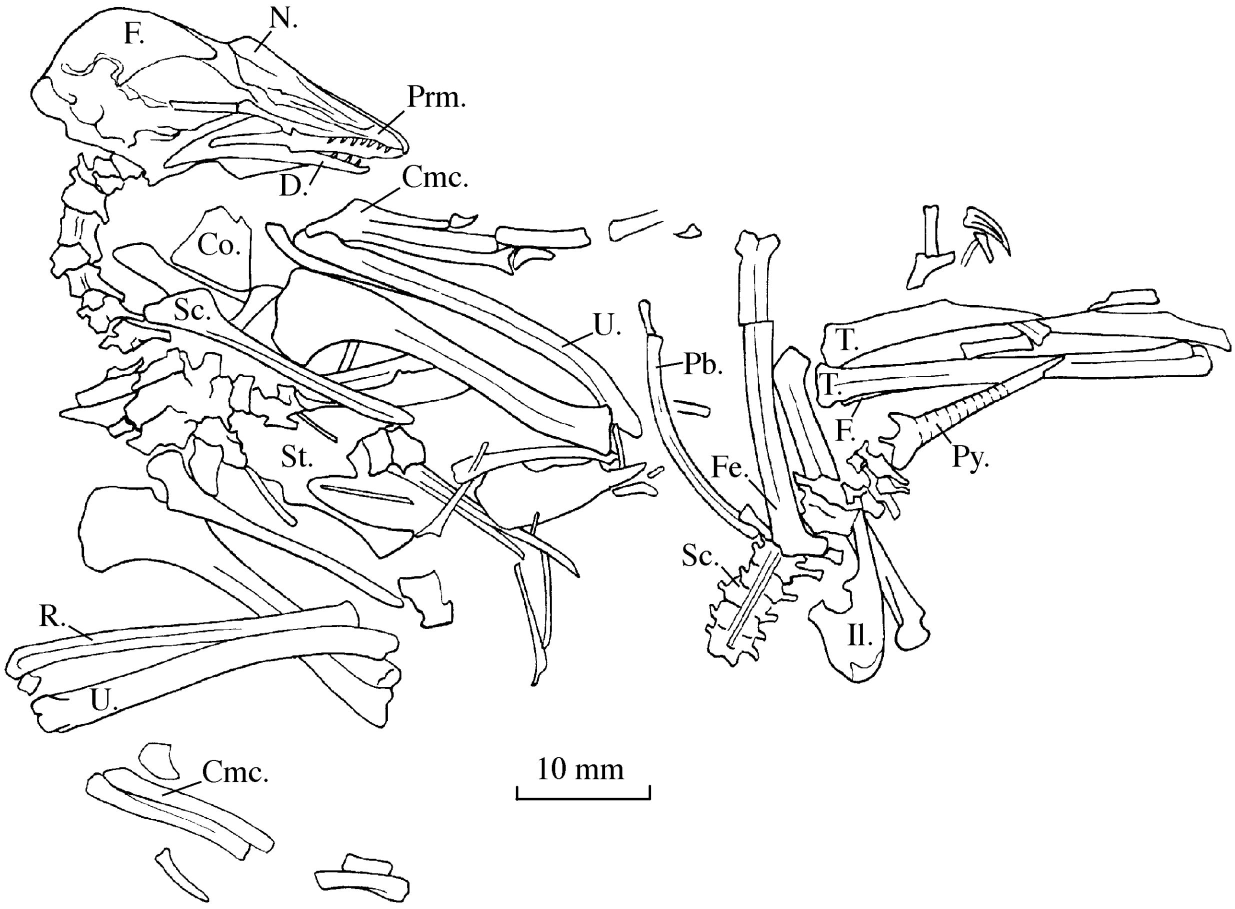

Figure 15. Drawing of *Cathayornis yandica* skeleton (from Zhou, 1994).

On all the primitive fossil birds to date, this is the first documentation of a fused carpometacarpus. On *Jibeinia* and *Sinornis* the carpals and metacarpals are unfused and thus are not recognized as a legitimate carpometacarpus. Phylogenetically, this character is extremely significant toward *Cathayornis.* In addition, the digits in this genus have been highly modified: digit II retains only two phalanges with an ungual, and digit III retains only a single phalanx, consistent with extant taxa. However the presence of two small unguals is distinct from extant forms and the digit II second phalanx has yet to become laterally compressed.

The sternum morphology is the most characteristic feature of the genus. Sanz and Buscalioni (1992) described an Early Cretaceous specimen from the Las Hoyas region of Spain that they named *Concornis lacustris.* It is regrettable that cranial material is not present, although the postcrania are relatively well represented. This genus shares numerous characters with *Cathayornis* including a fundamentally similar characteristic V-shaped furcula, an elongated furcular process, and clavicle branches that are straight and robust. The coracoid and sternum articulation is exceptionally broadened, the terminus is very slightly anteriorly concave, the proximal end is thin but the coracoid head is slightly broadened for articulation with the humerus. The sterna of each genus are similar, resembling a top or gyroscope. The anterior surface is acute and the posterior face is broadened. Both sterna have a low carina and elongated lateral processes that expand to terminate as a boot, and the posterior processes are also relatively long. However, the two are noticeably distinct in that the shafts of the *Cathayornis* lateral processes are extremely thin, whereas those of *Concornis* are relatively robust. The termini of the *Cathayornis* posterior processes are acute but on the latter are extremely robust and do not become reduced or thinned.

On *Cathayornis* the medial process of the sternum is short and blunt but on the Spanish form it is relatively long. Furthermore, anterior to the lateral process on *Concornis,* is a short process (process craniolateralis), but *Cathayornis* lacks this feature and its posterior process is shorter than its posterolateral process, whereas these counterparts on *Concornis* are nearly equivalent in length. *Concornis* therefore appears to be more derived.

Only a portion of the *Cathayornis* tarsometatarsus is preserved on the hindlimb but the femur and tibiotarsus are extremely well preserved despite being shifted in position. The femur resembles that of *Sinornis*. It is relatively long and robust, its head is large and distinctly projected, the shaft is slightly curved, and the distal medial and lateral condyles are well developed, with the lateral condyle being relatively large. The tibiotarsus is slightly longer than the femur, there is an expanded portion proximomedially, and the articular surface is slightly expanded and concave. At the distal end the condyles are not as distinctly laterally projected as on the femur. Only a portion of the tarsometatarsus is present and a majority of the digits are not preserved with only several slender phalanges and three unguals represented. The curvature of the unguals is unlike the strong arc seen in *Jibeinia, Sinornis,* or *Boluochia* and instead is more gently curved. By applying curvature parameters to determine habitat adaptation as conducted by Feduccia (1993), *Cathayornis* then falls out of the range of being a small perching form. Unfortunately, the tibiotarsus of this small form is not very diagnostic and complete digit measurements are not available for analysis. From the portion preserved, however, it is recognized that the three metatarsi are unfused, the phalanges represented are relatively long, and the talons do not display intense curvature. Thus this small form may be an Early Cretaceous analogue adapted to a shrub habitat. It may also have been adapted to riparian habitats based upon its relatively low skull with a rather planar and elongated bill, perhaps subsisting on small fish and foliage. Following a consistent increase in the adaptation to its environment, it perhaps evolved toward wading or more aquatic behavior. If this interpretation is accurate, then *Cathayornis,* together with *Gansus,* represent the most primitive morphology adapted to this type of avian behavior. The latter genus, although also an Early Cretaceous form, occurs stratigraphically higher.

Obviously, this behavioral interpretation is based primarily upon cranial morphology and talon curvature and is presented as a preliminary hypothesis. Remaining skeletal morphology of this genus has yet to become modified enough for determining adaptation to a riparian environment. But measurements of the forelimbs of wading and swimming birds, as well as those of *Jibeinia* and *Sinornis,* are compared, and show that the metacarpal and digit length are distinctly shorter than the humerus and radius/ulna length. These parameters in *Cathayornis* are basically consistent (humerus length 17 mm, ulna length 27 mm, radius length 26 mm, carpometacarpus and digit length approximately 26 mm) and are extremely close to indices of extant wading and natatorial taxa, representing sufficient supplemental evidence to support the interpretation of adaptation to riparian habitats.

The evolutionary level of *Cathayornis* has already been provided in the discussion of the forelimb. Within the framework of the continuity of avian evolution, *Cathayornis* is regarded as concrete evidence for the continuity of the *Confuciusornis-Jibeinia-Sinornis* lineage.

Cathayornis caudatus sp. nov.

In the fall of 1993, Zhonghe Zhou, Yucai Gu, Yutie Sun, and others collected Mesozoic vertebrates in the Boluochi Region of Chaoyang Co. where they recovered a well preserved specimen smaller than *C. yandica* from the same quarry. The specimen is extremely similar to *C. yandica* in morphology but also displays relatively distinctive characters including its small size and the presence of over 10 short caudals that composes a tail, which differs from the former because its caudals are fused into a pygostyle.

Diagnosis: A small species of *Cathayornis* with a transverse trough lying between the frontal and parietal. There is a minimum of three pairs of teeth on the mandible, a relatively well developed carina is present on the sternum, the tarsometatarsus is elongated and exceeds half the length of the tibiotarsus, caudals are unfused such that there is no pygostyle but instead a small tail is present.

Type. A complete skeleton represented in a positive and negative slab. V10917 is housed in the Institute of Vertebrate Paleontology and Paleoanthropology.

Locality and stratigraphic position: Gray mudstones of the Early Cretaceous Jiufotang Fm., village of Boluochi, Chaoyang Co., Liaoning Province.

Etymology: “Caudatus,” Latin for bearing a tail.

Description: This species is smaller than *C. yandica*. The skull is preserved in lateral perspective, the forelimb has been shifted in position, the pectoral girdle has been seriously compressionally distorted prohibiting an accurate description, cervicals are overlain by the forelimb, and digits are disarticulated and scattered within the matrix.

The specimen is preserved in lateral perspective and resembles *C. yandica* with a short skull, blunt rostrum, and a relatively short premaxillary process. The nasal process is slender and long, four pairs of relatively short teeth are present on the premaxilla, and the maxilla is a relatively large, representing the most robust element on the rostrum as a nearly obtuse triangular element located laterally on the rostrum. The dentition is unobservable. Nasals resemble those of *C. yandica*, being relatively expansive, large, and located posterodorsal to the rostrum. A small, irregularly shaped, and extremely projected lacrimal is located posterolateral to the nasals and anterolateral to the frontals. There is an obliquely elongated element interpreted to be the prefrontal which lies posterolateral to the nasals and posterodorsal to the maxilla. The nasal-frontal contact is expansive and the frontals are relatively thin with a thickened medial suture line. Thus it is determined that they are not fused and represent a primitive condition. The frontals also represent the entire posterior portion of the skull and at the contact with the parietals there is an extremely conspicuous transverse v-shaped groove, a character shared with the Jurassic *Confuciusornis* and *Archaeopteryx* and which represents a plesiomorphy. Posterolateral on the skull there is a small temporal recess, the posterior half of which is composed of the squamosal. A postorbital process is not recognized. The quadrate is obscured by the radius and ulna, prohibiting its description

The mandible is relatively broad and thick with a slightly curved ventral margin. Dentition is present anteriorly with a minimum of three teeth on each side. Posteroventral to the dentary there is a relatively well developed angular. Posterior to the dentary and dorsal to the angular is a conspicuous elongated mandibular fenestra. Additional mandibular elements are obscured by the forelimb.

The forelimb is disarticulated and scattered within the matrix, although its fundamental morphology is still discernable. The humerus is relatively long with minor curvature at its distal end. The most noticeable characters proximally include the well developed medial tuberosity and the large and spherical humeral head. The lateral tuberosity is also particularly enlarged and there is a relatively conspicuous capital groove which is distinct from *C. yandica*. A proximomedial circular depression on the humerus indicates the presence of a pneumatic fossa or foramen. Furthermore, there is a large deltoid crest proximolaterally which becomes a little inflated distally. It is possibly due to taphonomic conditions that the proximal end is broadened and the distal end is relatively narrow. Distally, the medial condyle is well developed and distinctly projected, while the lateral condyle is indistinct due to compressional distortion from the proximal ulna.

Table 7. Skeletal measurements of *Cathayornis caudatus* sp. nov. (mm).

Cranial length	28.0
Premaxilla length	~12.0
Frontal length	16.0
Cranial height	~15.0
Mandibular length	~21.0
Humerus length	26.0
Humerus proximal breadth	7.0
Humerus distal breadth	~5.0
Ulna length	26.0
Ulna transverse diameter	2.5
Radius length	~25.0
Carpometacarpus length	15.0
Manus digit ungual length	2.0
Sternum length	21.5
Sternum breadth	16.5
Posterior process length	11.0
Femur length	23.0
Femur diameter	2.5
Tibiotarsus length	27.0
Tibiotarsus proximal breadth	4.0
Tibiotarsus distal breadth	4.0
Fibula length	~7.0
Tarsometatarsus length	17.0
Tarsometatarsus proximal breadth	4.0
Tarsometatarsus distal breadth	5.0
Pes digit I ungual length	5.0
Pygostyle length	~12.0

Both ulnae are incomplete and poorly preserved at their distal end. The shaft is relatively slender and curved. There is a short olecranon process at the proximal end, associated with a relatively large medial cotyle distinct from the lateral cotyle. Due to the presence of the well developed lateral cotyle, it is determined that the distolateral condyle of the humerus is also well developed. It is possible that an incipient olecranon fossa is present on the distal humerus, which would be consistent with the other Early Cretaceous taxa. The ulna lacks secondary anconael or inner papillae.

The radius is extremely fragmentary but appears to resemble the basic avian condition with a straight shaft. It is a relatively robust element compared to the ulna and in cross-section is not much more slender. Its proximal articular end is planar, lacking a distinctive cotyle for the humerus.

A horseshoe-shaped carpal is preserved anteroventral to the rostral end of the skull. The carpometacarpus resembles that of *C. yandica* with an expanded and fused proximal end. A single independent ungual is still present and it is assumed a second ungual should also be present although verification of its presence is impossible. The base of the ungual is short and thick and the apex is hooked.

The pectoral girdle is basically overlain by the pair of humeri such that only a single scapula articulated with the coracoid is visible, being represented as an expanded plate. Remaining pectoral elements are not visible, with exception of the sternum which is relatively well preserved. It differs from *C. yandica* in possessing a relatively well developed manubrium, there is an extremely short anterolateral process (sternocoracoidal process), and the posterolateral process resembles the condition of *C. yandica.* Posteriorly there is an expanded boot-shaped medial process (trabecula) that is slightly longer than the lateral process, a character also distinct from *C. yandica*. A low carina extends posteroventrally from the midpoint, while anterodorsal to the midpoint there is a small pneumatocoel. Both of these characters are more derived than on *C. yandica*.

No cervical vertebrae are exposed but four to five amphicoelous thoracic vertebra are present that are not extremely elongated, a morphology that is consistent with the vast majority of Early Cretaceous taxa, or retaining the plesiomorphic reptialian condition. Lumbar and sacral vertebrae are tightly associated but have yet to become fused. This major plesiomorphic character is the derivation for the species nomenclature for it still preserves numerous caudals to compose a tail. Regardless of their extreme contraction, the morphology of each caudal is still distinctly discernable as is each neural spine. Within the evolutionary process, the representation of ancestral morphology, or plesiomorphic conditions, appears to be continuously preserved for a relatively long period of geologic history.

A large portion of the sacrum is obscured, such that all that is visible is a portion of the ilium and posterior half of the pubis, both of which basically resemble the condition of *C. yandica*, the distal pubes not being fused.

Hindlimb long bones are relatively well preserved and only a single side of the femur is damaged. The femur is shorter than the tibiotarsus, the shaft is not robust and is relatively curved. Its proximal end is medially curved and does not display a distinct femoral head, although this may be due to taphonomic conditions.

The tibiotarsus is long and straight with a slightly expanded proximal end but a cnemial crest is absent. A fibula lies proximolaterally which is not extremely long and resembles the condition of other Early Cretaceous taxa. Distal medial and lateral condyles are extremely distinct and spherical, while a distal trochlea is also relatively distinct. In anterior perspective there is a process dorsomedial to the medial condyle which is analogous to the supratendinal bridge on later taxa of Aves. Thus, this suggests that the phalangeal and tarsometatarsal musculature and tendons traversed laterally along the hindlimb.

The two tarometatarsi are excellently preserved with proximal end fused and length exceeding half the length of the tibiotarsus. Among the three metatarsals, MtII is the longest and most robust. The morphology of MtIII and IV are equivalent although the latter is slightly longer. There is no indication of an MtV. The pes digits are relatively slender and long, phalanges are disarticulated and widely dispersed within the matrix, although the relationship of the digits and unguals is relatively distinct. Among the unguals, that on digit I is rather intensely curved although the remaining unguals have less curvature. From the perspective of general morphology and particularly the digit I talon with its relatively intense curvature and an acute terminus, it is determined that this species had the facility for a relatively strong grip and thus it is determined to represent a perching form.

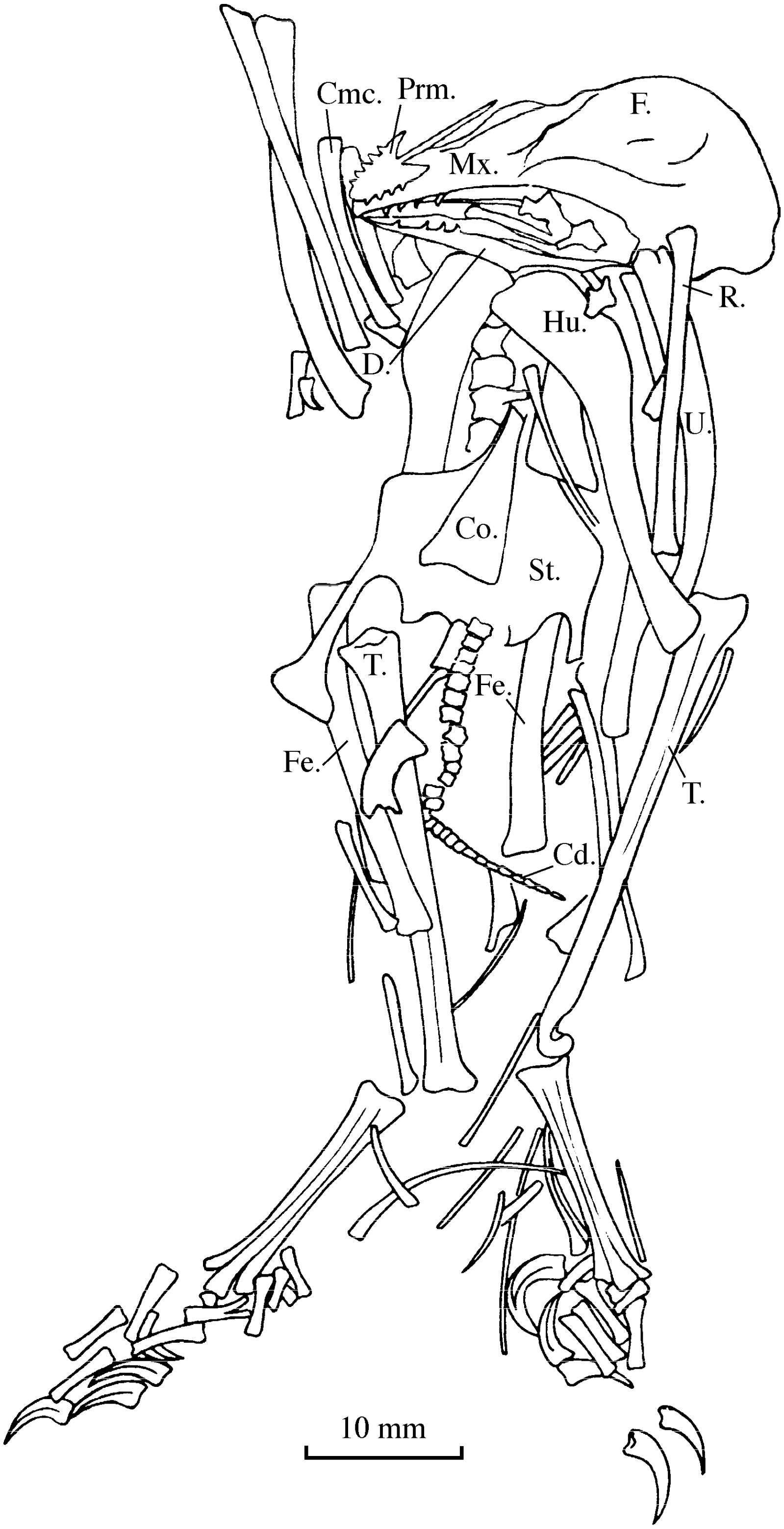

Figure 16. Drawing of V10917 *Cathayornis caudatus.*

Comparison and discussion: This small specimen is generally consistent with *Cathayornis* in its short skull, sternum, and pelvic morphology. But it also exhibitis extreme distinctions from other taxa excavated from Boluochi such as *Boluochia,* which has a strongly hooked beak, broadened tarsometatarsus, and particularly intensely recurved talons. *Cathayornis* is a little larger, approaching a moderate sized bird, has an increased dentition, and more derived characters including a more slender and elongated bill, humerus tuberosities are relatively well developed, and tibiotarsus maintains a cnemial crest. These characters also distinguish it from the other taxa described later in this text. With the exception of Early Cretaceous *Sinornis,* there are no other small avian forms such as this, with characters including the v-shaped groove between the frontals and parietals, teeth more numerous than *C. yandica,* sternum with a distinct manubrium, humerus being relatively long and equivalent in length to the ulna, femur head undeveloped, tibiotarsus lacking a cnemial crest, tarsometatarsus relatively weak with its length exceeding one-half that of the tibiotarsus, diameters of MtII and MtIV equivalent, and talons moderately curved. Its most conspicuous character is the unfused caudal vertebrae, or an approximate 12 mm tail.

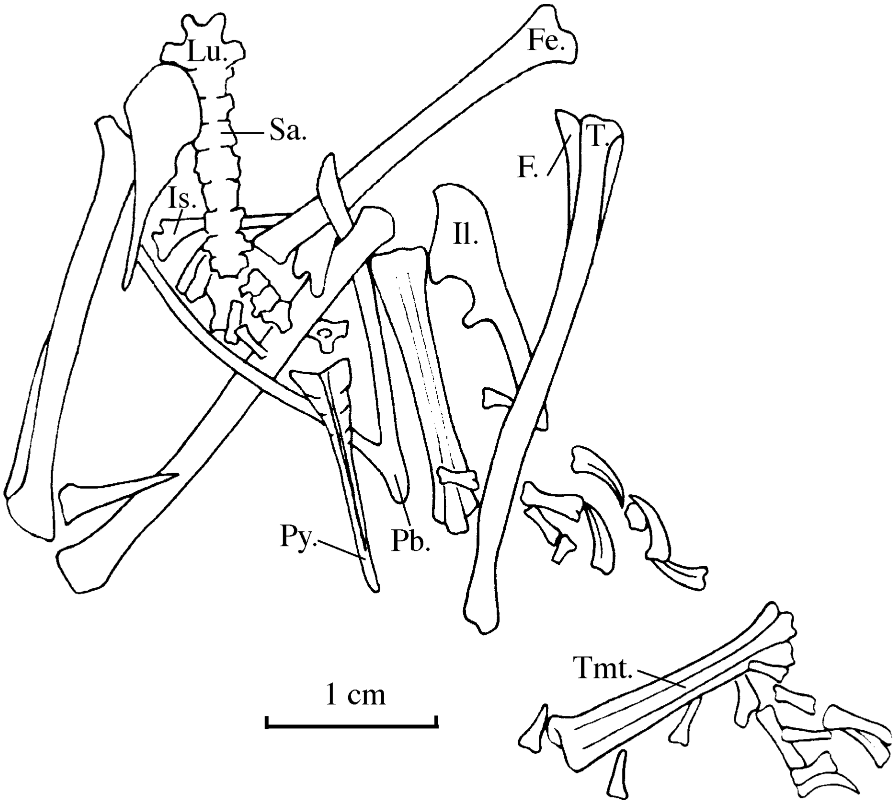

Figure 17. Drawing of specimen V.10533 *Cathayornis.*

C. caudatus shares plesiomorphic characters with Jurassic forms including the groove between the parietals and frontals, the primitive morphology of the femur and tibia, and particularly the presence of unfused caudals, characters absent on other Early Cretaceous taxa. But despite the distinctive plesiomorphic characters, *C. caudatus* also bears significant apomorphies including the small pneumatocoel on the humerus, ulna with a short olecranon process, the presence of a manubrium, the projected carina, and presence of an anterolateral processes on the sternum, all of which increase the functional ability for flight.

With regard to the behavioral adaptations of *C. caudatus,* it conforms to the Sinornithiformes by the presence of a short and straight rostrum, a robust and broadened tarsometatarsus, and large and recurved talons representing a typical perching form. Although *C.*

caudatus displays the neomorphic character of a reduced its body size, it still maintains a relatively long humerus and a short tail which are not adaptations for facilitating flight. Furthermore, its talons, are not as arced as those found on other Early Cretaceous taxa, with the exception of the relatively hooked ungual on digit I. Consequently, although this species is adapted for perching behavior, it's morphological modifications are relatively weak, and perhaps it represents a gradual transformation to a ground dwelling habitat.

Table 8. Measurements of *Cathayornis caudatus* specimen V.10533 (mm).

Synsacrum length	15.5
Tail length	15.0
Ilium length	13.0
Ilium height	5.0
Acetabulum diameter	3.0
Preserved length of pubis	20.0
Preserved length of ischium	10.0
Femur length	24.5
Femur proximal breadth	3.0
Femur distal breadth	4.0
Tibiotarsus length	30.5
Tibiotarsus proximal breadth	3.5
Tibiotarsus distal breadth	3.0
Fibula length	9.0
Tarsometatarsus length	16.0
Tarsometatarsus proximal breadth	3.5
Tarsometatarsus distal breadth	4.0
Ungual maximum length	5.0

Appended description: Two more specimens have been recovered which are housed in the Institute of Vertebrate Paleontology and Paleoanthropology and may supplement the description of the types. Specimen V.10533 (positive and negative) is an incomplete skeleton and V.10904 is a pair of hindlimbs.

V.10533 is a partial skeleton represented by the postsacral vertebral column, pelvic girdle, and nearly complete hindlimb. Vertebrae include incompletely fused sacrals, three relatively broadened lumbar centra, and seven centra posterior to them recognized as sacrals, the posterior of which have expanded diapophyses, have basically lost the boundary lines between centra, there is a unified neural canal, but diapophyses have yet to become fused. Posterior to the sacrals is a separate series of caudals with a length of approximately 16 mm, and which are basically fused into a pygostyle, resembling the condition on extant taxa. The centra of the pygostyle reduce in size posteriorly to compose an elongated slender cone, though the neural spines are not fused allowing the recognition of each element in the caudal series.

Elements on the pelvic girdle are unfused, ilia are widely spaced and pubes are disassociated, lying to the side of the ilia with distal ends in near contact but unfused. The ilia are fundamentally consistent with *C. yandica* in their preacetabular portion being particularly high, anterior margin rounded, and ventral margin being slightly embayed. They are distinct, however in their medial curvature and the postacetabular region being particularly low and becoming extremely slender with an acute terminus. The acetabulum is relatively large. Proximal pubis is obscured but its shaft is distinctly elongated and terminates with a slightly expanded pubic boot. Only a single side of the ischium is visible, being relatively short and robust with a relatively thickened short posterior branch.

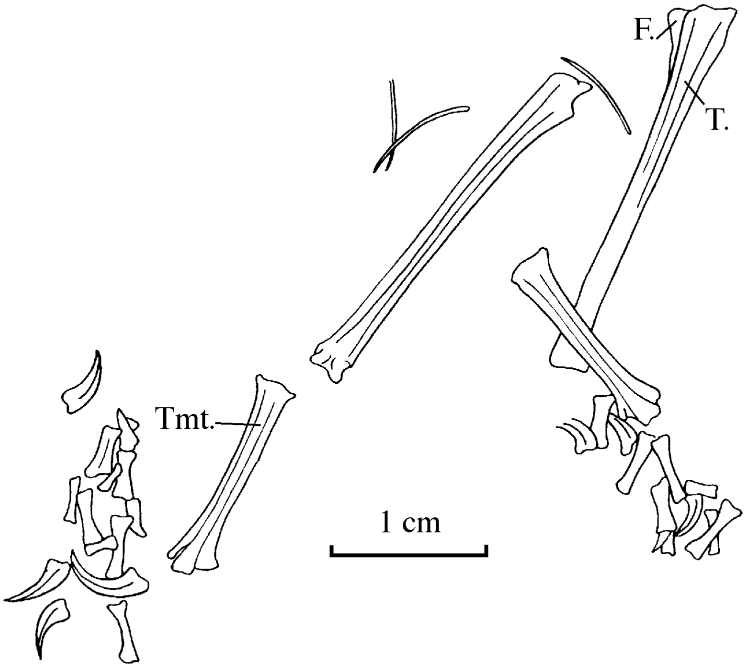

Figure 18. Drawing of *Cathayornis caudatus* specimen V.10904.

The femur on the relatively complete hindlimb is consistent with the type, being slender, long, and lacking a distinct head. Proximomedially it is merely slightly oblique for articulation with the acetabulum and distal condyles are not distinctly formed, although these nebulous characters may be the result of taphonomic conditions. However, the distal femora are distinctly represented, condyles are slightly expanded and project anteriorly but a distinct intercondylar fossa is absent. The tibiotarsus is also slender and long, being consistent with the type for *C. caudatus*, its proximal end lacks a distinct cnemial crest, distal end has a relatively narrow intercondylar depression, and condyles do not excessively expand laterally. The tarsometatarsi are consistent with the type but are a little more robust. Ungual curvature is slight and allows a further interpretation of *C. caudatus* to be a slender and long legged form that may have been adapted to both perching and riparian habitats.

Specimen V.10904 preserves only a pair of tibiotarsi, a pair of tarsometatarsi and digits with unguals. Aside from being relatively large, the remaining characters are all consistent with the type, with the exception of a distinct cnemial crest on the tibiotarsus. This specimen also preserves several slender gastric ribs.

Table 9. Measurements of *Cathayornis caudatus* specimen V.10904 (mm).

Tibiotarsus length	34.5
Tibiotarsus proximal breadth	4.5
Tibiotarsus distal breadth	4.5
Tibiotarsus breadth at midshaft	3.0
Tarsometatarsus length	19.0
Tarsometatarsus proximal breadth	4.0
Tarsometatarsus distal breadth	4.5
Maximum length of ungual	8.0

Longchengornis gen. nov.

Genus diagnosis: The parietal is posteriorly located, frontal is narrow and expanded posteriorly. Cervicals have a ventral keel, thoracic centra are amphiplatyan with elongated centra and relatively large lateral pleurocoels, and caudals are unfused to represent a relatively long tail. Proximal humerus is larger than on *Cathayornis*, is laterally expanded, there is a relatively large circular depression at its proximal midsection, and shaft is straight. Coracoid is relatively narrow and small with a linear distal terminus. Furcula is slender and the furcular process is extremely elongated. Tibiotarsus is slender and long and talons are large and recurved.

Genus etymology: Longcheng (dragon city) being pinyin romanization for the initial name of the city of Chaoyang, established in 341 AD. The nomenclature was sustained until its alteration to Chaoyang during the reign of Emperor Tianbao circa 742 AD. During this period the city represented the regional administrative, economic, and cultural center for the Northeast portion of China.

Longchengornis sanyanensis sp. nov.

Type: An incomplete skeleton (IVPP #V.10530).

Species diagnosis: As for genus. Humerus slightly shorter than ulna, manus retains ungual phalanges, sacral centra are fused but sacral girdle is still primitive, and distal metatarsals are still unfused.

Species etymology: Sanyan (three Yan kingdoms) being pinyin romanization for this region of China during the period of the Sixteen Kingdoms circa 341AD, represented by the Former Yan, Later Yan, and Northern Yan kingdoms established by the Tungusic tribes of Manchuria and eastern Mongolia.

Locality and stratigraphic position: Early Cretaceous Jiufotang Fm. at Boluochi, Chaoyang Co., Liaoning Province.

Description: *Longchengornis* is slightly larger then *Cathayornis caudatus.* The cranium is only represented by the frontals and parietals although additional cranial elements may lie within the matrix, but overlying postcranial elements prohibit further preparation. Furthermore, a portion of the skeleton has been lost due to pre-burial transportation of a short distance. Missing are portions of the forelimb and hindlimb, while elements that have been shifted in position include vertebrae, humerus, pectoral girdle, and hindlimb. The sternum is preserved in lateral perspective.

Parietals are positioned posteriorly on the skull and are isolated from the frontals by a distinct groove, which is a condition shared among all the most primitive avian taxa including *Confuciusornis* and *Archaeopteryx* and represents a plesiomorphic reptilian condition. The cranial elements are relatively thick and suture lines are conspicuous. The frontal is exposed only in lateral perspective, the remaining being obscured by the cervical vertebra. It appears to be relatively large and long with an arched posterior section.

The vertebrae are relatively well preserved compared to the other skeletal elements and represent nearly the entire column, particularly the posterior sequence. Cervicals have been rather shifted and scattered. The atlas is not recognized but the axis is present posterior to the skull and possesses a high spine, a conspicuous odontoid process, and an enlarged ventral process. Characters of the posterior cervicals include the presence of a slender ventral keel that extends along the entire midline of the centrum. This is a character shared with extant wading birds although they differ in that their ventral keel is present only on the anterior portion of the centra, as posteriorly the keel is either extremely low or absent. Both ends of the amphicoelous cervical centrae are expanded, the midsection is constricted, they have still not developed a heterocoelous condition, and posterior vertebrae are relatively elongated. Taphonomic conditions prohibit a description of neural spine morphology. The most conspicuous character of the thoracic vertebrae is the relatively large and deep lateral depressions on the centra. They also resemble the cervicals in being medially constricted. Posterior thoracic and lumbar centra are relatively short and slightly expanded. At least eight sacral centra are fused but a pygostyle is absent. Although the caudals are reduced and compressed, they remain numerous with at least 15 centra represented. Caudal length approaches 20 mm representing the longest caudal series among the specimens produced from the Boluochi quarries, as the series on *C. caudatus* is relatively short. This character may reflect the developmental condition of the forelimb and sternum, and would also noticeabley affect the ability for flight.

The left forelimb is nearly completely preserved but the right limb only preserves a humerus in good condition. This element differs from the other Early Cretaceous taxa in its shaft being relatively straight and the proximal end being extremely inflated and transversely expanded, resembling slightly the condition of *Confuciusornis,* although the lateral angle is not as extended. In basic outline, the proximal humerus is circular with a relatively large depression at its midsection. Because this feature is merely an impression it cannot be determined whether it represents a large pneumatocoel such as on *Confuciusornis*. At the dorsal margin of this depression is a moderate sized crest. Remaining morphological characters of the proximal humerus are vague. The shaft is relatively slender and there appears to be a shallow longitudinal groove at its midpoint. The distal end is relatively rounded, resembling the reptilian condition more than the derived condition of *C. caudatus*. The two distal condyles are not distinctly pronounced although the distal end displays an apomorphic condition, being modified to be laterally oblique to facilitate the functional flight stroke.

The left radius and ulna are completely preserved with the ulna being relatively robust, simple in morphology, proximal end is slightly curved to conform to the humerus, and there is a small underdeveloped anterior projection which is recognized as an incipient olecranon process. The distal end is relatively planar with a moderate longitudinal groove that represents an extremely rare character documented on early avian species, and as this end is not laterally expanded, it represents a plesiomorphic condition. The radius is correspondingly slender and straight with a planar proximal end and lacks a distinct gently depressed cotyle. Its distal end is also relatively flat, slightly medially curved, and does not exhibit the derived condition of a flattened and broadened morphology.

Two extremely conspicuous carpals are retained on the forelimb, one large and the other small, representing the ulnare and radiale. Conforming to the condition of the other Early Cretaceous avian taxa, McII and McIII are fused at their proximal ends. However it is also distinct from the other taxa excavated from the Boluochi quarries described earlier in the text in that although McII and III are fused proximately, a relatively long proximal projection (suture process) is still retained but other morphological features are absent. Furthermore, an McI process is still distinct and unlike the condition of *Jibeinia,* retains its independence. This specimen represents the only Cretaceous bird with forelimb morphology of Jurassic forms. It is thereby extremely significant that McII and III are not fused distally, being separated by a narrow vacuity which affects the associated phalanges of each digit. Digit I is still relatively elongated and its ungual is rather large, being the major character distinguishing *Longchengornis* from the other Early Cretaceous taxa. Only a single phalanx of digits II and III are preserved which also differ from the other avian taxa by not being expanded.

The pectoral girdle is well preserved, with the exception of the scapula. The dexterous coracoids have shifted in position and lie in opposition, being small, narrow, and slender. The proximal end is extremely slender and small with a small lenticularly shaped projection but lacking any other additional characters. This is extremely distinct from neornithine taxa from the same

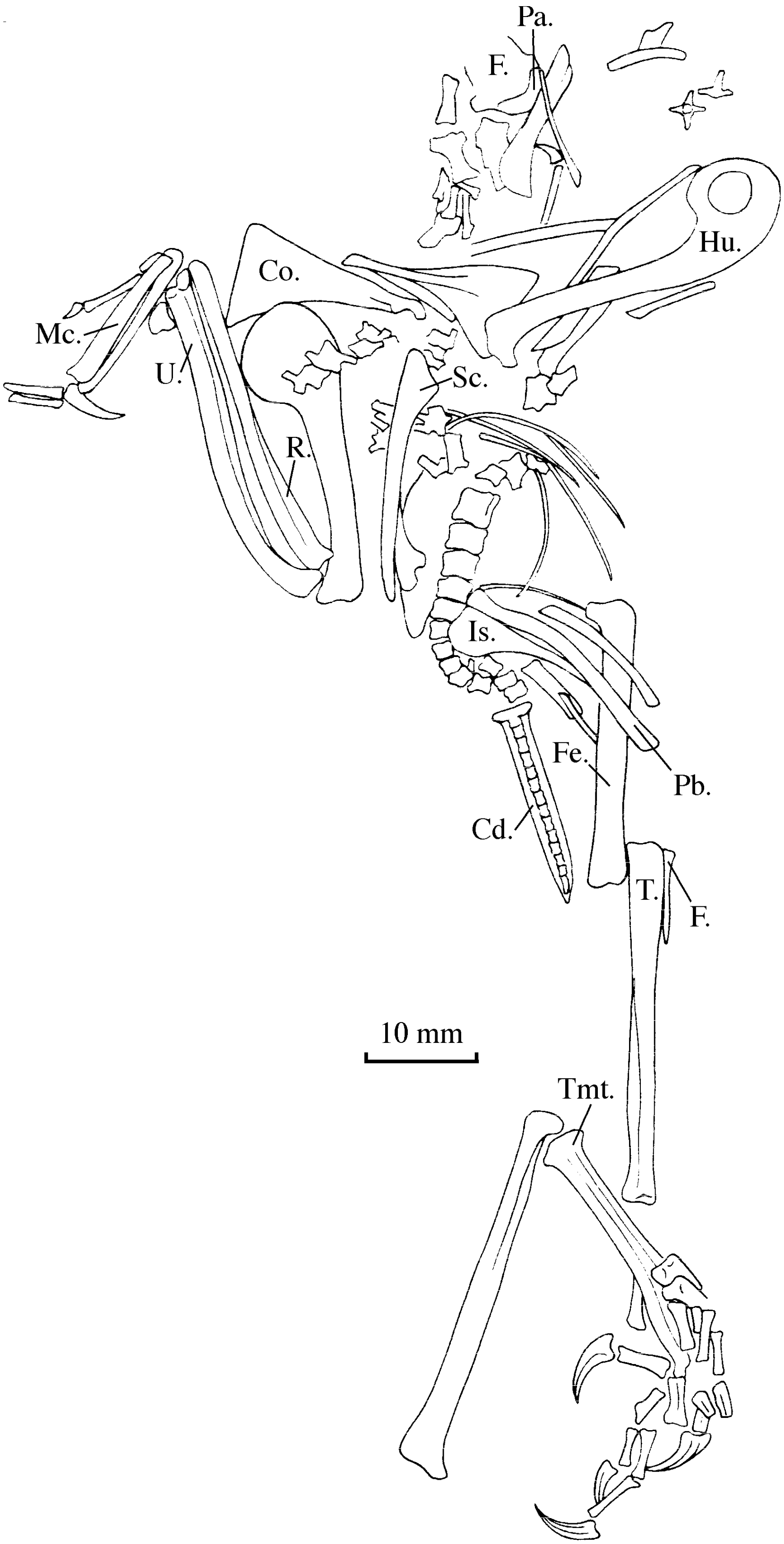

Figure 19. Drawing of *Longchengornis sanyanensis* specimen V.10530.

locality which will be described later in the text. The coracoid morphology is a 15° acute triangle with the hypotenuse side as a relatively thick margin, the ventral side is concave, and the contact with the sternum is linear, or lacks an elongated thickened margin. Neither medial nor lateral angles are expanded. The furcula of *Longchengornis* is also extremely autapomorphic, differing from all other known Early Cretaceous taxa in that the clavicle branches are extremely slender and relatively short, but the furcular process is longer than the clavicle branches with a rounded terminus. One side of the scapula is preserved which is not as characteristic as the coracoid or furcula, as it is relatively slender, long, narrow, and rather scimitar-shaped, resembling extant taxa. It displays a little curvature, the scapular crest is not expanded, and its terminus is not acute as on extant taxa.

The sternum is distorted, being laterally folded, such that its morphology can only be inferred. It appears to have been relatively elongated, lacks a carina, and it is unclear whether it posseses posterolateral processes. It does however appear to maintain a crescentic curvature anteroposteriorly, and although a carina is absent, it still possesses a low projection that is unlike the condition of Jurassic forms, which are relatively flattened or resemble a flattened plate. Rib preservation is extremely fragmentary and scattered, but heads are noted to be bicapitate, shafts are slender and long, and no gastric ribs are documented.

Each of the pelvic elements are preserved like the sternum and only visible in lateral perspective. A portion of the ilium is missing, although it is still quite evident that it is the largest element in the girdle. Its lateral perspective indicates it to be relatively high, its anterior portion is particularly broadened, posterior portion is slightly constricted, and the dorsal margin is crescentic. Preacetabular region is longer than the postacetabular region, and which differs from *Cathayornis* by being more posteriorly acute. The anterior ischium is expanded but it is undetermined whether a transverse process is present. The expansive proximal end composes the posterior and ventral wall of the acetabulum. The terminus is relatively narrow and unbifurcated. The pubis resembles the general condition of primitive birds, being the longest and most slender element in the pelvic girdle, however in this species its termini are rounded and not expanded although they are still not fused.

Of the left hindlimb, the femur is absent although an articulated tibiotarsus and tarsometatarsus is present isolated from the torso. On the right side, the proximal femur is overlain by the pelvic girdle and the tarsometatarsus is overlain by the left tarsometatarsus and digits. The hindlimb is autapomorphic in that the three long bones are all extremely similar in diameter while the femur and tarsometatarsus are shorter than the tibiotarsus. The femoral shaft is extremely straight, distal condyles are only very slightly laterally expanded and are not distinctly separated by a boundary, although this condition may be due to taphonomic processes. The tibiotarsus is long and straight with a planar proximal articular facet that is not laterally expanded, a cnemial crest is absent, and a moderate fibular crest lies proximolaterally. Distal condyles are relatively well developed, are anteriorly projected, and articulate well with the medial and lateral fossa of the tarsometatarsus. A fibula is extremely short and slender. The terminus of the tibiotarsus is relatively planar. From lateral perspective the ventral margin of the condyles are slightly rounded and predominantly project anteriorly.

The tarsometatarsus is slightly shortened, proximal end is fused, but its proximal articular surface is unlike any other Early Cretaceous species with a relatively large fused cap overlying the proximal end. This proximal surface is convex at its midsection which both sides slightly depressed to form the lateral and medial articular fossae. The distal end is not fused although the three trochlea are damaged prohibiting a precise description. However, from the morphology of the phalanges it may be determined that digit III is the longest, representing the standard avian configuration of the pes. Pes digit I is relatively elongated with a relatively large ungual. Phalangeal formula is recognized as 1, 2, 3, 4. Unguals are all relatively large and recurved, with curvature parameters that indicate *Longchengornis* is a perching form. Digit I and III unguals are the most robust and longest indicating that they were the major functional mechanisms for grasping.

Table 10. *Longchengornis sanyanensis* skeletal measurements (mm).

Preserved length of skull	1.0
Cervical 2 length	3.0
Coracoid length	17.0
Distal coracoid breadth	19.0
Clavicle branch length	9.0
Furcula process length	10.0
Scapula length	23.0
Humerus length	32.5
Proximal humerus breadth	12.0
Distal humerus breadth	5.0
Humerus shaft diameter	12.0
Ulna length	45.0
Radius length	29.0
Metacarpal length	15.0
Manus digit I length	8.0
Synsacrum length	14.0
Ilium length	17.0
Ischium length	~11.0
Pubis length	~21.0
Caudal vertebrae length	21.0
Preserved length of femur	21.5
Distal femur transverse breadth	4.0
Tibiotarsus length	~34.0
Tibiotarsus proximal breadth	3.5
Tibiotarsus distal breadth	3.0
Tarsometatarsus length	~21.5
Tarsometatarsus proximal breadth	4.0
Pes digit I phalanx length	5.5
Pes digit I ungual length	7.0
Pes digit II ungual length	8.0

Comparison and discussion: To date, eight genera assigned to the subclass Sauriurae have been excavated from the Mesozoic of China. In addition to the relatively primitive Jurassic *Confuciusornis,* there are Early Cretaceous taxa with a wide degree of morphological variation. This variation is due to the radiation into various habitats or a differential degree of evolutionary development. The species *Longchengornis sanyenensis* appears geologically later than *Cathayornis caudatus*; it has caudal vertebrae reduced in size and which compose a tail. Although the pelvic girdle resembles the posteriorly oblique condition of *Cathayornis* allowing its assignment to that family, *Longchengornis* also possesses characters distinct from the members of the Cathayornithidae including a ventral keel on the cervicals, large lateral recesses on the thoracic vertebrae, proximal humerus rounded, laterally expanded, and maintaining a large and circular depression; tibiotarsus and tarsometatarsus are relatively slender and long, and talons are particularly intensely recurved. These characters justify the erection of a new genus.

Longchengornis displays a derived condition in its humerus being shorter than the radius-ulna, which promotes a strengthening of the flight stroke. The intense curvature of the pes talons also indicates that is adapted to perching behavior. The relatively slender and weak tarsometatarsus and tibiotarsus also indicate a dexterous hindlimb on this species. Furthermore, in general morphology it retains plesiomorphic characters such as the loose contact relationship between the frontals and parietals where there is a relatively deep groove, resembling the condition on *Confuciusornis* and *Archaeopteryx.* Also, the pectoral girdle is not as well developed as on other Early Cretaceous taxa as the coracoid is relatively small with a simplified proximal morphology, while articulation with the sternum is relatively planar and not extremely laterally expanded, furcula branches are extremely short, proximal humerus resembles the condition of *Confuciusornis* by being laterally expanded with a depression at its midpoint which may be analogous to the *Confuciusornis* pneumatocoel, and there is still a distinct first metacarpal process. The most noticeable plesiomorphy of *Longchengornis* lies in the retention of a large series of caudal vertebrae to compose a tail. Although these caudals are reduced in size, in combination with its other plesiomorphic characters, this genus represents a lower evolutionary grade than its contemporaneous taxa, representing an intermediate or transitional phase between the Late Jurassic *Jibeinia* and other Cretaceous taxa.

Otogornis Hou, 1994

Otogornis genghisi Hou, 1994

In 1990, under the leadership of X.J. Zhao and D. Russell, the Sino-Canadian Dinosaur Project collected an incomplete avian specimen from the banks of the Taostu River in the Ordos region of Inner Mongolia. A preliminary description of the specimen was conducted by Dong (1993) followed by a more detailed description by Hou (1994).

Type: Both scapulae and coracoids, a pair of humeri and forelimbs including a portion of the metacarpals and two feathers. IVPP specimen V9607.

Diagnosis: Moderate in size; walls of the long bones are thickened, and scapula is an elongated and thickened plate with an anteriorly projected acromion. The coracoid head is inflated, distal end is an expanded plate, and the shaft maintains a supracoracoidal foramen. Humerus is relatively robust, is shorter than the radius-ulna, proximal end lacks a pneumatocoel, a capital groove is well developed, deltoid process is small, the olecranon fossa is shallow, and the tricipital groove is a deep depression. Radius and ulna are elongated, ulna is laterally compressed, and lacks secondary feather papillae. Metacarpals are unfused and manus unguals are present. Feather barbules are not in compact alignment.

Locality and Stratigraphic position: Gray-green mudstones of the middle to upper section of the Early Cretaceous Yijinhuoluo Fm., Zidan Group, at Chabu Sumu, west of Otog Qi, Yike Zhaomeng, Inner Mongolia.

Description: In order to facilitate a more detailed description, after the specimen was photographed it was imbedded in resin and the reverse side was prepared. Although the distal ends of the two scapulae are missing the perserved morphology is unlike that of extant taxa which is elongated and scimitar shaped, and instead the *Otogornis* scapula is relatively primitive as a thickened plate with minor curvature at its proximal end, resembling the condition on *Archaeopteryx lithographica* (de Beer, 1954) and *A. bavarica* (Wellnhoffer, 1993). Proximodorsolaterally on the scapular column a long and narrow groove initiates and extends to the distal end. This is a character that rather resembles the extant *Threkiornis aethiopica* (wading), *Anser fabalis* (wading) and *Accipiter nisus* (raptor), only their scapular grooves are shallower. The majority of extant taxa lack this character. The scapular crest is relatively projected, the proximal breadth of the scapula is 6.0 mm, and the shaft breadth is 3.0 mm. The glenoid fossa is relatively large, elliptical, and located laterally. The contact with the coracoid cannot be described due to its fusion although it may be noted that the contact surface is relatively large and probably obliquely elongated. The contact for the furcula is unknown as the medial side of the left scapula is overlain by the humeral head and the proximomedial right scapula is damaged.

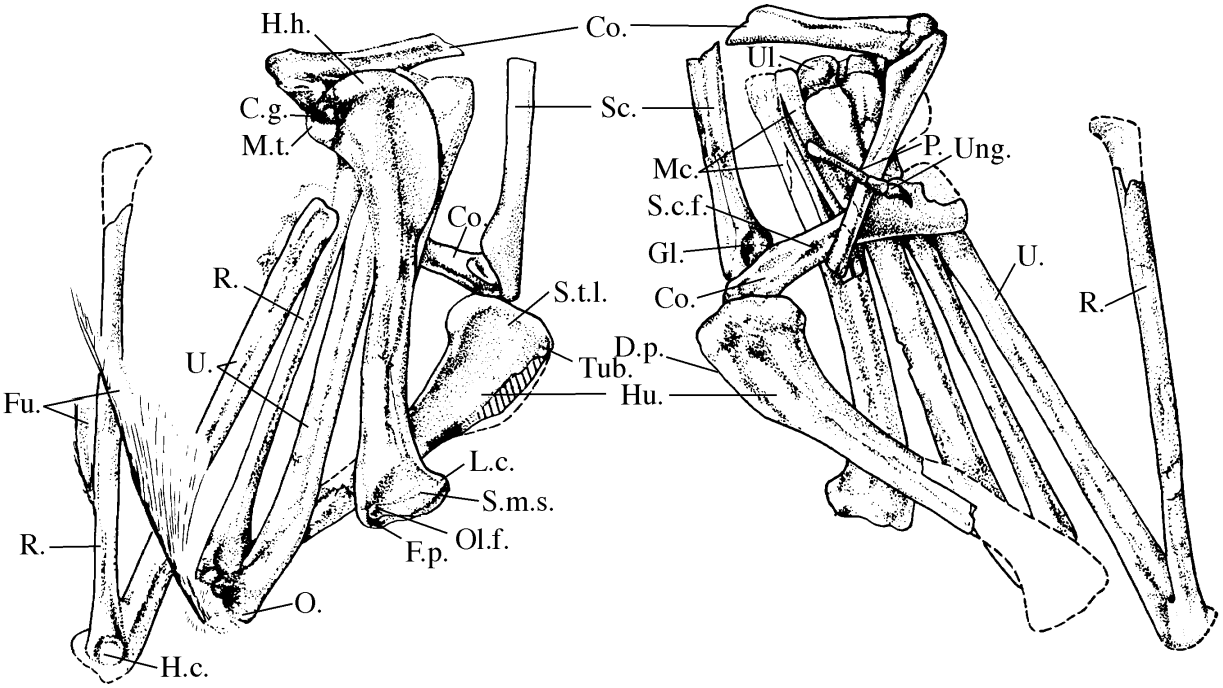

Figure 20. Drawing of alternative views of *Otogornis genghisi* V9606 (after Hou, 1994).

The coracoid is basically complete with the exception of some slight damage to the medial margin. It differs from the plate-shaped coracoid on the London specimen of *Archaeopteryx* and is more consistent with the morphology of *Sinornis* and *Cathayornis* in its relatively thin and slender proximal end, broad and spacious distal end, and a slight constriction of the shaft approaching the proximal end. The head is slightly inflated and there is a distinct supracoracoidal foramen on the dorsal midpoint of the shaft. This character is shared with extant taxa only the foramen is situated at a different location. On *Otogornis* there is a relatively large triangular prominence located anteromedial to the foramen which is analogous to the precoracoid process on extant taxa. On the coracoid head, there is a lateral articular facet for the humerus, a medial facet for the scapula, and a third articular fossa between both. Proximal coracoid morphology differs from that on extant taxa with its medial side displaying a posteriorly extended groove, which may represent the incipient stage of the large and deep coracoid fossa that is present on extant forms. The distal end is 7.0 mm in breadth and although neither a spacious contact or lateral process is present for contact with the sternum, it is possible that such a contact occurred due to the broad and spacious morphology of the distal end.

The right humerus and radius are overlain by the anconeal side of the left humerus, while the proximal half of the right humerus palmar surface is overlain by the metacarpals. The right humerus is exceptionally complete, represents the most robust forelimb element, and is extremely close in morphology to that of *Archaeopteryx* with a very slight sinuous curvature. The walls of this element are extremely thick, the proximal end lacks a pneumatocoel, and a capital groove is extremely well developed, which is a character present on all extant volant birds. However, on *Otogornis,* there is a low projection at the midpoint of the capital groove which divides the groove into two sections. The humeral head is large, a lateral deltoid process is undeveloped, a medial tuberosity is well developed and is distinctly projected, but a pneumatocoel at its posterior surface is absent as there is only a depression present. A cotyle is present on its proximal surface for articulation with the coracoid. The medial shaft of the humerus is linear and a single shallow groove extends from the proximal end to attenuate as it approaches the distal end. Distally, an olecranon fossa is shallow, the tricipital groove differs distinctly from those on extant taxa by being a deep depression instead of a legitimate groove. Furthermore, a legitimate flexor process is absent and instead there is merely a circular medial process. An ectepicondyle is also situated extremely low. The palmar surface of the humerus is concave due to compressional distortion but there is an elongated ligamental sulcus posterior to the head with two mound-shaped processes on its distal margin, of which the lateral is relatively high and the medial slightly lower. A large trough is present posterior to these two processes. The proximomedial side is circular in morphology. On the lateral side of the palmar surface, an inflation to facilitate the Brachial biceps is absent and a dorsal tuberosity is extremely weak. Determination of the presence of a depression for the Brachialis anticus is impossible due to compressional distortion.

The ulna is relatively robust, the shaft is laterally compressed, and there is an extremely primitive but conspicuous olecranon process. The lateral cotyle on the palmar surface is small and projects laterally with an extremely well developed sulcus on its medial side to facilitate the attachment of the Scapulotricipital. A medial cotyle is basically absent. On the medial section of the palmar surface there lies a longitudinal groove resembling that on the humerus. The distal ulna is not expanded and an ulnare remains articulated.

The radius is more slender than the ulna, and is slightly laterally compressed with an extremely linear shaft. The distal end is missing from the right radius although its impression in the matrix is quite distinct indicating that it is slightly expanded. The radial head is large with an enlarged humeral cotyle but a distal bicipital tuberosity is extremely weak. Its contact relationship with the ulna is obscured by its tight articulation.

Among the carpals, only the ulnare is preserved and is irregular in morphology. At least two metacarpals are preserved in extremely tight association and are equivalent in length in addition to diameter. It may be discerned that they were not fused due to the distinct boundary between them. A distal and ungual phalanx are preserved with distinct articular facets. The ungual is not very large, neither is it very recurved, and its terminus is damaged.

Two feather impressions are present; one is relatively complete and located at the proximal left radius, the other is only represented by a small portion of barbs located by the proximolateral shaft of the right radius. The well preserved feather does not preserve a complete basal shaft and barbs are rather indistinct. It is morphologically distinct from the feathers of other Mesozoic birds in that it displays only a single pinna with an opposing pinna being nearly non-existent. It is not known whether or not this is due to asymmetry. The pinna is extremely well developed although barb count is small at approximately 25 with poorly preserved barbules. It is impossible to determine whether radioli are present. Furthermore, the extremely low barb count is due to the feather being extremely short, and thus it cannot represent a primary flight feather, nor can it represent a down feather because barbs on down feather shafts are not as conspicuous as those on medial and lateral pinnae. Consequently, this very possibly represents one of the small wing feathers which generally have asymmetrical pinnae and are extremely short.

Comparison and discussion: The primitive nature of this archaic bird from Inner Mongolia is evident. Its most significant character is that the long bones are not pneumaticized, as they maintain thickened walls, and particularly the humerus which maintains neither pneumatic foramina or fossae. In this respect it is more primitive than the taxa recovered from the Chaoyang region of Liaoning, but it shares several characters with the Cathayornithidae, and is relatively close to the genus *Longchengornis*, thus its assignment to this family.

Archaeopteryx is considered to have had a weak ability for functional flight. This hypothesis is based not only on the presence of a tail, but also on the extremely short pectoral girdle, particularly the short elliptically shaped coracoid which was incapable of facilitating flight musculature such as the Supracoracoideus. The coracoid on *Otogornis* is elongated and its proximal end still lacks a hooked process to facilitate the Supracoracoideus such as on extant taxa. But the proximal end does display a slender and constricted region and the coracoid head is inflated, which would facilitate implantation of pectoral musculature. Furthermore, the distal end of the coracoid is well developed as a broadened plate, providing expansive facility for the attachment of the powerful Sternocoracoidei and greatly increasing the strength and articular surface area for the sternum. This is quite unlike the counterparts on *Archaeopteryx,* where the coracoid is arched and sternum and coracoids both lack spacious regions for facilitating musculature. Although the *Otogornis* scapula is relatively straight and thick, its possesses an anteriorly projected scapular spine at its proximal end. This differs from the transversely expanded morphology of *Archaeopteryx* which more closely resembles several reptiles and particularly the ornithomimid dinosaurs. The scapular shaft of *Otogornis* has relatively rounded margins unlike the sharp dorsal margined and elongated scimitar-shaped morphology of extant taxa. However, it is also unlike the *Archaeopteryx* scapula, which is thickened and slightly curved, and more closely resembles the morphology of *Sinornis* or *Cathayornis,* though it is obviously has not attained the derived condition of *Cathayornis* on which the scapular spine is even more anteriorly projected.

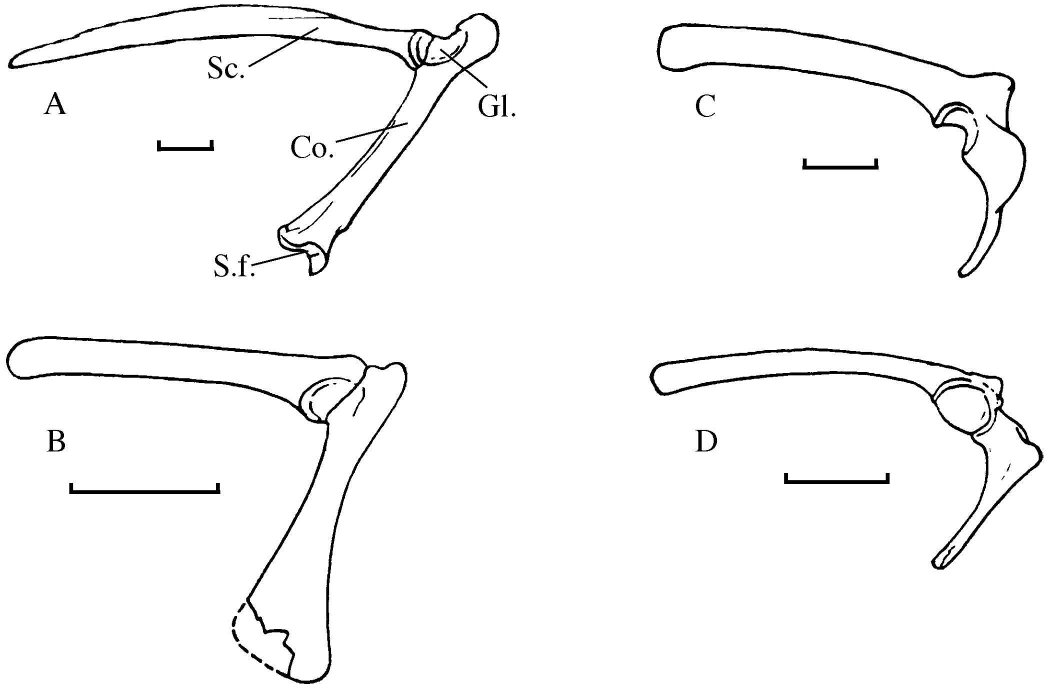

Figure 21. A comparison of archaic and modern scapulacoracoids. A. *Phasianus colchicus,* B. *Otogornis genghisi,* C. *Archaeopteryx lithographica* (from Ostrom, 1976), D. *A. bavarica* (from Wellnhofer, 1993) (scale bar is approximately 1 cm).

The humerus is the most characteristic element on *Otogornis*, being more derived than *Archaeopteryx* but more primitive than both *Sinornis* and *Cathayornis.* A shared character with *Archaeopteryx* is the absence of pneumatic fossae or foramina. However, the proximal humerus of *Archaeopteryx* resembles extremely closely that of small ornithomimid dinosaurs (de Beer, 1954) but *Otogornis* exhibits the more generalized avian condition by the presence of a capital groove and a relatively well developed medial tuberosity, while distally it maintains an extremely shallow olecranon fossa. The humeral shaft of *Archaeopteryx* is relatively slender and weak, its distal end maintains condyles for the radius-ulna, and lacks any other characteristic features (Ostrom, 1976). Both *Sinornis* and *Cathayornis* possess well developed proximal pneumatic fossae on both sides of the medial tuberosity in addition to a fully pneumaticized shaft with relatively thin walls, an extremely well developed medial tuberosity, and a short and deep tendinal groove. Distally they display a deep medially situated olecranon fossa and a well developed flexor process. These characters strengthen the ability for flight and are much more derived than those on *Otogornis.*

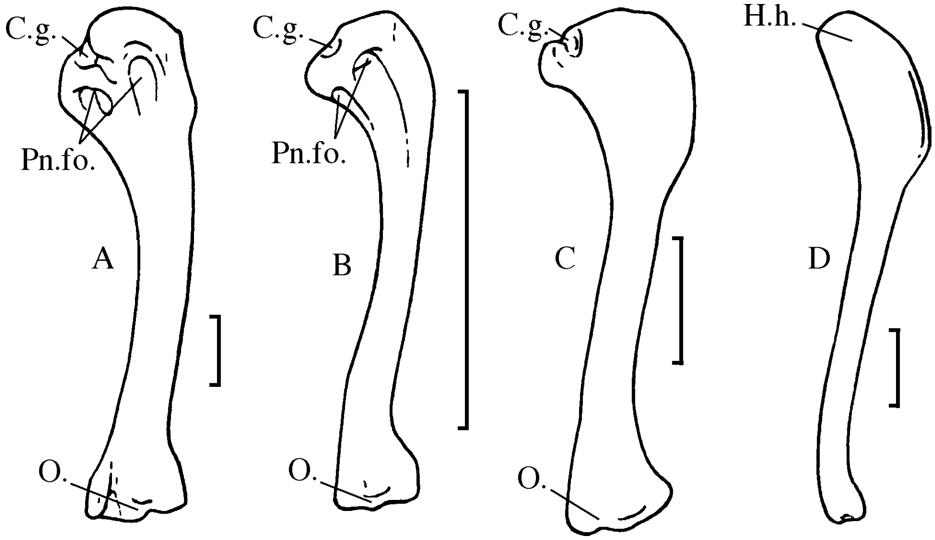

Figure 22. A comparison of archaic and modern humeri (from Hou, 1994a). A. *Phasianus colchicus,* B. *Cathayornis* (from Zhou, 1992); C. *Otogornis,* D. *Archaeopteryx* (scale bare is 1 cm).

The principle function of the ulna lies in the facilitation of the secondary flight feathers. The ulna's morphology, particularly the degree of adaptive morphology at its termini for flight, is a significant aspect in the study of the evolution of archaic avian forms. On *Otogornis* the shaft has been modified to be laterally compressed and the proximal end is slightly curved with an incipient olecranon process, while the radial shaft is linear with its two termini slightly inflated. Although they are still not very modified, they are still much more derived than the condition of *Archaeopteryx* and quite distinct from both *Cathayornis* and *Sinornis,* as the latter two maintain ulnae with distinct and differentially sized lateral and medial cotyles and relatively conspicuous humeral musculature scars on their proximal palmar surface. On *Cathayornis,* the distal articular facet for the radiale is relatively well developed.

Otogornis shares several characters with *Enantiornis* from the Late Cretaceous of South America (Walker, 1981) both of which resemble *Archaeopteryx* with unfused metatarsals but are more derived in their relatively elongated coracoid with the presence of a supracoracoidal foramen and a relatively well developed capital groove on the humerus. *Enantiornis* maintains even more apomorphies, such as the presence of a proximal coracoidal sulcus, a conspicuous distal sterno-coracoidal musculature scar, a well developed sterno-coracoidal process, and an elongated, narrow, and concave articular surface. Furthermore, its humerus maintains relatively well developed pneumatic fossae, a fully pneumaticized shaft, an olecranon fossae that has migrated medially, and an extremely well developed flexor process. In conclusion, although *Otogornis* shares several characters with *Enantiornis,* they do not necessarily share a close phylogenetic relationship due to the autapomorphic characters of *Otogornis* and the numerous derived characters on *Enantiornis* which are shared with extant taxa, such as the relatively slender and narrow fourth metatarsal.

Cuspirostrisornithidae Fam. nov.

Cuspirostrisornis Gen. nov.

Genus diagnosis: Beak is slender and acute with an elongated and thin nasal process of the premaxilla and short maxillary process. Five pair of teeth are present on both the premaxilla and the mandible. The mandible is slender and linear. Humerus is slightly shorter than the radius-ulna with a relatively well developed pneumatic fossa and capital groove, dorsal and ventral tuberosity are extremely distinct, and shaft curvature resembles that on extant taxa. A manubrium is present on the sternum, as is a short anterolateral process, the carina is relatively well developed, and lengths of the posterior and posterolateral processes are equivalent. The distomedial condyle on the femur is enlarged, a cnemial crest is present on the tibiotarsus, and the talons have intense curvature.

Etymology: Cuspirostris - Latin for sharp-beaked.

Cuspirostrisornis houi sp. nov.

Species diagnosis: A small species with a potentially more flexible neck, pelvic girdle is unfused, femur is relatively long with well developed distal condyles and a slightly broadened intercondylar groove, proximal tarsometatarsus is fused, MtIII is the longest in the series, and MtII is the shortest.

Etymology: Named in honor of the collector of the specimen, Mr. Jinfeng Hou, who is also the premier illustrator at the Institute of Vertebrate Paleontology and Paleoanthropology.

Type: Positive and negative of a complete skeleton (IVPP #V10897)

Locality and stratigraphic position: Early Cretaceous light gray mudstones of the Jiufotang Fm. approximately two km west of the village of Boluochi, Chaoyang Co., Liaoning Province.

Description: At the beginning of summer 1993, Lianhai Hou traveled to western Liaoning to conduct research upon Mesozoic birds and specifically to map the quarries producing the avian specimens. For this reason, Mr. Jinfeng Hou, the illustrator at IVPP was requested to accompany the expedition. In addition to his illustration duties, Mr. Hou also diligently assisted in the excavations.

The specimen is excellently exposed with the exception of the distorted dorsal cranium, cervical region and pelvic girdle. The premaxilla lies isolated from the rest of the skull and is exceptionally well preserved as an arrow-head shaped element, although the apex of the premaxilla is not extremely acutely elongated and is instead short and conical with five pair of relatively short teeth, the anterior most being the smallest, tooth roots are not noted, and cusps are slightly posteriorly inclined. The left and right premaxillae are fused anteriorly but posteriorly are distinct from each other. The suture line on the main body of the premaxilla is conical, the slender posteriorly projected nasal process is particularly elongated to reach the ventral surface of the nasals, and the lateral maxillary process is extremely short. The maxilla is a relatively broadened and elongated plate with no indication of a dentition. The zygomatic arch is incomplete but the large trapezoid shaped quadrate on the posterior cranium is extremely conspicuous with a relatively large jugal process. The squamosal in the vicinity of the temporal fossa is a thin irregularly shaped plate dorsal to the quadrate. An extremely projected opisthotic lies posterior and slightly ventral to the squamosal in addition to being posterodorsal to the quadrate. The presence of this element is rarely documented on the other known Early Cretaceous taxa.

On the anterodorsal portion of the skull, the nasals are represented merely by a narrow linear element. Frontals are large and constitute the entire top of the skull with a relatively broad groove separating them from the midportion of the posteriorly located, relatively narrow parietals, which overly the occipital. The presence of a parietal crest cannot be determined due to damage. The ventral portion of the skull is difficult to determine due to its exposure in lateral perspective but the basitemporal process of the basisphenoid is relatively long. Only a single side of the pterygoid is exposed indicating that it is relatively robust. At the most anterior end of the rostral process there is a distinct pair of palatines with a large and expansive basal section, although its anterior morphology, and particularly that of the vomer, cannot be determined. The entire occipital region is obscured by cervical vertebrae.

The narrow and long mandible is basically represented only by its anterior half, where the symphysis is divided by a loose suture line. Five small extremely reduced tubercular-shaped teeth are present. At the posteromedioventral margin of the dentary, an extremely projected splenial crest is present and a small portion of the anterior boot of the angular is visible.

The morphology of the short cervical centra is unknown because they are obscured by the proximal humerus and the well developed neural spines are distorted. The cervical count is also unclear. There are perhaps four to five cervicals visible between the cranium and the proximal humerus, the diapophyses are well developed, and a ventral process is present. Dorsal to the sternum there are extremely well preserved impressions of five to six dorsal vertebrae which are distinctly amphiplatyan, the centra are slender and long with expanded termini, are medially constricted, and a ventral process is absent. Posterior to the dorsals are at least seven sacral vertebrae basically composing a synsacrum. The centra are fused although their count is still discernible. A single unified synsacrum is rare among the Early Cretaceous taxa. There is a narrow ventral crest on the synsacrum and a relatively deep longitudinal groove lies laterally on the centra between the relatively expanded parapophyses. Posteriorly there are several caudal vertebrae independent from the synsacrum, the count of which is unclear, although it is extremely evident that a relatively robust pygostyle is present which is relatively long with an acute terminus, and at its proximal end several incompletely fused caudal centra are still discernable.

The forelimb on *Cuspirostrisornis* is more derived than *Cathayornis.* The humerus not only displays the S-shaped sinuosity of extant taxa, it also has a relatively large and deep proximal pneumatic fossa, a distinct capital groove, and a particularly projected humeral head. The medial tuberosity is larger than the lateral tuberosity, and a deltoid process is extremely well developed. On the palmar surface, the bicipital groove is still extremely narrow and shallow representing an incipient stage. Distally, the medial condyle is particularly well developed and projects extremely medially, while the lateral condyle projects laterally off the shaft, and between both lies a small but distinct trochlear condyle, although a genuine medial or lateral trochlear region is not present. There is a shallow and relatively broad depression above the trochlear condyle which may represent an incipient olecranon fossa. Furthermore, a relatively small mound-shaped entepicondyle is present proximal to the medial condyle.

The radius and ulna are poorly preserved and are obscured by the humerus and other elements that prohibit the interpretation of several characters. The outline of the radius indicates it to be an extremely robust element nearly equivalent to the ulna, both of which are relatively straight. The only curvature on the ulna occurs proximally, as its remaining morphology is relatively simple, its proximal surface is relatively planar, and neither an olecranon process or humeral cotyle is present, although their is a proximolateral projection which may represent an incipient lateral cotyle. The medial margin is rounded, as is the distal end, upon which there is a process which may have facilitated musculature and which is located at the position of the tendinal depression on modern taxa. The radius proximomedial surface is concave but not expanded, representing an extremely undeveloped humeral cotyle. The distal end is also not expanded.

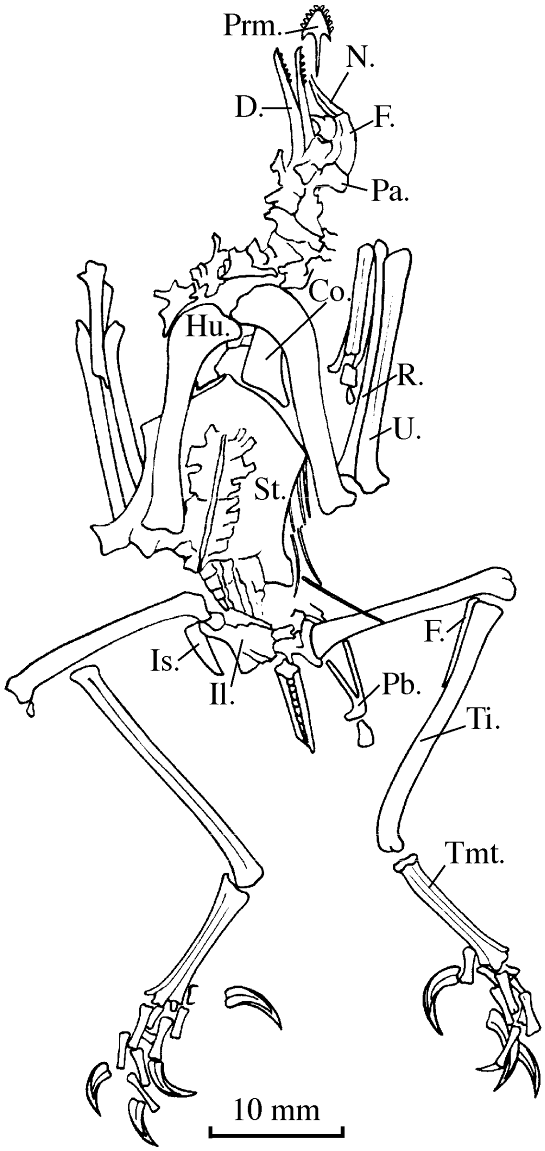

Figure 23. Drawing of *Cuspirostrisornis houi* (V.10897).

The most prominent feature of the carpometacarpus is the well developed carpal trochlea and a distinct process on metacarpal I. A small ungual phalanx is still retained, a process is present proximolaterally which may represent a pisiform process, and a seam and small fissure divides the McII from the McIII.

The pectoral girdle is basically obscured due to distortion of its elements, although the coracoid head is extremely distinct with a concave furcular articular facet.

Although the sternum is relatively broad, its carina is more pronounced than on *Cathayornis;* the posterolateral process resembles that on *Cathayornis* only it is slightly shorter, as its length does not exceed that of the posterior process. A medial process is absent between the posterolateral and posterior processes. Anteriorly there is a short and distinct anterolateral process which slightly resembles that of *Cancornis lacustris* from the Early Cretaceous of Spain only it is even more distinct. There is a relatively deep and broad coracoid sulcus and a manubrium is also present, clearly indicating that this species was completely adapted for flight. Furthermore, anterodorsally on the sternum and posterior to the manubrium there are several small pneumatic foramina. On extant taxa, the foramina at this location are enlarged.

The pelvic girdle has also suffered from compressional distortion, prohibiting a complete description. The elements are slightly smaller than those on the pectoral girdle. The ilium resembles that of *Cathayornis* with an expanded preacetabular region and constricted postacetabular region with an acute termination. At the acetabulum, the proximal ischium is relatively broad but its distal end is vague. The pubis is elongated with its distal end expanded into a small pubic boot but not fused with its counterpart. This is an extremely significant character as it is an indication that the primitive fused pelvic girdle has been modified to the open avian configuration which in turn influences the modification of the internal organs and particularly the reproductive system to represent modern avian ovovipary. Without an open pelvic girdle the avian egg could not have become modified as it is today.

The hindlimbs are the best preserved elements on the specimen, although the phalanges have been shifted in position. Each femur is preserved unilaterally, resembling the condition of the forelimbs. The shaft is straight, relatively elongated, and is slightly shorter than the tibiotarsus. The femur head is relatively enlarged, projects laterally from the shaft with a short neck, and there is a short trochanteric crest present. Distally, the most significant character lies in the medial condyle being larger than the lateral condyle, which is in distinct contrast to extant taxa and differs from *Cathayornis,* but resembles the condition of *Chaoyangia.* The lateral condyle is not laterally expanded and an intercondylar fossa is extremely narrow.

The tibiotarsus is thin and elongated, the shaft is straight, the anteroproximal end has a longitudinal groove, a cnemial crest is well developed, a lateral cnemial crest is relatively small and lies next to the fibula. The medial cnemial crest is relatively well developed and projects off the proximal surface to represent the highest process on the element. The proximal articular surface is vague and resembles a cap that covers the proximal end. The distal condyles are well developed with the medial condyle large, the lateral condyle relatively small, and there is a moderate and extremely distinct lateral ligamental prominence, a supratendinal bridge is absent, and instead there is a depression that may represent a tendinal groove. The anterior intercondylar fossa is relatively broad, a fibular crest is absent, and the posterior intercondylar groove is obscured, prohibiting description. Both fibula are preserved as relatively short elements at the lateral side of the tibia and their distal ends are slender.

The tarsometatarsus is relatively short. Proximally the tarsals are fused and resembles a cap on the proximal end of the metatarsals to compose a single shaft, however boundary lines between MtII, III, and IV are still quite distinct. Mt IV is the most slender resembling the Enantiornithes such as *Jibeinia*, Mt II and III are relatively robust, the trochlea of Mt III is the longest, MtII is the shortest, and Mt IV is the smallest. This condition is distinct from extant taxa and in general morphology appears relatively primitive.

Digit III is the longest among the pes elements with a long and intensely curved ungual although it is simple in morphology and lacks flexor tuberositys. The digit I ungual is large. Clearly it is adapted for perching behavior.

Comparison and discussion: The derived characters on *Cuspirostrisornis* are multifaceted: The temporal fossae is quite distinct from the reptilian condition; dentition is reduced, particularly on the mandible; sacral vertebra are fused; humerus is derived in the presence of a pneumatic fossa, capital groove, and distal end is modified into a more complex morphology; carpometacarpus is fused and a McI process is present; on the sternum a manubrium is present and the carina is more well developed; and the distal pubes are unfused. These apomorphic characters distinguish this genus from all other known Early Cretaceous taxa.

Autapomorphic characters of *Cuspirostrisornis* include a premaxilla with five pair of teeth, medial condyle of the distal femur is larger than the lateral condyle, tibiotarsus is more slender than the femur, numerous small pneumatic foramina are present on the dorsal sternum, and the diameters of MtII and MtIII are equivalent.

Table 11. *Cuspirostrisornis houi* measurements (mm).

Preserved length of skull	~27.0
Skull height	~14.0
Premaxilla length	~11.0
Humerus length	29.0
Proximal humerus breadth	8.0
Distal humerus breadth	6.5
Humerus midshaft breadth	3.5
Ulna length	32.0
Proximal ulna breadth	4.0
Distal ulna breadth	4.0
Radius length	29.5
Proximal radius breadth	3.0
Distance between sternum anterolateral processes	18.0
Distance between distal ends of sternum posterolateral processes	24.0
Sternum length	~23.0
Femur length	27.3
Femur proximal breadth	5.1
Femur distal breadth	4.5
Femur midshaft breadth	3.1
Tibiotarsus length	32.5
Tibiotarsus proximal breadth	3.2
Tibiotarsus distal breadth	~3.5
Tibiotarsus midshaft breadth	2.2
Fibula length	~8.5
Tarsometatarsus length	19.0
Tarsometatarsus proximal breadth	4.5
Tarsometatarsus distal breadth	5.0
Tarsometatarsus midshaft breadth	5.0
Digit I ungual (along curvature)	8.0
Digit II ungual (along curvature)	8.0
Digit IIII ungual (along curvature)	9.0
Digit IV ungual (along curvature)	6.0

Plesiomorphic characters shared with contemporaneous taxa include the unfused cranial elements; cervical centra have still yet to become heterocoelous; sternum is yet to be fully developed; proximal sacral girdle is still unfused, the ilium and synsacrum are not expanded; supratendinal bridge is absent on the tibiotarsus; distal tarsometatarsus is incompletely fused, particularly MtIV, and unguals are simple in morphology.

Cuspirostrisornis shares numerous characters with *Cathayornis* including the primitive skull, basic morphology of the sternum, and characters of the wing and pelvic girdle. But the former genus is quite distinct in numerous characters, such as the slender and elongated rostrum with premaxilla bearing five pair of teeth, the most anterior of which are the smallest; the wing is more derived, particularly the humerus; sternum displays a more enlarged carina, a manubrium, anterolateral processes, and small pneumatic foramina are present, posterolateral and posterior processes are equivalent in length; synsacrum is present; distal tarsometatarsi are unfused despite their close proximity, medial condyle of the femur is enlarged; and talons are particularly recurved.

The aforementioned autapomorphies and apomorphies justify the erection of the new family Longirostrisithidae, recognized with an elongated beak, slightly more elongated distal wing, relatively more well developed sternum, and intensely recurved talons. It represents a typical small perching form, but it does not conform in morphology with the majority of the Passiridae, despite its small body size and its beak resembling the morphology of the extant genus *Motacilla.*

Several characters are shared with *Concornis* from the Early Cretaceous of Spain, including similar dorsal centra, presence of anterolateral processes on the sternum, distal pubes unfused, MtIV relatively slender, and the intense curvature of the talons. But these characters are not the result of a close phylogenetic relationship, for *Concornis* displays numerous distinctions including a depression on its rounded and projected proximal humerus, the sternum possesses few small foramina, the carina is not as developed, the distal pubes display a portion that is elongated, straight, and are in extremely close proximity; and there is a well developed fibular crest on the tibia. Further comparisons are considered unnecessary.

Largirostrornis Gen. nov.

Genus diagnosis: Skull is elongated with a large extended rostrum, cranium is shorter than rostrum, nasals are elongated, frontals are expanded, parietal posterior margin is rounded, and maxilla bears six acute posteriorly recurved teeth. Vertebrae are amphicoelous with particularly high neural spines and sacrum is basically fused. Sternum lateral processes are extremely elongated with expanded termini, furcula is short and robust, coracoid is relatively elongated with an arched articular surface for the sternum. Humerus has a capital groove and a sinuous shaft, carpometacarpus is basically fused, and a curved manus unguals are still present.

Etymology: “Large,” being Latin for plentiful or bountiful. “Rostrum” being Latin for bill or mouth, with reference to the large beak on this genus.

Largirostrornis sexdentoris sp. nov.

Type: Positive and negative slabs of a complete skeleton (IVPP #10531).

Locality and Stratigraphic position: Gray mudstones of the Early Cretaceous Jiufotang Fm. at Boluochi, Chaoyang Co., Liaoning Province.

Species diagnosis: As for genus. Torso longer than all other known Early Cretaceous taxa, rostrum relatively large, femur slightly curved with a small head that is extremely projected, tibiotarsus particularly inflated proximally and with distal condyles laterally expanded, tarsometatarsus is short with digit III trochlea the longest, Mt I is positioned high, and talons are large and hooked.

Etymology: “Sex” being Latin for the numeral six and “dent” being Latin for teeth.

Description: This specimen is slightly larger than *Cuspirostrisornis* and is preserved differently, with each of the skeletal elements being slightly shifted in position, particularly the pelvic girdle and hind limbs. The femora are upside down, and the pelvic girdle, caudal vertebrae and phalanges have all been scattered within the matrix, providing some difficulty in the recognition and diagnosis of some elements.

The skull is basically preserved in dorsoventral perspective with the distal ulna obscuring a portion of it. On the positive slab the cranium is relatively well preserved and on the negative slab the rostrum and palate are relatively distinct. The premaxilla is relatively short and small, resembling *Cuspirostrisornis*, and has been displaced very slightly anteriorly to the anterior position of the mandible. Six pair of small teeth are present, the nasal process of the premaxilla resembles *Cuspirorstrisornis* by being elongated and thin, and the maxilla is relatively broad and elongated. Nasals have also been displaced to lie lateral to the skull, with only a portion of them exposed with a distinct medial suture line between the two broadened foliate plates. The suture line between the broad and short frontals is also conspicuous, ventrolaterally to them there is a compressionally distorted depression which is located precisely in the analogous position of the temporal fossa on extant taxa, though on this specimen it cannot represent this character. The contact between the frontals and parietals is unclear as the latter is not exposed. Both quadrates are exposed posterolaterally as triangular elements with relatively elongated anterior and posterior branches. The body of the quadratojugal is relatively short and robust.

The palate is relatively well exposed with a pair of narrow vomers lying between the large expansive palatines, anterior to which there appears to be a weakly developed, relatively short maxillopalatine process. It is noteworthy that the pterygoids are extremely broadened or well developed with an extremely prominent posteromedial sphenoidal-rostral process, while at their midpoint there is a shallow longitudinal groove posterolateral to which is an extremely distinct external auditory meatus. Further posteriorly, the basitemporal plate is not expansive and posterolaterally on it there is a large foramen for the Vagus nerve (X). The basioccipital is even more reduced, being short and small, and the occipital condyle is relatively projected.

The ventral mandible is relatively distinct, displaying two relatively narrow and elongated dentaries bearing six pair of acute, short, thick, and posteriorly recurved but slightly anteriorly oblique teeth. Anteriorly the symphysis is extremely short, posteriorly the dentary is relatively broad, an elongated and linear angular lies at the ventral margin, and only a portion of the surangular and prearticular are preserved. A coronoid process does not appear to be present, the articular is not preserved, the slightly posteriorly placed splenial is thin, plate shaped, and fused to the medial side of the dentary.

One of the more notable characters of this new genus is the particularly elongated neural spines on the vertebrae, which are basically consistent in height from the cervical to the caudal region, although in the thoracic region they are very slightly higher and in the cervical region are slightly lower. Diapophyses are relatively long. Centra differ markedly from the heterocoelous condition of extant taxa by being cylindrical and relatively short. Further cervical descriptions cannot be made because the elements are scattered within the matrix, being incompletely preserved, a portion are distorted by the cranium, and their remaining portion is obscured by the forelimb. Several thoracic vertebrae are obscured by the sternum although one side is visible indicating that the centra are long and neural spines are high. Caudals are also incompletely preserved, a pygostyle is not recognized, and a single synsacrum lies in a transverse orientation in the vicinity of the pelvic girdle, which from ventral perspective appears to be basically fused, although transverse processes are still separated.

The coracoids are the best preserved elements of the pectoral girdle and differ from the morphology of *Cuspirostrisornis* and *Cathayornis* by being elongated, head is not expanded, and distal articular surface for the sternum is crescentic. Only the two clavicle branches of the furcula are exposed and appear to be more slender than on *Cuspirostrisornis*. On the sternum, there is a low but extremely distinct carina running anteroposteriorly, the sternum posterolateral process is extremely elongated, greatly exceeds the posterior process in length, and resembles *Cuspirostrisornis* and *Cathayornis* in morphology. The basic morphology of the sternal body consists of a relatively rounded anterior margin with an extremely small carinal apex at its midpoint, relatively deep coracoidal sulci lateral to the carina, and its dorsal surface is a shallow basin with a medial longitudinal carinal groove. However, this taxon lacks an anterior process differing from *Cuspirostrisornis* and *Concornis* but resembling *Cathayornis.*

There are no complete ribs preserved and exceptionally slender fragments may represent gastral ribs.

Completely preserved forelimb elements include a humerus, ulna, carpometacarpus, and an ungual. The remaining limb elements are either not preserved or are distorted beyond recognition. The right humerus is relatively robust. It has an S-shaped sinuous curvature and an enlarged proximal end. Its most prominent characteristic is the small but deep pneumatic fossa on the proximomedial side which is situated slightly more proximal than its homologue on extant taxa. The humeral head is relatively large and rounded. Distal to it is a scar for musculature that facilitates the attachment for the posterior portion of the Latissimus dorsi. Distally, the medial, lateral, and ectepicondylar processes are all relatively distinct and the distal end is expanded with condyles laterally projected; however, an olecranon fossa is absent.

The shaft of the left ulna has a slight curvature, and the proximal end is slightly hooked. The medial side of its apex is slightly more projected, and may represent an incipient olecranon process. The lateral side is situated slightly lower and perhaps represents an incipient lateral cotyle. In anconeal perspective, the distal end is rounded and slightly more expanded than the shaft with a relatively distinct medial condyle. The radius is more slender and weaker than the ulna and has a straight shaft. The distal end is short and conical, the planar proximal end is slightly expanded, and in proximal perspective it displays a shallow cotyle.

The carpometacarpus is preserved in transverse orientation just beneath the skull. It is distinctly fused, and resembles that of several moderate-sized species in the Passeridae. Proximally, the carpal trochlea is well developed and the process of metacarpal I is small but quite distinct. There is a distinct intermetacarpal fissure between McII and the slender McIII, and the distal end is also fused. At least one ungual phalanx is retained. Unfortunately the manus digits are dispersed within the matrix.

The pelvic girdle is incomplete, the best preserved elements being represented by the pubi. The ilia and ischia are isolated from the torso and are upside down. The pubis is slender, elongated, posteriorly extended with a slightly inflated distal end, and is not fused to but in close proximity to its counterpart. Its proximal end composes the ventral portion of the acetabulum. One ischium lies medial to the pubis while the other lies lateral to it. It is relatively broad and thick, shorter than the pubis, and particularly broad where it composes the acetabulum. The ilium is basically consistent with the morphology of *Cathayornis*, with a particularly broadened preacetabular portion and an attenuated postacetabular portion.

The hindlimb is better preserved than the forelimb. The femur is preserved upside down and phalanges are all dispersed within the matrix beneath the tarsometatarsus. The femur is only three mm shorter than the humerus, but is less robust, and relatively weak. Its shaft is slightly curved, its proximal surface is very slightly convex, femur head is distinctly isolated from the shaft, and a small distinct trochanteric crest lies proximolaterally. The distal end is broader and thicker than the proximal end and has laterally expanded distal condyles. The lateral condyle is projected and is larger than the medial condyle, a distinct medial ligamental fossa is present on the medial condyle, and on the lateral side of the lateral condyle there is a distinct scar for flexor musculature. In general morphology, this femur is more derived than both *Cuspirostrisornis* and *Cathayornis* although the posterodistal rotular groove remains extremely narrow. The entire element has become modified to possess the fundamental characters of extant taxa.

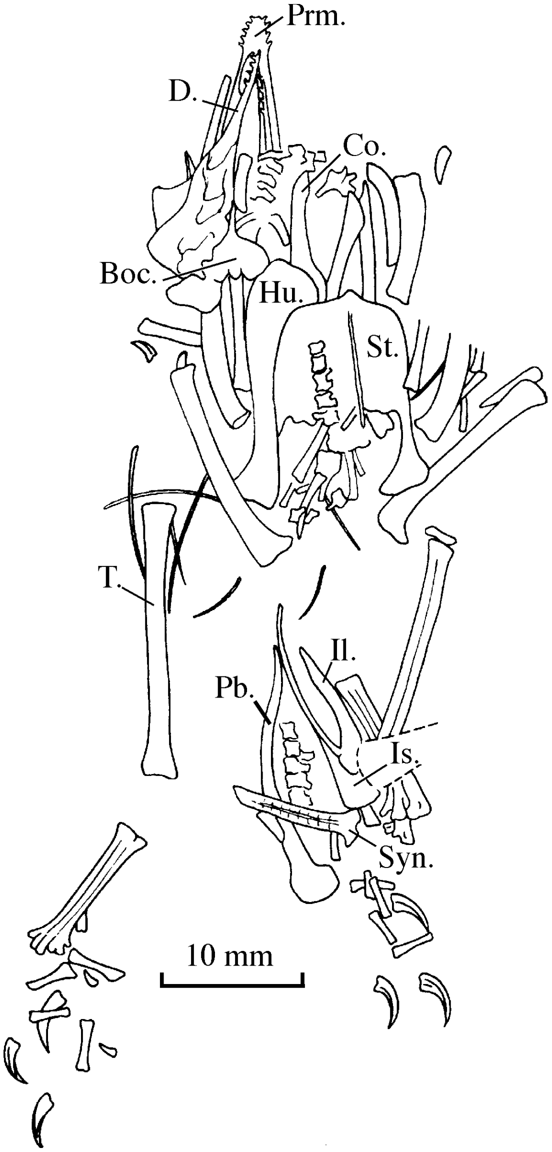

Figure 24. Drawing of *Largirostrornis sexdentoris* specimen V10531.

The tibiotarsus is longer than the femur. The proximal end displays some slight curvature, a short cnemial crest is present, the proximal surface is expanded and relatively planar, and resembles a cap overlying the shaft. The distal medial and lateral condyles are exceptionally projected. The lateral condyle is relatively large and the medial condyle small, the intercondylar fossa is extremely small, and a supratendinal bridge is absent. The fibula is represented on the lateral side of the tibia as a relatively compressed elongated cone.

A pair of tarsometatarsi are preserved, one of which is complete. It is shorter than both the femur and tibiotarsus and resembles the condition in *Cuspirostrisornis,* being slightly more than half the length of the tibiotarsus. Like *Cuspirostrisornis,* it has an ossified or fused cap covering its proximal end, although the distal end is not fused. MtI differs from other known Cretaceous taxa by being positioned relatively high. MtIII is the longest, MtII is the shortest, and MtIV is slightly slender. Because the digits are so disarticulated, the only observations that can be made is that they are relatively elongated and have large and recurved talons.

Table 12. *Largirostrornis sexdentoris* measurements (mm).

Skull length	32.0
Rostrum length	17.0
Humerus length	31.0
Proximal humerus breadth	8.5
Distal humerus breadth	6.0
Ulna length	~31.5
Carpometacarpus length	15.0
Carpometacarpus proximal breadth	4.5
Carpometacarpus distal breadth	3.5
Ungual length	2.0
Coracoid length	19.0
Coracoid distal breadth	10.5
Sternum anterior breadth	~17.5
Sternum midline length	~22.0
Femur length	28.5
Femur proximal breadth	6.0
Femur distal breadth	5.0
Tibiotarsus length	33.0
Tibiotarsus proximal breadth	5.0
Tibiotarsus distal breadth	5.0
Tarsometatarsus length	19.0
Tarsometatarsus proximal breadth	5.0
Tarsometatarsus distal breadth	5.5

Comparison and discussion: The above description notes several characters that are more derived than in other known Early Cretaceous taxa. These include the rather distinctly modified skull with a particularly elongated rostrum and a correspondingly relatively small cranium; the humerus has a small pneumatic fossa and its shaft shares the same sinuosity with extant taxa; the carpometacarpus is fused and has a well developed first metacarpal process; the sternum has a low carina that is continuous from the anterior to posterior ends, and an incipient manubrium; the coracoid is relatively slender and elongated with an arched articular surface for the sternum; the femur head is distinctly isolated from the shaft, and the distal femur morphology is relatively complex; the tibiotarsus maintains a cnemial crest, and the distal pubes are unfused.

Several of these characters are shared with *Concornis* from the Early Cretaceous of Spain, including the presence of a small pneumatic fossa on the proximal humerus, although on the Spanish specimen this fossa is at the midpoint just distal to the humeral head instead of medially as on *Largirostrornis*. The *Concornis* carpometacarpus is fused and between MtII and MtIII a slender intermetacarpal fissure is also present. Its tibiotarsus not only possesses a cnemial crest, but also displays a short and well developed fibular crest. The distal pubes are unfused although they differ in not being expanded into a boot.

Although these two genera share numerous characters, there is no real evidence that they are phylogenetically closer to each other than to any other Early Cretaceous genus. *Concornis* is distinct in its extremely broad coracoid and elongated humerus which greatly exceeds the length of the femur (representing an apomorphy), whereas on the new Chinese genus the humerus is just barely longer than the femur. Also, the posterior carina on the *Concornis* sternum is extremely elongated and there is an anterolateral process, but on *Largirostrornis* the anterolateral process is incipient. The femur head is not distinctly defined on *Concornis* and its tarsometatarsus is more elongated. Another Early Cretaceous genus that maintains a cnemial crest includes the Australian genus *Nanantius,* but it is otherwise vastly distinct from *Largirostrornis* and thus further comparisons are unnecessary. However, it is worthy of note that the new genus has a first metatarsal that is positioned particularly high, which is unique among Early Cretaceous genera and is a character shared with extant wading birds.

Largirostrornis appears to be phylogenetically closest to genera produced from the same locality such as *Cathayornis* and particularly *Cuspirostrisornis,* based upon characters including the reduced dentition. *Cathayornis* has four premaxillary and two mandibular teeth, *Cuspirostrisornis* has five pairs of teeth on the premaxilla and mandible, and *Largirostrornis* has five premaxillary and six mandibular teeth. In addition the anterior cranial elements, including the nasals and maxilla, are basically similar, as are other cranial features such as the unfused frontals and parietals. Also similar are forelimb-hindlimb indexes, sternum morphology, hindlimb proportions, and talon morphology, thus allowing the assignment of *Largirostrornis* to the Cathayornithiformes, which currently contains two families: Cathayornithidae and Cuspirostrisornithidae. As stated earlier, *Largirostrornis* approaches *Cuspirorstrisornis* with its relatively elongated rostrum and similar dentition count, particularly on the maxilla; the carpometacarpus is fused, and humerus-femur index is consistent, thus allowing an assignment of *Largirostrornis* to the Cuspirostrisornithidae. Its erection as a new genus is justified by the autapomorphic and apomorphic characters listed above.

The co-occurrence of the more derived *Largirostrornis* with other more primitive taxa from the same locality is further evidence of a mosaic fauna, as will be further documented in following descriptions. The four genera just described (*Boluochia, Cathayornis, Cuspirostrisornis,* and *Largirostrornis*) were derived from the same stratigraphic level at the same locality. These four genera are classified in three families within two orders. The several species described prior to *Largirostrornis* are all morphologically distinct and represent different evolutionary stages, but are not quite as distinct as *Largirostrornis.* Furthermore, the several species recognized from Spain also represent distinct evolutionary phases. For example, *Iberomesornis* is more primitive than *Concorsnis* in having a planar distal coracoid, extremely short clavicle branches, and a humerus that is simple in morphology.

Ornithurae

The extant Ornithurae occupy an extensive range of geologic time with a large quantity of fossil specimens extending through the Cenozoic to Cretaceous and Late Jurassic. In one respect, this indicates that extant taxa are descendants of various diachronous primitive forms and also indicates that there is an intimate phylogenetic relationship among the extinct taxa of various geological ages and extant taxa. Furthermore, avian fossil specimens increase with advancing geologic history, and there is now a large quantity of extinct taxa that are regarded as having phylogenetic relationships with the Ornithurae, several of which are recognized from the Mesozoic of China. This extends the history of the suborder back 142 million years and fills significant vacancies in the evolution of the group.

Primary characters of the Ornithurae include fused premaxillae and complete loss of dentition; the nasal process of the premaxilla overlies the nasals, the carpals and metacarpals are completely fused, the caudal vertebrae are fused and fewer than 15, a pygostyle is present, ribs bear ossified uncinate processes, three pelvic elements are basically parallel, fibula is reduced and shortened, tarsometatarsus is basically fused, MtV is completely lost, well developed hypotarsal ridges are present, sternum maintains a generally well developed carina, tibiotarsus bears a well developed lateral cnemial crest, humeral head is distinct and the morphology of its distal end resembles the extant condition, coracoid is a single columnar unit, and a supracoracoid process is present.

Liaoningornithiformes Hou, 1996

Liaoningornithidae Hou, 1996

Liaoningornis Hou, 1996

Genus diagnosis: Sternum possesses a well developed carina, presternum is present, ribs are robust, distolateral condyle of the humerus is enlarged, femur head is particularly well developed, and distal condyles are enlarged, tarsometatarsus is only half the length of the tibiotarsus, and length of the medial pes digit (not including the ungual) exceeds the tarsometatarsus.

Liaoningornis longidigitus Hou, 1996

Type: An incomplete skeleton (positive and negative slabs) including a portion of the forelimb, pectoral girdle with sternum, ribs, and hindlimb (IVPP specimen V11303.2).

Species diagnosis: As for genus. Sternum is goblet-shaped, distal terminus of coracoid is expanded, tarsometatarsus is robust, and unguals are as long as to the most distal phalanges, which maintain autapomorphic lateral grooves.

Locality and Stratigraphic position: Base of the Late Jurassic Yixian Fm. at the village of Sihetun, town of Shangyuanzhen, Beipiao Co., Liaoning Province.

Description: A majority of the skeletal elements is preserved on the positive slab (V11303-1). The sternum is complete and differs morphologically from those of extant taxa by being goblet-shaped with its anterior portion laterally expanded. It gradually constricts posteriorly and becomes most slender approaching the distal end in the pelvic region, though it again expands laterally at its terminus to abruptly compose two angles. Its posterior margin is slightly anteriorly embayed. A well developed carina, approximately three mm high, extends along the midline from the anterior to posterior margins but approaching the posterior margin it bifurcates into two crests.

Liaoningornis differs from all known genera by the presence of a pair of vestigial presterna, which are rhomboid with a small mammary projection on their lateral angle that resembles the anterior processes of the sternum. The anterior margin of the presternum contacts the coracoid with an enlarged and deep articular groove.

Only portions of a coracoid, a scapula, and a furcular process are preserved. The distal coracoid is expanded and its length cannot be determined. Both ends of the scapula are damaged but its shaft is relatively thick with a slight curvature. Between the two presterna there is a relatively long projection resembling a furcular process. This element is incomplete and may actually represent a vestigial interclavicle because in general a furcula is not as elongated as this element.

Ribs are incomplete and dispersed within the matrix. Those that are preserved are relatively large and broad although there are two slender ribs that may represent gastric ribs.

Only the distal end of the humerus is preserved which has a slight amount of curvature, although the rest of the shaft is basically straight. The lateral condyle is enlarged and transversely expanded. The ulna is relatively robust and curved with medial and lateral cotyles lying on different planes. The radius is more slender than the ulna and has a straight shaft and a humeral cotyle. Distal ends of the radius and ulna are not preserved.

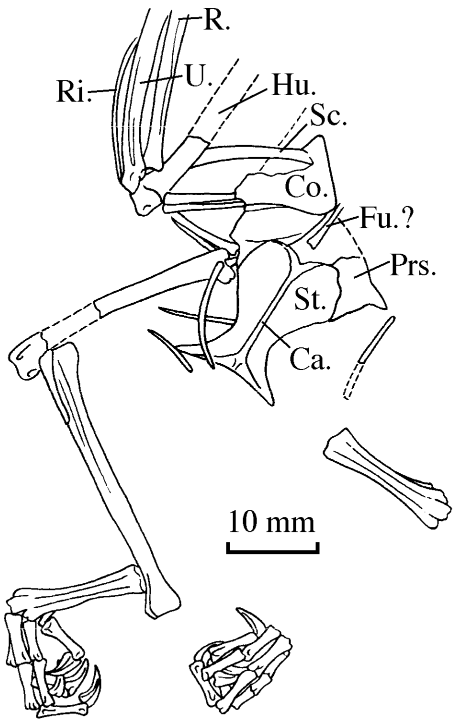

Figure 25. Drawing of *Liaoningornis longidigitus* V.11303-1 (positive).

The femur is long with very slight curvature. The head is particularly well developed, there is conspicuous scarring to facilitate the attachment of the Teres ligament, and the medial condyle is enlarged with a depression for facilitating ligament attachment. The tibiotarsus is slightly longer than the femur with expanded termini, a relatively planar proximal end, well developed distal condyles (particularly the projected lateral condyle), and a lateral longitudinal trough which may represent a tendinal groove, although a supratendinal bridge is absent. The fibula is slender with a length half that of the tibiotarsus and a fused proximal end.

Among the metatarsals preserved, MtIII is the longest and MtIV is not as slender as MtII. The pedal digits are slender and elongated; the length of the medial digit (excluding ungual) greatly surpasses that of the tarsometatarsus. A large lateral groove on each side of the phalanges for the unguals represents an autapomorphy not documented on any other species. Talons are large and acute with well developed lateral tendinal grooves, but the unguals are not very recurved and their lengths are equivalent to the phalanges they are articulated with.

The majority of the feathers have become carbonized and thus are obscure. Those on the ulna are still recognizable and are shorter than those on *Confuciusornis* and *Archaeopteryx.*

Comparison and discussion: To date, *Liaoningornis* represents the only Late Jurassic taxon that possesses a carina, a presternum, and a forelimb with numerous characters which allow an assignment to the Ornithurae. It also represents the smallest body size of any avian fossil. Plesiomorphic characters shared with the Reptilia include the presence of a presternum and possibly an interclavicle. Jurassic members of the Sauriurae include only *Confuciusornis* and *Archaeopteryx,* which maintain not only numerous avian characters (with *Confuciusornis* being a little more derived) but also numerous reptilian characters, though neither share the autapomorphic characters of *Liaoningornis,* and consequently it is inappropriate to assign the latter genus to the family Sauriurae. From a comprehensive perspective, *Liaoningornis* is dominated by apomorphic characters, particularly in its well developed sternum and carina, which are vastly more derived and modified than on the contemporaneous *Confuciusornis* and suggest better flight capability. Its hindlimb is also more derived and distinctly modified, providing a second justification for its taxonomic assignment. Consequently, the retention of distinctly plesiomorphic characters does not exclude *Liaoningornis* from an assignment to the Ornithurae.

The identification of a presternum is based an the following factors: It has an intimate relationship to the sternum by its sutural contact and it replaces the anterior process of the sternum with an anterolateral mammary process. At its anterior margin there is a deep transverse groove for the contact with the broad and circular coracoid. Furthermore, if this element was instead interpreted as another portion of the pectoral girdle, its location and morphology would suggest it to be the coracoid, currently recognized in association with the precoracoid or epicoracoid on extant taxa, and which would also be isolated and lie in opposition to the articular surface of the sternum.

The developmental history of the presternum indicates that it becomes prominent in the early stages of the Reptilia and Mammalia. Later, what is regarded as the legitimate sternum is composed of the presternum, sternum, and xiphisternum. It is generally recognized that mature vertebrates that retain a presternum include members of the Mammalia in addition to the reptilian forms including *Sphenodon,* the Lacertilia, and Crocodylia, although recognition of this element is controversial as some interpret it in the Mammalia to have become modified into the manubrium while in the Lacertilia it is retained as an independent element. Its presence in the Crocodylia is also disputed, but some recognize it as the expanded anterior portion of the sternum which is in contact with the coracoid and procoracoid. On *Liaoningornis* it is distinct from the sternum in its lateral expansion. Thus its presence indicates an intimate relationship to the Reptilia, and within the context of avian origin and evolution represents a significant topic of discussion among ornithologists. The identification of a presternum on *Liaoningornis* undoubtedly represents a significant discovery in Ornithology.

Characters shared between *Liaoningornis* and volant birds include the presence of a well developed carina on the sternum, well developed medial and lateral cotyles on the proximal ulna, and a well developed femur head with scars facilitating the attachment of the Teres ligament.

Plesiomorphic characters include the presence of a presternum, sternum as a thickened plate that lacks lateral processes, proximal tibiotarsus lacking a cnemial crest and distal end lacking a supratendinal bridge, distal tarsometatarsus is incompletely fused, and radius is relatively robust.

Autapomorphic characters of *Liaoningornis* include the extreme lateral expansion of the distal humerus with an enlarged lateral condyle, similar diameters of radius and ulna shafts, distinct morphology of the sternum with the presence of a presternum, relatively elongated femur which is only slightly shorter than the tibiotarsus, and a tarsometatarsus shortened to one-half the length of the tibiotarsus.

Liaoningornis was excavated from the same locality that produced the new species of *Confuciusornis.* Both share the character of a well developed sternum, although each is morphologically distinct. Both genera are also more derived than *Archaeopteryx* in their well developed lateral humeral condyle and presence of medial and lateral cotyle on the ulna. It is possible that *Liaoningornis* is ancestral to *Hesperornis* and *Ichthyornis* because the *Liaoningornis* sternal morphology in addition to its tarsometatarsus-tibiotarsus length indices are consistent with *Hesperornis, Ichthyornis* and other aquatic birds, particularly diving birds. *Liaoningornis* is quite distinct from *Confuciusornis* in its adaptation to aquatic or riparian habitats as opposed to perching. Furthermore its morphology, particularly the pes, is similar to specimens representing Coraciiformes described from the Middle Eocene of Germany. Its phylogenetic relationship to later avian taxa is illustrated in Figure 84.

The large and diverse quantity of specimens from the basal Yixian Fm. of Beipiao, Liaoning, is an indication that avian diversity had already initiated by the Late Jurassic. The relatively derived genus *Liaoningornis* documents the earliest member of the Ornithurae and indicates that the Jurassic was the period of avian origin and diversity. *Liaoningornis* gave rise to the later radiation of Early Cretaceous ornithurids with *Chaoyangia*, *Songlingornis*, and *Gansus* representing the main lineage of avian evolution. *Liaoningornis* not only distinctly expresses a derived condition but also, due to its antiquity, retains reptilian characters such as a presternum and possibly an interclavicle, characters that were lost with the appearance of *Jibeinia*. In the Early Cretaceous, avian taxa radiate toward extant morphology as exemplified by *Chaoyangia*, which possesses characters shared with extant and younger fossil birds such as *Ichthyornis* and *Hesperornis* including an uncinate process on the gastric ribs, although its pelvic girdle is still extremely primitive. Not only does the *Songlingornis* sternum possess a carina, it also maintains posterolateral sternal foramina and its coracoid morphology approaches the complexity of extant forms. *Gansus* is even more derived: its tarsometatarsus is basically fused and digit IV is the longest in the series, being fully adapted for riparian habitats.

Gansuiformes Hou and Liu, 1984

Gansuidae Hou and Liu 1984

Gansus Hou and Liu 1984

Gansus yumenensis Hou and Liu 1984

The description of *Gansus yumenensis* in 1980 constituted the first record of Mesozoic birds in China, initiated the study of paleornithology in the country, and aroused extensive attention in the academic realm. At that time, with the exception of *Archaeopteryx*, *Gansus* represented the oldest record of Aves. Furthermore, its morphology reflects adaptations for a riparian or aquatic habitat although its unguals are autapomorphic and to date workers are still perplexed by their morphology.

Specimen: A portion of a left hindlimb including a distal tibiotarsus, complete tarsometatarsus and digits with unguals. (IVPP specimen V6862).

Locality and stratigraphic age: Gray-black mudstones of the Early Cretaceous middle Xiagou Fm., northwest of the village of Chenjiawan, Changma perfecture, Yumen Municipality, Gansu Province.

Ammended Diagnosis: A small form with recurved talons maintaining well developed flexor tuberosities: digits that are slender, elongated, and composed of phalanges with inflated termini; depressions are present to facilitate the tendons of the Flexor longus digitorum; and digit IV is the longest in the series. The tarsometatarsus is slightly shorter than the longest digit, is slightly laterally compressed incompletely fused distally, and a distal haemal foramen is well developed and placed nearly at the terminal end within the intertrochlear recess. Mt IV is shorter than MtIII. Proximally the sulcus for the extensor musculature is shallow and small, posterior to which there are no well developed calcaneal ridges or tendinal canals, but on the proximal surface there is a pronounced crest separating the anteroposteriorly elongated cotyles. On the distal tibiotarsus a supratendinal bridge is absent, the medial condyle is particularly narrow with an acute lateral margin, the lateral condyle is particularly broadened, and the medial side of the posterior intercondylar groove is more excavated.

Summary: In August, 1983, the paleoichthyologists Fengchen Ma, Zhicheng Liu, and Shaochu Huang were conducting Mesozoic research in the Changma region of Yumen Municipality. During their excavations, Professor Liu uncovered a hindlimb, whereupon all expedition members recognized it as an extremely significant specimen of a bird and not that of a pterosaur. Professor Ma took particular care to preserve the specimen and presented it to Lanzhou University where L.H. Hou provided a diagnosis. At that time Hou was visiting the Department of Biology where he was conducting joint research with the anatomist Linyu Cong, dissecting a specimen of *Alligator sinensis.*

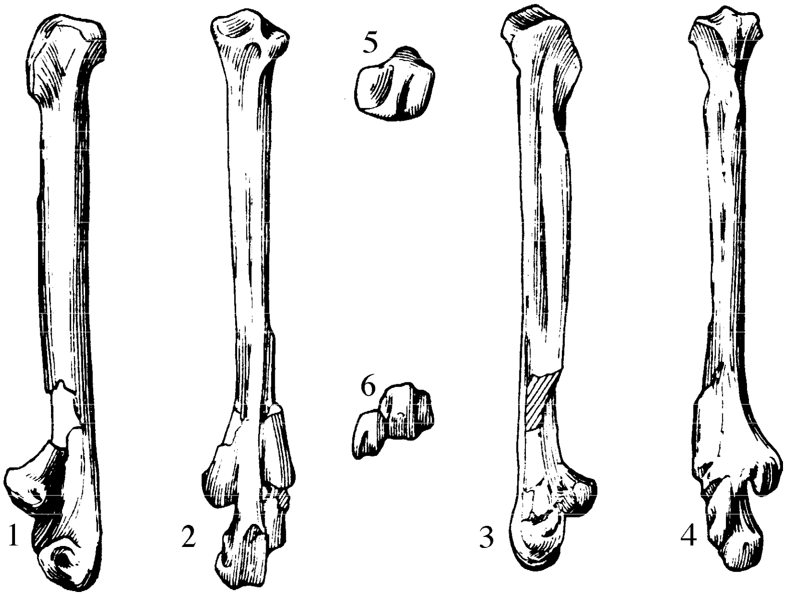

Figure 26. Left tarsometatarsus of *Gansus yumenensis* (After Hou, 1984)
1. Left lateral perspective; 2. Anterior perspective; 3. Right lateral perspective. 4. Posterior perspective; 5. Proximal perspective; 6. Distal perspective.

After a careful analysis of the specimen, he identified it as avian on the basis of several aspects: The distal tibia of a pterosaur has two extremely small articular condyles that are not laterally expanded; they articulate with two tarsals and lack trochlear depressions. Also, the distal hindlimb of pterosaurs maintains five fully formed tarsals, and as in other reptiles, displays five anteriorly directed metatarsals that are approximately four times the length of the digits. This is completely distinct from the avian tarsometatarsal condition.

Gansus maintains numerous autapomorphic features, among which are several characteristic of the avian condition. These include the distal tibia with two differentially sized condyles, tarsals have all become fused with the tibia and metatarsals to compose a tibiotarsus and tarsometatarsus, the metatarsals have varying lengths; MtIII trochlea is the longest, only four digits are present, and the pollex is in opposition to the other three digits.

Only the distal tibiotarsus is preserved with both condyles complete, the lateral side of which is slightly longer. In anterior perspective a supratendinal bridge is absent, the distal shaft is relatively flat, and lacks any depressed regions; thus it represents the plesiomorphic condition. The two condyles are relatively distinct from each other. The lateral condyle is distinctly larger, its dorsal margin is quite distinctly delineated from the shaft, its articular surface is reduced, its lateral margin is rather rounded, and it is not laterally expanded. The medial condyle is distally extended and medially oblique with an anteriorly projected anterior margin that composes an obtuse angle with the shaft. Its posterodorsal margin is particularly low and only reaches a point just proximal to the midline of the lateral condyle. The intercondylar depression is V-shaped and distinctly medially inclined. The posterior trochlea is predominantly laterally inclined. A characteristic feature of the medial condyle is a thinly crescentic depression at its midpoint, anterodorsal to which a thick inflation extends to the dorsal margin of the condyle. The lateral condyle is slightly convex with a small thickened inflation at its midpoint and a transverse depression between the dorsal margin of the condyle and the shaft. There is an oblique truncated surface on the shaft above the condyles and the shaft is elliptical in cross-section with relatively thick walls.

Table 13. *Gansus yumenensis* tibiotarsus measurements (mm).

Preserved length	9.5
Medial and lateral condyles lateral breadth	4.4
Medial and lateral condyles anterior breadth	4.4
Trochlea posterior breadth	4.0
Medial condyle anteroposterior length	4.5
Medial condyle anterior process height	2.7
Lateral condyle anteroposterior length	4.2
Lateral condyle maximum length	3.4
Distal breadth	3.0
Anteroposterior length	3.5

The tarsometatarsus is complete and basically fused with a straight shaft that is very weakly anteriorly concave and posteriorly convex at its midpoint. The lateral side has been subjected to compressional distortion such that it is medially depressed, and a portion of its wall is damaged. The articulation on digit I with the tarsometatarsus is not very distinct. The proximal surface of the tarsometatarsus maintains distinct medial and lateral cotyles lying at different levels. The medial cotyle is relatively large, shallow, positioned relatively high, is nearly rectangular in anteroposterior orientation, and there is an anteroposteriorly directed fissure at its midpoint. The lateral cotyle projects laterally from the shaft, is positioned slightly lower, and is relatively flattened with a linear lateral margin. A relatively pronounced rounded crest between the two cotyles represents a vestigial metatarsal boundary line.

Table 14. *Gansus yumenensis* tarsometatarsus measurements (mm).

Length	31.6
Proximal transverse breadth	4.3
Proximal anteroposterior breadth	4.2
MtIII trochlea breadth	4.2
MtIII anteroposterior breadth	4.2
MtIV trochlea breadth	3.1

In anterior perspective the tarsometatarsus has been slightly laterally distorted but it may still be inferred that the anterior surface of the shaft is relatively flat, or slightly depressed, based upon the relatively short and shallow anterodorsal metatarsal groove and the very slightly convex distal end. Proximally, there is a distinct but small and shallow intercotylar fossa. A proximal haemal foramen is either absent or obscured due to compressional distortion, and the tuberosity for the Tibialis anticus is low and medially situated.

Approaching the distal end the shaft becomes slightly arched but lacks a conspicuous depression on the shaft proximal to the trochleae. The trochleae are not expanded. MtIII is the longest with a broad articular surface and a terminus with a relatively deep medial groove that extends to the medial and lateral sides, and there are well developed lateral fossae for ligament attachment. MtII is the shortest, posteriorly obliquely inclined, and positioned higher than in any known avian taxon. Its terminus reaches only to the base of the MtIII tochlea. A relatively small transverse groove is also present at its terminus, there is a small acute process directed posteriorly, and a pair of slightly small lateral ligament fossae are present, the lateral of which is larger. MtIV is incomplete at its distal end but is tightly fused to the lateral side of MtIII. It is slightly gracile, slender, and shorter than its lateral counterpart.

The *Gansus* pedal phalangeal formula is 2-3-4-5. The digits are distinctly slender and elongate with the lengths of digits III and IV exceeding that of the tarsometatarsus. The proximal phalanges are all extremely expanded and have relatively deeply excavated articular surfaces, the distal ends are dorsoventrally compressed, and there are lateral ligament fossae on all phalanges. The four unguals are slightly compressed and recurved; they have well developed flexor tuberosities at their bases, particularly on digits II and IV. Ventrally on the unguals is an acute process that is undoubtedly intimately related to habitat adaptation. Furthermore, there are relatively deep lateral ligament grooves on the talons. Among the four talons, that on digit II is relatively large while the remaining are basically consistent in size.

Table 15. *Gansus yumenensis* digit measurements (mm).

Digit I phalanx I length	8.4
Digit I ungual length	4.1
Digit II phalanx I length	10.1
Digit II phalanx II length	11.5
Digit II ungual length	5.0
Digit III phalanx I length	13.0
Digit III phalanx II length	10.8
Digit III phalanx III length	8.0
Digit III ungual length	5.0
Digit IV phalanx I length	11.1
Digit IV phalanx II length	8.6
Digit IV phalanx III length	8.4
Digit IV phalanx IV length	7.5
Digit IV ungual length	4.0

Discussion: From one aspect, *Gansus* displays derived characters of extant forms, but it also retains several primitive characters in addition to autapomorphic characters. It represents an archaic avian evolutionary phase. Consequently, it was initially erected within a new order to represent a transitional phase within Aves. Currently, there is abundant supplemental Early Cretaceous specimens but these do not diminish the significant phylogenetic position represented by *Gansus* and to date supplemental taxa or specimens resembling *Gansus* are still absent. In 1996, correspondence was received from Richard C. Fox, from the University of Alberta, Canada, stating that he recovered a tarsometatarsus from the Early Cretaceous of northwest Alberta that may be comparable to *Gansus*, thereby suggesting the potential extensive distribution range of this genus 130 million years ago.

Gansus shares the following characters with extant taxa: distal tibia has become modified into a tibiotarsus, the metatarsals and portion of the tarsals have become fused to compose a tarsometatarsus with concave proximal medial and lateral cotyles, a conspicuous distal haemal foramen, and digit I lies in opposition to the other three digits. These characters are also more derived than the homologues on the abundant specimens from the Early Cretaceous Jiufotang Fm. in the Chaoyang region of Liaoning Province, on which concave proximal medial and lateral cotyles are indistinct, the distal tarsometatarsi are all unfused, and a haemal foramen is absent.

However, *Gansus* retains the plesiomorphic characters of the absence of a supratendinal bridge on the tibiotarsus, the presence of which is a synapomorphy shared among archaic birds;

also on the proximal tarsometatarsus a haemal foramen is absent, as is a tuberosity for the Tibialis anticus, and a canal for the flexor tendons. Their symplesiomorphic characters are shared with taxa from the Chaoyang region and are more primitive than the conditions in *Ichthyornis* and *Hesperornis.*

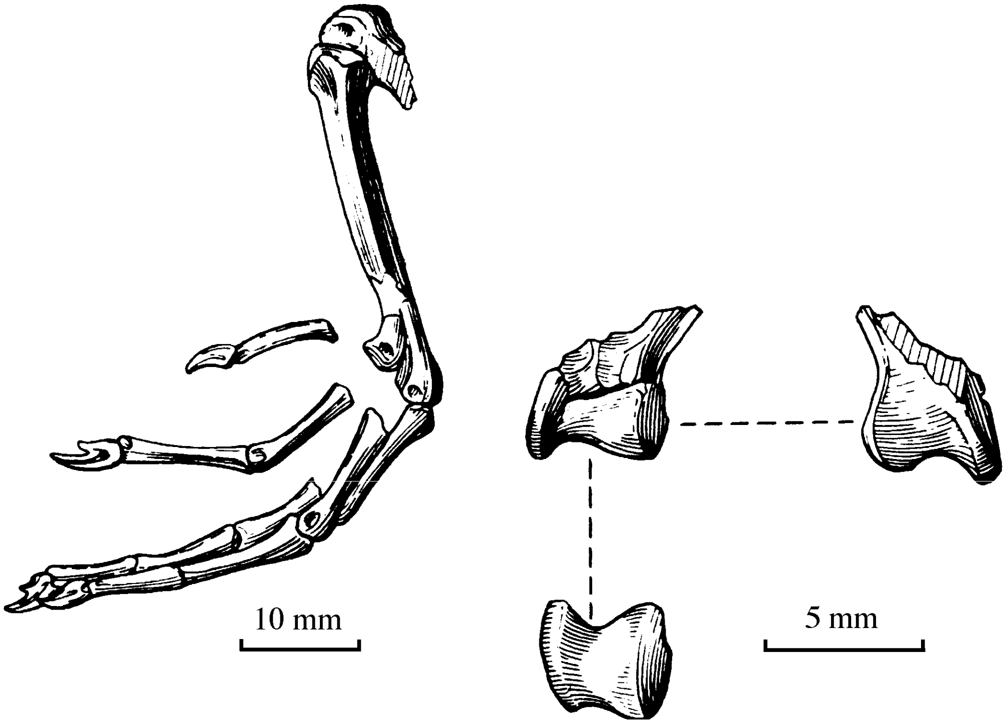

Figure 27. Medial view of *Gansus yumenensis* distal left hindlimb (left) and anterior, posterior and ventral view of left distal tibiotarsus (right) (after Hou, 1984).

Autapomorphic characters of *Gansus* include the following: (1) Tibiotarsus with thick walls, distal medial and lateral condyles are extremely distinct from each other with the lateral being broad and enlarged and the medial being narrow and medially oblique, and its anterior margin is anteriorly projected to compose a obtuse angle with the shaft. (2) The anterior surface of the tibiotarsus is flattened; there is a thinly crescentic trough on its medial side, and a very slightly convex lateral side with a small inflation at its midpoint. (3) The tibiotarsus is shorter than digits III and IV, sizes of the medial and lateral cotyles are vastly distinct and its cotyles are separated by a high longitudinal crest. (4) The anterodistal shaft of the tibiotarsus and the extended tubular-shaped Mt III trochlea differ from the anserine condition of being thin and flat or concave; nor does it resemble the arched condition of riparian taxa, but more closely approaches the morphology of the Charadriidae. (5) MtII is positioned particularly high and is located quite distant from MtIII. (6) Digit I is relatively elongated and is vastly distinct from the condition in extant taxa, in which this digit generally tends to be reduced. Digit IV is the longest in the series, exceeding the length of digit III, which resembles the condition of several extant taxa including the pelicans.

Gansus occupies a significant position in the evolution of archaic birds and is quite distinct not only from extant taxa but from Early Cretaceous taxa including those from Spain, *Ambiortus* from Mongolia, and all the taxa from the Chaoyang region of Liaoning Province. *Gansus* shares a tarsometatarsal character with *Enaliornis* from the Early Cretaceous marine deposits of the United Kingdom: MtIV is longer then its MtIII. *Enaliornis* is regarded as having an intimate relationship with *Hesperornis,* both being typical diving forms. This then indicates either a shared behavioral or habitat adaptation or a definite phylogenetic relationship among the three.

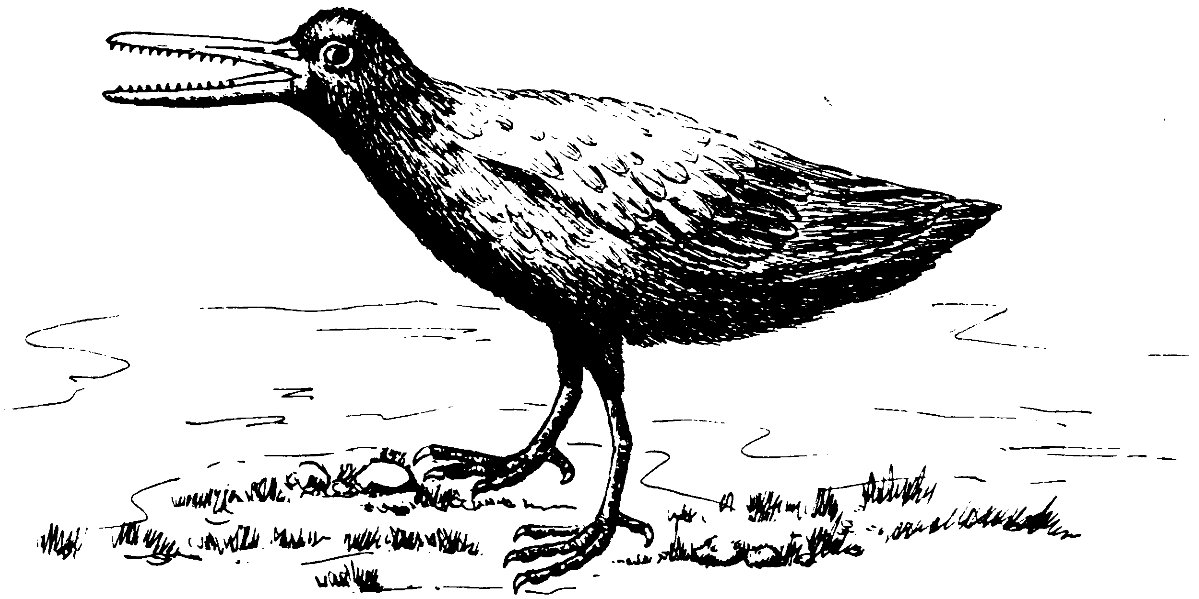

Figure 28. Restoration of *Gansus yumenensis* (revised from Feduccia, 1996).

The autapomorphic characters of *Gansus* distinguish it from all the Liaoning taxa regardless of some of their morphology reflecting an adaptation for riparian habitats. Additional distinctions of *Gansus* lie in its talons, which have well enveloped flexor tuberosities, and that its digit IV is the longest in the pes. Moreover, the long bones on the Chaoyang taxa all differ by being relatively thin-walled. Worthy of note is that the talon morphology of *Gansus* is extremely close to the charadriid genus *Scalopax,* which also maintains particularly projected flexor tuberosities on the ventral aspect of its five talons. But on *Gansus* the tuberosities on digits I and II are not as well developed, which may imply that it was fully adapted to a riparian habitat. In addition to the ungual flexor tuberosity of digit three, which resembles that of *Scolopax,* the degree of talon curvature is also nearly identical, the hallux is shortened, and the tarsometatarsus is similar in morphology. Thus, it would appear that *Scolopax* is the closest relative to *Gansus* and that the charadriid lineage is descended from this genus. Obviously, the hiatus of over one hundred million years between these two genera would certainly result in morphological discrepancies, as exemplified by the relatively primitive nature of the *Gansus* tarsometatarsus that is slightly shorter than the longest digit, digits being relatively slender and weak, presence of a relatively deep sulcus for the Flexor longus digitorum, and digit IV being the longest. These plesiomorphic characters distinguish it from later avian forms, which underwent a trend of gradual adaptive modifications. For instance, the reason the sulcus for the Flexor longus digitorum is deeper than on *Scolopax* is that the archaic avian muscular system was not completely developed for fully functional flight, whereas in extant Aves are not only fully adapted for functional flight, but is also fully adapted for activities including perching, predation, terrestrial mobility, wading, swimming, and diving.

Furthermore, the digits on *Gansus* are long, slender, and weak, whereas the charadriid forms, although they lack webbed feet, have digits that are relatively robust and fortified for mobility in regions such as beaches or paludal habitats, and thus the majority of taxa display a tendency to reduce pedal digit I. Some species retain only three anterior digits, and the occasional charadriid evolves webbed feet. *Scolopax* has relatively thick ventral ‘dermal cushions’ on its pes which further facilitates floatation and terrestrial surface contact. This adaptation is absent on *Gansus.* Its phalangeal articular surfaces are not as well developed, its digits are slender and weak, and even though digit IV is elongated, this is not sufficient justification for the interpretation of webbing. Among those extant taxa with an elongated digit IV none maintains webbed feet, as exemplified by *Hydrophasianus*. But the elongated digit IV and slender and long digits on *Gansus* resemble *Hydrophasianus*, further indicating a close descendant relationship to the Charadriidae. However, *Hydrophasianus* has a distinct autapomorphy in that its opposable digit I ungual is relatively elongated, whereas in *Gansus* the ungual of digit I is only half the length of its associated phalanx.

Chaoyangiformes Ord. nov.

Chaoyangidae Fam. nov.

Chaoyangia Hou and Zhang, 1994

Chaoyangia beishanensis Hou and Zhang, 1994

Type: An incomplete skeleton lacking the head, forelimb, and hindlimb (IVPP specimen V9934).

Locality and stratigraphic position: Middle to upper mudstones of the early Early Cretaceous Jiufotang Fm., from the Beishan quarry, Chaoyang Co., Liaoning Province.

Diagnosis: Vertebral centra are not heterocoelous, sacrals exceed eight, and are unfused. Ribs bear a proximal longitudinal groove and an ossified uncinate process. Sacral girdle is unfused, pubis is posteriorly inclined, pneumaticized, and has fused termini, ilium is reniform (kidney-shaped), and preacetabular section is longer than the unreduced postacetabular section. Long bones are thinly walled and pneumaticized. Femoral head and shaft are well developed and fourth trochanter has become lost. Cnemial crest on the tibia is enlarged and fibula is not fused to the tibia.

Description: *Chaoyangia* was discovered serendipitously in the fall of 1990 when an expedition was concluding its excavations in the Boluochi region of Chaoyang Co after the collection of several avian specimens. On the last day, upon closing the quarry, a brief perusal of the spoil pile was conducted for potential specimens that were missed. A massive chunk of shale was split to reveal the *Chaoyangia* specimen, which differed from the others collected from the quarry by being larger, and displaying an exceptionally distinct sacral girdle. The vertebral column was primitive and resembled that of *Archaeopteryx*, whereas the pelvic girdle resembled that of the Dinosauria, but its thoracic ribs were like thos of extant birds in having a well developed uncinate processes. Because this was the first discovery of a specimen with such mosaic characters, an intensive search was initiated to try to find the associated portions of the skeleton, particularly the skull, pectoral girdle, and forelimb. The search ensued until nightfall without success, and the team ultimately departed the quarry with a deep sense of regret. Continuous annual excavations have been conducted at this quarry since 1990 and to date supplemental material of this genus has yet to be recovered, despite the addition of numerous typical specimens.

Recently, in addition to the continuous production of Early Mesozoic birds from China, other Early Cretaceous discoveries have been made in Mongolia, Spain, Canada, South America, and Australia, but there are still no specimens resembling *Chaoyangia*, which is the principle justification for the erection of the new order.

The specimen is preserved in natural configuration, with the posterior three cervicals in tight association with their corresponding thoracic vertebrae. Right gastric ribs are in their natural configuration as is the pelvic girdle, which maintains enlarged ilia flanking the sacral vertebrae. The acetabulum is distinctly exposed, and the right femur is shifted anteriorly. On the left side, only three gastric ribs are preserved and have shifted in position. As in the other specimens from this quarry, feathers are not preserved.

The three cervicals are tightly articulated, resembling the condition of *Confuciusornis* and *Archaeopteryx.* The centra are not heterocoelous and increase in size posteriorly. Although the centra are relatively short, lateral pleurocoels are relatively well developed, and neural spines are relatively low with their height increasing posteriorly. Short cervical ribs are retained and become progressively elongated posteriorly. There are approximately seven thoracic vertebrae with distinctly elongated centra and high neural spines that differ from those of extant taxa by being unfused. The several posterior thoracic dorsal spines are particularly high, attaining 6 mm in height and 5.5 mm in length, whereas centra are 3.5 mm high and have a slightly concave ventromedial margin. A ventral keel is not noticeable. At least one lumbar is detached from the column; its neural spine is also relatively high, and its morphology resembles the thoracic condition, but features posterior to it are obscured by the ilium. There are at least eight sacral centra with neural spines that are particularly pronounced but are not in contact, and diapophyses are relatively elongated, contacting the dorsomedial margin of the ilium. Fusion has clearly begun in anterior caudal centra although neural spines are still unfused.

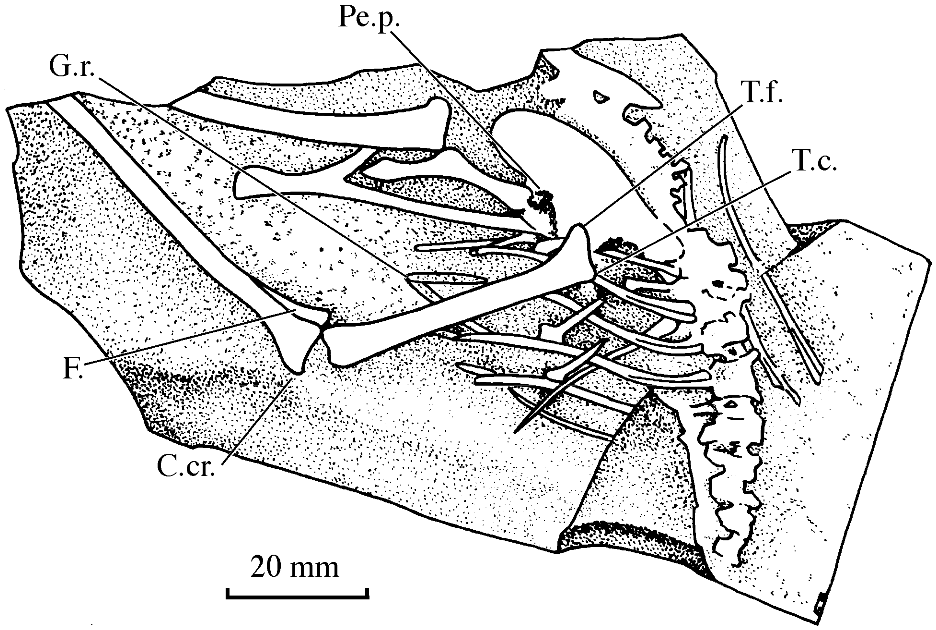

Figure 29. Drawing of right lateral view of *Chaoyangia beishanensis* partial skeleton (V19934) (after Hou and Zhang, 1993)

The most notable character of *Chaoyangia* lies in its thoracic ribs, which have well developed ossified uncinate processes which resemble the extant condition as well as that of *Hesperornis* and *Ichthyornis*, and are a unique morphology among Early Cretaceous taxa. Eight typically bicapitate ribs are represented (three on the left side and five posterior ribs on the right) as relatively complete shafts in natural position. These indicate a relatively large chest cavity in outline. Proximal ribs display the extremely autapomorphic character of longitudinal grooves 10 to 15 mm long. Ribs also resemble the extant condition: The have a longitudinal dorsal process for facilitating attachment of intercostal musculature, although the shafts are relatively slender and elongated. This differs from the extant condition in which ribs are expanded to facilitate the stability of the thoracic cavity, or expand the surface area for facilitating intercostal musculature for functional flight (Fig. 78). Although the ribs on *Chaoyangia* are extremely elongated, facilitation for intercostal musculature is rather weak. Obviously, in order to fortify the thoracic chamber, *Chaoyangia* ossified its uncinate processes, which have become elongated to surpass the intercostal vacuities and almost attain the next anterior rib, resembling the condition of extant taxa. The uncinate processes are posteriorly oblique; they have an extremely expanded base and an acute termination, resembling an elongated cone. Two to four uncinate processes are present that are two-thirds the length of the rib shaft itself.

It is extremely noteworthy that *Chaoyangia* maintains ossified gastric ribs, and although they are neither as numerous nor as complete as the dorsal ribs, they are sufficient to indicate that the genus had a relatively derived thoracic cavity. The gastric ribs are preserved in natural configuration, with their termini in contact with the distal dorsal ribs. Both termini of the gastric ribs are not expanded as in the extant condition. Two additional gastric ribs lay isolated between the dorsal ribs.

In contrast to the derived thoracic cavity is the presence of an exceptionally primitive pelvic girdle resembling that of the Dinosauria. Elements on the right side are relatively well preserved. A basically complete reniform ilium has a relatively elongated preacetabular section that has been medially depressed due to compressional distortion. The postacetabular portion of the ilium is only slightly reduced and is extremely broadened. It has a relatively rounded terminus which differs distinctly from that of *Cathayornis* from the same locality. The acetabulum is small and circular and the entire dorsal wall is composed of the ilium, although its anterior portion is incomplete. The dorsal margin of the ilium is very slightly dorsally crescentic, lies lateral to the centra, and is not fused with the lumbar or sacral centra.

The right pubis is complete but only the posterior portion of the left pubis is visible. Its shaft is relatively cylindrical and pneumaticized. The portion of the pubis that composes the anteroventral acetabulum, or the prepubic process, has been greatly reduced, representing only an extremely short pectineal process. The pubis extends posteriorly from the acetabulum; its distal end contacts its counterpart via a slight inflation. The distal region of contact is relatively elongated, being 17 mm in length. This condition resembles that of *Archaeopteryx* although it lacks a dorsally hooked process.

The right ischium is also relatively complete and forms an irregularly shaped linear element that is broader than the pubis and slightly resembles the condition in *Archaeopteryx*. The ischium extends posteroventrally between the two pubes and has an undulating expansion. Its distal end does not reach the medial margin of the distal pubes and terminates to become narrow and acute. The proximal end forms the posteroventral portion of the acetabulum. Its ventral margin is a dorsally arched embayment, and it differs from *Cathayornis* by lacking a dorsal process. All three pelvic elements are unfused and do not bear an intimate relationship with the sacral vertebrae. Thus in this respect, it closely resembles *Archaeopteryx.*

Although the hindlimb preserves only the femur and a portion of the tibiotarsus, it appears to be relatively robust. Both femora are preserved, with the one on the right side being nearly perfect. The right shaft is relatively straight but the left is slightly curved. The proximal end bears a relatively high trochanteric crest, and a shallow trochanteric fossa. The femoral head is relatively large and projects relatively distinctly medially, although a neck is basically absent. The fourth trochanter has become lost. The shaft is more slender than the proximal end; it has a pneumatic foramen on the proximolateral side, is highly pneumaticized, and has relatively thin walls. Distally, the rotular groove is relatively expanded and a scar for ligament attachment is relatively distinct on the medial side of the medial condyle. Whether or not an attachment point to facilitate flexor musculature is present on the lateral side of the lateral condyle is unknown due to being obscured. The distal end is slightly concave, quite distinct from the extant condition. The distal end of the left femur is not preserved; the element has been shifted in position to lie posteroventral to the ilium, and overlies the proximal left ischium and pubis.

The right distal tibiotarsus is missing and the left side only preserves a portion of its proximal end. Like the femur, it is relatively robust, the shaft has a slight curvature, and it possesses the distinct character of a relatively well developed medial crest resembling the extant condition of projecting medially, however, its extension to the proximal surface is vague. Proximally, it is represented by a single very slightly concave articular surface that has yet to become divided into two facets; this is a direct reflection of its articular relationship with the rather planar distal femur. There is a slight proximolateral expansion but a distinct lateral cnemial crest is absent.

Only a slender and short right fibula is preserved in addition to an extremely short portion of the right tarsometatarsus, but it cannot be determined whether it resembles *Cathayornis*. The tarsals appear to have become fused to compose a cap on the shaft of the fused tarsometatarsus.

Table 16. Measurements of *Chaoyangia beishanensis* (mm).

Vertebral column preserved length	88.0
Second to last right rib length	~36.0
Second to last right uncinate process length	8.0
Second to last right proximal rib to uncinate process length	25.0
Third to last right rib length	40.0
Longest right uncinate process	11.1
Fourth to last right rib length	37.5
Ilium length	32.0
Pubis length	~51.0
Distal pubis contact length	17.0
Ischium length	30.0
Femur length	45.0
Femur proximal breadth	9.5
Femur distal breadth	7.2
Tibiotarsus preserved length	5.3
Tibiotarsus proximal breadth	8.5

A cursory observation of the *Chaoyangia* specimen would cast doubt upon its veracity as a member of Aves because the skull, forelimb, and sternum are absent, hindlimb is incomplete, there are no feather impressions, and the pelvic girdle is extremely primitive. However, careful examination of the specimen documents fundamental avian characteristics that alleviate all suspicions. These include the relatively thin-walled and highly pneumaticized long bones, the presence of ossified uncinate processes, preacetabular region of the ilium exceeds the length of the postacetabular region, the short prepubic process is represented as the avian pectineal process, pubis is distinctly posteriorly oblique, femur has a relatively high trochanteric crest, and tibiotarsus maintains a well developed medial cnemial crest.

The characters documented above indicate that *Chaoyangia* has a modern avian morphology in addition to retaining primitive characters, excluding its assignment to any known avian orders. Although numerous specimens are produced from the same quarry that are also small and retain primitive characters, none displays characters as apomorphic as *Chaoyangia*, which include the presence of uncinate processes on the ribs, resembling the condition of *Hesperornis, Ichthyornis,* and other extant carinate birds, in addition to the presence of ossified gastric ribs that probably indicates a stabilized thoracic cavity, thinly walled and pneumaticized long bones, sacral vertebrae exceed eight in count, femur is enlarged with the fourth trochanter lost, and distal end bears depressions for facilitating ligament attachment; and a medial cnemial crest is present on the tibiotarsus.

Plesiomorphic characters retained by *Chaoyangia* include the non-heterocoelous cervical centra, unfused lumbar and sacral centra, and unfused pelvic girdle. Its autapomorphic characters include a medial longitudinal groove on the proximal dorsal ribs, apparently for the facilitation of intercostal musculature, the reniform ilium with a relatively large discrepancy between preacetabular and postacetabular length, and a rounded posterior end; and a pneumaticized pubic shaft with an elongated contact of the distal pubis.

Chaoyangia shares plesiomorphic characters with the Sauriurae including the non-heterocoelous vertebral centra, sacral girdle is not fused, and pubis is posteriorly oblique with fused termini. The most notable characters shared with extant taxa to the exclusion of the Sauriurae include the presence of uncinate processes on the dorsal ribs; ossified, elongated, and pneumaticized gastric ribs; and a well developed cnemial crest on the tibiotarsus. Thus, *Chaoyangia* is justifiably assigned to the Ornithurae.

Relatively contemporaneous taxa include not only the Chinese *Confuciusornis, Liaoningornis, Jibeinia, Sinornis, Cathayornis,* and *Gansus,* but also *Archaeopteryx,* the Mongolian *Ambiortus,* and the European *Enaliornis, Limnornis, Noguerornis, Concornis,* and *Iberomesornis.* The Late Jurassic *Confuciusornis* and *Archaeopteryx* represent the most primitive members of Aves to date, sharinga a similar pelvic girdle morphology of a thin and narrow postacetabular region which differs greatly from that of*Chaoyangia.* Also, the *Confuciusornis* ischium is short and broad with an expansive terminus and a dorsal process which also differs markedly from that of *Chaoyangia.* The *Confuciusornis* pubis differs by being relatively thin and weak with an unexpanded terminus.

Liaoningornis is the most recently erected small genus derived from the same stratigraphic level as *Confuciusornis,* but it compares poorly to *Chaoyangia.* Although it maintains a well developed carina, it still retains particularly primitive characters such as the presence of a presternum, which differ greatly from *Chaoyangia.* The genus *Jibeinia* occupies an extremely significant position in avian phylogeny. It is produced from latest Jurassic sediments and represents a transitional phase between the morphologies of *Confuciusornis-Archaeopteryx* and the diverse assemblage of Early Cretaceous genera. Its most notable characters lie in its wing and sternum morphology. Obviously it could not have maintained an advanced rib morphology or derived condition of the tibiotarsus such as on *Chaoyangia.*

Despite *Sinornis* and *Chaoyangia* being derived from different localities, they are both produced from the Early Cretaceous Jiufotang Fm. and share several characters such as an unfused pelvic girdle, although other pelvic characters are quite distinct, (e.g. *Sinornis* possesses a curved pubic boot) and a small cnemial crest on the tibiotarsus, it lacks uncinate processes on the ribs, and its gastric ribs lie distant from the dorsal ribs.

Cathayornis is an archaic form that is smaller than a sparrow-sized passerid, is produced from the same quarry as *Chaoyangia,* and differs in its absence of uncinate processes on its ribs, a smaller acetabulum, and a smaller and more narrow postacetabular region of the ilium.

The Mongolian genus *Ambiornis* represents an archaic member of carinate birds, approaches the size of a corvid, is represented only by a forelimb, a portion of vertebrae, and sternum, and is diagnosed with a distinct carina and extremely well developed proximomedial and lateral tuberosities on its humerus. It is regrettable that the corresponding counterparts of *Chaoyangia* are not preserved.

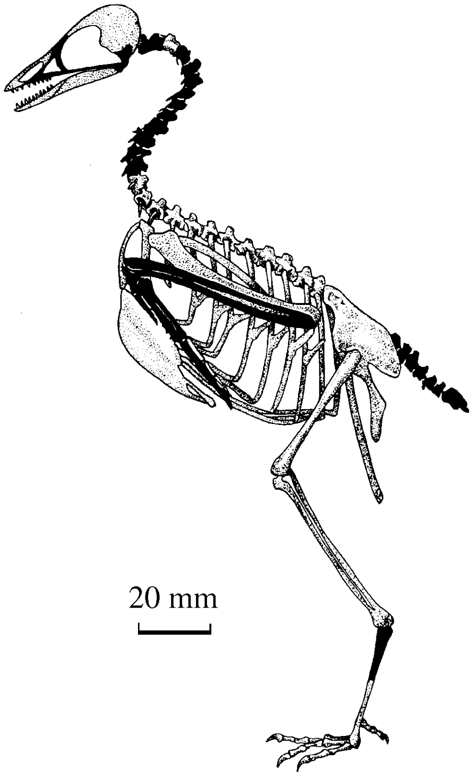

Figure 30. Restoration of *Chaoyangia beishanensis* (after Hou, Zhou, and Feduccia, 1996).

Noguerornis, Concornis, and *Iberomesornis* are all produced from the Early Cretaceous of Spain. The former is derived from limestones at the locality of Montsec in Laerido Province, while the latter two are produced from limestones at Las Hoyas, Cayenca Province. *Noguerornis* is principally represented by a forelimb, partial vertebrae, furcula, and a fragmentary tibia. Thus it cannot be compared to *Chaoyangia,* although it represents an evolutionary stage that closely approaches that of *Sinornis* and *Cathayornis.* The two latter genera are represented by incomplete skeletons; *Iberomesornis* is more complete. Although it lacks a skull, the remaining skeleton is complete, resembling *Cathayornis* by being small and primitive but with relatively derived forelimb characters, although talons are retained. Its ribs lack uncinate processes, sacral girdle and distal tibiotarsus are not fused, a relatively long pygostyle is present, preacetabular portion of the ilium is elongated and broad, posterior portion is reduced and relatively narrow, and only five sacral centra are present. These features distinguish it distinctly from *Chaoyangia.*

The genus *Limnornis* is produced from the Early Cretaceous of Romania and is represented only by a right distal humerus, several right metacarpals, and a portion of the left femur which has a projected distolateral condyle, a rounded medial condyle, a deep popliteal fossa, and a narrow intercondylar fossa, indicating a more derived condition than *Chaoyangia.* It is regrettable that its ribs are not preserved for a more complete comparison.

It is appropriate here to conduct a comparison of several morphological aspects of *Archaeopteryx, Confuciusornis,* and *Chaoyangia.*

There is a relatively large size discrepancy between the current specimens of *Archaeopteryx. Chaoyangia* approaches the size of the Berlin specimen and further resembles it by having amphicoelous vertebral centra and relatively elongated lateral centra depressions or pleurocoels. It is noteworthy that on the cast of the London specimen presented to IVPP, there is a rib that resembles the condition on *Chaoyangia,* where a distinctly elongated groove lies on the dorsal surface, although the ribs are relatively short and no gastric ribs are noted, indicating its more primitive condition. The presence of this groove, however, indicates that *Archaeopteryx* possessed a rather stabilized intercostal musculature system. The dorsal ribs of *Chaoyangia* are elongated with relatively long uncinate processes and distal ends that are in contact with the gastric ribs. The interconnection of intercostal uncinate processes is a further adaptation for flight and reinforces the rigid thoracic lattice structure, representing the most conspicuous apomorphy of the genus. The thoracic condition of *Confuciusornis* resembles *Archaeopteryx* but its ribs are more slender and longitudinal grooves are shallower.

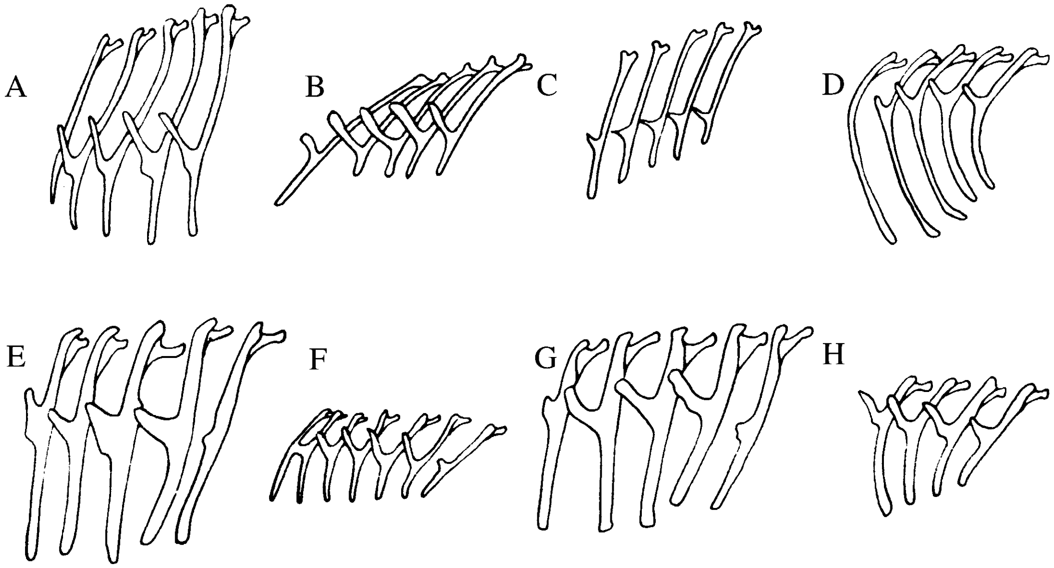

Figure 31. A comparison of *Chaoyangia* rib morphology to other avian taxa (After Hou and Zhang, 1993) A. *Chaoyangia;* B. *Hesperornis;* C. *Icthyornis*; D. Gruidae; E. Anseriformes; F. Falconiformes; G. Galliformes; H. Passeriformes.

Chaoyangia represents the most archaic avian form with uncinate processes on the ribs. Within the evolution of the avian thoracic cavity, the development of the uncinate process is extremely significant. Thus a comparison of uncinate processes is conducted between Mesozoic and extant genera to attempt to decipher an evolutionary pattern. Figure 81A, B, and C illustrates Mesozoic forms, in which it may be noted that the uncinate processes are all located distally on the ribs. On the extant forms the anterior uncinate processes are positioned slightly distal but do not exceed the point two-thirds the length of the rib. Posteriorly along the rib cage the uncinate processes migrate dorsally; the one on the terminal rib is dorsal to the midpoint of the shaft.

Rib morphology is based upon differential habitat adaptations. *Hesperornis* and other extant natatorial birds maintain relatively robust ribs, with uncinate processes that are particularly broadened at their termini. However, other extant taxa display uncinate processes in which the base is the broadest. Wading birds possess ribs that are narrow and elongated with proximoventral pneumatic foramina; thus *Ichthyornis* rib morphology more closely resembles that of wading birds. Raptor rib morphology is broad and thin with numerous pneumatic foramina from the proximal end to the midportion of the rib. Dense forest taxa generally maintain a fortified rib that is moderate in thickness but is particularly strong in morphology with only a small quantity or a single pneumatic foramen at the proximal end. *Chaoyangia* most closely approaches *Ichthyornis* in morphology and thus resembles a wading bird, although no extant taxa have the longitudinal groove on the ribs such as on *Chaoyangia.*

Several reptiles tat maintain uncinate processes on their ribs, including the genus *Sphenodon* and members of the Crocodylia, although these are cartilaginous and not fully ossified. Ostrom (1960) states that *Dromaeosaurus* also possesses uncinate processes but these are probably a homoplasy.

The pelvic girdle on the fossil specimens indicates the following evolutionary trends: (1) The preacetabular portion of the ilium becomes extended concurrent with the increase of sacral fusion, while the postacetabular portion becomes reduced as an adaptation for the shortened caudal series and to reduce weight for the flight load. (2) The ischium becomes an irregularly shaped thin plate that extends and expands posteriorly to gradually approach the ilium and as in the extant condition, to finally fuse with the ilium. The ischium of *Chaoyangia* is longer and thinner than *Confuciusornis* or *Archaeopteryx* in addition to lacking a proximal ischial fenestra. (3) The prepubic process becomes reduced with the entire pubis becoming posteriorly elongated to form the longest and thinnest element on the pelvic girdle as in the extant condition. The distal pubes eventually diverge whereas the distal ischia become fused. The *Chaoyangia* pubis is not only longer than *Confuciusornis* and *Archaeopteryx*, it is pneumaticized, which is a highly autapomorphic condition. The pubes on *Archaeopteryx* and *Confuciusornis* are distinct. (4) The hindlimb of *Chaoyangia* is more derived than its predecessors and distinctly closer to the morphology of later forms; its femur resembles those of ground dwellers. The femoral head on *Confuciusornis* and *Archaeopteryx* is undeveloped and the tibia retains the reptilian condition.

Early Cretaceous avian specimens from China and other regions of the world share numerous characters with their Late Jurassic predecessors in addition to maintaining more derived characters. *Chaoyangia* is the most characteristic and derived of these genera due to its thoracic construction, which provides the most effective adaptability for flight among all the Early Cretaceous species.

Songlingornithidae Fam. nov.

Songlingornis gen. nov.

Diagnosis: Presence of a relatively compact abundant dentition; relatively well developed carpometacarpus; proximal coracoid maintains a well developed head with a distinct procoracoid, coracoid fossae, and haemal foramen, while distally there is a relatively large sterno-coracoidal process and a depression to facilitate sterno-coracoidal musculature. The furcular process has become reduced to resemble the condition on extant wading birds. Sternum is elongated and broadened with a distinct carina, a well developed lateral process, and a posteriorly expanded foot that greatly exceeds the distal end of the sternum body, and elliptical fenestrae are present posteriorly.

Etymology: Songling (pine ridge in English) being Pinyin Romanization for the name of the northeast-southwest oriented mountain range to the southeast of the fossil quarry, which is the second largest range in Chaoyang Co.

Songlingornis linghensis gen. et sp. nov

Species diagnosis: As for genus, slender and elongated mandible with more than nine teeth; vertebral centra are not heterocoelous; ribs are slender and elongated; femoral head is well developed; sternum bears a relatively deep coracoid groove and a prominant manubrium; and scapula is straight.

Species etymology: Linghe, being Pinyin Romanization for the Linghe River, which is the largest river in the fossiliferous region of Western Liaoning and traverses the region from the northeast to southwest.

Type: An incomplete skeleton lacking the head and forelimb (IVPP specimen V10913).

Locality and stratigraphic age: Early Cretaceous Jiufotang Fm. at Boluochi, Chaoyang, Liaoning Province.

Description: The specimen was collected in 1992 from a fossiliferous unit which is thinly laminated and interbedded with muddy sands. These muds obscure the specimens unless painstaking care is taken when scrutinizing a split piece of matrix. A specimen is generally revealed only after the muddy matrix has been scraped away and therefore, due to these taphonomic conditions, an entire specimen may be damaged. Fortunately, impressions of lost bone are extremely distinct and reflect the precise morphology of the elements. It is extremely regrettable that due to this sedimentological condition a counterpart is not preserved.

Only a small portion of the skull is preserved, and as with the remaining portion of the skeleton it is exposed in ventral perspective with portions represented only by impressions in the matrix. Represented are the nasals, premaxilla, quadrate, and well preserved left and right mandibles. The premaxilla has a minimum of five teeth, its nasal process is extremely elongated, nasals are relatively broad, short, and have been displaced to the posterior portion of the skull. The well preserved mandibles are extremely slender and elongated with up to twelve teeth in the ramus, representing the most numerous dentition among all the taxa produced from the Boluochi region.

Teeth all maintain a substantial root with a conspicuous constriction beneath the crown, which is short, posteriorly oblique on all teeth, and resembles the morphology of *Archaeopteryx.* The mandible is extremely narrow with a relatively linear ventral margin and a retroarticular process is present. The posterior portion of the second mandible is lost but the dentition is long with 12 teeth. A disassociated slender elongated plate at the posterior half of the mandible may represent the splenial, and an irregularly shaped piece of the quadrate may be represented posterodorsally. A portion of the maxilla overlies the mandible and has an extremely narrow posterior flange. It is presumed that this genus possessed a relatively long skull, based upon the narrow and long mandible with a retroarticular process. It bears some resemblance to the extant charadriid genus *Haematopus.*

The vertebrae are widely scattered within the matrix. None of the cervicals is completely preserved, and the centra morphology is indeterminate, but the neural spines resemble several avian taxa in being relatively high. Several thoracic vertebrae are preserved between and (or) lateral to the coracoids, but because they are not exposed in lateral or anteroposterior perspective it is difficult to determine their precise morphology, although it is quite evident that they are not heterocoelous. No vertebrae posterior to the sternum are preserved. There are impressions of two slender and elongated ribs articulated with the centra which do not bear uncinate processes. Two additional incomplete distal portions of ribs lie within the matrix.

The pectoral girdle is relatively well preserved. A scapula, probably from the right side, appears relatively weak, slender, and elongated and has a relatively well developed proximal articular facet. There is a relatively large acromion process and an oblique anterolateral articular facet for the furcula. The blade has yet to become modified into the extant scimitar-shaped morphology and is instead relatively linear with the distal end being rather expanded.

The coracoids are extremely well preserved. Their morphology basically resembles the extant condition and particularly that of the extant Threskiornithidae, although they are much smaller. Compared to its contemporaneous taxa, the *Songlingornis* coracoid is distinctly more derived but differs from extant morphology in that its neck is extremely short, nearly to the point of being absent, the procoracoid lies dorsally close to the coracoid head as an extremely large process but not acutely tapered, which differs from the condition in threskiornithids. At the base of the

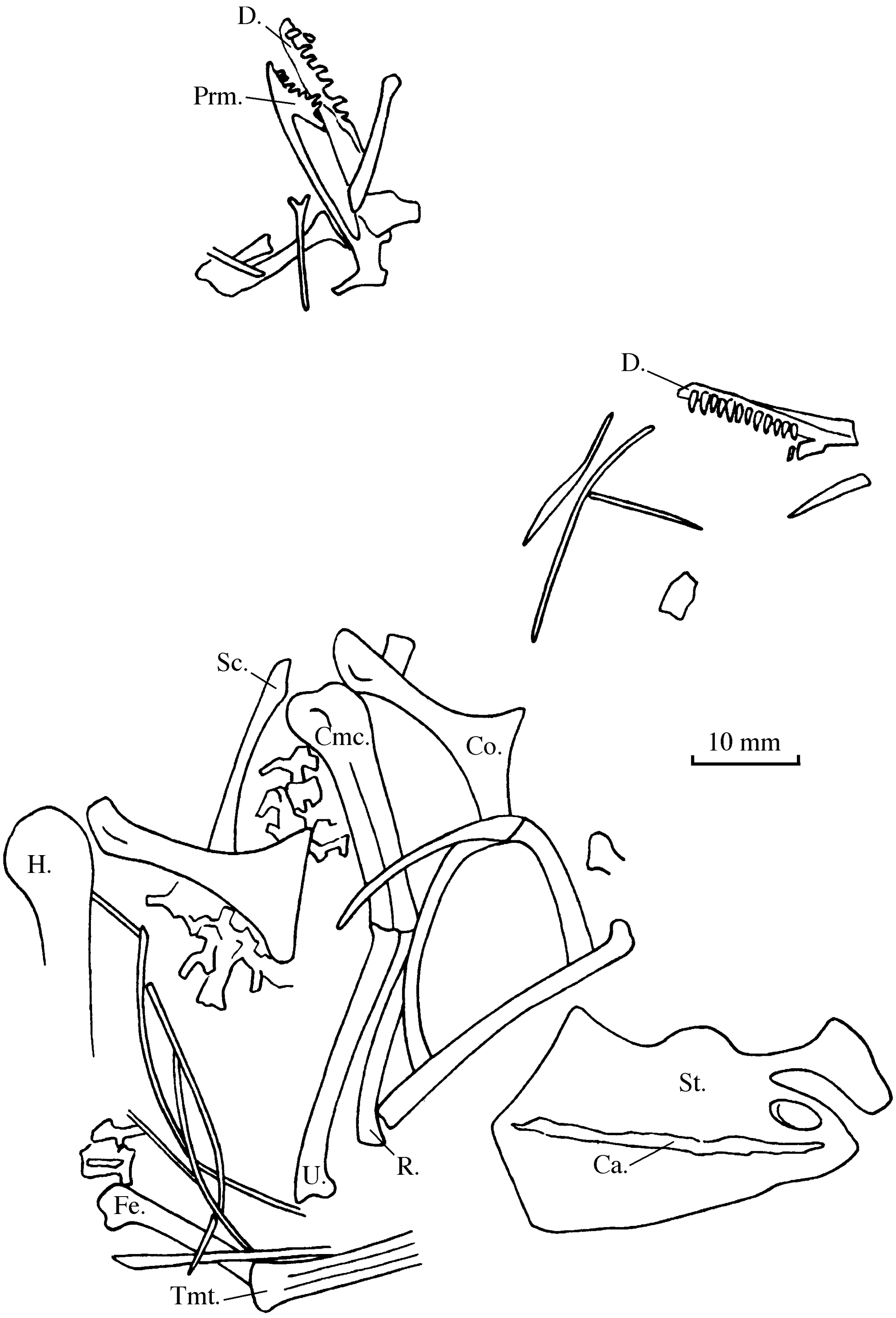

Figure 32. Drawing of *Songlingornis linghensis* specimen V.10913.

procoracoid on the proximal shaft there is a coracoid foramen, which is a character shared with the Threskiornithidae, Sphenisciformes, Lariformes and the Charadriiformidae, and Haematopidae, although the location of this foramen is variable. In extant forms, a coracoid fossa lies between the procoracoid and the head representing a major conduit for musculature, but on *Songlingornis* this character is represented only by a groove on the dorsal side of the procoracoid and a mound-shaped projection lies distal to the head, where the fossa should lie. Because the neck is extremely abbreviated, this fossa is nearly circular. At the base of the procoracoid, approaching the coracoid shaft, is an articular surface for the scapula. The rather rounded coracoid head is relatively large and has a very slightly hooked proximal end and an anteroventrally oblique humeral articular facet. In actuality there are two facets at the proximal end: one that lies proximodorsally and the other for the scapula lies distal to the neck. The distal end is relatively expanded and has a transversely broadened and slightly depressed articular facet for the sternum. Distolaterally there is a particularly elongated sterno-coracoidal process which is just as prominent as on several extant taxa such as the Threskiornithidae and Haemotopidae. Medially, there is an extremely projected distomedial angle. At the distal expansion, there is a slight ventral projection while on the dorsal side there is a very slight but distinct depression for the attachment of the Sternocoracoidei.

The furcula is one of the best preserved elements on this specimen. Its left branch is more complete than the right and lies obliquely beneath the right coracoid. Its interclavicle or furcular suture line is extremely distinct and its furcular process is extremely short. The furcular suture line is arcuate, unlike the V-shaped configuration on the other specimens from the same locality. This morphology resembles that of Threskiornithidae and several families in the Charadriiformes. However, the furcular branches of *Songlingornis* are still rather thick and heavy, unlike the light, slender, and dexterous morphology of extant taxa. Nevertheless, the branches have become modified to be relatively elongated, and as such it may be determined that they not only provided functional support for the pectoral girdle and sternum, but also supported a relatively large crop, which is a significantly derived character in the digestive system of Aves.

The sternum is ventrally exposed and is exceptionally autapomorphic as an elongated, irregular, and multifaceted element. It has an extremely long carina that extends from the anterior to posterior margins and although it is extremely distinct it is not exceptionally pronounced. It is of interest that narrow grooves run along each side of the carina and gradually shallow anteroposteriorly. These grooves represent the intermuscular line between the carina and sternum, resembling later avian morphology. The anterior carina is still relatively unprojected and a genuine carinal apex has yet to be formed, although there is a small mound-shaped projection anteroventrally. The posterior carina is even less projected as a low and flat line that lies between two medial fenestrae. Anteriorly, there are two relatively deep grooves or sulci to accommodate the coracoid. Each is associated with an extremely thick and broadened dorsal lip but an extremely thin ventral lip. The most anteromedial end has been damaged, prohibiting a description of the manubrium. Lateral to the coracoid sulci are a pair of anterolateral sterno-coracoidal processes. Generally, a sternum in this derived condition would maintain articulated gastric ribs, however on this specimen, where the gastric ribs would be present, there is a relatively large arcuate shaped medial embayment. At the posterior end, there is a large arcuate projection anterior to the posterolateral process, that creates an undulating margin on the posterolateral expansion. The terminus of the posterolateral process is shorter than in any other Early Cretaceous genus but it still surpasses the posterior end of the sternum as an expansive fan-shaped feature that circumscribes the posterior margin. Two extremely distinct oval fenestrae perforate the posterior portion and serve to lighten the weight of the element.

The forelimb is incompletely preserved. It is represented only by two distal ulnae, a radius, and a single carpometacarpus. The proximal right ulna is overlain by the carpometacarpus and is located lateral to the left branch of the furcula and anterior to the sternum. It has a straight shaft, a slightly expanded distal end with an extremely distinct tendinal depression, and a relatively projected lateral condyle, but its distal trochlea is neither concave or planar, as the lateral condyle is distally projected due to compressional distortion. Only the distal end of the left unla is preserved as a relatively rounded element. The radius is missing its distal end, has a slender and linear shaft, proximal end is not expanded, and the humeral cotyle is relatively flat.

Table 17. *Songlingornis linghensis* skeletal measurements (mm).

Premaxilla length	19.0
Nasal length	9.5
Mandible length	25.5
Longest rib length	31.0
Coracoid length	22.5
Proximal coracoid breadth	5.5
Distal coracoid breadth	10.5
Distal furcula breadth	12.0
Furcula branch length	25.0
Sternum length	35.0
Preserved breadth between sterno-coracoid processes	23.0
Sternum posterolateral process length	38.0
Sternum posterolateral process terminus breadth	10.0
Sternum fenestra longitudinal diameter	7.5
Ulna preserved length	28.0
Radius preserved length	21.0
Carpometacarpal length	25.0
Femur length	11.0
Femur proximal breadth	7.5

The right carpometacarpus is relatively well preserved, lying between the coracoids and more closely to the right coracoid. It is completely fused at the proximal process of metacarpal I, which is relatively thick and enlarged. The proximal articular surface, or the carpal trochlea, is relatively well developed, there is a pisiform process medially, and the ligament attachment of the pisiform process is extremely conspicuous. In addition, there is a relatively well developed and large medial ligament fossa proximal to the pisiform process. MtII is robust and linear but MtIII is relatively curved, both have been shifted in position, and the distal metacarpal fusion is rather complete. Taphonomic conditions do not allow the determination of the presence of an intermetacarpal vacuity.

Of the hindlimb, only the proximal femur and a portion of the tarsometatarsus are exposed. The femur is relatively robust and has a well developed dorsally projected proximolateral trochanter. A small trochanteric fossa is also present proximally. The femoral head is large and has a well developed depression for the attachment of the teres ligament, and the head is distinctly separated from the shaft by a relatively well developed neck. Another portion of a vague long bone is present near the terminus of the left furcular branch, anterior to the sternum, and right posterior side of the ulna. Its terminus is represented as an irregularly shaped impression of three trochlea, and thus may represent the tarsometatarsus or three juxtaposed phalanges.

Discussion and comparison: *Songlingornis* was collected in the Boluochi region of Chaoyang Co. from the same locality that produced the genera *Cathayornis, Boluochia, Cuspirostrisornis, Largirostrisornis,* and *Chaoyangia*. It represents a form with a derived pectoral girdle and abundant dentition. It is smaller than *Chaoyangia* and more closely approaches *Largirostrisornis,* while morphologically it is more derived than *Cathayornis, Cuspirostrisornis,* or *Largirostrisornis.* It is the only Early Cretaceous avian genus with a procoracoid, coracoid fossa, and coracoid foramen, in addition to medial fenestrae on the sternum, which thus justifies the erection of a new genus and species and its assignment to the Ornithurae despite the presence of a full dentition.

Songlingornis shares several characters with the Sauriurae *Cathayornis,* including the morphology of its dentition which has a rather slender constriction beneath the low, acute, and posteriorly curved crown. The premaxilla is extremely similar, being conical with a relatively short body and a slender and elongated nasal process. The relatively thin and elongated mandible is also similar. Although the limbs and vertebrae are incompletely preserved, there are distinct similarities to *Cathayornis* such as the non-heterocoelous centra, ribs are slender, long, and lack uncinate processes, and ulna is relatively straight, lacking any trace of papillae of caudal remiges.

Characters of *Songlingornis* that are autapomorphic for Early Cretaceous taxa, are more derived than the other members of the Sauriurae from the Boluochi quarry, and justify its exclusion from the subclass Sauriurae include a mandible with a relatively well developed retroarticular process (which is also present on several extant wading birds), the extremely short furcular process with an arcuate ventral suture; the coracoid with extant morphology and being primitive only in the absence of a neck, causing the element to be relatively short; and a sternum with an elongated carina, a distinct intermuscular lineation, and well developed posteromedial fenestrae.

In addition to *Gansus* and *Chaoyangia,* other Early Cretaceous ornithurines include the English *Enaliornis* (Seeley, 1864), the Mongolian *Ambiortus* (Kurochkin, 1982), and the French *Gallorais* (Lambrecht, 1933). It is not necessary to reiterate a description of these taxa, however it should be noted that the specimens of *Gansus* and *Chaoyangia* preserve portions of their skeletons that are not represented on *Songlingornis.* On *Chaoyangia* this includes the derived uncinate processes on the ribs.

As previously stated, the coracoid, furcula, and sternum of *Songlingornis* are comparable to extant morphology and reflect habitat adaptations. A comparison of the furcula to extant orders indicates an affinity to the Galliformes that dwell partially in shrub habitats or on the ground, as reflected by the relatively elongated fusion of their furcular process, the majority of which is composed of thin plates that are expanded into differential morphologies. The morphology of *Songlingornis,* however, is quite distinct from these extant taxa, indicating a different behavioral modification. In the Falconiformes, the furcular process is thinner and more slender and has an extremely short posteriorly directed process off the suture zone; its arc is much broader, its distal margin is flat, clavicle branches are not extremely elongated, and proximal termini become gradually expanded and widely divergent, which is quite distinct from *Songlingornis.* The songbirds in the Passeriformes have a quite distinct furcula that is relatively narrow; the termini are medially thinly crescentic at their fusion point, clavicle branches are slender and long and have a moderate degree of divergence, and the ventral margin is very slightly but distinctly convex. The *Songlingornis* furcula differs not only in being relatively robust, but also by its very slightly concave ventral margin. Thus it is distinct from song birds and other dense forest taxa. The diving taxa, represented by the Anseriformes, have several characters in their furcular morphology that resemble the raptors, including the large degree of arc, branches which are not extremely elongated, and which have a slight proximal expansion. However, the suture zone is not thinned and projects slightly laterally to appear as a small ventrally directed mound, which differs from the condition of the raptors. The *Songlingornis* furcula compares to the Anseriformes in its robusticity, but it is quite distinct in that its branches are not expanded, the suture zone lacks the small mounded projection, and the arc of the furcula is not as expansive. Charadriifomes represent the riparian wading birds, with the basic morphology of their furcula being consistent, and expressed as relatively elongated and slender branches that do not become expanded. The suture zone rather resembles that in the Passeriformes although the crescentically shaped process is more inconspicuous, while it projects very slightly dorsoventrally. The *Songlingornis* furcula, with its extremely expansive branches, slightly resembles wading birds but its furcular branches are more robust, the suture zone only projects dorsally, and its ventral margin is concave.

The comparisons conducted above indicate that the *Songlingornis* furcula is more derived than any other Cretaceous taxon, but that it is also distinct from every modern form, and thus it is recognized as a transitional morphology which represents a specialized environmental adaptation, but what it is modified for is not clear. Obviously, its robusticity is a plesiomorphic condition.

The *Songlingornis* coracoid morphology more closely resembles that of extant taxa, which generally conforms to the following morphologies. The Galliformes and other shrub- and ground-dwelling forms have a relatively long and robust coracoid shaft with an extremely short proximal coracoid neck and with extremely conspicuous and very projected proximoventral furcular articular facets. The most significant character on this coracoid is that the procoracoid is extremely short or absent, the distal end is rather unexpanded, and the angle of the distomedial margin and sterno-coracooidal process is extremely small or undeveloped. *Songlingornis* is vastly distinct from this morphology.

In the Falconiformes the coracoid shaft is relatively short and has rather expanded proximal and distal termini, and the proximal head has no medial curvature but is instead in direct alignment with the shaft. The furcular articular facets are extremely large and medially situated as oblique facets. Distally, the sterno-coracoidal process is extremely large although the distomedial angle is correspondingly very small. The presence of a coracoid foramen is a variable character, but when it is present, it is situated more distant from the shaft. The procoracoid is relatively well developed. *Songlingornis* shares characters with Falconiformes including the relatively short coracoid shaft, well developed sterno-coracoidal process, and well developed procoracoid, although the two are also extremely distinct in that the *Songlingornis* coracoid head is slightly medially curved, there is a relatively large angle of the distomedial margin, and the coracoid foramen is placed closer to the shaft.

The Passeriformes coracoid has a thinly elongated shaft and a particularly recurved proximal end with a medially hooked process extending from it. The coracoid fossa is extremely elongated, the distal sterno-coracoidal process is extremely weak, the posteromedial angle is relatively acute, and the procoracoid is well developed. This is quite distinct from *Songlingornis* in all aspects of its morphology.

Numerous characters are shared with the Anseriformes, including the relatively robust shaft, the slightly medially oblique proximal end, the well developed sterno-coracoidal process, and a relatively large distomedial angle. However, there are also numerous distinctions, because the Anseriformes have an undeveloped procoracoid, the coracoid fossa is elongated, a coracoid foramen is absent, and the sterno-coracoid process is relatively long and projected.

The numerous extant riparian wading taxa share characters including the robust coracoid shaft, expanded termini, presence of a coracoid foramen, and a relatively large sterno-coracoidal process. With the exception of the Ciconiiformes, the remaining wading forms have a well developed procoracoid. *Songlingornis* shares characters with them, including the robust shaft, well developed procoracoid, and an enlarged sterno-coracoidal process, although it is distinct in its particularly narrow coracoid fossa, the straight procoracoid, and the coracoid foramen being situated near the dorsal margin of the procoracoid. In general morphology the coracoid of *Songlingornis* resembles that of wading birds and thus there is a potential ancestral-descendant relationship.

Finally, the sternum of the Galliformes is typified by a long anterior process, two pairs of lateral processes, the medial process being the longest and most slender, and an extremely narrow posterior xiphial process associated with deep elongated reentrants. Falconiformes lack lateral processes, the posterior portion is expanded, as is the terminus, the posterior margin is relatively linear or slightly convex, the xiphial process is particularly short or very undeveloped, and there is a pair of medial fenestrae. Passeriformes have particularly well developed anterior processes which facilitate gastric ribs, the posterior sternum is very slightly reduced, posterolateral processes are short with shallow reentrants, and the posterior terminus is relatively flat, lacking a xiphial process. The sternum in Anseriformes is basically rectangular with a relatively well developed anterior process, lateral processes are not extremely elongated, v-shaped embayments are present, xiphial process is absent, and the posterior terminus extends as a bifurcation. Riparian and wading birds differ slightly by maintaining a thinly rectangular sternum with undeveloped anterior processes; lateral processes are shorter than the sternal body, long and narrow reentrants are present, the posterior terminus is either arcuate or relatively flat, and there is a short xiphial process. It is thereby evident that the sternum of *Songlingornis* differs distinctly from the Galliformes and other ground or shrub dwelling taxa. The presence of the medial fenestrae resembles the condition of Falconiformes although its remaining characters are quite distinct. Thus the sternum of *Songlingornis* is relatively distinct from the Galliformes and other ground dwelling or shrub habitat forms.

The distinction of the *Songlingornis* sternum from both the passeriform song birds but similarity to the Galliformes is quite evident. Firstly, the anterior process on the Passeriformes is particularly well developed and facilitates contact with the gastric ribs, medial fenestrae are absent, and the distal margin is relatively linear, suggesting a rather distant phylogenetic relationship. Compared to the anseriform diving birds, its morphology is quite distinct although they are both proportionately relatively large elements on the skeleton. *Songlingornis* posterolateral processes with their exaggerated termini are not only distinct from the Anseriformes but also from any known extant form. The presence of medial fenestrae is also distinct from the Anseriformes. Compared to wading and riparian habitat forms, there are also extreme distinctions in morphology, particularly posteriorly, but there is some resemblance in that they have very undeveloped anterior processes.

Songlingornis has a relatively well preserved scapula, coracoid, and furcula that are morphologically distinct from extant taxa that inhabit multiple habitats, although there are slight resemblances in the furcula and coracoid to riparian and wading forms. The morphology of extant multi-habitat forms is basically plesiomorphic, and has become modified through geologic time to represent environmental adaptations, although their adaptive plasticity is extremely limited due to the general absence of any major global climatic change after the Quaternary glacial stages, which represents a long stage of environmental stasis. An intensive fluctuation in a short interval of time, to the extent of partial environmental oscillation, would thereby force an extinction event among these species. The currently extinct or endangered avian species, as exemplified by the Chinese terrestrial crested ibis (*Nipponia nipon*), are not isolated phenomena. As the entire global climate is now under the influence of human activity, the destiny of species, including avian forms, is under the affects of human civilization, and thus it is the responsibility of the entire human race to preserve ecological equilibrium.

The morphological distinctions between *Songlingornis* and extant forms represent relatively plesiomorphic characters, although they are derived for the Early Cretaceous and represent individual habitat adaptations. It is unclear what these modifications represent, although they must lie in the adaptation for flight. The extremely unpronounced carina is as underived compared to Late Cretaceous forms as to extant forms and thus still represents a phase of strengthening pectoral musculature for increased velocity. The Early Cretaceous therefore appears to be a period of stasis in the evolutionary transformation between the Late Jurassic and Late Cretaceous and represents climatic conditions distinct from those today.

Songlingornis apomorphic characters suggest an incipient modification for a riparian habitat or wading behavior. The dentition is the most complete of all known Early Cretaceous taxa and thus it represents a primitive taxon. The morphology of the dentition resembles, among others, those of *Cathayornis, Largirostrisornis,* and *Archaeopteryx,* all of which maintain a large tooth root, a constricted crown base, and a low but acute apex that is slightly posteriorly curved, and thus they must all share a common ancestor.

Chapter 3. The significance and phylogenetic development of Chinese Mesozoic birds.

Mesozoic Avian biogeography.

To date, Chinese Early Cretaceous and older avian fossils are restricted to North China between north latitude 35° and 45°, where nine localities are represented. These consist of Tuanwang, Laiyang Co., Shandong Province; Senjitu, Fengning Co., Hebei Province; three localities in Liaoning Province including Boluochi and Meileyingzi, Chaoyang Co., and Shangyuan, Beipiao Co.; Chabu Sumu, Otog Qi Co., Inner Mongolia; Zhonghe Co., Ningxia Autonomous Region; and the Changma region of Gansu Province. The chronology of these localities spans Late Jurassic to Early Cretaceous. Currently described from these localities are 12 genera and 14 species, including the subclass Sauriurae with three orders, four families, eight genera, and ten species and the subclass Ornithurae with three orders, four families, four genera, and four species. The Late Jurassic produces two orders, two genera, and three species, the remaining are all Early Cretaceous. Distribution of specimens are as follows: Shandong and Ningxia only produce feather impressions. Hebei, Inner Mongolia, and Gansu produce only single diachronous specimens. The vast majority of specimens is produced from the Chaoyang and Beipiao regions of Liaoning, the Chaoyang region representing only Early Cretaceous specimens and the Beipiao only Late Jurassic.

The only other Late Jurassic site producing fossil birds is the Bavarian region of Germany, but additional Early Cretaceous sites are relatively numerous, in Asia represented in Mongolia and in Europe represented in Spain, Rumania, and Russia, while an additional occurrence lies in Australia. But with the exception of the Spanish specimens, the remaining specimens are all fragmentary.

The Mesozoic birds of China display a strong provincialism and distinct evolutionary stages compared to contemporaneous taxa from other regions of the world. The Late Jurassic *Confuciusornis* is differs from *Archaeopteryx* by its possession of a keratinous beak replacing the dentition, its humerus maintains a pneumatocoel, and its sternum is relatively large and plate-shaped. *Liaoningornis* cannot be compared to *Archaeopteryx,* because it is the earliest member of the Ornithurae. Several Early Cretaceous Chinese forms compare to the major taxa from Spain such as *Noguerornis, Concornis,* and *Iberomesornis.* These Chinese taxa include *Cathayornis, Boluochia,* and *Cuspirorstrisornis,* all representing members of the subclass Enantiornithes. However, there are also several derived Ornithurae in China including *Gansus, Chaoyangia,* and *Songlingornis.* Thus the Chinese avian fauna from the Late Jurassic to Early Cretaceous is distinctly autochthonous.

Among the Enantiornithes, the Chinese forms are extremely distinct from contemporaneous forms in the Western Hemisphere, as exemplified by the tarsometatarsus and phalangeal morphology of *Sinornis* and *Boluochia,* which resemble several extant raptors, and thus may represent incipient predatory behavior. On *Cuspirostrisornis* and other genera, the relatively elongated and acute beak associated with numerous teeth indicates that although they may be adapted to a perching habitat they perhaps used ground feeding behavior like the short skulled forms such as *Cathayornis.* Moreover, they co-occur with more primitive taxa such as

Cathayornis caudatus and *Longchengornis,* which retain a tail. Nowhere on earth is there such a diversity and complexity of evolutionary levels of fossil birds as in East Asia.

Avian biostratigraphy.

The chronology of Chinese Mesozoic birds is globally unique because it includes numerous stratigraphic levels, all representing terrestrial sediments. The stratigraphic sequence is illustrated in Table 18:

Table 18. Correlation chart of Chinese Mesozoic avian localities.

		Formation	Lithology	Locality	Taxa
Cretaceous	Aptian	Maodongshan Fm.	Gray mudstones	Dongxin, Ningxia	Feather impressions
	Berremian	Xiagou Fm.	Gray-black mudstones	Yumen, Gansu	*Gansus*
	Hauterivian	Yijinhuoluo Fm.	Brown mudstones	Otog Qi Inner Mongolia	*Otogornis*
	Berriasian	Jiufotang Fm.	Blue-gray mudstones	Chaoyang, Liaoning	*Sinornis, Cathayornis, Boluochia, Chaoyangia, Cuspirorstrisornis, Largirostrornis, Songlingornis*
Jurassic	Tithonian	Laiyang Fm.	Gray-brown shales	Laiyang, Shandong	Feather impression
		Yixian Fm.	Gray mudstones	Beipiao, Liaoning Fengning, Hebei	*Confuciusornis, Liaoningornis*

With regard to the age of the Yixian Fm., prior to the 1980's the general consensus was that it represented the Late Jurassic. In the 1980's controversy regarding this age assignment erupted, resulting in a revised consensus among a large portion of geologists and paleontologists. Jin (1996) recognized the terrestrial Jurassic-Cretaceous boundary in the lower member of the Yixian Fm. based upon paleontological data and stratigraphic correlations. Zhao (1985) derived a 146-147 Ma date in the formation based upon potassium-argon dating of biotites. Li et al. (1995) believed the age to be Late Jurassic based upon a symmetrodont mammal excavated from the same locality as *Confuciusornis.* Wang (1990) correlated the formation to the Tithonian Stage of the Late Jurassic based upon multiple paleontological phyla. This text regards the Yixian Fm. as Late Jurassic based upon the evolutionary level of *Confuciusornis* compared to *Archaeopteryx,* though the former genus may be slightly younger.

The influence of two events upon avian evolution and radiation.

After the publication of Charles Darwin's Origin of Species (1859), the concept of natural selection dominated the realms of Biology and Geology for over one hundred years. The core of Darwin's theory lies in individual biotic elements systematically passing through stages of superiority and inferiority, revolving its genetic components toward a higher degree, while becoming modified from a simple to more complex element. The concept of natural stasis indicates that within the process of biotic evolution it is impossible for large or sudden modifications to take place, as biotic development can only proceed through extremely short and slow intervals. In the past several decades abundant new data have been provided from the fields of astronomy, astronavigation, geophysics, and geochemistry, but particular advancements have been made in biological evolution. It is not possible here to conduct a review of all the theories and schools of thought, but merely to conduct an abbreviated introduction to the discoveries and research recently undertaken in the Mesozoic of North China.

The preceding text is an introduction to fossil birds from the Late Jurassic to Early Cretaceous of China that have been discovered only since 1984 from six provinces in at least four stratigraphic units. These extremely rare archaic birds are recovered most notably from the Early Cretaceous of Chaoyang, Liaoning, and the Late Jurassic of Beipiao, Liaoning. Several tens of specimens, which have not been subjected to extensive fluvial transportation prior to burial, are particularly concentrated within several stratigraphic units less than six meters thick and less than 100 square meters in area. This is a phenomenon rarely observed in the field of vertebrate paleontology within sediments as archaic as this, with the exception of fish beds. From the perspective of geologic time and quantity of specimens, the two localities of the Late Jurassic Yixian Fm. at Beipiao and the Early Cretaceous Jiufotang Fm. at Chaoyang represent extremely short intervals of extremely distinct evolutionary levels, one of which is particularly expressed by the avian characteristics at the base of the Yixian Fm. that have only been revealed in the past two years. In 1994, only three specimens of *Confuciusornis* and several isolated feather impressions were recovered. From that time to 1996, specimens of *Confuciusornis* in paleontological repositories and those that have filtered to private collectors are estimated to amount to nearly 100, with the vast majority representing relatively complete skeletons. Preliminary research upon the avifauna indicates that it is relatively complex, for as stated previously, not only are there abundant primitive forms such as *Confuciusornis*, which is comparable to *Archaeopteryx*, but there are derived taxa such as *Liaoningornis* that represent the oldest member of the Ornithurae, or the ancestor of modern birds. Additional specimens currently under study will result in even more abundant new scientific literature concerning the genesis of the second Jurassic avifauna known to the world and how it subsequently evolved.

The Beipiao and Chaoyang faunas constitute new members of the renowned East Asian Late Jurassic to Early Cretaceous Jehol Fauna, which has an extensive geographic distribution extending from the south at the Dabieshan-Qinling mountain ranges, north to Inner Mongolia and the eastern Baikal region of Russia, while from the east at Shandong, Liaoning, and Jilin Provinces of China, it extends west to the Hexizoulang Corridor of Gansu Province.

The development or evolution of any biotic element, including birds, is dependent upon both intrinsic and extrinsic factors. Intrinsic factors depend on inherited mutations, whereas extrinsic factors depend on habitat. It is quite evident that the Late Jurassic *Confuciusornis* evolved quite rapidly with distinct autapomorphic characters to represent the singular basal stock of its lineage, although the genesis of its lineage predated this genus. In the late Middle Jurassic (~152 Ma), North China and its neighboring regions were subjected to a phase of aridification (this climate was not conducive to biotic genesis or development and represented a period of relative stasis). Subsequently, in the Late Jurassic, the climate gradually rebounded to a more tropical regime which generated numerous lacustrine bodies to promote initial development and proliferation of nearly every order of plant, providing excellent environmental conditions for the development of faunas. Primarily, there existed invertebrates such as ostracods and insects which later become more prolific in association with fish, amphibians, reptiles, birds and mammals, representing a magnificent period of history in biotic evolution. Every class of vertebrates developed and radiated within its environment to attempt to dominate its own habitat.

There is an extensive set of geologic data that indicates that North China was subjected to extremely frequent episodes of orogenic and igneous activity during the Late Jurassic. At the *Confuciusornis* locality of Jianshangou there are several levels of mudstones interbedded with igneous rocks. In addition, both overlying and underlying the *Confuciusornis* beds are sequences of one cm thick mudstones and limestones which appear to represent cyclothems. Additional contemporaneous volcanic events are represented by relatively thick pyroclastic units associated with regional orogenic activity represented by faulting and deformation, suggesting contemporaneous earth tremors. The *Confuciusornis* fauna evolved rapidly and radiated within this turbulent but favorable environment.

The taphonomic conditions of this fauna, however. are quite distinct from those of *Archaeopteryx,* which is found in sediments representing a marine saline lacustrine body and actually represents an “allochthonous” taphonomic condition as opposed to an “autochthonous” condition. The presence of *Archaeopteryx* in its depositional setting was due to either being the object of predation or accidentally falling into the saline lake from the surrounding arboreal habitats, and consequently there is no fixed pattern regarding its taphonomic conditions. A comparison of the two basically contemporaneous paleoenvironments indicates that the preservation of the *Confuciusornis* fauna was possibly the result of environmental fluctuation which provoked abrupt genetic mutation. Consequently, there suddenly arose a new regional fauna characterized by *Confuciusornis* which differed distinctly from the single taxon *Archaeopteryx* fauna of Germany. It may be confidently assumed that the ancestor to *Confuciusornis* resides in the underlying terrestrial sediments of the lower Yixian Fm. which would also represent the genuine ancestor to Aves.

It is worthy of note that the East Asian Late Jurassic avian fauna with *Confuciusornis* is represented by at least two stratigraphic positions. Only two specimens of *Confuciusornis,* representing the type and the specimen described in this text, are produced from the most basal units of the Yixian Fm. at Beipiao. Overlying this horizon is an approximately one meter thick unit of mudstone that is currently producing a large quantity of *Confuciusornis* specimens. The specimen described in this text is the largest individual of the genus known to date. Although the distance between the two productive stratigraphic levels is extremely short, it is evident that evolution is occurring through a radical stage of radiation as represented by the occurrence of *Liaoningornis* in the upper unit.

During the Early Cretaceous deposition of the Jiufotang Fm., environmental conditions altered with a reduction of volcanic activity, although intense orogenesis continued. The locality producing *Chaoyangia* and *Boluochia* displays taphonomic conditions that are distinct from the underlying Yixian Fm., with the presence of multiple taxa that perhaps represent residual forms from the Late Jurassic. Preservation of specimens in the Yixian Fm. is extremely good, as represented by skeletons of Mammalia, Aves, Amphibia, and Pisces, which are osteologically exceptionally well-preserved as is feather microstructure. However, specimens from the Boluochi region, including Aves and Pisces, are predominantly preserved as impressions, whether they are untransported complete skeletons or disarticulated transported specimens. The preservation is similar among both avian and fish specimens; skeletal elements are extremely compressed or paper thin. One locality in the Boluochi region represents less than 50 square meters where several dozen avian specimens have been produced. Resembling the condition of the Yixian Fm., there are two productive stratigraphic levels, the lower of which consists of a thick gray-white mudstone and which produces the vast majority of the avian specimens. Approximately 50 cm above this unit is a dark gray relatively thinly laminated mudstone which first produced an avian specimen in 1994; in 1995 a second specimen was recovered. Although its productivity does not equal that of the lower unit, preservation is similar. Feather impressions are not preserved in the Boluochi region.

Boluochi produces seven genera and eight species among which are the two species of Ornithurae (*Chaoyangia beishanensis* and *Songlingornis linghensis*), both of which are intimately related to extant forms. The former possesses uncinate processes on its ribs and the latter not only possesses a well developed carina on its sternum, it also maintains posteromedial sternum fenestrae, and a furcula and sternum which closely resemble the condition of shore birds. The Boluochi Sauriurae taxa are also relatively distinct. *Boluochia* displays incipient modifications for predation; *Cuspirostrisornis* and *Largirostrornis* have become modified for riparian habitats; and *Cathayornis* is very possibly a small songbird. From the perspective of evolutionary rank and morphology, the Early Cretaceous birds of Chaoyang can be compared to those from contemporaneous localities such as Spain, in the derived morphology of the forelimb and sternum; also, the fifth metatarsal has become lost, but the pelvic girdles retain their primitive morphology. As the general characteristics of the Chinese Early Cretaceous birds are not entirely distinct, they may reflect contemporaneous evolutionary conditions in the Old World or the possibility of interchange between eastern and western Eurasia. All avian taxa were evolving a relatively strong adaptation toward flight, coordinated with a reduction in body size for increased habitat adaptation.

The Chaoyang region is quite distinct not only from the Late Jurassic locality of Beipiao but also from other Early Cretaceous faunas; most noticeable distinction lies in the evolutionary level of the fauna. In addition to the close geographic proximity (less than 100 km separates the Late Jurassic and Early Cretaceous localities), the chronologic proximity is also rather close. Faunal complexions, however are clearly distinct. The Late Jurassic taxa are either edentulous or have their dentition in a state of reduction with a cartilaginous beak replacing it. But cranial morphology is still extremely primitive because the cranial elements are both thick and unfused. The Early Cretaceous taxa all maintain a dentition but the frontals are all extremely derived.

The Chinese Early Jurassic taxa maintain forelimbs that resemble *Archaeopteryx*, with carpals, metacarpals, and digits all unfused. The first metacarpal is still extremely prominent, and digits I, II, and III are all still independent with particularly enlarged unguals, particularly that of digit I which greatly exceeds the length of the first phalanx. Using *Cathayornis* as a basis for Early Cretaceous comparison, it may be noted that the forelimb is more derived: a portion of the carpometacarpus is fused, McI is basically reduced, digits I and III are also in a state of reduction, the manual unguals are extremely small and have a low degree of curvature, the fundamental wing morphology is present, and the walls of the long bones have become thinned, representing adaptations for flight. Although the sterna on the Late Jurassic taxa are relatively large, the morphology is still primitive because they all lack a carina. The sterna on the Early Cretaceous taxa are all more derived because they possess a carina and well developed posterior processes. Other portions of the pectoral girdle on the Chinese Late Jurassic taxa also resemble *Archaeopteryx* in their extreme primitive condition: they have extremely short and robust furcula and an unexpanded distal coracoid, whereas the pectoral girdles of Early Cretaceous taxa are more derived and functionally adapted to their forelimbs. These have an enlarged furcula with elongated furcular branches, the termini of the coracoid approach extant morphology by being extremely expanded, the shaft has become thinned, and there is a more fortified contact with the sternum.

The pelvic elements of the Late Jurassic forms are all relatively small and the distal pubes are fused, closely resembling the reptilian condition. Although their counterparts among the Early Cretaceous taxa are still unfused, they have become rather enlarged and basically lie posteriorly oblique, the ilia and sacral vertebrae have developed a more intimate relationship, and the distal pubes have initiated separation. The Late Jurassic forms retain five metatarsals but in the Early

Cretaceous, MtV has become lost. Furthermore, with the exception of *Liaoningornis* the Late Jurassic taxa are all larger, representing the plesiomorphic condition.

Worthy of note here is that the latest Jurassic avian specimen from Hebei Province is at an evolutionary level between *Confuciusornis* and *Cathayornis.*

The simplified comparisons undertaken above display the extremely distinct character states represented in the avian taxa from the chronologically distinct Yixian and Jiufotang formations. From the perspective of the entire faunal assemblages, the traditional concept of gradualism cannot be applied to their condition and it is only the concept of saltationism through genetic transmission that sufficiently explains their contrasting faunas. However, total reliance upon abrupt mutation is also not adequate for the explanation of the co-existence of the primitive *Confuciusornis* with the derived *Liaoningornis.* Furthermore, the presence of the intermediate *Jibeinia* is reliable data indicating that the concept of gradualism is viable. Consequently, in the preceding description of specimens, it is proposed that evolution occurs through an extremely complicated systematic process of biotic genesis, development, modification, and radiation. Current disciplines including geophysics, geochemistry, astronomy, physics, and particularly biology indicates catastrophism is a significant natural factor. But it is impossible to apply a single theory or hypothesis to explain biotic origin and evolution. Therefore, the fossil avian specimens currently produced in China document both evolutionary models of gradualism and saltationism. Different evolutionary levels are illustrated between various taxa within the same fauna from the same locality in both the Yixian and Jiufotang formations.

To date, there has been no discussion of the radiation of Late Jurassic birds due to the sole presence of the most primitive genus *Archaeopteryx.* Most recently, a large collection of specimens has been made from the *Confuciusornis* locality, and the vast majority of specimens represent or approach the evolutionary level of that genus, although there are morphological distinctions, particularly in the large variation of sternum morphology. Extant variation of sternum morphology coincides with different habitat adaptations. Thus it may be deduced that the Late Jurassic did not represent the genesis of the class Aves but instead probably represents an initial radiation after its divergence from the Reptilian stem group. During this period the avian condition was still not adapted to genuine flight, and although the forelimb possessed feathers, it still did not form a legitimate wing, and the primitive birds mosstly relied upon their sharp talons for terrestrial locomotion and climbing in arboreal habitats. This conclusion is the major contribution to the ornithological world from the study of the Mesozoic birds of China. In addition, these specimens provide further data for the origin and evolution of the class.

The problem concerning the vast majority of specimens preserved as impressions in the Boluochi quarries is hereby addressed. At the outset of this chapter, the Late Jurassic to Early Cretaceous climate was described as temperate and mesic, providing suitable conditions for the rapid origin and evolution of species. Concurrently, this period witnessed frequent orogenic and volcanic activity that created numerous conditions for extinction. The principal cause of mortality in the Late Jurassic Yixian Fm. was volcanic activity because the related geological data indicates moderately silicic volcanic flows in the Late Mesozoic of western Liaoning Province. The corresponding ash and toxic airborne particles may have created an umbrella resulting in atmospheric cooling, acid rain, and moderately toxic atmospheric conditions that could have led to mass mortality and extinction. In this manner, the Late Jurassic volcanic activity had a double affect: As stated previously, this activity provoked speciation and morphological development, as exemplified by the contemporaneous ostracods and insects, and thus the avian speciation is merely an example of the general trend. But in the Jiufotang Fm. of the Boluochi region the physical mechanisms controlling sedimentation, speciation, biological evolution, and extinction are more complex, because volcanic activity during this period is diminished, although orogenic activity is more dynamic. At the Boluochi locality there is a five meter-thick sedimentary package which lacks any trace of igneous components, although lithologic deformation is quite distinct. It is possible that the intense orogenic activity created partial crustal fracturing which in effect released extensive quantities of high temperature gas, causing ambient temperature fluctuation and the infusion of toxic chemical agents into the atmosphere which resulted in acid rain and a fluctuation of pH levels in the lacustrine bodies, in addition to affecting the lake levels themselves, thus creating mass mortality among the fauna dependent upon the lakes.

Additionally, geologic data indicates that in Hebei Province during the period represented by the early Late Jurassic Dabeizhou Fm. to the middle Early Cretaceous Fuxin Fm. there were frequent geomagnetic reversals. Therefore, some workers have hypothesized that during these periods of polarity reversals there was a weakening of the geomagnetic shield, allowing greater penetration of cosmic rays which subsequently provoked the mutation of genes, rapidly increasing biotic extinction and speciation. Furthermore, in recent years there are workers who have proposed other extra terrestrial agents of mass extinction such as the eruption of solar flares resulting in a sudden increase in ambient temperature to the point of conflagration, or perhaps toxins released by passing comets. In conclusion, the climates of the Late Jurassic Yixian Fm. and the Early Cretaceous Jiufotang Fm. express both continuity and discontinuity but within this time period there also occurred minor events which created the exceptional taphonomic conditions in the Boluochi region. To date, another locality resembling these conditions has not been found and as yet not a single fossil feather has been recovered at Boluochi which it is believed here to be due to the aquatic chemistry of the original lacustrine body.

The significance of Chinese Mesozoic birds in the systematic evolution of the class Aves.

I. The two Late Jurassic and Early Cretaceous avian faunas from China represent the most abundant and diverse Mesozoic assemblages of the class in the world today. The *Confuciusornis* Fauna confirms that the Late Jurassic is not the period of origin of the class Aves and that *Archaeopteryx* is not the common ancestor. The origin of the class and its common ancestor arethus determined to lie in an earlier stage. A large quantity of *Confuciusornis* and *Liaoningornis* specimens is currently under study and represents irrefutable evidence that the origin of the class predates the Late Jurassic and could lie in the Middle Jurassic to Early Triassic. There is a great possibility that this ancestor resides in China.

II. The two avian faunas provide evidence that within the process of biotic evolution gradualism and saltationism are co-occurring phenomena. Different evolutionary ranks occur contemporaneously and within the same fauna. Derived taxa constitute a minority, or are rare, but represent the fundamental lineage from which a further derived phase is generated. Taxa such as these are represented by the Late Jurassic *Liaoningornis* and the Early Cretaceous *Chaoyangia* and *Songlingornis.*

III. Two major events occurred within the origin and early evolution of the class: The relatively late diversification and radiation in the Late Jurassic, and diversity and radiation of even larger scope in the Early Cretaceous. These two events were the foundation for avian evolution.

IV. The Chinese paleontological data confirms that the origin or co-occurrence of the two suborders Sauriurae and Ornithurae was present at least in the Late Jurassic.

V. The earlier an avian taxon occurs in geologic history the more autochthonous characteristics are present. This suggests a polyphyletic origin for the class.

VI. Avian-Dinosaurian relationships are not as intimate as some workers believe. The class Aves is not a descendent lineage of the Dinosauria but has a closer relationship to more primitive members of the Archosauria.

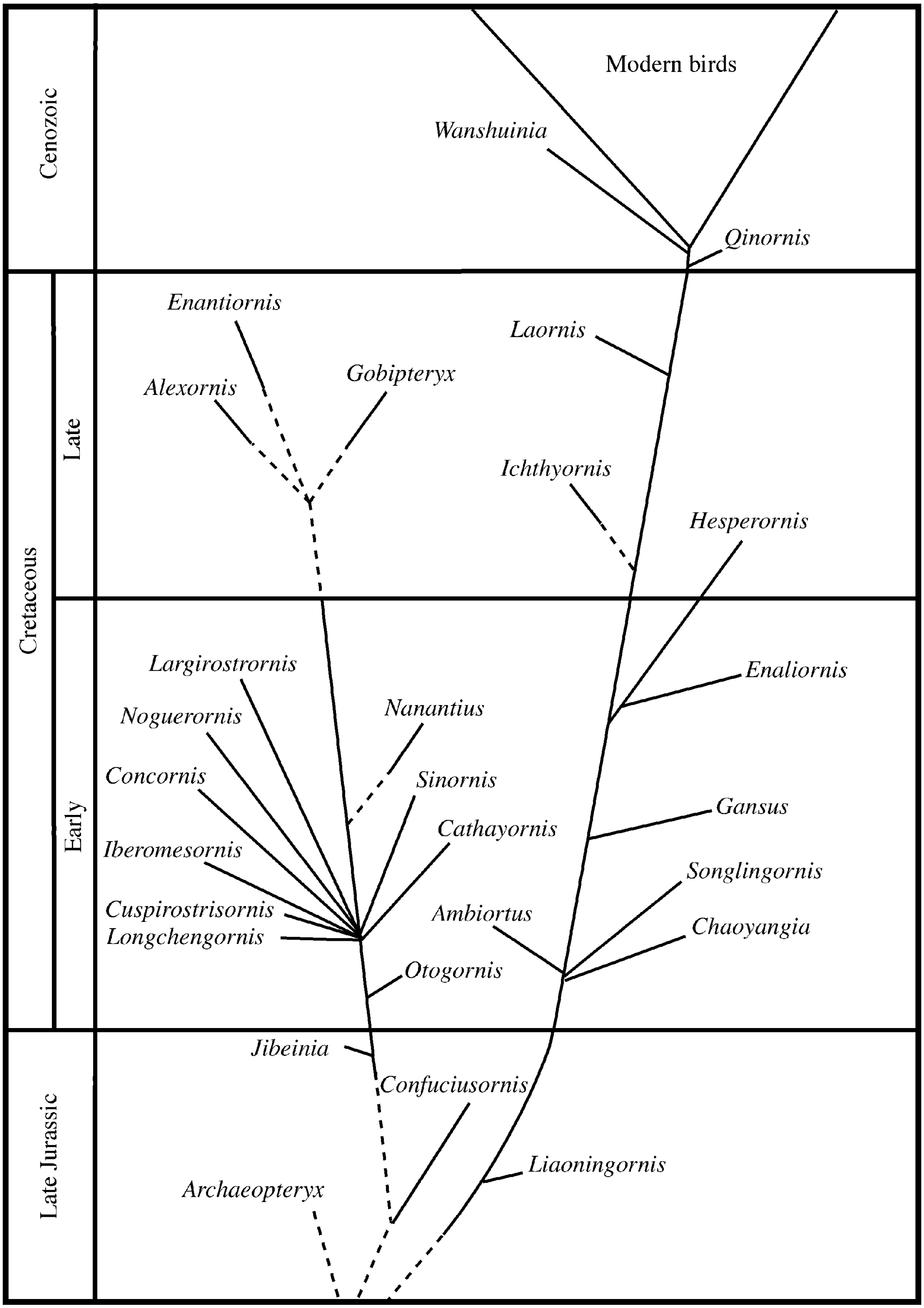

Figure 33. Early avian systematic evolution.

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