ANATOMY AND SYSTEMATICS OF THE CONFUCIUSORNITHIDAE (THEROPODA: AVES) FROM THE LATE MESOZOIC OF NORTHEASTERN CHINA

LUIS M. CHIAPPE

Research Associate, Department of Ornithology
American Museum of Natural History
Current address: Associate Curator, Vertebrate Paleontology
Natural History Museum of Los Angeles County
900 Exposition Boulevard, Los Angeles, CA 90007

JI SHU'AN

National Geological Museum of China
Yangrou Hutong 15, Xisi, 100034 Beijing, China

JI QIANG

National Geological Museum of China
Yangrou Hutong 15, Xisi, 100034 Beijing, China

MARK A. NORELL

Chairman
Division of Paleontology
American Museum of Natural History

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ABSTRACT

The osteology and plumage of *Confuciusornis sanctus* and *Changchengornis hengdaoziensis* from the Chaomidianzi Formation (previously referred to as the lower section of the Yixian Formation) of western Liaoning Province (China) are described in detail.

Confuciusornis sanctus and *Changchengornis hengdaoziensis* have toothless, beaked skulls (the tomial crest is straight in the former species and strongly curved in the latter) and retain the dorsal portion of the nasal process of the maxilla. The skull of *Confuciusornis sanctus* is of typical diapsid plan. It possesses a triradiate postorbital that with the squamosal forms a complete supratemporal arcade. Furthermore, a robust jugal–postorbital contact completely separates the infratemporal fenestra from the orbit. Although the postorbital region is not preserved in *Changchengornis hengdaoziensis*, it likely resembles that of *Confuciusornis sanctus*.

Both species have abbreviated tails with long pygostyles, not the long, bony tail originally reconstructed in *Confuciusornis sanctus*. Scapulae and coracoids are fused to form scapulocoracoids. The coracoids are strutlike but much shorter than the scapulae. The furculae are robust and boomerang shaped. The sterna are long and nearly flat. A complete basket of gastralia follows the sternum caudally. The wing elements are short, and proportions among individual bones are primitive in that the hand is longer than either the humerus or the ulna and the ulna is shorter than the humerus. The pelvis is opisthopubic. The postacetabular wing of the ilium is much shorter than the preacetabular wing. Differences in plumage, namely the presence or absence of two very long tail feathers, are observed among several well-preserved specimens of *Confuciusornis sanctus*. This difference is likely the expression of sexual dimorphism, although other biological attributes known for extant populations (e.g., differential molting, correlation between sexual maturity and ornamental plumage) indicate that alternative explanations may also account for the observed plumage variation among specimens of *Confuciusornis sanctus*.

Given the latest Jurassic–earliest Cretaceous age of the Chaomidianzi Formation, *Confuciusornis sanctus* and *Changchengornis hengdaoziensis* are surely among the oldest known birds after the Early Tithonian *Archaeopteryx lithographica*. *Confuciusornis sanctus* and *Changchengornis hengdaoziensis* thus furnish the earliest record of beaked birds.

The fully diapsid skull of *Confuciusornis sanctus*, and presumably of *Changchengornis hengdaoziensis*, and the absence of a bending zone on the base of the snout suggest that earlier interpretations of the skull of *Confuciusornis sanctus* as prokinetic are incorrect. *Confuciusornis sanctus* probably had very limited cranial kinetic capabilities, if any. Optimization of the postorbital–jugal contact, a character intimately correlated with intracranial kinesis, in a phylogeny of basal avians indicates that the essentially akinetic condition of the skull of *Confuciusornis sanctus* is a reversal derived from forms possessing kinetic properties.

Recent recognition of two additional species of *Confuciusornis*—*Confuciusornis chuonzhous* and *Confuciusornis suniae*—are based on anatomical misinterpretations. Thus, *Confuciusornis suniae* and *Confuciusornis chuonzhous* are regarded as junior synonyms of *Confuciusornis sanctus*. *Confuciusornis sanctus* is the sister-taxon of *Changchengornis hengdaoziensis*, and both are placed within the Confuciusornithidae. Some of the synapomorphies supporting this grouping include the presence of edentolous jaws, a rostrally forked mandibular symphysis, a reduced claw of manual digit II, and a V-shaped caudal margin of the sternum. The Confuciusornithidae is considered to be the sister-group of a clade composed of the Enantiornithomorpha and the Ornithuromorpha. This phylogenetic interpretation is far more parsimonious than previous systematic hypotheses placing the Confuciusornithidae as either within the Enantiornithes or as its sister-group.

Purported climbing specializations of *Confuciusornis sanctus* are evaluated in light of the available anatomical evidence. We conclude that both *Confuciusornis sanctus* and *Changchengornis hengdaoziensis* were ill suited for tree climbing. The foot of *Changchengornis hengdaoziensis*, however, suggests a greater grasping ability than that of *Confuciusornis sanctus*. It is argued that both *Confuciusornis sanctus* and *Changchengornis hengdaoziensis* were able to fly and take off from the ground.

The remarkable concentration of specimens of *Confuciusornis sanctus* from a relatively small quarry near the village of Sihetun (Liaoning Province) suggests several events of mass mortality and, perhaps, a gregarious behavior.

INTRODUCTION

The Late Jurassic–Early Cretaceous deposits of western Liaoning Province (northeastern China) are famous for the extraordinary preservation of fossils (e.g., Zhou Z.-H. et al., 1992; Hou et al., 1995b, c, 1996; Ji Q. and Ji S.-A., 1996, 1997a, b; Hou, 1997; Chen et al., 1998; Ji Q. et al., 1998). These deposits have furnished one of the most important, and certainly the most abundant, collections of Mesozoic birds. Taxa discovered in these deposits include *Sinornis santensis* (Sereno and Rao, 1992), *Cathayornis yandica* (Zhou Z.-H. et al., 1992), *Chaoyangia beishanensis* (Hou and Zhang, 1993), *Boluochia zhengi* (Zhou Z.-H., 1995a), *Liaoningornis longiditris* (Hou et al., 1996), *Liaoxiornis delicatus* (Hou and Chen, 1999), *Changchengornis hengdaoziensis* (Ji Q. et al., 1999), and *Confuciusornis sanctus* (Hou et al., 1995b, c).

Confuciusornis sanctus from the Chaomidianzi Formation (previously referred to as the lower section of the Yixian Formation) is one of the oldest known birds. Hundreds of nearly complete specimens, including juveniles and fully grown individuals, often preserved with full plumage, have been recovered from the Chaomidianzi beds of the Sihetun-Jianshangou area (fig. 1). Although many of these specimens have unfortunately been smuggled out of China and sold on the international commercial market, many others have been deposited in Chinese and foreign institutions. This high number of extraordinarily preserved specimens affords an unprecedented opportunity to investigate intraspecific variation, allometric growth, and sexual dimorphism in one of the earliest and most primitive lineages of birds. Although several recent papers have dealt with *Confuciusornis sanctus*, its anatomy has only been cursorily described (e.g., Hou et al., 1995b, c, 1996; Hou, 1995; Peters, 1996; Guan et al., 1997; Viohl, 1997; Martin et al., 1998; Zhou Z.-H. and Hou, 1998) and its phylogenetic relationships only superficially explored (Hou et al., 1995b, c, 1996; Chiappe, 1997a). Here we provide full anatomical descriptions of several specimens of *Confuciusornis sanctus* and of its close relative, *Changchengornis hengdaoziensis* (Ji Q. et

Fig. 1.   Geographic location of the area of Sihetun–Jianshangou, Province of Liaoning, northeastern China.

al., 1999). Additionally, we present a phylogenetic discussion of the interrelationships of these species to other basal birds.

The anatomical terminology and orientation of skeletal elements used here follows the one proposed by the *Nomina Anatomica Avium* of Baumel et al. (1993). However, for osteological features, Latin terms are replaced by their English equivalents.

Anatomical Abbreviations

ace	acetabulum
ang	angular
anf	antorbital fenestra
ce	centra of synsacrum
cmf	caudal mandibular fenestra
cv	caudal vertebrae
cve	cervical vertebrae
co	coracoid
d	dentary
dc	dorsal condyle of humerus
dlp	dorsolateral process of last free caudal vertebra
dlr	dorsolateral ridges of synsacrum
dpc	deltopectoral crest of humerus
ept	ectopterygoid
enr	external nares
f	frontal
fem	femur

fib	fibula
fo	fossa on deltopectoral crest of humerus
fur	furcula
gas	gastralia
hum	humerus
hyo	hyoid
idp	dorsal process of ischium
ili	ilium
isc	ischium
itf	infratemporal fenestra
j	jugal
lac	lacrimal
lcv	last free caudal vertebrae
lec	lateral excavations of thoracic centra
mcI-III	metacarpals I-III
mtV	metatarsal V
mx	maxilla
mxf	maxillary fenestra
n	nasal
o	orbit
ost	orbital septum
p	parietal
pa	palpebral
pal	palatine
par	prearticular
ph1I	phalanx 1 of digit I
ph1II	phalanx 1 of digit II
ph2II	phalanx 2 of digit II
ph2III	phalanx 2 of digit III
ph3II	phalanx 3 of digit II
ph3III	phalanx 3 of digit III
pmx	premaxilla
po	postorbital
pt	pterygoid
pub	pubis
py	pygostyle
q	quadrate

r	thoracic ribs
rad	radius
rdl	radiale
rmf	rostral mandibular fenestra
sa	surangular
sc	scapula
scl	sclerotic plates
sp	splenial
sq	squamosal
st	sternum
stc	sternal carina
stf	supratemporal fossa
syn	synsacrum
tdt	tubercle on distal tibiotarsus
tib	tibiotarsus
tmt	tarsometatarsus
tub	tubercle for insertion of *m. tibialis cranialis*
tv	thoracic vertebrae
uln	ulna
up	uncinate process
vc	ventral condyle of humerus
vep	ventral epicondyle of humerus
vr	ventral ribs
I-IV	manual or pedal digits

Institutional Abbreviations

BPV	Natural History Museum, Beijing (China)
GMV	National Geological Museum of China, Beijing (China)
JM	Jura-Museum, Eichstätt (Germany)
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing (China)
SMFAv	Forschungsinstitut Senckenberg, Frankfurt (Germany)

GEOLOGICAL SETTING

Chinese scientists have tended to regard the strata bearing *Confuciusornis sanctus* as the basal section of the Yixian Formation (e.g., Hou et al., 1995a, b, c; Wang et al., 1998). According to recent investigations, however, the beds bearing *Confuciusornis sanctus* should not be grouped into the Yixian Formation (Ji Q. et al., in press). The Jurassic–Cretaceous transitional deposits in the western part of Liaoning Province are better subdivided into three formations (in ascending order): the Chaomidianzi Forma-tion, the Yixian Formation, and the Jiufotang Formation. The newly established Chaomi-dianzi Formation has its type section at the village of Sihetun, approximately 25 km south of Beipiao City (Ji Q. et al., in press).

In the Sihetun–Jianshangou region and ad-jacent areas (figs. 1–3), the Chaomidianzi Formation uncomformably overlies the Mid-dle Jurassic Tuchengzi Formation and com-formably underlies the Yixian Formation. Three members can be recognized within the Chaomidianzi Formation (in ascending or-

Fig. 2. View of the main fossil quarry of the Chaomidianzi Formation near the village of Sihetun. Most specimens of *Confuciusornis sanctus* come from this quarry.

der): the Sihetun Member, the Jiulongsong Member, and the Hengdaozi Member.

The Sihetun Member consists mainly of yellow, thick-bedded conglomerates; grayish yellow and grayish green, median-bedded tuffaceous sandstones with pebbles; and grayish green, median- to thin-bedded tuffaceous sandstones and siltstones yielding theropod footprints and, more recently, the partial skeleton of a nonavian coelurosaur.

The Jiulongsong Member is lithologically composed of a series of grayish white, thin-bedded tuffs intercalated with tuffaceous shales and mudstones and containing a rich ensemble of plants (e.g., Filicophyta, Cycadicae, Ginkgoatae, Coniferae, and Angiospermae; Zhou Z.-Y., 1995), gastropods, bivalves, ostracods, conchostracans (e.g., *Eosestheria jinganshanensis*), insects, shrimps, fishes (e.g., *Peipiaosteus pani*, and *Lycoptera* spp.; Jin, 1996), pelobatid frogs

(e.g., *Liaobatrachus grabaui*; Ji S.-A. and Ji Q., 1998), turtles (e.g., *Manchurochelys* sp.), lizards (e.g., *Dalinghosaurus longidigitus*; Ji S.-A., 1998), pterosaurs, mammals (e.g., *Jeholodens jenkinsi*; Ji Q. et al., 1999), psittacosaurids (Ji S.-A. and Bo, 1998; Xu and Wang, 1998), and other dinosaurs such as *Sinosauropteryx prima* (Ji Q. and Ji S.-A., 1996), *Protarchaeopteryx robusta* (Ji Q. and Ji S.-A., 1997a), and *Caudipteryx zoui* (Ji Q. et al., 1998). Most specimens of *Confuciusornis sanctus* are also from this member. Because most of the fossils from this member have been collected by local farmers, their precise stratigraphic position within the Jiulongsong Member remains tentative (e.g., Wang et al., 1998; Zhou Z.-H. and Hou, 1998). According to our investigations and conversations with local farmers, the specimens of *Confuciusornis sanctus* occur in beds that are stratigraphically higher than those containing specimens of *Sinosauropteryx prima, Protarchaeopteryx robusta*, and *Caudipteryx zoui* (fig. 4). This interpretation, however, differs from that given by other authors (e.g., Chen et al., 1998; Wang et al., 1998), who identified the stratigraphic provenance of *Sinosauropteryx prima* as higher than the lower-most occurrence of *Confuciusornis sanctus* at the Sihetun section (fig. 5).

The Hengdaozi Member, the upper portion of the Chaomidianzi Formation, consists of grayish yellow and grayish green tuffaceous sandstones, siltstones, and silty mudstones. It is well developed and exposed in the village of Jianshangou (approximately 3 km northeast from the village of Sihetun; fig. 3), yielding fragmentary plant remains, a diverse insect fauna (e.g., Odonata, Phasmatodea, Mecoptera, Raphidioptera, Neuroptera, Diptera, Homoptera, and Orthoptera; Ren et al., 1997; Ren, 1998), conchostracans (e.g., *Eosestheria* spp.), fishes (e.g., *Peipiaosteus pani*; Jin, 1996), turtles (e.g., *Manchurochelys liaoxiensis*; Ji S.-A., 1995), pterosaurs (e.g., *Eosipterus yangi*; Ji S.-A. and Ji Q., 1997; Ji S.-A. et al., 1999), mammals (e.g., *Zhangheotherium quinquecuspidens*; Hu et al., 1997), and birds (e.g., *Confuciusornis sanctus* and *Changchengornis hengdaoziensis*).

There is still no consensus on the chronology of the sedimentary deposits bearing fossils of *Confuciusornis sanctus* and its as-

Fig. 3.   Fossil site of the holotype of *Changchengornis hengdaoziensis*. This quarry of the Chaomidianzi Formation is located near the village of Jianshangou. Some specimens of *Confuciusornis sanctus* have also been collected at this locality.

sociated biota (Smith et al., 1995; Chiappe, 1995a, in press a; Hou et al., 1995a, b, c, 1996; Jin, 1996; Ren et al., 1997). Early Cretaceous intrusive rocks are very common in the Sihetun-Jianshangou area, and the sedimentary tuff beds seem to be cut through, capped, disturbed, heated, and metamorphosed by intrusive basalts and andesites (Ren et al., 1997).

Samples from intrusive rocks from the Sihetun-Jianshangou area were collected by Jin et al. (1993), and radiometric analysis was used to date the Yixian Formation (in the broad sense, the Chaomidianzi and Yixian formations of this study) as Early Cretaceous. Smith et al. (1995) provided dates of approximately 122 million years B.P. for these intrusive volcanics, providing a minimum age for the fossil-bearing deposits.

Biostratigraphic correlations of the tuffaceous rocks of the Chaomidianzi Formation have given conflicting results. An Early Cretaceous age is generally supported based on the palynological association (Mao et al., 1990; Li and Liu, 1994). The endemic nature of the fish community yields no resolution other than the Late Jurassic–Early Cretaceous transition (Jin, 1996). This lack of resolution appears to be the same for the ostracod microfauna, which has been argued to be either Early Cretaceous or Late Jurassic age (Zhang, 1985). The occurrence of the ornithischian dinosaur *Psittacosaurus*, a common element of the Early Cretaceous dinosaur faunas from the Gobi Desert and other regions of Asia, has been used to claim such an age for the Chaomidianzi Formation (Xu and Wang, 1998), but the recent discovery of a long-tailed pterosaur—otherwise unknown for any Cretaceous site—supports an older, Late Jurassic age (Ji S.-A. et al., 1999). Furthermore, recent radiometric dates of a large number of samples of the tuffaceous sediments of the Chaomidianzi Formation also support its assignment to the latest Jurassic (Chen P.-J., Nanjing Geological Institute,
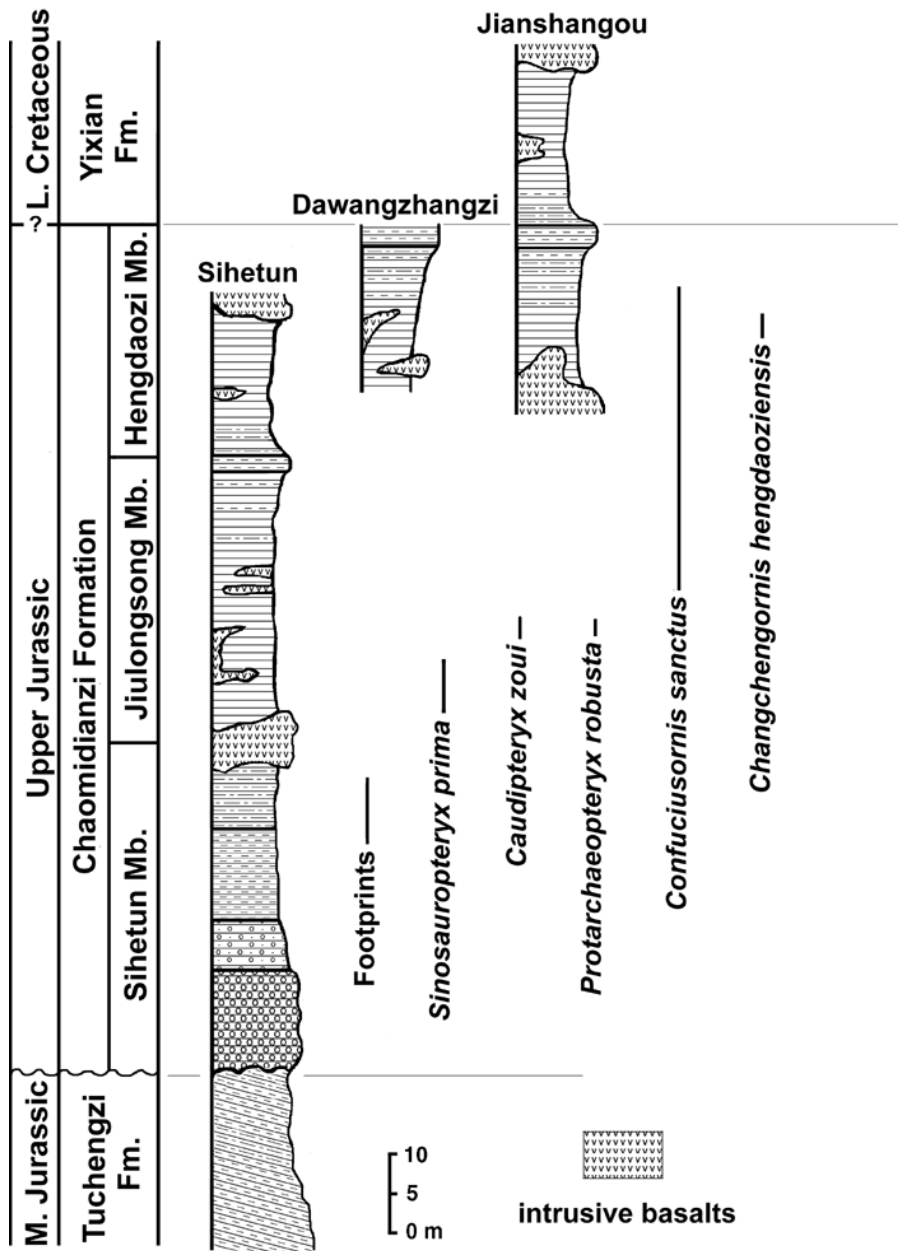
Fig. 4. Stratigraphic section and fossil horizons of the Chaomidianzi Formation; this section follows data by Ji Q. et al. (in press).

personal commun.), but other radiometric analyses of the tuffaceous beds indicate an Early Cretaceous age ($\sim$ 124 million years B.P.) (Swisher et al., 1999).

Sedimentological studies of the Chaomidianzi Formation (lower section of the Yix-ian Formation of other authors) indicate that these strata represent a transition from fluvial (Sihetun Member) to lacustrine facies (Jiu-longsong Member and lower section of Hengdaozi Member), followed by the grad-ual infilling of the lake system (Hengdaozi
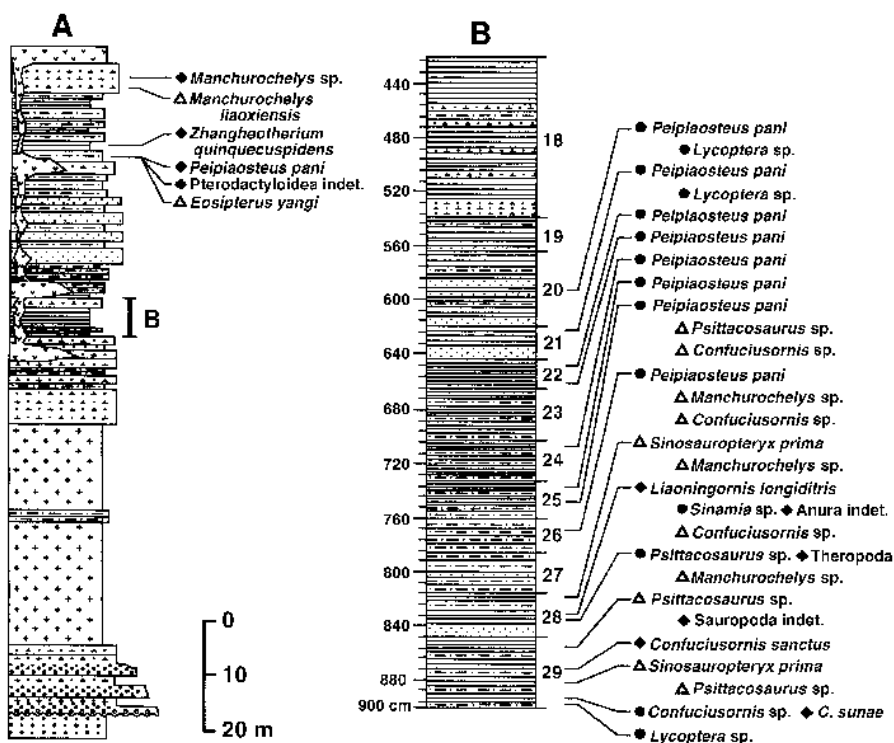
Fig. 5.   Stratigraphic section and fossil horizons of the Chaomidianzi Formation **(A)** as proposed by Wang et al. (1998). Symbols are as follows: ● fossils collected during Wang et al.'s excavation; ◆ fossils with "confirmed" horizons according to Wang et al.; and △ fossils with "investigated" horizons according to Wang et al. Figure modified from Wang et al. (1998). **(B)** detail of A.

Member). The fine lamination of many of the fossiliferous layers of the Sihetun and Hengdaozi members suggests that the lake was periodically large and deep. The abundance of tuffaceous sediments and intrusive volcanic rocks documents the influence of volcanic activity in the depositional sequence (Wang et al., 1998).

SYSTEMATIC PALEONTOLOGY

AVES LINNAEUS, 1758

CONFUCIUSORNITHIDAE HOU ET AL., 1995

DEFINITION: A node-based phylogenetic definition (see de Queiroz and Gauthier, 1992) is here applied to the Confuciusornithidae. This clade is defined as the common ancestor of *Confuciusornis sanctus* and *Changchengornis hengdaoziensis* plus all of this ancestor's descendants.

INCLUDED SPECIES: *Confuciusornis sanctus* (Hou et al., 1995b) and *Changchengornis hengdaoziensis* (Ji Q. et al., 1999) from the Chaomidianzi Formation of northeastern China.

DIAGNOSIS: Birds with toothless jaws; rostral end of the mandibular symphysis forked; distinct, round foramen (presumably the maxillary fenestra) pneumatizing the ascending ramus of the maxilla within antorbital cavity; deltopectoral crest of the humerus prominent and subquadrangular; metacarpal I not coosified to the semilunate-metacarpal II and III complex; proximal phalanx of manual digit III much shorter than remaining nonungual phalanges; claw of manual digit II much smaller than the claws of digits I and III; and caudal end of the sternum V shaped.

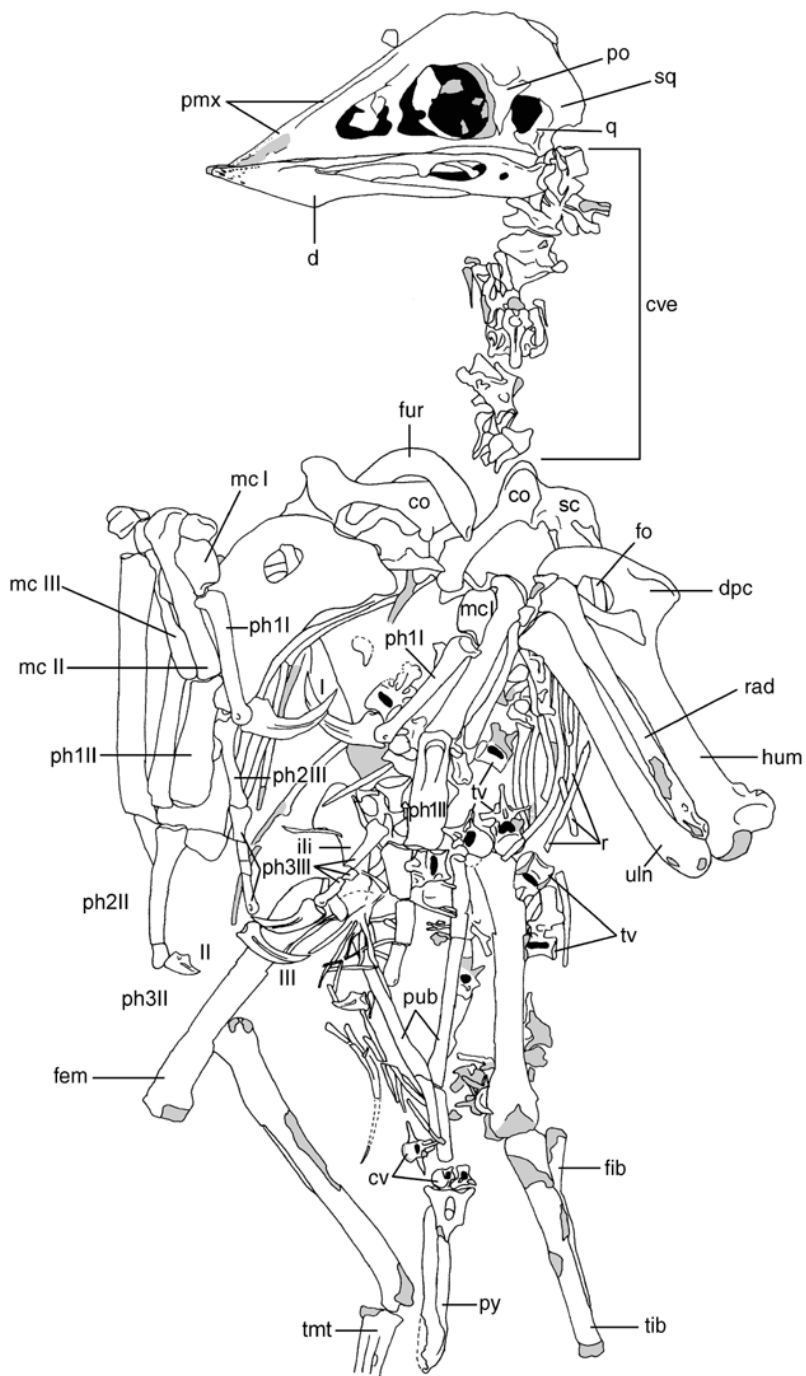Fig. 6. *Confuciusornis sanctus* (GMV-2132). See Anatomical Abbreviations for definition of labels.

Fig. 6. Continued.

2 cm

Fig. 7.   *Confuciusornis sanctus* (GMV-2133). See Anatomical Abbreviations for definition of labels.
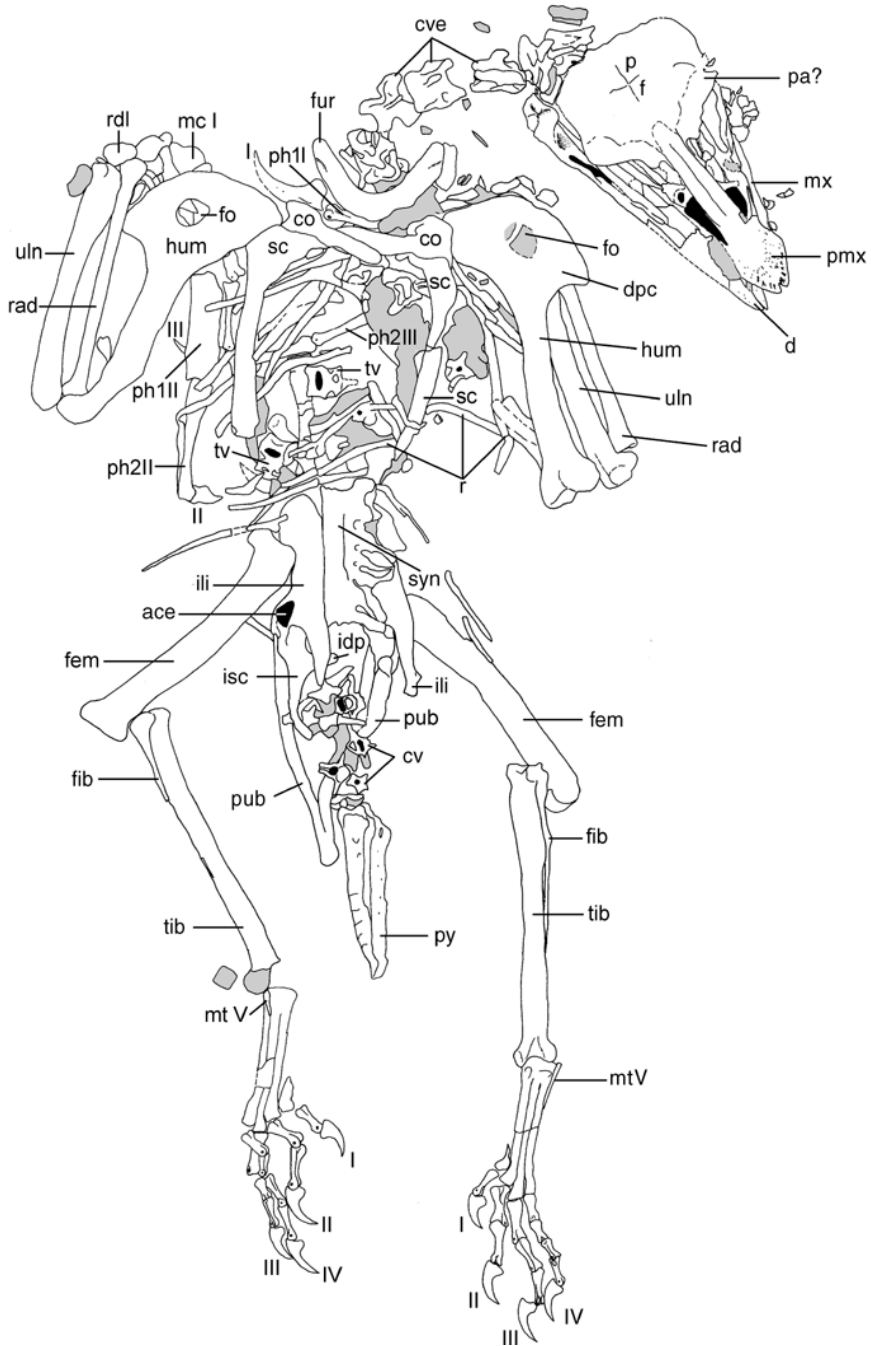
Fig. 7.   Continued.

Fig. 8.   *Confuciusornis sanctus* (GMV-2130).
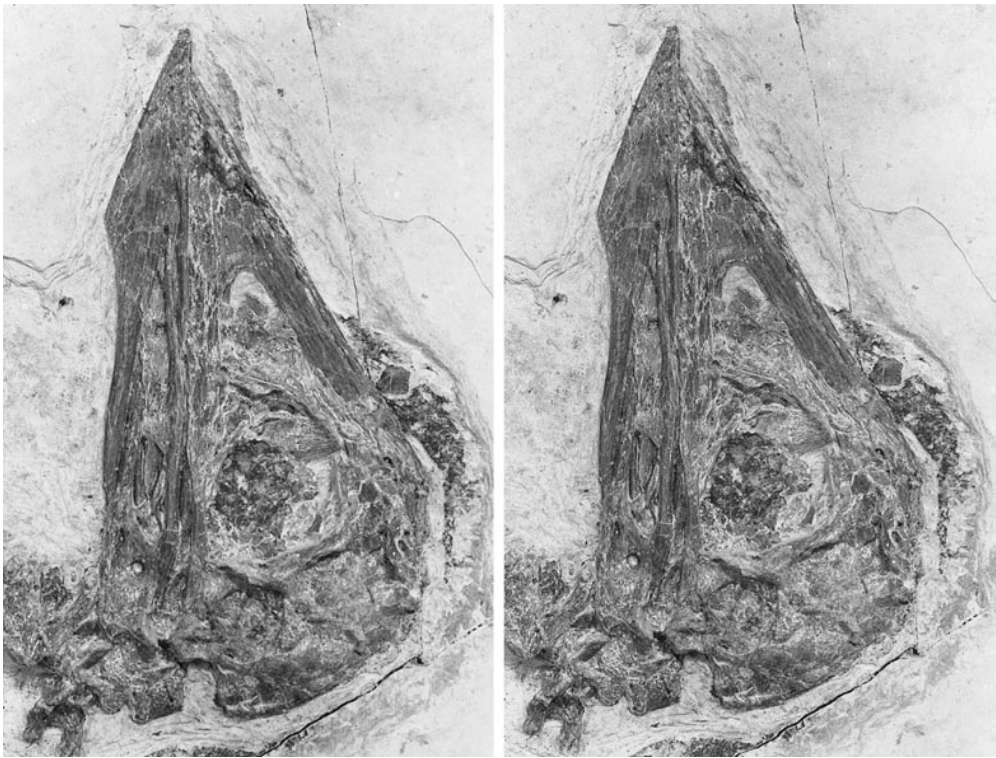
Fig. 9. *Confuciusornis sanctus* (GMV-2131).

Fig. 10. *Confuciusornis sanctus* (GMV-2132). See Anatomical Abbreviations for definition of labels.

Confuciusornis sanctus Hou et al., 1995
Figures 6-49, 60-63, 70

HOLOTYPE: IVPP-V10918, incomplete specimen including skull and forelimb elements (Hou et al., 1995b).

REFERRED SPECIMENS: Hou et al.'s (1995b, c) original description referred two slabs with hindlimb elements (IVPP-V10895 and IVPP-V10919) to *Confuciusornis sanctus* despite their being no elemental overlaps with the holotype (Chiappe, 1995a). The later discovery of numerous articulated specimens have shown that the three specimens assigned by Hou et al. (1995b, c) to *Confuciusornis sanctus* indeed belong to this species. Although many specimens of *Confuciusornis sanctus* are housed in private collections, and thus are often unavailable for study or reference in scientific publications, many specimens are in Chinese and foreign institutions. The National Geological Museum of China in Beijing has an extensive collection (nearly 100 specimens). Of these, specimens GMV-2130, GMV-2131, GMV-2132, and GMV-2133—all nearly complete specimens and some (GMV-2130 and GMV-2131) preserving feathers in their natural position—and the more incomplete GMV-2141 and GMV-2142 were fully prepared at the American Museum of Natural History and are the nucleus of this study (figs. 6–9). In addition, we have drawn information from the many partially prepared specimens at the National Geological Museum of China (GMV-2146–54), those available at the Beijing Natural History Museum (BPV-2066; see Guan et al., 1997), the Forschungsinstitut Senckenberg (SMFAv-412, SMFAv-416, SMFAv-421, SMFAv-423; see Peters, 1996; Peters and Ji, 1998), and the Jura-Museum (JM-UKr-1997/1, JM-Ukr-1996/15; see Viohl, 1997) and those reported by Hou et al. (1995b, c, 1996), Zhou Z.-H. and Hou (1998), and Martin et al. (1998).

LOCALITY AND HORIZON: Although most specimens of *Confuciusornis sanctus* are from the villages of Sihetun (fig. 2) and Jianshangou (fig. 3) within the town of Shangyuan (25 km south of Beipiao City, Liaoning
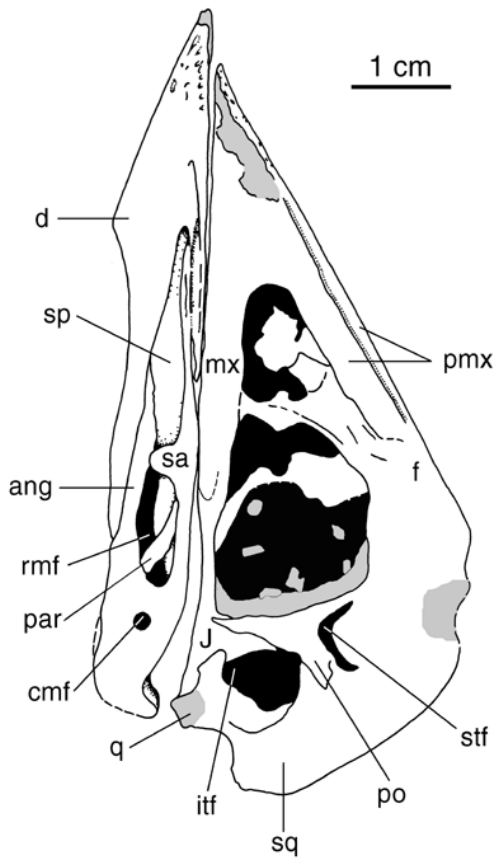
Fig. 10. Continued.

a straight culmen and mandible; rostral margin of the premaxilla notched; large round to oval foramen piercing through the deltopectoral crest of the humerus; intermediate phalanx of manual digit II bowed; prominent tubercle centered on the cranial surface of the distal end of the tibiotarsus; short hallux, not exceeding in length 50% of pedal digit II.

Changchengornis hengdaoziensis
Ji Q. et al., 1999
Figures 50–59

HOLOTYPE: GMV-2129, complete specimen split in a slab and a counterslab (Ji Q. et al., 1999) (figs. 50–51).

LOCALITY AND HORIZON: Jianshangou village (fig. 3) in the town of Shangyuan (approximately 25 km south of Beipiao City, Liaoning Province, China); Hengdaozi Member, Chaomidianzi Formation.

DIAGNOSIS: A confuciusornithid bird with a prominently curved and sharp rostrum; rostrum proportionally shorter than that of *Confuciusornis sanctus* (approximately one-third the skull's length in *Changchengornis hengdaoziensis* versus one-half in *Confuciusornis sanctus*); mandible significantly shorter than skull and high caudally; cross section of furcula in shape of a horizontal 8 and not suboval as in *Confuciusornis sanctus*; distinct tubercle on caudal surface of furcula at junction between clavicular rami; caudal margin of sternum forming a much steeper V than that of *Confuciusornis sanctus*; humeral deltopectoral crest not pierced by foramen as in *Confuciusornis sanctus*; metacarpal I nearly 50% the length of metacarpal II; intermediate phalanx of manual digit II shorter than proximal phalanx (opposite is true for *Confuciusornis sanctus*); distal fusion between metatarsals III and IV; tarsometatarsus not excavated plantarly as in *Confuciusornis sanctus*; hallux proportionally longer than in *Confuciusornis sanctus*.

Province), two specimens have been recently found near the village of Dawangzhangzi (Lingyuan City, Liaoning Province), approximately 180 km southwest of Beipiao City. All specimens from the Sihetun—Jianshangou region come from the Jiulongsong and Hengdaozi members of the Chaomidianzi Formation (Ji Q. et al., in press). Specimens collected at Dawangzhangzi are from the Hengdaozi Member. The Chaomidianzi Formation has been regarded as of latest Jurassic age, although its age is still under debate.

DIAGNOSIS: A confuciusornithid bird with

ANATOMY OF *CONFUCIUSORNIS SANCTUS*

SKULL AND MANDIBLE

The skulls of all specimens studied here are crushed, often making it difficult to visualize sutures separating individual bones. Comparing the several specimens, however, enables a reliable representation of its cranial morphology.
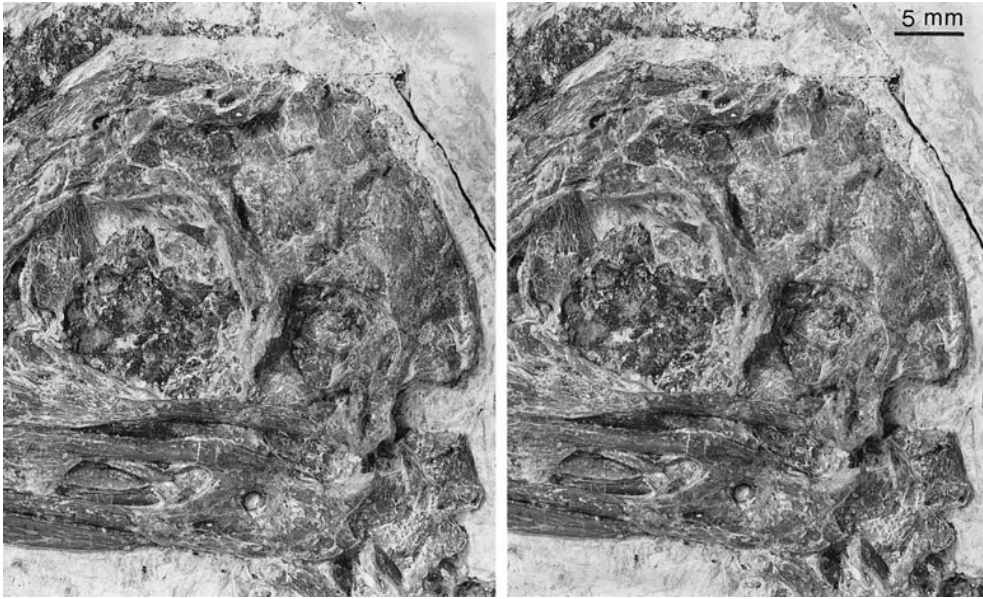
Fig. 11.   Detail of the orbital and postorbital region of the skull of *Confuciusornis sanctus* (GMV-2132). See fig. 10 for labels.
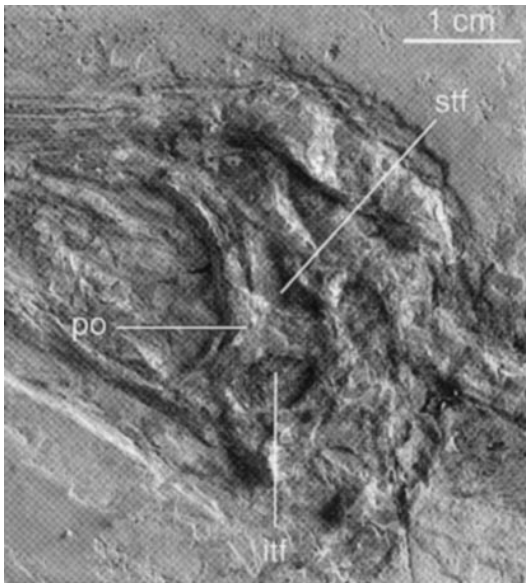

Fig. 12.   Detail of the postorbital region of the skull of *Confuciusornis sanctus* (GMV-2153). See Anatomical Abbreviations for definition of labels.

In lateral view, the skull is subtriangular, without teeth, and with a robust, pointed beak (figs. 10, 13, 15, 16, 20). Smaller specimens appear to have lower skulls than those of the larger specimens (cf. figs. 10, 15, 16); this same condition has been noticed for specimens of *Archaeopteryx lithographica* and several nonavian theropods (Houck et al., 1990). The rostral portions of both the premaxilla and dentary are scarred by deep, neurovascular foramina and grooves. The presence of these foramina provides evidence for the existence of a rhamphotheca (Peters, 1996). As Hou et al. (1995c) emphasized, *Confuciusornis sanctus* provides the earliest record of a toothless, beaked bird, showing once again that tooth loss is common in the evolution of theropod dinosaurs. Toothlessness has evolved at least three times within birds (Confuciusornithidae, Enantiornithes, and Neornithes) and several other times within nonavian theropods (e.g., Oviraptoridae and Ornithomimidae) (fig. 65).

The subtriangular external nares open far from the rostrum's tip (figs. 10, 13, 15, 16, 20). They are bounded dorsally by the premaxilla and ventrally by the maxilla. Caudally, they are demarcated by the nasal wall of the maxilla and, apparently, by a contribution of the nasal to their dorsocaudal corner. The antorbital cavity, the osseous correlate of the antorbital sinus (Witmer, 1997),
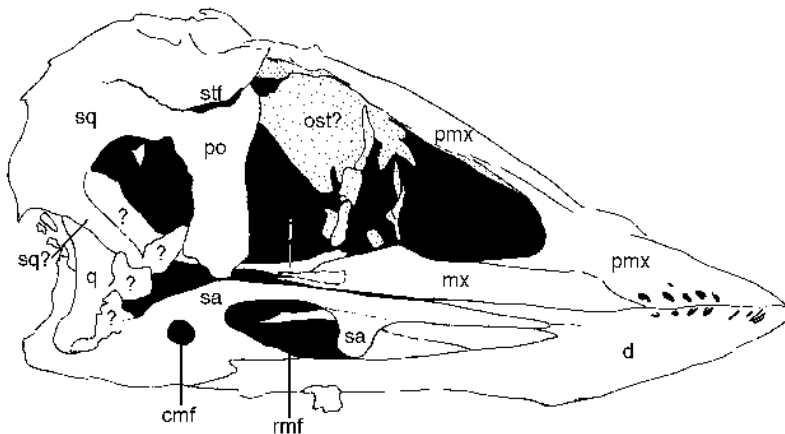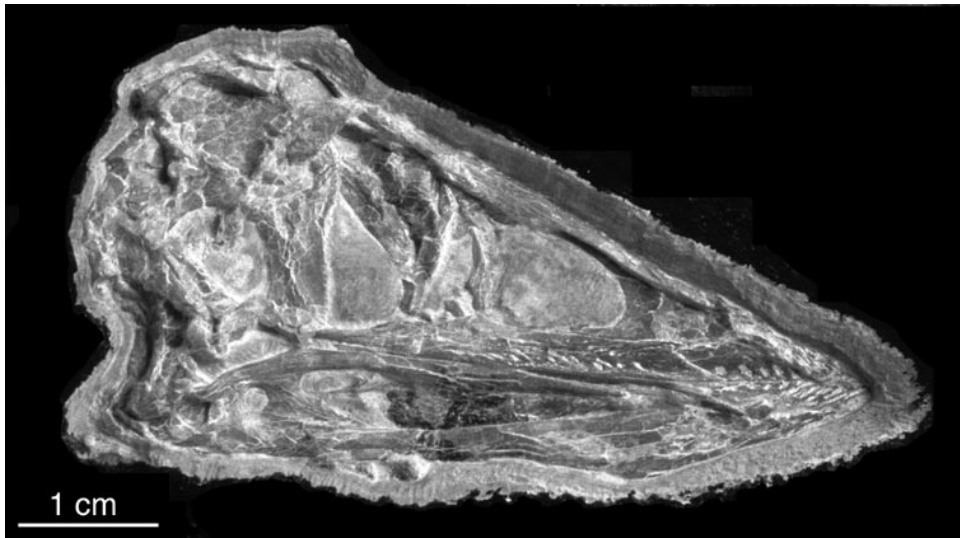
Fig. 13.   Skull of *Confuciusornis sanctus* (SMFAv-416). See Anatomical Abbreviations for definition of labels.

is not clearly defined in any of the studied specimens. Nevertheless, it was evidently enclosed between the maxilla rostrally and ventrally, the lacrimal caudally, and the nasal dorsally. The jugal contributed to its caudoventral corner (figs. 10, 13). The participation of the nasal in the antorbital cavity is characteristic of most birds and juvenile troodontids (M. Norell, personal observation) but unlike many adult nonavian theropods, in which a lacrimomaxillary contact excludes the nasal from the dorsal margin of the antorbital cavity (Witmer, 1997). The rostral portion of the antorbital cavity was medially

walled by a recessed nasal process of the maxilla (figs. 14–16). This process is much broader than the tapering nasal process illustrated by Martin et al. (1998). The retention of the dorsal portion of the nasal process of the maxilla is a primitive condition also present in *Archaeopteryx lithographica* (Wellnhofer, 1974), the alvarezsaurid *Shuvuuia deserti* (Chiappe et al., 1998a), and nonavian theropods (Witmer, 1990, 1997). The caudal margin of this process would have formed the rostral border of the internal antorbital fenestra (Witmer, 1997). Although the fenestra's precise shape remains unclear in all
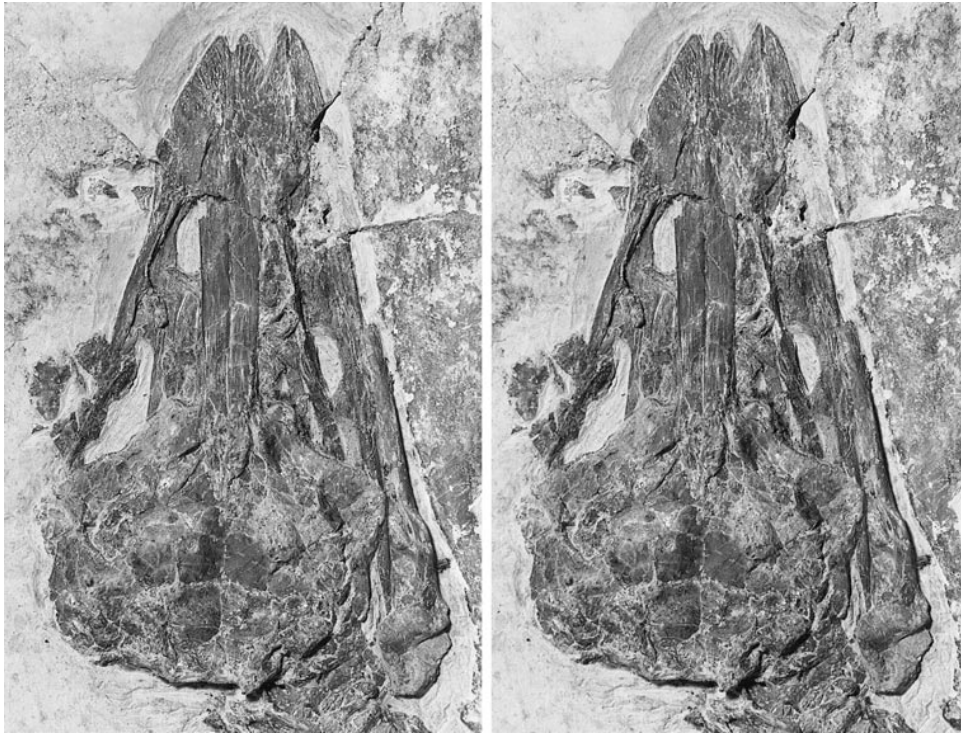
Fig. 14. Skull of *Confuciusornis sanctus* (GMV-2133). See Anatomical Abbreviations for definition of labels.

studied specimens, it is evidently narrow and small, a conclusion also reached by Martin et al. (1998). In contrast to *Archaeopteryx lithographica*, the nasal process of the maxilla of *Confuciusornis sanctus* is perforated by a single, round foramen (figs. 14–16) rather than two (Witmer, 1997). This foramen is separated from the internal antorbital fenestra by a robust pila interfenestralis (Witmer, 1997). Even though it is uncertain whether this foramen is homologous to either the maxillary or the promaxillary fenestra of *Archaeopteryx lithographica* and nonavian theropods, its round morphology and position approaches more that of the former (Witmer, 1997). In any case, the morphology of the rostral portion of the antorbital cavity of *Confuciusornis sanctus* is intermediate between that of *Archaeopteryx lithographica* and its modern counterparts.

The skull's tomial crest is straight throughout its length. The boundary between the maxillary process of the premaxilla and the maxilla is clear in GMV-2133, GMV-2146, and SMFAv-416 (figs. 13, 14). This process is short, tapering caudally and overlapping the maxilla dorsally. Hou et al.'s (1995c) interpretation of *Confuciusornis sanctus*' premaxilla as large and elongated at the expense of the maxilla is clearly wrong. The premaxillae fused to each other for most of the rostral half of the snout, although their rostral tips are separated by a V-shaped notch (fig. 14). Caudally, the premaxillae project into long and robust frontal processes (figs. 10, 13–16). These frontal processes are separated by a straight suture for most of their length, although they fuse to each other in their rostral portion. Caudally, these processes reach the rostral margin of the orbit, joining the frontals. In contrast to the observations of Hou et al. (1995c) and Martin et al. (1998), the junction of the frontal processes of the premaxillae with the frontals is not marked by any apparent hinge or bending zone as in typical prokinetic birds (Zusi, 1993; see Implications for the Evolution of Avian Cranial Kinesis, below). On the contrary, the caudal
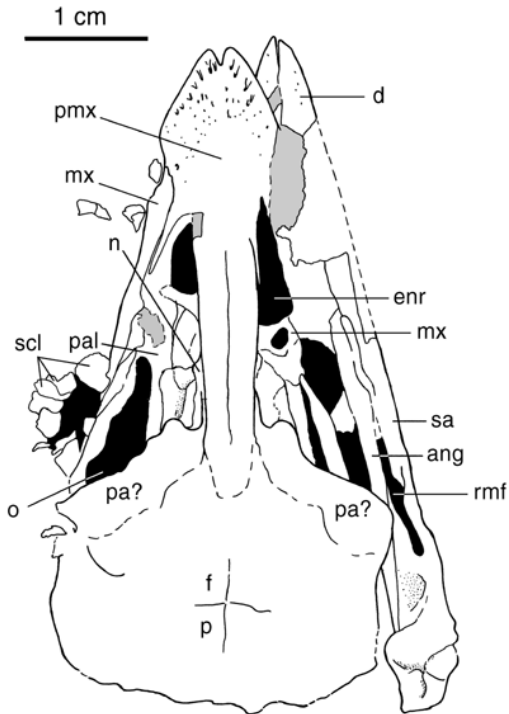
Fig. 14. Continued.

portion of the frontal processes of the premaxillae are robust and broadly overlap the frontals (figs. 10, 14). In GMV-2133 and GMV-2150, a small, thin bone lies lateral to the frontal process of the left premaxilla along its caudal margin (fig. 14). A similar ossification forms the dorsal margin of the antorbital cavity in GMV-2130 (fig. 15); in this specimen, this element has a distinct ventrolateral process overhanging the caudal portion of the nasal process of the maxilla. This bone can be confidently interpreted as the nasal. Thus, the nasals of *Confuciusornis sanctus* did not contact each other along the midline but were separated by the broad frontal processes of the premaxillae.

On the top of the skull, the frontals are inflated, forming two distinct lobes (fig. 14). In GMV-2133 and GMV-2150, these bones appear to be laterally bordered by rectangular ossifications, that cap the orbit dorsally (fig. 14). The identity of these supraorbital ossifications is problematic. They may be symmetrical fractures of each frontal, although the fact that the pattern occurs in two spec-

imens suggests that they are sutures demarcating independent ossifications. If they are indeed separate ossifications, their position suggests they may be palpebral bones. Palpebral bones are common among birds, often occurring in Tinamidae, Accipitridae, and other modern lineages (Jollie, 1957). The orbit of *Confuciusornis sanctus* is round, and partially articulated sclerotic plates can be seen inside or in the vicinity of the orbit of several specimens (e.g., GMV-2132 and GMV-2133). In SMFAv-416, the dorsal half of the orbit is medially walled by a wide sheet of bone with its caudal margin slanting rostroventrally; this ossification may be part of the interorbital septum (fig. 13). The frontals are separated from the parietals by a suture perpendicular to the interfrontal suture. The parietals are large and are separated by a sagittal suture (fig. 14). The remaining bones of the braincase are crushed in all specimens, and the sutures demarcating them are not discernible. The foramen magnum is approximately the same size as the occipital condyle (Guan et al., 1997). In ventral view, rostral to the occipital condyle there is a deep subcondylar fossa.

The caudal and caudodorsal margins of the orbit are formed by a triradiate postorbital, bearing processes for the frontal, jugal, and squamosal (figs. 10–13). The presence of a postorbital in *Confuciusornis sanctus* is unequivocal (contra Hou et al., 1995c). The tapering caudal process of the postorbital overlaps an equally tapering rostral process of the squamosal dorsally. Martin et al.'s (1998) skull reconstruction lacking a squamosal is incorrect (fig. 20). The postorbital–squamosal bar separates a supratemporal fossa from an infratemporal one (Chiappe et al., 1998b; Peters and Ji Q., 1998). A similar separation between these two diapsid fenestrae is preserved in several specimens (e.g., GMV-2153 and SMFAv-416) (figs. 10, 12, 13).

The ventral margin of the squamosal is arched strongly, apparently bearing a rostroventral process that overlaps the lateral surface of the quadrate (fig. 13). In GMV-2133, two bone fragments were preserved in disarticulation, caudal to the right articular area of the skull. Based on morphology and position, these two fragments are interpreted as the mandibular and otic processes of the right
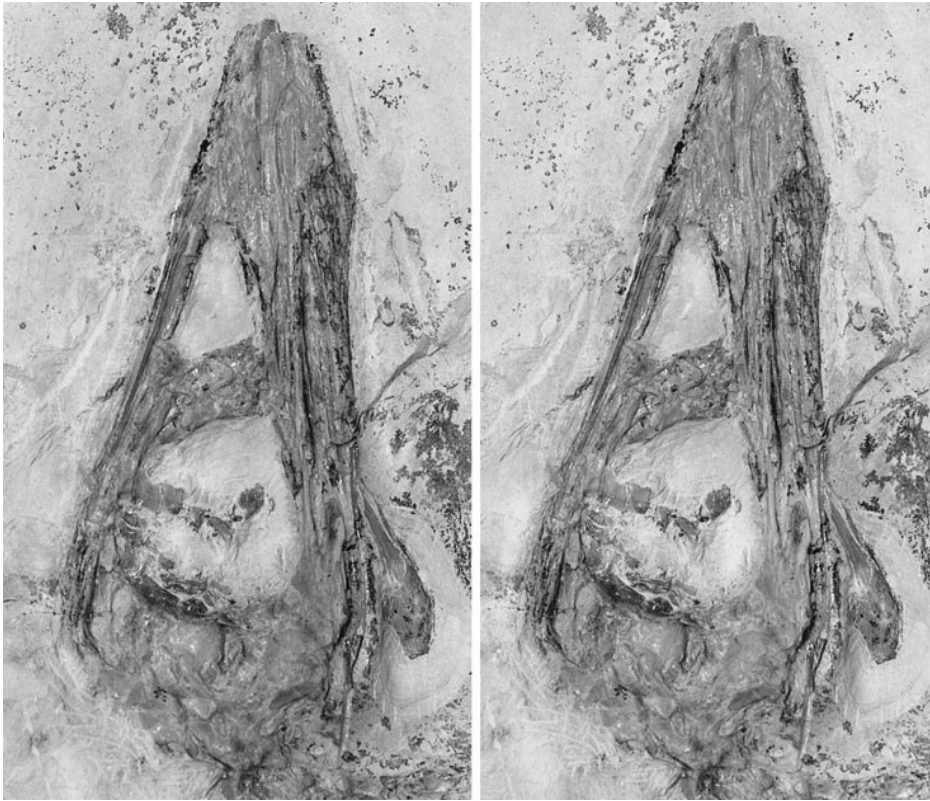
Fig. 15.   Skull of *Confuciusornis sanctus* (GMV-2130). See Anatomical Abbreviations for definition of labels.

quadrate (figs. 17, 18). These bones were removed from the matrix. The mandibular process shows a craniocaudally expanded medial condyle and a much smaller lateral condyle (fig. 18F). The medial condyle is crescentic in medial view. Laterally, the lateral condyle bears a small, shallow depression for articulation of the quadratojugal (fig. 18E). The otic process bears two distinct, head like projections (fig. 18A, B), suggesting that the quadrate of *Confuciusornis sanctus* articulated with both the squamosal and the braincase. A braincase articulation for the quadrate is present in all birds—other than *Archaeopteryx lithographica*—for which relevant skull material is preserved. This condition has recently been reported for the alvarezsaurid *Shuvuuia deserti* (Chiappe et al., 1998a) as well as for oviraptorid theropods (Maryanska and Osmólska, 1997). The otic process of the quadrate of several Mesozoic birds (e.g., hesperornithiforms, ich-

thyornithiforms, and *Patagopteryx deferrariisi*) is not differentiated in well-defined capitula.

The orbit is defined ventrally by a robust and straight jugal bone. This bone is high at the level of the rostral margin of the orbit, becoming substantially narrower caudally. In GMV-2132, immediately behind the orbit, the jugal expands dorsally into a tall, triangular process (fig. 10). This process abuts most of the caudal margin of the ventral process of the postorbital. Interestingly, in SMFAv-416 the ventral process of the postorbital does not appear to taper (Peters and Ji, 1998); a thick process overlaps the jugal laterally (fig. 13). It is not possible to discern whether the jugal had a dorsal process because this may be covered by the overlapping ventral process of the postorbital. A condition comparable to that of SMFAv-416 appears to be present in GMV-2153 (fig. 12) and is apparent in Martin et al.'s (1998) re-
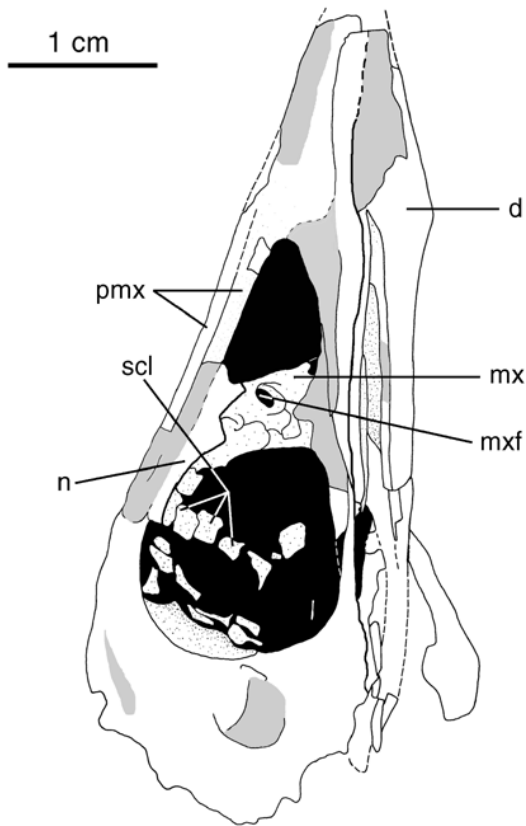
Fig. 15.   Continued.

construction of the skull (fig. 20). Additional specimens with adequate preservation of this region are needed to decide whether these apparently different conditions represent a common polymorphism or whether the morphology of GMV-2132 is pathologic. In all these specimens, however, the solid postorbital–jugal bar completely separates the orbit from the infratemporal fenestra. Thus, the skull of *Confuciusornis sanctus* is of primitive diapsid configuration (Romer, 1956), not that of a "typical avian highly modified diapsid type" as postulated by Hou et al. (1995c).

Early workers on Mesozoic birds regarded this fully diapsid condition to be present in *Archaeopteryx lithographica* (e.g., Heilmann, 1926), yet subsequent studies of the available skulls have been unable to identify confidently a postorbital–jugal contact (Wellnhofer, 1974; Bühler, 1985; Elzanowski and Wellnhofer, 1996). A postorbital bone is clearly present in *Archaeopteryx lithographica* (contra Martin, 1991), as is evident in the Berlin specimen (L. Chiappe, personal observation) and inferred by the presence of a postorbital facet in the squamosal of the Aktien-Verein specimen (Elzanowski and Wellnhofer, 1996; this specimen has been considered to be the holotype of *Archaeopteryx bavarica* by Wellnhofer [1993]). The jugal of *Archaeopteryx lithographica* presents a caudodorsal tapering process that some have suggested may have directly contacted the postorbital (e.g., Wellnhofer, 1974; Elzanowski and Wellnhofer, 1996). This process, however, appears to be located too caudally to contact the postorbital directly (Elzanowski and Wellnhofer, 1996: fig. 7B). Furthermore, in a recently described enantiornithine from Catalonia (Sanz et al., 1997), an identical process abuts the lateral surface of the quadrate and not the postorbital. Thus, although *Archaeopteryx lithographica* clearly has a postorbital bone with a ventrally directed jugal process, it seems unlikely that this process established a direct contact with the jugal. If this is the case, then *Confuciusornis sanctus* is the first and only known bird for which a direct contact between the postorbital and the jugal can be unquestionably documented (see Implications for the Evolution of Avian Cranial Kinesis, below).

Very little information is available on the palatal structure of *Confuciusornis sanctus*. A portion of the palate is observed through the prepared areas of the external nares, antorbital fossa, and orbit of GMV-2133 (fig. 14). The maxilla has a medial expansion contributing to the palate. Caudally, this bone joins an elongate, belt like bone that is interpreted as the palatine. Comparable paired bones are preserved in JM-UKr-1997/1. A few fragmentary palatal elements are also visible through the space of the left naris and antorbital cavity of specimen GMV-2146 (fig. 19). A long bone with rostral and caudal expansions is tentatively interpreted as the left pterygoid. Although the rostral and caudal boundaries of this element are not clear, a rostral triangular expansion appears to mark the rostral end of this bone (fig. 19). A similar rostral expansion is present in the pterygoid of *Archaeopteryx lithographica* (Elzanowski and Wellnhofer, 1996). Dorsal-
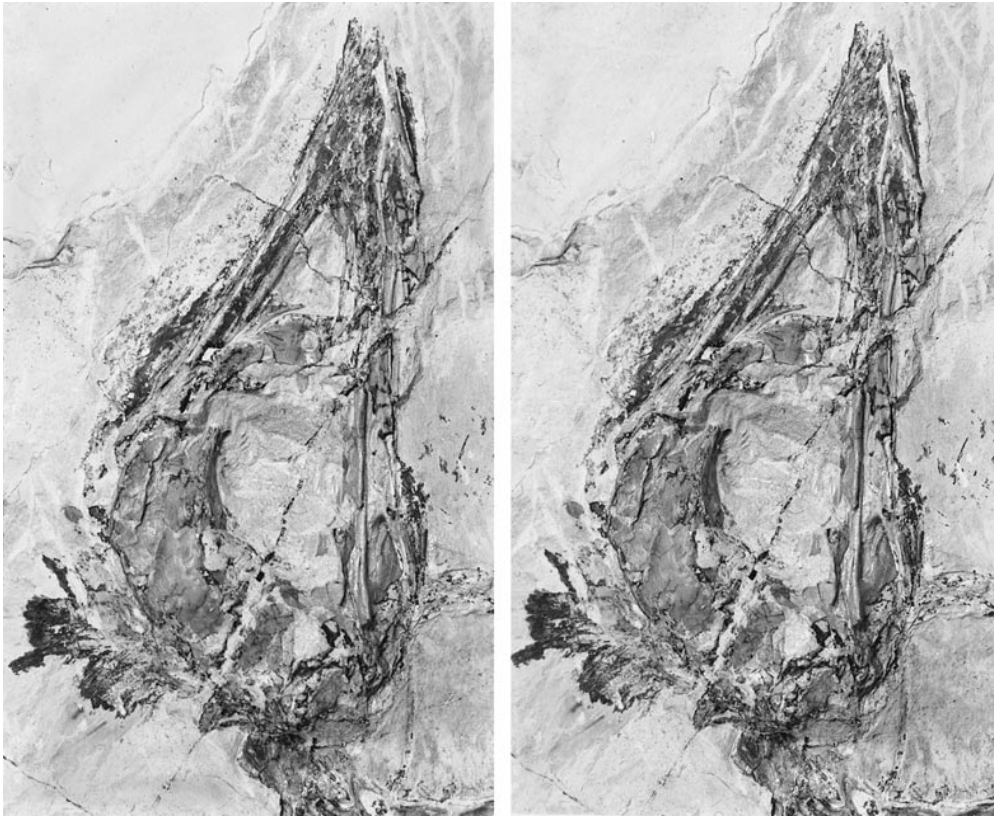
Fig. 16.   Skull of *Confuciusornis sanctus* (GMV-2131). See Anatomical Abbreviations for definition of labels.

ly, this bone is recessed by a shallow depression. Lateral to this bone, just caudal to the triangular expansion, is an incomplete but crescentic bone. Its caudomedial portion is dorsally excavated by a round, shallow depression. Although incomplete, the morphology and position of this bone suggests it may be an ectopterygoid. This bone, absent in the palate of modern avians (Jollie, 1957), is present in *Archaeopteryx lithographica* (Wellnhofer, 1974; Elzanowski and Wellnhofer, 1996; contra Martin, 1991), and it has been tentatively reported for the Late Cretaceous enantiornithine *Gobipteryx minuta* (Elzanowski, 1995).

The mandible of *Confuciusornis sanctus* is robust, especially in its symphysial and rostral third (figs. 10, 13, 15, 20). As in the skull, the tomial crest is straight throughout its entire length, and the mandible's sharp tip is indented by a notch (fig. 14). The mandib-

ular rami are firmly joined at their symphyses. In GMV-2132 and GMV-2133, however, they remain unfused; a distinct suture separating both mandibular rami is also present in SMFAv-412 (Peters, 1996). From its tip, the ventral margin of the mandible slants caudoventrally for most of its rostral third. This gives the mandible a spear-shaped aspect in lateral view (figs. 10, 13, 15, 20). The jaw is tallest at a point one-third from its tip. Caudally, the lower margin of the jaw slants caudodorsally, becoming horizontal.

In the rostral third of the jaw, the dentary bifurcates into long dorsal and ventral processes (figs. 10, 13, 15, 20). The ventral process tapers caudally, reaching almost the end of the mandible in some specimens (e.g., JM-UKr-1997/1). The dorsal process, which is shorter and more slender than the ventral one, also tapers caudally, ending somewhat beyond the mandible's midpoint. This pro-
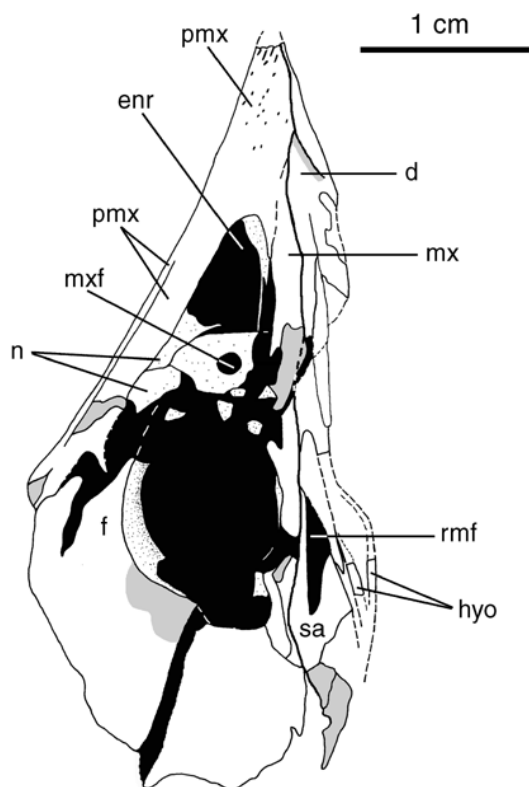
Fig. 16.   Continued.

cess is ventrally lined by a long, slender projection of the surangular. The surangular forms the entire dorsal margin of the suboval rostral mandibular fenestra, and, by means of a subtriangular, ventrally directed process, it also bounds the fenestra rostrally (figs. 10, 13, 20). The caudalmost portion of the surangular is perforated by a small, round foramen, comparable in position to the surangular foramen of nonavian theropods and the caudal mandibular fenestra of many modern birds (figs. 10, 13). The angular overlaps dorsally the ventral process of the dentary, forming the complete ventral margin of the rostral mandibular fenestra. Caudally, the angular is fused to the articular, a condition also known for the Patagonian Late Cretaceous *Patagopteryx deferrariisi* (Chiappe, 1996). In GMV-2132, in front of the rostral mandibular fenestra, there is a flat bone lying within an elongate depression between the surangular and the dentary–angular (fig. 10). This bone presumably corresponds to the splenial,

which is exposed in lateral view. The fact that it is visible in lateral view indicates that the area between the surangular and the dentary–angular was not walled laterally. This same configuration of the lateral surface of the jaw is present in GMV-2130, GMV-2131, and SMFAv-416. In SMFAv-416, the lateral surface of the splenial is also visible through the depression in front of the rostral mandibular fenestra (fig. 13). A dorsorostrally directed bar, within the rostral mandibular fenestra of this specimen, is interpreted as the prearticular (fig. 10).

The articular surface of the mandible of *Confuciusornis sanctus* exhibits two well-developed cotylae. The main axis of each is rostrolaterally oriented (Guan et al., 1997). The medial cotyla is wider than the lateral cotyla and oriented somewhat more laterally. The retroarticular process is either reduced or poorly developed.

VERTEBRAL COLUMN

The cervical vertebrae are poorly preserved in most of the studied specimens. The atlas and axis are preserved in SMFAv-412. The atlas is ring shaped and has a depressed centrum. The cranial surface of the centrum bears a craniodorsal facet for articulation with the occipital condyle. Ventrally, the atlantal centrum projects into a faint keel. The axis has an expanded spinal process and a centrum that is laterally excavated by an elongate fossa.

Six post atlantal cervicals are clearly distinguishable in GMV-2132 and JM-UKr-1997/1 and seven in GMV-2131 (fig. 21). The spinal processes are reduced throughout the series (fig. 22). The postzygapophyses of the middle and caudal portions of the cervical series are ample and semilunate; their lateral margin is convex. The postzygapophysial facets are distinctly concave in the rostral cervicals, and they become flat in the caudal elements of the series. Evidence of central pneumatization is equivocal. Pneumatic foramina are not visible in the rostral cervical centra of GMV-2131 and GMV-2147. However, a rostral centrum of JM-UKr-1997/1, presumably that of the third cervical, is pierced by a small foramen just caudal to its center. Cervical central pneumatization is

widespread among nonavian theropods (Britt, 1993), and among basal birds it has been reported for *Archaeopteryx lithographica* (Britt et al., 1998). The presence of a distinct foramen on a rostral cervical centrum of JM-UKr-1997/1 suggests that this primitive system of cervical pneumatization may have also been present in *Confuciusornis sanctus*—this pneumatization may not be distinguishable in the poorly preserved cervicals of the remaining studied specimens.

The third vertebrae of GMV-2147 shows that its ribs were not fused to the para- and diapophyses. Peters (1996) reported that the cervical centra of SMFAv-412 are heterocoelic; a disarticulated caudal cervical of SMFAv-412 indeed shows an incipient degree of heterocoely on its cranial articular surface. Other studied specimens (e.g., JM-UKr-1997/1) also show a certain degree of heterocoely for the cranial articular surfaces of the cervical vertebrae (contra Martin et al., 1998). A comparable condition, in which the cranial articular surface is heterocoelic whereas the caudal one is not, is known for enantiornithine birds (Chiappe, 1996; Sanz et al., 1996; Chiappe and Walker, in press). Specimens GMV-2147 and JM-UKr-1997/1 show well-developed cranioventral fossae in the rostral cervicals. Ventrally, the centra are compressed, and a well-developed ventral process can be seen in the last preserved cervical of GMV-2132 (fig. 21).

In GMV-2132 there are 12 disarticulated thoracic vertebrae (fig. 6), but more may have formed the thoracic series of *Confuciusornis sanctus*. Thirteen thoracic vertebrae compose the trunk of *Archaeopteryx lithographica* and many nonavian theropods, and a reduction to 11 or fewer thoracic vertebrae appears to have evolved among ornithothoracine birds (Chiappe, 1996). The thoracic vertebrae of *Confuciusornis sanctus* have subcircular, amphiplatian articular surfaces and relatively small vertebral foramina (the ratio between the height of the cranial articular surface and that of the vertebral foramen is approximately 0.4) (fig. 25). They show no evidence of hyposphene–hypantrum accessory articulations. Their spinal processes are tall and craniocaudally narrow in lateral view (fig. 25). Deep fossae for the insertion of elastic ligaments carve the rostral and cau-
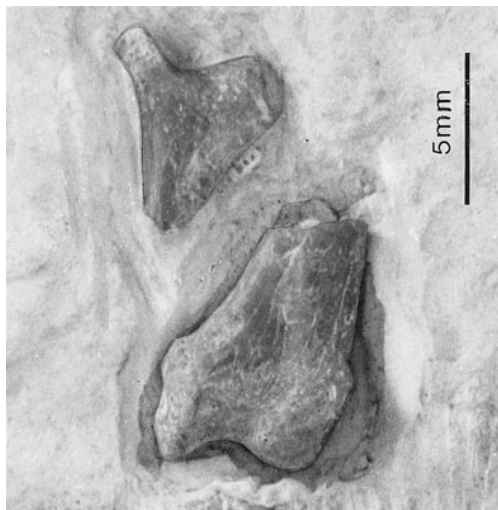

Fig. 17. Detail of the proximal and distal ends of the quadrate of *Confuciusornis sanctus* (GMV-2133) as exposed on the slab near the right caudolateral corner of its skull.

dal bases of the spinal processes. The transverse processes project laterally in a plane perpendicular to that of the spinal processes. The caudal bases of the transverse processes are deeply excavated by infrapostdiapophysial fossae. The centra bear large, suboval excavations on their lateral sides (figs. 6–9, 25, 30). Comparable lateral excavations are known for a variety of enantiornithines (Chiappe and Walker, in press), ichthyornithiforms, and hesperornithiforms (Marsh, 1880) and several modern lineages. The parapophyses (costal fovea) of these vertebrae rest over tall peduncles located rostral to the transverse process.

Seven vertebrae form the synsacrum of the two individuals of GMV-2153 (fig. 23) and JM-UKr-1997/1—molds of these vertebrae are also visible in GMV-2146. An identical number of synsacral vertebrae was reported by Peters (1996). Synsacral vertebrae are completely fused to each other (figs. 23, 24). In the smaller individual of GMV-2153 (fig. 23), the two terminal thoracic vertebrae appear to be fused to the synsacrum. This condition is either due to diagenetic processes or is pathologic because it has not been observed in any other specimen. The cranial articular surface of the synsacrum is round and distinctly concave, as in Enantiornithes, *Pa-*
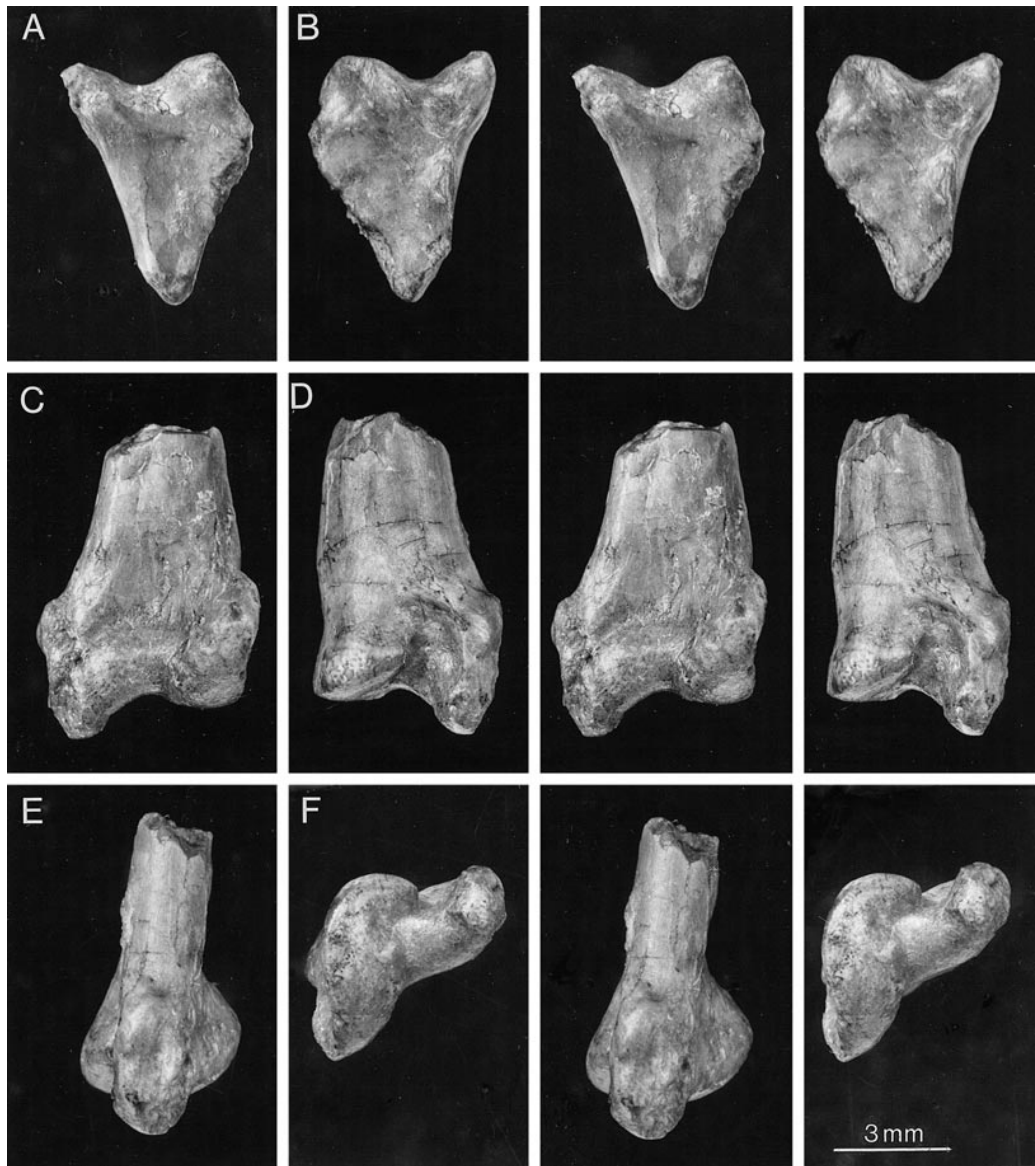
Fig. 18.   Otic process (A, B) and articular process (C–F) of the quadrate of *Confuciusornis sanctus* (GMV-2133). (A, C) caudal, (B, D) cranial, (E) lateral, and (F) distal views. Stereopair.

tagopteryx deferrariisi, and the Alvarezsauridae (Chiappe et al., 1996). Laterally, the vertebral centra of the cranial half of the synsacrum are excavated by fossae comparable to those of the thoracic centra. Robust transverse processes of the synsacral vertebrae separate the iliac blades (figs. 24, 25).

Hou et al. (1996) and Martin et al. (1998) reported four or five free caudals for *Con-*

fuciusornis sanctus. Nevertheless, seven disarticulated caudal vertebrae are preserved in GMV-2133 (fig. 7), and the same number of elements are articulated between the synsacrum and the pygostyle of the smaller individual of GMV-2153 (fig. 23). The proximal and middle caudals have round and slightly concave cranial articular facets (fig. 25). These caudals have tall and compressed spi-

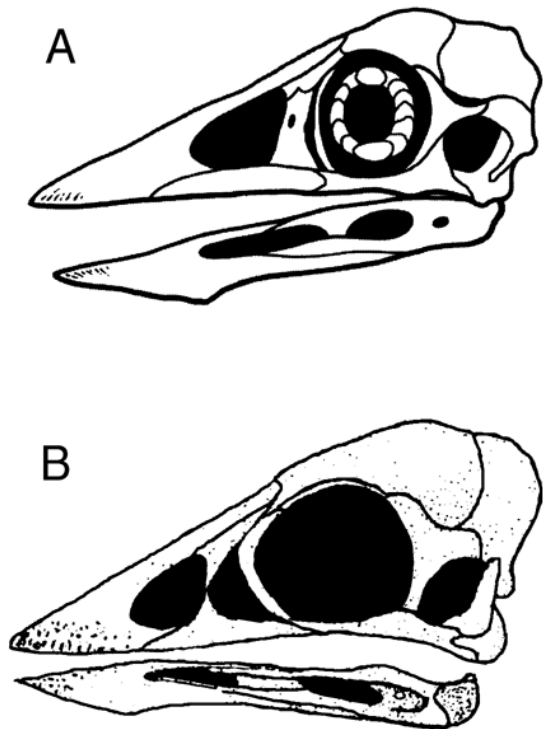Fig. 19. Palatal view of the skull of *Confuciusornis sanctus* (GMV-2146). See Anatomical Abbreviations for definition of labels.

Fig. 20. Skull reconstruction of *Confuciusornis sanctus*: (A) this study and (B) after Martin et al. (1998).

nal processes and robust transverse processes that project laterally and perpendicular to the spinal processes. These vertebrae have relatively elongate prezygapophyses and postzygapophyses that project from the spinal processes. The last free caudal is smaller than the preceding ones (fig. 24). The centrum of this vertebra is subrectangular (fig. 25); its vertebral canal is round. The vertebral arch of this apparent last caudal bears short, dorsolateral projections (fig. 25).

The caudal series of *Confuciusornis sanc-* *tus* ends in a long pygostyle (contra initial reports of a long, squirrel-like, bony tail by Hou et al. [1995b, c]) (figs. 6–9, 23–25). Hou et al.'s (1996) report that this composite bone is present in only some of the specimens of *Confuciusornis sanctus* they studied is puzzling because this bone has been seen in all the specimens we have observed (several dozen). The pygostyle of *Confuciusornis sanctus* ends in a transversally rounded tip (fig. 24). The pygostyle is slightly more than half the length of the tibiotarsus (60% in GMV-2133) and, based on GMV-2131 and the smaller individual of GMV-2153, is about 140% the length of the combined lengths of the free caudals (figs. 6–9). Hou et al. (1996) and Martin et al. (1998) described the pygostyle as being formed by 8 and 10 elements, respectively. The exact number of caudals involved in the pygostyle, however, is uncertain due to their complete coossification. Ventrally, the pygostyle bears a prominent axial keel along its entire length.
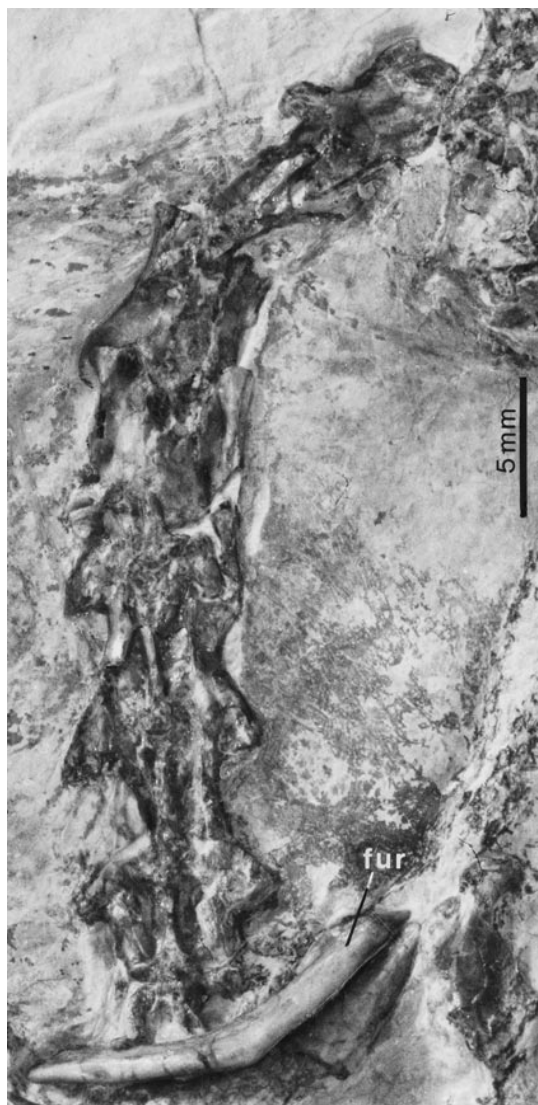
Fig. 21. Detail of the cervical vertebrae of *Confuciusornis sanctus* (GMV-2131). See Anatomical Abbreviations for definition of label.

A longitudinal furrow lying between strong, lateral ridges is visible on the dorsal surface of the pygostyle of GMV-2133 (fig. 25).

THORACIC GIRDLE

The scapula and coracoid are fused to each other (fig. 26), as in the adults of other basal birds such as *Archaeopteryx lithographica* and some nonavian theropods such as *Velociraptor mongoliensis* (Norell and Makov-

icky, in press), oviraptorids, and troodontids (P. Currie, Royal Tyrrell Museum of Paleontology, personal commun.). The shafts of these two bones join at an angle of approximately 90° (fig. 26). This angle, however, is not present at the level of the glenoid facet; the main axis of the glenoid facets of the scapula and coracoid are on the same plane. This configuration is identical to that of *Archaeopteryx lithographica*, the alvarezsaurids, and nonavian theropods. The modern condition of coracoidal and scapular glenoid facets (in addition to their shafts) angled to each other at approximately 90° is a synapomorphy of the Ornithothoraces (Chiappe, 1996).

The coracoid is robust and strutlike but short in relation to the scapula; the coracoid is roughly half the length of the scapula (figs. 26, 27). The scapula fuses to the shoulder end of the coracoid; consequently, the acrocoracoid process is not developed. The coracoid also lacks both procoracoid and sternocoracoid processes. The scapula is straight and costolaterally compressed (fig. 27). It bears a large and subtriangular acromion, which ends in a transversely straight margin. The distal end of the blade is not sharp, as in more advanced birds (Chiappe, 1996), but instead expands gradually toward its tip as in nonavian theropods (fig. 27).

The morphology of the furcula of *Confuciusornis sanctus* is remarkably similar to that of *Archaeopteryx lithographica* (Hou et al., 1996). It is robust, boomerang shaped (interclavicular angle of about 85°), and craniocaudally compressed (figs. 6, 7, 9, 26, 27, 29). It lacks a hypocleideum, although the junction of the clavicular rami is marked by a slight caudal swelling in certain specimens (e.g., GMV-2131 and larger individual of GMV-2153). Each clavicular ramus ends in a round, inflated area, projected caudally (fig. 27). This area most likely articulated to the shoulder end of the coracoid, thus being homologous to the acrocoracoidal articular facet of modern birds (Baumel and Witmer, 1993). A distinct acromial process is not developed.

STERNUM, RIBS, AND GASTRALIA

The sternum of *Confuciusornis sanctus* is relatively long (e.g., GMV-2130 and GMV-
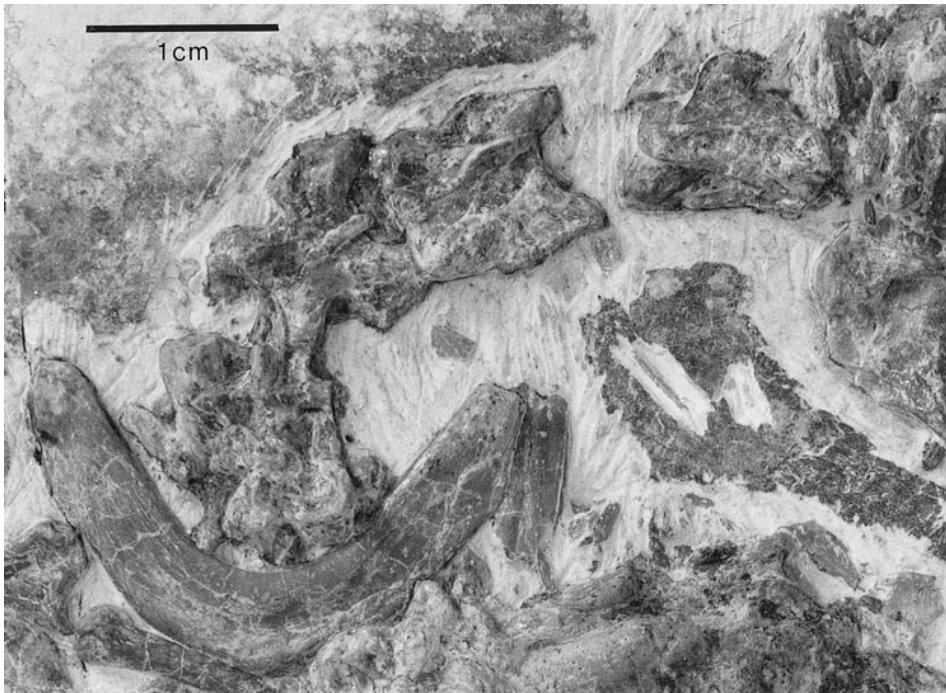
Fig. 22.   Detail of the cervical vertebrae of *Confuciusornis sanctus* (GMV-2133). See fig. 7 for labels.

2131) and in most specimens is virtually flat, lacking any significant development of a keel (figs. 28–30). Specimens GMV-2147 and SMFAv-423, however, show a faint, sagittal ridge on its caudal portion (figs. 31, 32). This ridge is interpreted as an incipient sternal carina. As in some other primitive birds (e.g., *Concornis lacustris* and *Cathayornis yandica* [Sanz et al., 1996]), it is higher toward the caudal margin of the sternum. Whether this ridge anchored a larger, cartilaginous carina is unknown.

The rostral margin of the sternum is straight to slightly convex. Laterally, on the rostral half, there are distinct facets for five sternal ribs (figs. 28–32). These ribs are preserved in articulation in GMV-2131. The sternal ribs are relatively flat and expand gradually toward their preserved proximal ends (fig. 31; GMV-2147). Ossified sternal ribs, which indicate a two-segment thoracic rib (vertebral and sternal elements), are known for other basal birds (e.g., *Iberomesornis romerali* [Sanz and Bonaparte, 1992], *Neuquenornis volans* [Chiappe and Calvo, 1994]) and several nonavian theropods

(Clark et al., 1999; Norell and Makovicky, in press). The number of sternal ribs varies among modern birds. The five sternal ribs of *Confuciusornis sanctus* fall within the range of modern birds, which may be as low as two (e.g., certain dinornithids) and as high as nine (e.g., swans) (Fürbringer, 1888).

Caudal to the sternal rib facets, the sternum bears a stout, broad lateral process (figs. 28–30). A similar process, also expanded immediately caudal to the sternal rib articular area, is present in oviraptorid and dromaeosaurid theropods (Norell and Makovicky, 1997, in press; Clark et al., 1999). This process tapers on its rostral and caudal corner and is laterally concave. The pointed caudal corner of the lateral process is more prominent and narrower than the rostral corner. The sternal body ends caudally in a V-shaped margin, with its apex centered on the midline (fig. 30).

As in several other basal birds (e.g., *Archaeopteryx lithographica*, *Sinornis santensis*, and *Changchengornis hengdaoziensis*), *Confuciusornis sanctus* retained a complete basket of gastralia caudal to the sternum. At
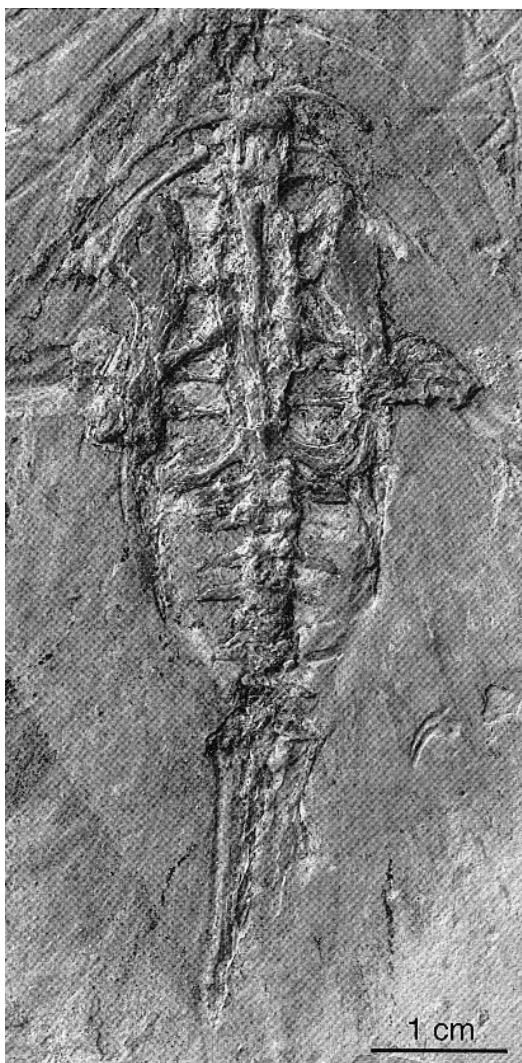
Fig. 23. Detail of the synsacrum, free caudal vertebrae, and pygostyle of *Confuciusornis sanctus* (GMV-2153, smaller individual, see fig. 62).

Fig. 24. Detail of the synsacrum, free caudal vertebrae, pygostyle, and pelvis of *Confuciusornis sanctus* (GMV-2131), ventral view.

least eight rows of gastralia are present in specimen GMV-2152 (fig. 33)—the gastral basket, however, is largely incomplete and disarticulated (e.g., GMV-2149) or not preserved (e.g., GMV-2130 and GMV-2131) in many studied specimens. Even though eight rows may not be the exact number of gastral rows in *Confuciusornis sanctus*, the fact that the caudal-most rows approach the pelvic region in articulated specimens suggests that this number was most likely not exceeded by more than one or two rows. This makes the

gastral basket of *Confuciusornis sanctus* much shorter than that of nonavian theropods such as dromaeosaurids (Norell and Makovicky, 1997). In GMV-2153, the caudal end of the sternum overlaps the first row and the very tip of the second row (fig. 33). With the exception of the first row, composed of single elements, each row of gastralia is formed by four rodlike elements—a medial and a lat-
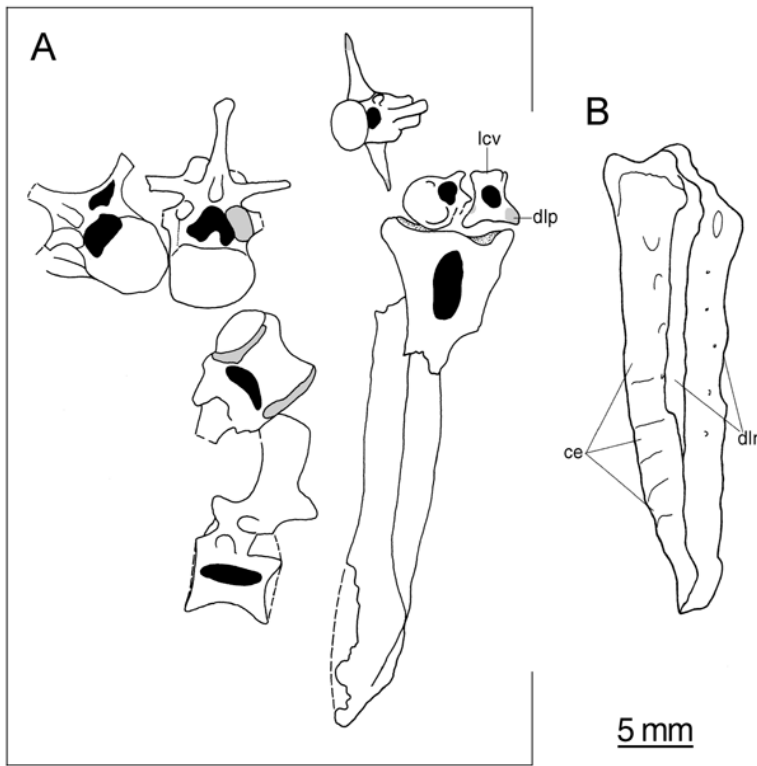
Fig. 25.   (A) Detail of the thoracic vertebrae, free caudal vertebrae, and pygostyle of *Confuciusornis sanctus* (GMV-2132; thoracic vertebrae removed from original position; see fig. 6). (B) Detail of pygostyle of *Confuciusornis sanctus* (GMV-2133). See Anatomical Abbreviations for definitions of labels.

eral one on each side. Left and right single elements also form the first gastral row of dromaeosaurids (Norell and Makovicky, 1997) and all other nonavian theropods (Claessens, 1996; P. Currie, personal commun.). The medial elements are laid in a zig-zag pattern, with the left element abutting against the preceding right element, which in turn contacts its preceding element of the left side. The individual elements become thinner caudally; the lateral elements are more slender than the medial ones. In specimen GMV-2152, although the gastral basket is exquisitely preserved and articulated, elements of the right side exceed those of the left side by two. The fact that several specimens of *Confuciusornis sanctus* do not show any evidence of gastralia raises questions regarding the proposed absence of gastral elements in other basal birds (e.g., Sanz et al., 1988).

The absence of uncinate processes in the rib cage of *Confuciusornis sanctus* was re-ported by Hou et al. (1996) and Peters (1996). Nevertheless, specimen GMV-2149 shows distinct uncinate processes articulating with six ribs (fig. 34). Remnants of uncinate processes or their caudodorsally oriented molds are also visible in several other specimens (e.g., GMV-2130, GMV-2146, and GMV-2147) (figs. 28, 31). The uncinate processes are long and often extend over nearly two subsequent ribs. Ossified uncinate processes have often been regarded as synapomorphic of ornithurine birds (e.g., Chiappe, 1996; Hou et al., 1996). These processes, however, have been found in oviraptorid and dromaeosaurid theropods (Clark et al., 1999). The presence of ossified uncinate processes in these nonavian theropods and in the confuciusornithids—clearly not ornithurine birds (see Systematics of the Confuciusornithidae, below)—suggest that their absence in other basal birds (e.g., *Archaeopteryx lithographica* [Martin, 1991], *Cathayornis yandica*
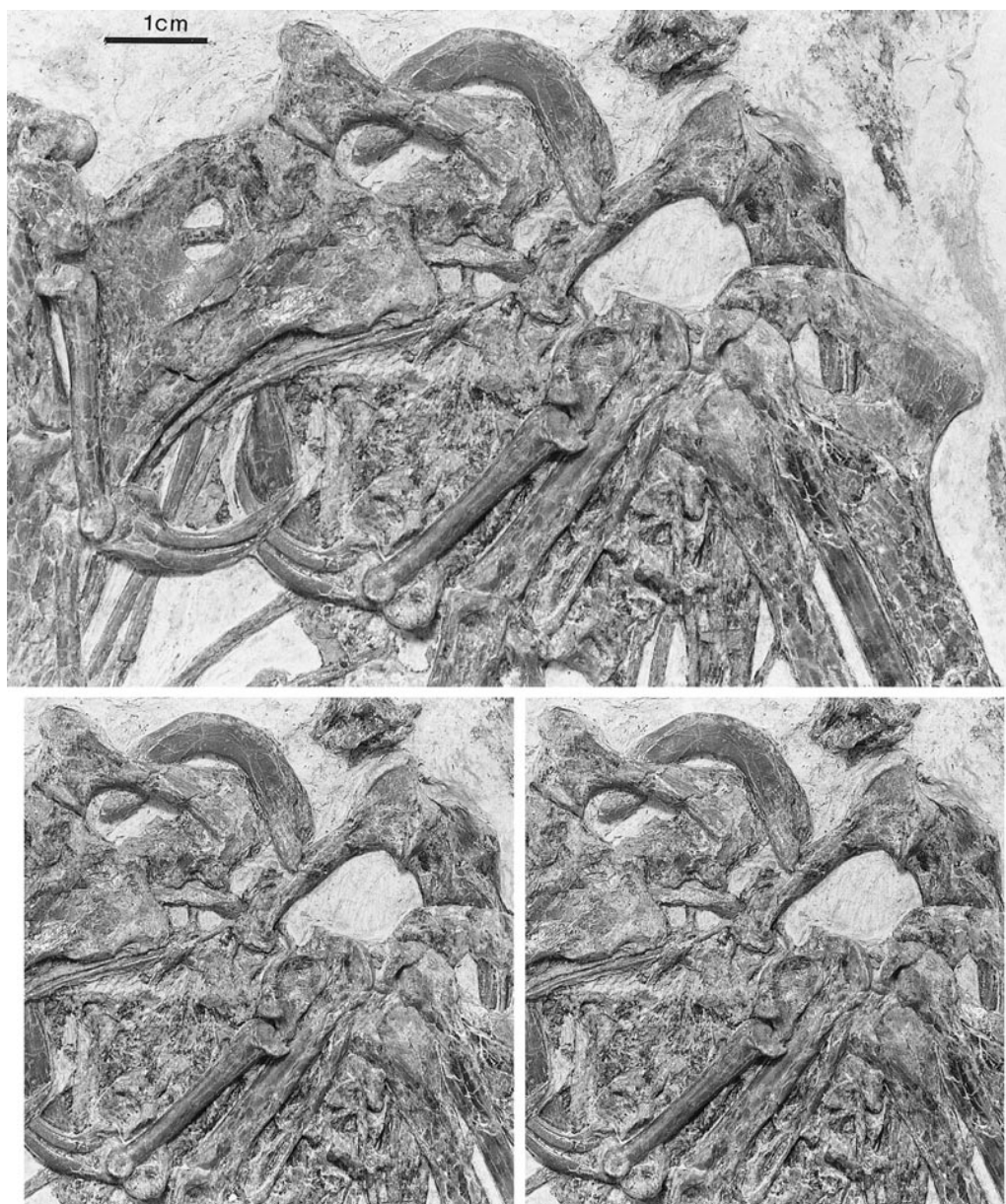
Fig. 26. Detail of the furcula, scapulocoracoid, proximal end of humeri, and metacarpals and digit I of *Confuciusornis sanctus* (GMV-2132). Furcula, scapulocoracoids, and left metacarpals and digit I in stereopair. See fig. 6 for labels.

[Zhou Z.-H. et al., 1992], *Concornis lacustris* [Sanz et al., 1995]) may be due to preservational factors or ontogenetic development. The fact that these processes are ossified in both oviraptorids and dromaeosaurids suggests that their ossification may be primitive for birds.

THORACIC LIMB

The forelimb is robust and bears powerful claws. Proportions among its elements are clearly primitive: the humerus is longer than the ulna, and the hand (based on digit II) is longer than either the humerus or the antebrachium (figs. 6–9; table 1).

Fig. 27.   Detail of the thoracic girdle and limbs of *Confuciusornis sanctus* (GMV-2133), dorsal view (humeri in caudal view). See Anatomical Abbreviations for definition of labels.

The humeral head is flat to slightly concave in caudal view (figs. 27, 37). The ventral corner of the proximal end prominently projects ventrally (fig. 26). The deltopectoral crest is large and dorsally expanded, extending for more than one-third the length of the humerus (figs. 27, 35–37). Cranially, the margin of this crest forms a distinct ridge (fig. 36); this ridge is not present in the crest's caudal margin (fig. 37). Opposite to the deltopectoral crest, the ventral margin of the humerus is concave, with no significant development of a bicipital crest (figs. 26, 35). On the caudal surface, the humerus lacks both a pneumotricipital fossa and foramen, as well as any evidence of a ventral tubercle (fig. 27).

A unique feature of *Confuciusornis sanctus* is that the deltopectoral crest is centrally pierced by a large, oval foramen that opens both cranially and caudally (figs. 26, 27, 35–37). We disagree with Martin et al.'s (1998) claim that this foramen is the result of an artifact created during preparation of the deltopectoral depression—many of the speci-

mens studied here have been carefully prepared, and there is little doubt that this foramen was a true feature of *Confuciusornis sanctus*. The functional interpretation of this foramen is complex. It is unlikely to be a pneumatic foramen (Hou et al., 1995b), which in neornithine birds constitutes the entrance of the humeral diverticulum of the clavicular air sac. In neornithine birds, however, this pneumatic foramen (or, in some instances, the multiple pneumatic foramina) is located inside the pneumotricipital fossa on the caudal surface of the proximal end and never on the deltopectoral crest (Baumel and Witmer, 1993). Furthermore, it never pierces the humerus from side to side. Among non-neornithine birds, a humeral pneumatic foramen is known only for an enantiornithine humerus from the Late Cretaceous of El Brete (Chiappe and Walker, in press). Thus, the unique configuration and position of the humeral foramen of *Confuciusornis sanctus* prevents its positive identification as a pneumatic feature.

There seems to be a degree of torsion be-

Fig. 28. Detail of the sternum, thoracic vertebrae, and ribs of *Confuciusornis sanctus* (GMV-2130). The sternum and thoracic vertebrae are in ventral and left lateral views, respectively. See Anatomical Abbreviations for definition of labels.

tween the proximal and distal ends of the humerus (fig. 27). Although the precise magnitude of this humeral torsion cannot be calculated due to the flattening and crushing of all available specimens, it appears that it was smaller than that of *Archaeopteryx lithographica* or the Enantiornithes (Chiappe, 1992).

The distal end of the humerus is significantly narrower than the proximal end (fig. 35). Caudally and cranially, there is no sign of either an olecranal fossa or a depression for the brachialis muscle (fig. 38). The condyles are primarily placed on the cranial surface (figs. 35, 36, 38). The dorsal condyle is suboval, and its main axis is inclined at approximately 66° with respect to the shaft's axis. The ventral condyle is smaller than the dorsal one and rounder. There is a robust

ventral epicondyle, cranioventrally located; two distinct fossae are present immediately distal to it (fig. 38). A round fossa excavates the dorsal margin of the distal end of the humerus. The flexor process is not developed.

The ulna and radius are essentially straight (figs. 35–37), although the former appears somewhat more bowed in GMV-2133. The ulna lacks any trace of quill knobs for the insertion of the follicular ligaments of the secondary flight feathers. The olecranon is feeble (figs. 36, 37). The proximal end of the ulna bears a bowl-shaped, round ventral cotyla and a slightly convex dorsal cotyla, projected cranially. The impression for the brachialis muscle is well developed. Proximally, the radius has a round articular facet. Just distal to it, on the interosseal surface, there
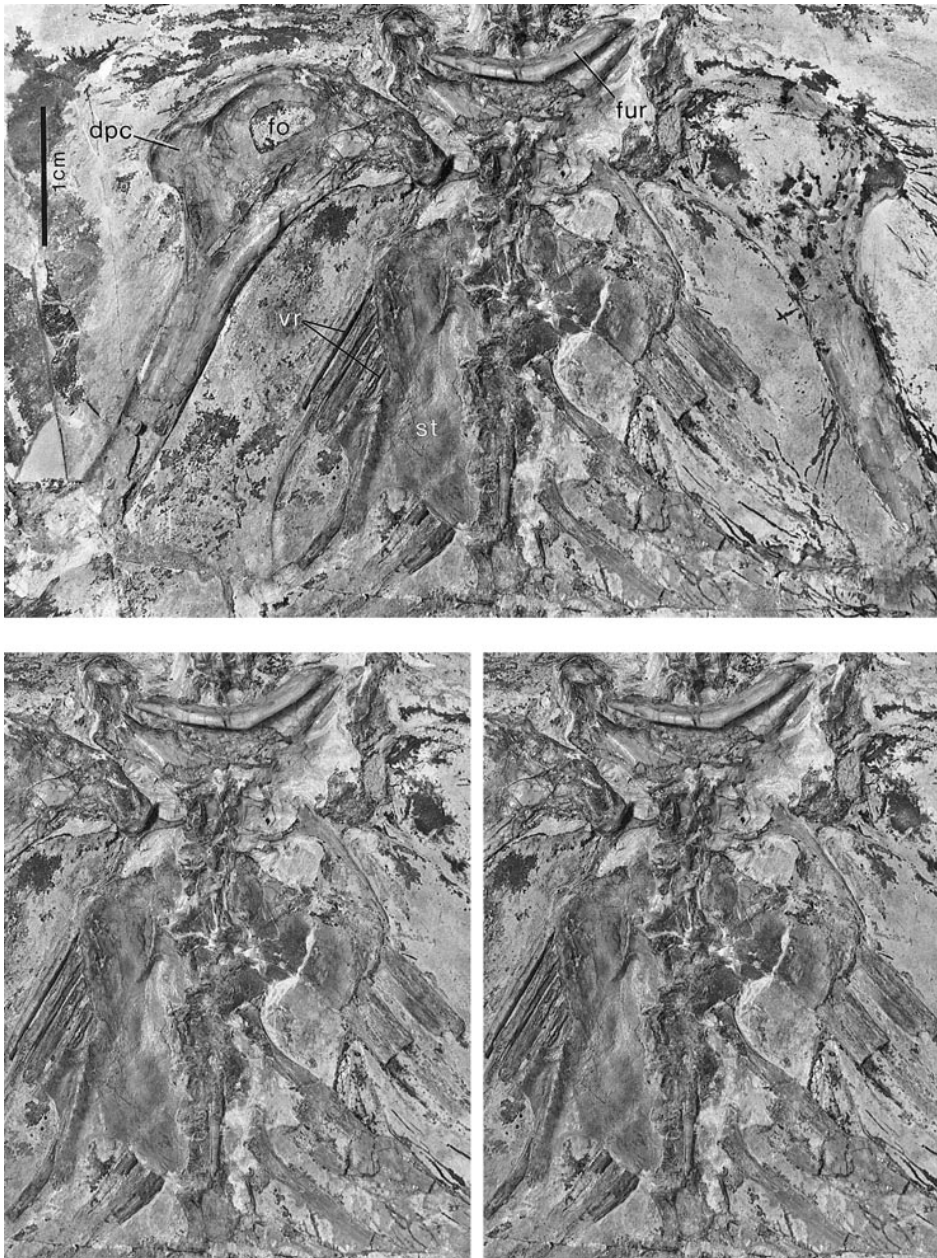
Fig. 29.   Detail of the sternum, furcula, ventral ribs, and humeri of *Confuciusornis sanctus* (GMV-2131). Furcula, sternum, and ventral ribs in stereopair. The sternum and humeri are in ventral and cranial views, respectively. See Anatomical Abbreviations for definition of labels.

is a small bicipital tuberculum. The shaft of the radius is cylindrical, lacking the longitudinal groove typical of enantiornithine birds (Chiappe and Calvo, 1994) (figs. 35–37). At midshaft, the radius is roughly 60%

the width of the ulna, a proportion that falls within the range of more advanced birds (Chiappe, 1996)—a similar proportion is also visible in some nonavian theropods. Distally, the radius widens and forms a transversally,
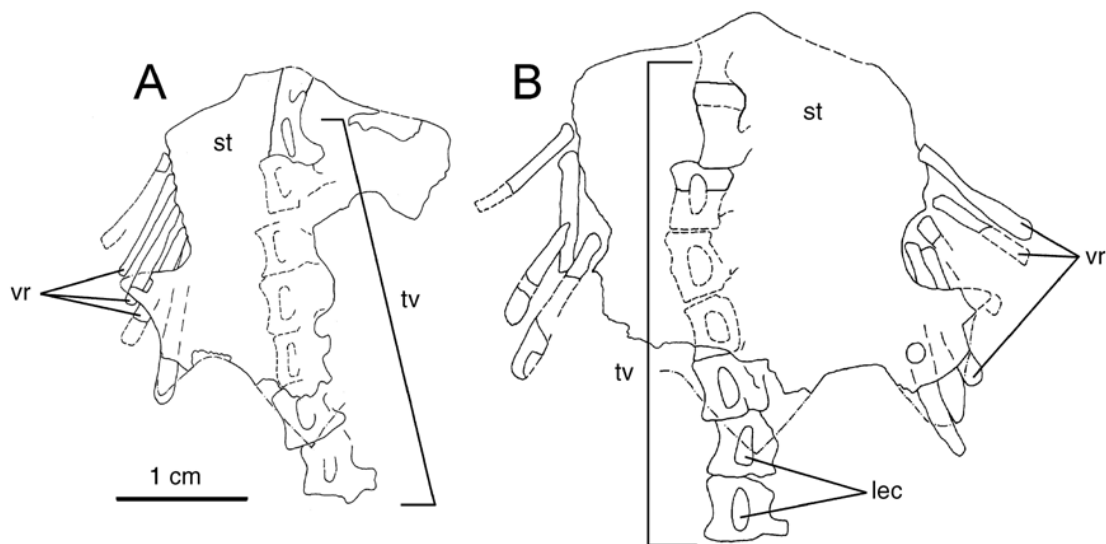
Fig. 30. Sternum, ventral ribs, and thoracic vertebrae of *Confuciusornis sanctus*: (A) GMV-2131 and (B) GMV-2130. The sternum and ventral ribs are in ventral view; the thoracic vertebrae are in left lateral view. See Anatomical Abbreviations for definition of labels.

subrectangular facet for the articulation with the radiale.

The radiale is subtriangular (fig. 37). Its dorsal aspect is saddle shaped, with a subtriangular metacarpal facet. Ventrally, it bears a deeply grooved, radial articulation by which it wraps around the distal end of the radius (this articulation is visible in the left radius of GMV-2132). The ulnare is also subtriangular but much smaller than the radiale (JM-UKr-1997/1).

The proximal end of the carpometacarpus forms a pulleylike carpal trochlea (figs. 26, 39). Even though metacarpals II (major) and III (minor) are fused proximally (contra Hou et al., 1995b, c), and with the semilunate carpal, they are not fused distally (figs. 6, 7, 26, 35, 39). Metacarpal I (alular) is not fused to metacarpal II (major). Metacarpal I is subrectangular and somewhat concave ventrally, lacking any sign of the extensor process. Its proximal end is concave, indicating the development of an incipient cranial carpal fossa. The distal articulation of metacarpal I forms a saddle-shaped ginglymous. Metacarpal I is roughly one-third the length of metacarpal II (figs. 26, 35, 39). This latter metacarpal is the longest and most robust of all three. The midshaft width of metacarpal II is more than twice that of metacarpal III. Proximally, the ventral face of metacarpal II bears an elongate tubercle somewhat displaced toward the metacarpal's caudal margin. The distal end of metacarpal II is formed by a robust ginglymous. The thin metacarpal III has a subcylindrical shaft. In contrast to what was stated by Hou et al. (1995b, c), this metacarpal is shorter than metacarpal II (figs. 26, 35, 39)—the opposite condition of enantiornithine birds. The intermetacarpal space between metacarpals II and III is relatively narrow, roughly as wide as the shaft of metacarpal III.

Digit I is composed of two phalanges—a long and straight proximal phalanx, which tapers toward its distal articulation, and a large, sharp, sickle-shaped claw, which in most specimens preserves remnants of its horny sheath (figs. 6, 8, 9, 26, 35, 39). The lateral and medial sides of this claw are marked by a wide, deep groove. The ungual phalanx of digit I bears a prominent flexor tubercle with a central depression.

Digit II is subequal in length to digit III (fig. 39; table 1), a condition comparable to that of oviraptorid theropods (Norell et al., 1995) but different from that of dromaeosaurids and *Archaeopteryx lithographica*.
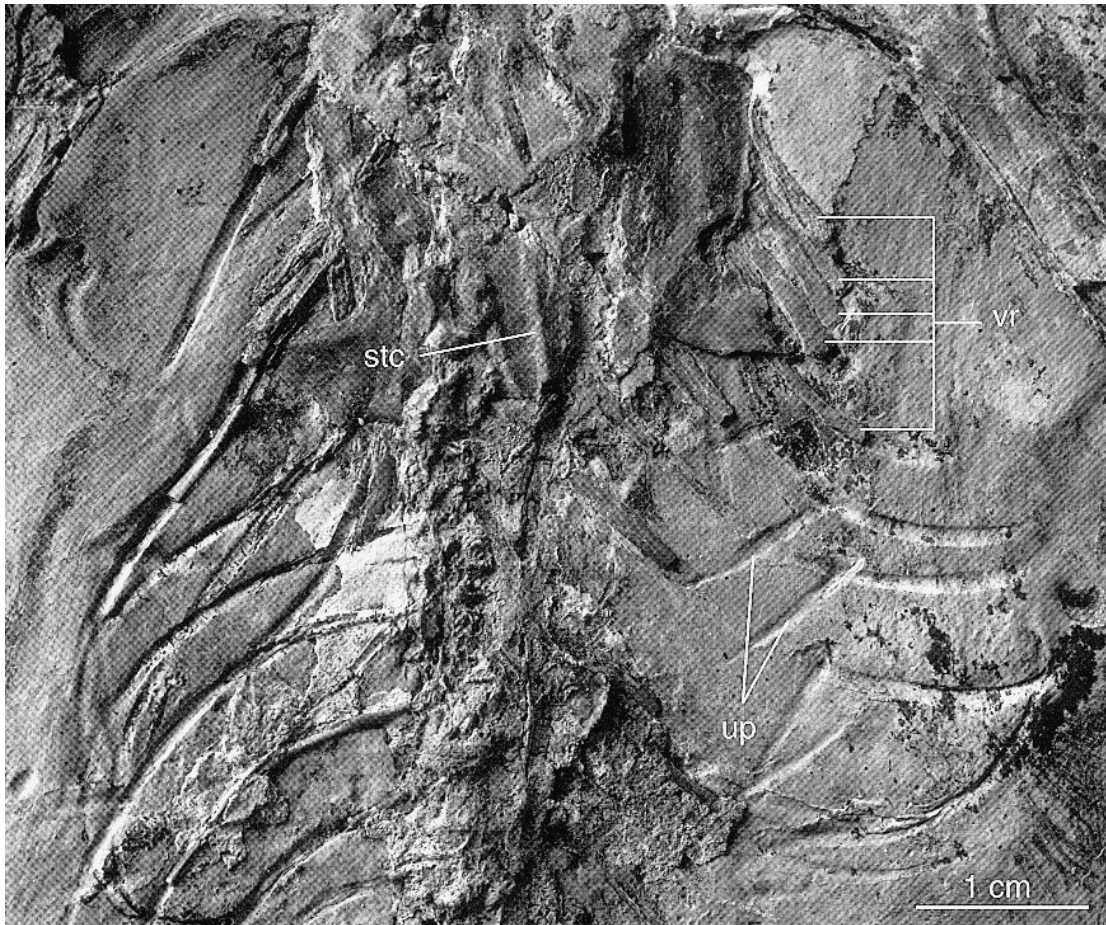
Fig. 31. Detail of the sternum and sternal and thoracic ribs of *Confuciusornis sanctus* (GMV-2147). See Anatomical Abbreviations for definition of labels.
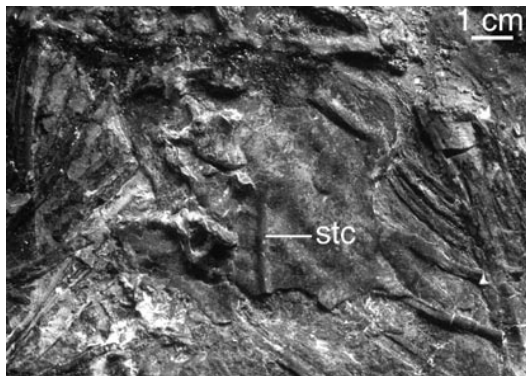

Fig. 32. Detail of sternum and ventral ribs of *Confuciusornis sanctus* (SMFAv-423). See Anatomical Abbreviations for definition of label.

The proximal phalanx of digit II is the most robust of all manual phalanges (figs. 6, 39). It is straight and of subequal width throughout its length. The intermediate phalanx of this digit is distinctly bowed (figs. 6, 39). It is longer, but much thinner, than the proximal phalanx. An intermediate phalanx longer than the proximal phalanx is a primitive condition found in *Archaeopteryx lithographica*, *Patagopteryx deferrariisi*, and nonavian theropods (Chiappe, 1996). Remarkable is the fact that digit II bears a very small claw (figs. 6, 39) with a weak flexor tubercle. This claw is significantly smaller than those of digits I and III, a condition strikingly different from that of other basal birds and nonavian theropods in which the size of the claw is at

Fig. 33.　Detail of gastralia and caudal end of the sternum of *Confuciusornis sanctus* (GMV-2152). See Anatomical Abbreviations for definition of label.
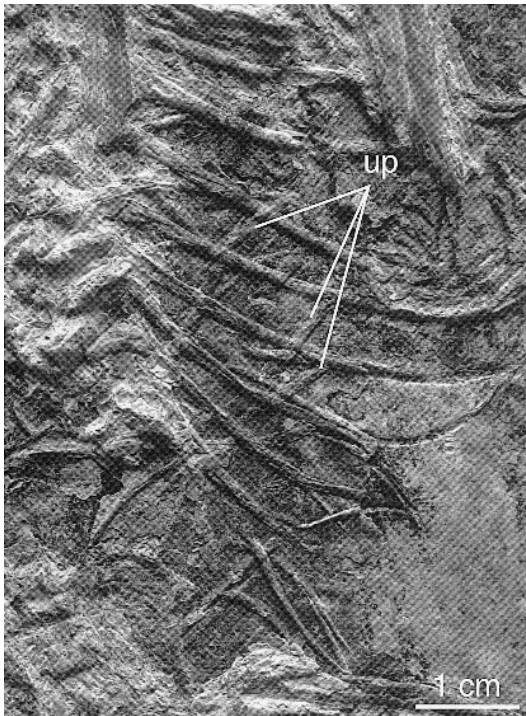
Fig. 34. Detail of the thoracic ribs and uncinate processes of *Confuciusornis sanctus* (GMV-2149). See Anatomical Abbreviations for definition of label.
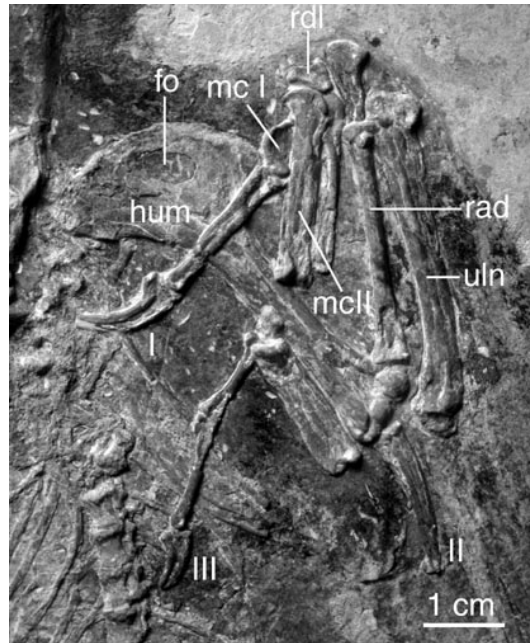

Fig. 35. Detail of left forelimb of *Confuciusornis sanctus* (JM-UKr-1997/1). See Anatomical Abbreviations for definition of labels.

best slightly smaller than that of digit I (e.g., Wellnhofer, 1985; Weishampel et al., 1990; Sanz et al., 1995; P. Currie, personal commun.).

Digit III contrasts with digit II in that it has a short and robust proximal phalanx and two long, slender, intermediate phalanges of roughly the same length (contra Martin et al., 1998) (figs. 6, 35, 39). This character is in contrast to the condition of most other birds, in which the proximal phalanx of digit III is

TABLE 1
Measurements (mm) of Forelimb of *Confuciusornis sanctus*

Maximum length measurement	Specimen							
	GMV-2130		GMV-2131		GMV-2132		GMV-2133	
	Left	Right	Left	Right	Left	Right	Left	Right
Humerus	47.86	47.69	41.01[a]	41.86	68.10	69.15	52.58	53.53
Radius	38.87	—	35.21	34.89	56.55	56.53	43.65	—
Ulna	40.73	—	—	—	—	58.45	45.38	—
Metacarpal III[b]	—	—	—	18.38	25.54	25.91	—	—
Metacarpal II[b]	—	21.11	—	20.78	32.86	33.15	—	—
Metacarpal I	—	5.99	—	6.45[a]	11.66	11.51	—	—
Digit III	—	—	—	32.61	—	—	—	—
Digit II	39.20	—	—	33.46	57.08[a]	60.03	45.69	—
Digit I	31.28	28.90[a]	26.01	26.38	46.60	46.69	—	—

[a] Estimated value.

[b] Includes semilunate carpal.

Fig. 36. Detail of humerus and ulna–radius of *Confuciusornis sanctus* (GMV-2132); humerus in cranial view. See fig. 6 for labels.

the longest (and usually the only one of this digit in extant birds), and that of *Archaeopteryx lithographica*, for which the first intermediate phalanx is the shortest of all (Wellnhofer, 1985). This digit ends in an arched ungual phalanx, somewhat smaller than that of digit I (figs., 6, 35, 39). Like that of digit I, this claw bears a well-developed flexor tubercle, which also possesses a central depression.

PELVIC GIRDLE

The ilium is long and low (fig. 40). The preacetabular wing has a round cranial end and a slightly concave lateral surface. The postacetabular wing is approximately 60% the length of the preacetabular wing. It is robust and tapers caudally. There is no brevis fossa in the postacetabular wing, unlike nonavian theropods. On the dorsal margin of the ilium of SMFAv-416, at the level of the acetabulum, there is a subtriangular and laterally projected process; a comparable process is known for *Rahonavis ostromi* (Forster et al., 1998a, b), Enantiornithes (Chiappe and Walker, in press), and a variety of extant lineages of birds. The length of the acetabulum is about 13% that of the ilium; this proportion is comparable to that of *Archaeopteryx lithographica* and several enantiornithine birds (Chiappe, 1996), but it is much smaller than that of nonavian maniraptorans (e.g., oviraptorids and dromaeosaurids). On its caudodorsal corner, there appears to be a small antitrochanter. Specimen BPV-2066

TABLE 2
Measurements (mm) of Hindlimb of *Confuciusornis sanctus*

Maximum length measurement	Specimen							
	GMV-2130		GMV-2131		GMV-2132		GMV-2133	
	Left	Right	Left	Right	Left	Right	Left	Right
Femur	41.78	—	—	—	—	—	46.85	—
Tibiotarsus	48.70	—	—	—	—	66.05	53.29	52.99
Tarsometatarsus	23.21	23.28	20.52	20.65	—	—	25.64	25.48
Metatarsal I	5.48	5.50	4.43	—	—	—	6.48	—
Digit I	9.61	10.11	7.65	7.95	—	—	11.41	11.06
Digit II	19.80	19.71	16.14	16.48	—	—	20.51	20.44
Digit III	25.23	25.11	19.94	20.00	—	—	22.79	25.34
Digit IV	—	21.76	17.03	—	—	—	29.22	24.05

Fig. 37.   Detail of humerus and ulna–radius of *Confuciusornis sanctus* (GMV-2133); humerus in caudal view. See fig. 7 for labels.
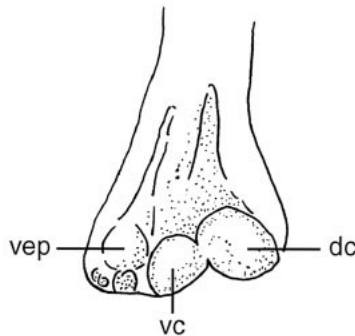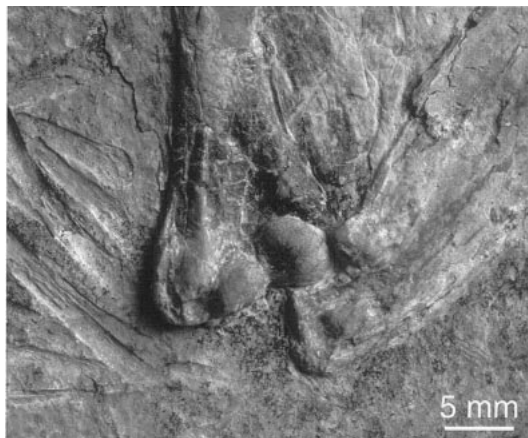

Fig. 38.   Detail of distal end of the left humerus (cranial view) of *Confuciusornis sanctus* (GMV-2154). See Anatomical Abbreviations for definition of labels.

(Guan et al., 1998) indicates that the ilia did not meet each other in the midline.

The ischium is relatively short: only 44% the length of the pubis (fig. 40)—a primitive condition shared by *Archaeopteryx lithographica* and nonavian maniraptorans (Chiappe et al., 1996). It is laterally compressed and tapers distally. Its caudal margin bears a long dorsal process (fig. 40). Although directed toward the postacetabular wing of the ilium, this process does not abut against the ilium; the overlapping seen in GMV-2133 is clearly due to crushing (fig. 40). A comparable ischial process is known for a variety of enantiornithine birds (Chiappe and Walker, in press), and less-developed processes of similar position are present in *Archaeopteryx lithographica* (Wellnhofer, 1974, 1985) and *Rahonavis ostromi* (Forster et al., 1998a, b), as well as in the nonavian theropod *Unen-*

lagia comahuensis (Novas and Puerta, 1997). The occurrence of this process in the ischium of *Confuciusornis sanctus*, Enantiornithes, and *Archaeopteryx lithographica* has been used to argue for a common origin exclusive of these three taxa (Hou et al., 1995c, 1996). Its presence in certain nonavian theropods (e.g., *Unenlagia comahuensis*), however, indicates that this character is most likely primitive. *Confuciusornis sanctus* lacks an ischiadic symphysis, a condition shared by dromaeosaurids (Norell and Makovicky, 1997) and most ornithothoracine birds (Chiappe, 1996).

The pubis is retroverted but not parallel to the postacetabular wing. It is not compressed laterally as in ornithurine birds (Chiappe, 1996), but it is thick and with a subtriangular to suboval cross section. The shafts of the two pubes converge distally to form a

Fig. 39. Detail of the right hand *Confuciusornis sanctus* (GMV-2132). Stereopair. See fig. 6 for labels.

straight symphysis that extends for 25–30% the total length of the pubis (figs. 40, 41). Each pubis can be individualized for most of the symphysis, but in the majority of the studied specimens they completely fuse to each other at the symphyseal tip. The distal end of the pubic symphysis is somewhat inflated, but it lacks any sign of a boot like expansion, as in *Archaeopteryx lithographica* (Wellnhofer, 1985), *Rahonavis ostromi* (Forster et al., 1998a, b), and several enantiornithines (e.g., *Cathayornis yandica* [Zhou Z.-H., 1995b] and *Sinornis santensis* [Sereno and Rao, 1992]).

PELVIC LIMB

The femur is typically straight (fig. 41), with only a slight craniocaudal curvature (figs. 7, 8). Its proximal end bears a round head, separated from the trochanter by a robust neck. In GMV-2154, the proximomedial surface of the head is excavated by a round capital fossa; this fossa can also be seen in SMFAv-423. Nothing hints at the presence of a notch separating lesser and greater trochanters, as in *Archaeopteryx lithographica* and many nonavian theropods. On the contrary, there seems to be a trochanteric crest, as in more advanced birds (Chiappe, 1996). Distally, the cranial surface lacks a patellar groove. On the lateral surface of the distal end, there is a well developed fibular trochlea, clearly distinguishable from the tibiofibular crest.

The tibiotarsus is straight and slightly longer than the femur (figs. 6–8; table 2). The
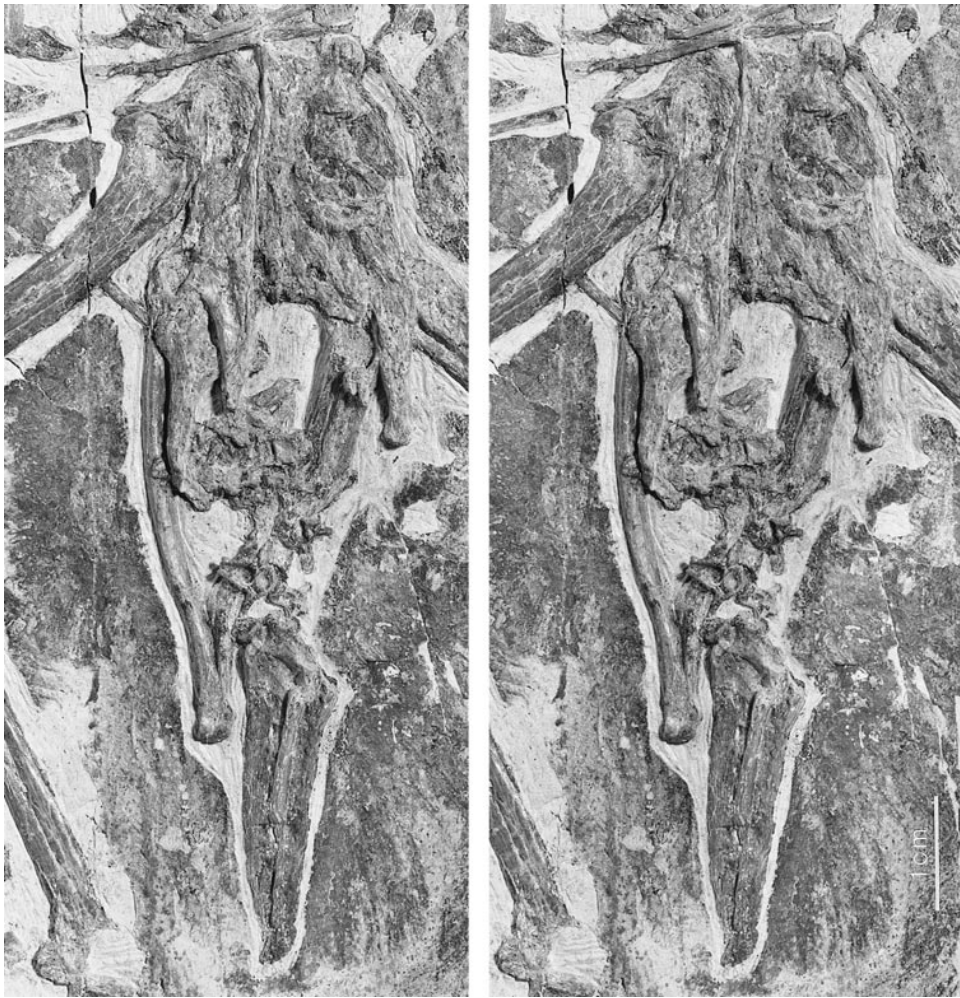
Fig. 40. Detail of the pelvis, free caudal vertebrae, and pygostyle of *Confuciusornis sanctus* (GMV-2133). Stereopair. See fig. 7 for labels.

fibular crest extends distally for the proximal two-fifths of the tibiotarsus. Caudally, on the proximal end of GMV-2133, there is a deep but short flexor fossa and a prominent popliteal tubercle (fig. 42). Distally, the proximal tarsals appear to be completely fused to each other and to the tibia; not a single suture separating these elements has been observed on any of the study specimens. Centered on the cranial surface of the distal end is a prominent oval tubercle (fig. 43). Such a tubercle is not known for other basal birds. Both the extensor groove and the supratendinal bridge are absent. In cranial view, the distal condyles of the tibiotarsus have an hour-glass

shape (fig. 43). These condyles are not proximally undercut by a deep groove, as is the case in Enantiornithes, *Patagopteryx deferrariisi*, and *Vorona berivotrensis* (Forster et al., 1996). The medial condyle is slightly wider than the lateral one, a primitive condition shared by other nonornithurine birds and nonavian theropods.

The fibula is slender and subcylindrical. The medial surface of its proximal end does not appear to be excavated by a fossa, as in some nonavian theropods. The elongate tubercle for the iliofibularis muscle projects laterally, as in *Patagopteryx deferrariisi* and the alvarezsaurids (Chiappe et al., 1996). Distal-
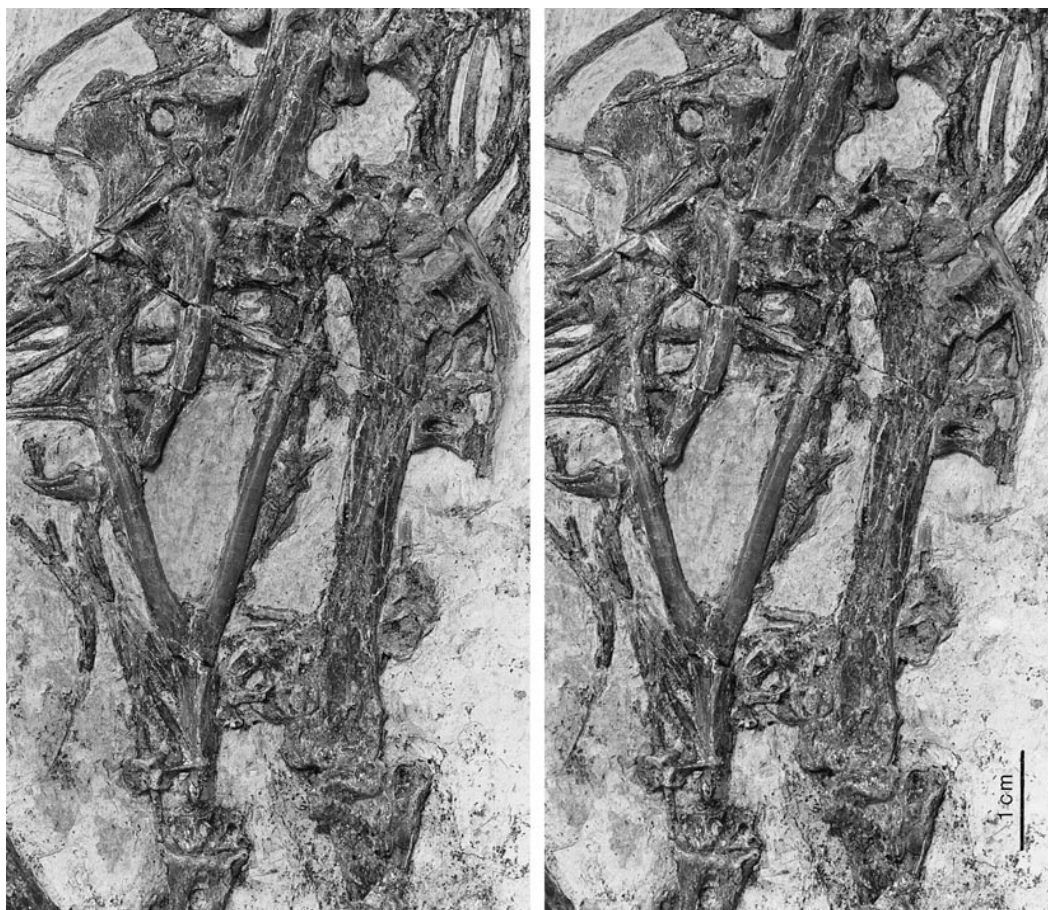
Fig. 41. Detail of the pubes and left femur of *Confuciusornis sanctus* (GMV-2132). Stereopair. See fig. 6 for labels.

ly, the fibula does not reach the proximal tarsals, but it extends considerably toward them, nearly reaching the level of the centrocranial tubercle of the distal end of the tibiotarsus.

The metatarsals are short, roughly half the length of the tibiotarsus (figs. 7–9; table 2). The metatarsals superficially resemble those of the Enantiornithes, although in detail they show significant differences. Metatarsals II–IV are proximally fused to each other (Hou et al., 1995b, 1996) and to the distal tarsals forming a tarsometatarsus (figs. 44, 45), a condition known for a variety of basal birds (e.g., *Archaeopteryx lithographica* and Enantiornithes) and nonavian maniraptorans (e.g., *Avimimus portentosus* [Kurzanov, 1987; Rich et al., in press] and *Elmisaurus*

rarus [Osmólska, 1981]). There is no evidence of an intercotylar eminence or a hypotarsus.

Metatarsal III is the longest; metatarsal IV is somewhat longer than metatarsal II (figs. 44, 45). Proximally, the contact between metatarsals III and IV is gapped by a short slit comparable to the lateral proximal vascular foramen of modern birds. The nearly undistorted tarsometatarsus of GMV-2131 shows that the cross sections of the midshafts of metatarsals II–IV are approximately ellipsoidal, subtriangular, and round, respectively. Although differently shaped, the cross section of metatarsal IV of *Confuciusornis sanctus* (e.g., GMV-2131) is slightly smaller than those of metatarsals II and III; this is minor compared with the difference between these
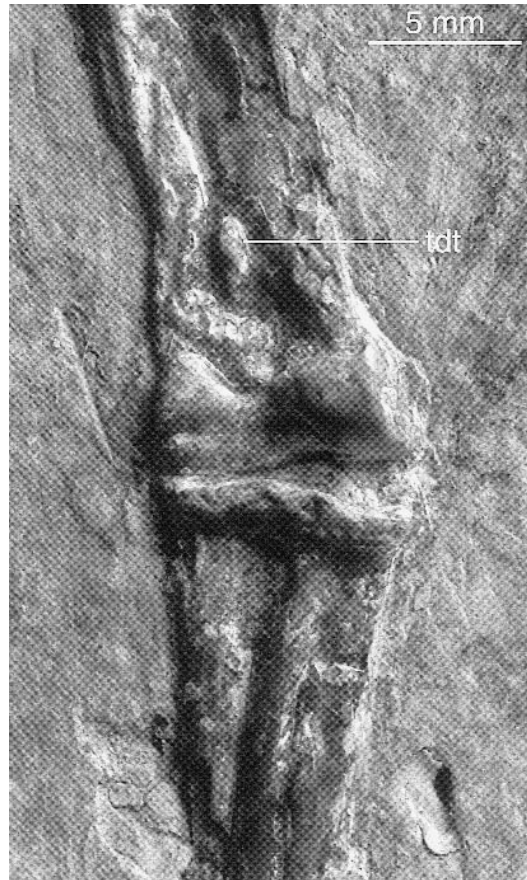
Fig. 43. Detail of distal end of the right distal end of tibiotarsus and proximal end of tarsometatarsus of *Confuciusornis sanctus* (GMV-2154). See Anatomical Abbreviations for definition of label.

Fig. 42. Detail of distal end of left femur and tibiotarsus (excluding distal end) of *Confuciusornis sanctus* (GMV-2133); feathers of the left wing are visible on the left half of the image. See fig. 7 for labels.

metatarsals in Enantiornithes (Chiappe, 1993; Chiappe and Calvo, 1994). On the dorsal surface of metatarsal II, somewhat proximal to its midshaft, there is an elongate tubercle, which is displaced toward the margin of metatarsal III (figs. 44, 45). This tubercle, comparable in position to that of Enantiornithes and some nonavian theropods (e.g., Rowe, 1988; Norell and Makovicky, 1997),

is presumably the area of attachment of the tibialis cranialis muscle (Chiappe, 1996). Initially interpreted as an enantiornithine synapomorphy (Chiappe, 1993), the presence of this tubercle on metatarsal II is probably a synapomorphy of a much more inclusive clade. Centered on the shaft of metatarsal III of SMFAv-423 and SMFAv-421, just proximal to the level of the tubercle of metatarsal II, there is another tubercle, although much smaller than that of metatarsal II. Most likely, the tibialis cranialis muscle also attached to this tubercle; this insertion has not left a scar (i.e., a tubercle) on the remaining specimens examined. Distally, the trochlea of metatarsal III bears a well-formed gingly-
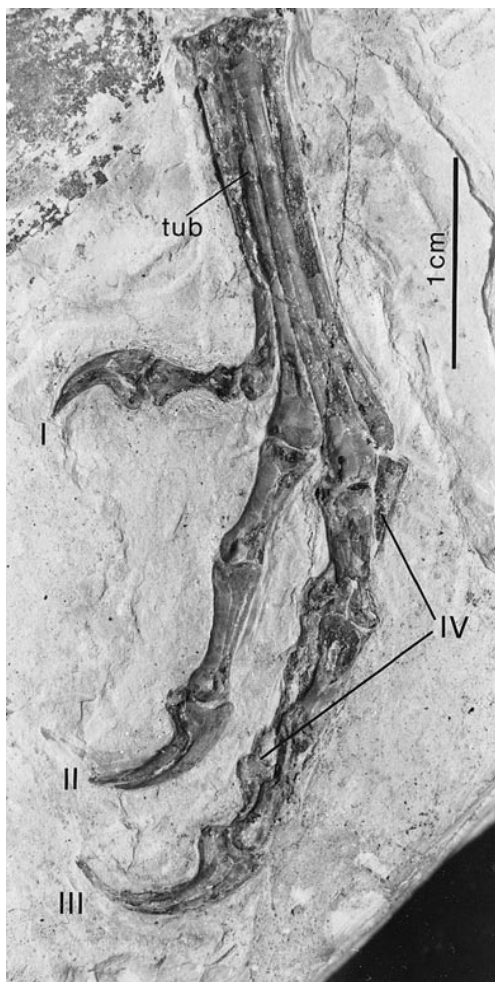
Fig. 44. Detail of left tarsometatarsus and foot of *Confuciusornis sanctus* (GMV-2130), dorsal view. See Anatomical Abbreviations for definition of labels.

moideal articulation (fig. 44). A ginglymous is not present in the trochlea of metatarsal IV, which is formed by an inflated, laterally compressed condyle (fig. 45). The distal trochlea of metatarsal II also lacks a ginglymoideal articulation. This trochlea is subequal in width to that of metatarsal III; in enantiornithine birds, this trochlea is significantly wider than that of metatarsal III (Chiappe, 1993). A gap between the distal ends of metatarsals III and IV corresponds to the distal vascular foramen.

Metatarsal I is attached distally to the lateral side of metatarsal II (fig. 44). The artic-

ulation for digit I is ball-like, protruding medially (fig. 45). The medial projection of the digital articulation of this metatarsal gives it a J-like appearance in dorsopalmar view (figs. 44, 46). This condition, however, should not be confused with the J-like morphology of avisaurid enantiornithines, in which this curvature is observable only in mediolateral view (Chiappe, 1993; Chiappe and Calvo, 1994). Metatarsal V is represented by a long, splintlike bone (Hou et al., 1995b) that extends for about one-third the length of the tarsometatarsus—retention of a metatarsal V is not uncommon among nonornithurine birds (e.g., *Archaeopteryx lithographica* [Ostrom, 1976] and *Vorona berivotrensis* [Forster et al., 1996]).

The foot of *Confuciusornis sanctus* is anisodactyl (figs. 44, 45). Its phalangeal formula is 2-3-4-5-x. Digit III is the longest toe (fig. 46; table 2), being subequal in length to metatarsal III. Digit IV is only slightly shorter than digit III and significantly longer than digit II. Digit I, the hallux, is short and lies in an elevated position. This digit is roughly 50% the length of digit II (table 2).

The proximal phalanx of the hallux is slightly shorter than its ungual phalanx (figs. 45, 46). This and the remaining ungual phalanges bear well-formed flexor tubercles and are approximately of the same size. In this latter respect, *Confuciusornis sanctus* differs from several enantiornithine birds (e.g., *Neuquenornis volans* [Chiappe and Calvo, 1994] and *Concornis lacustris* [Sanz et al., 1995]) in that the hallux's claw is not much larger than those of the remaining toes. *Confuciusornis sanctus* lacks the predatorial specializations of digit II seen in *Rahonavis ostromi* (Forster et al., 1998a, b) and retained to a lesser degree in certain more advanced birds, such as *Patagopteryx deferrariisi* (Chiappe, 1996). The proximal and intermediate phalanges of this digit are of subequal lengths (figs. 44–46). In digit III, the proximal phalanx is slightly longer than the two intermediate ones, which are roughly of the same length. Digit IV bears preungual phalanges that are shorter than all other phalanges (fig. 46). The proximal and last intermediate phalanges of this digit are of about the same length and slightly longer than the second and third phalanges. All preungual phalanges
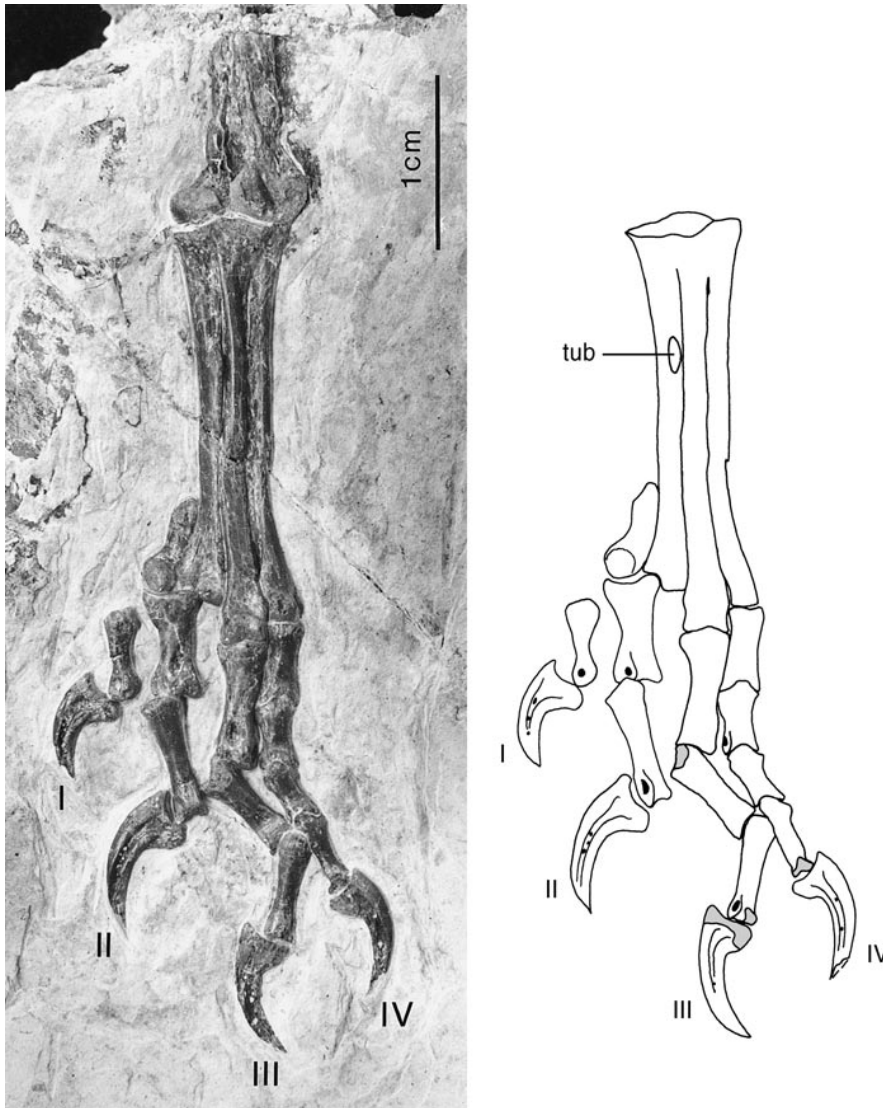
Fig. 45.   Left metatarsus and foot, and interpretive drawing, of *Confuciusornis sanctus* (GMV-2141), dorsal view. See Anatomical Abbreviations for definition of labels.

have well-developed collateral fossae on each side of their distal articular ends.

PLUMAGE

The plumage is well preserved in a large number of specimens (e.g., GMV-2130, GMV-2131, GMV-2146, GMV-2147, and GMV-2154) (figs. 8, 9, 47, 48). None of these specimens show any indication of the presence of an alula. Manual digit I lies completely outside the area of the wing (figs. 8,

9). This, combined with the fact that the claw of digit I is large, sharp, and massive, indicates that (1) *Confuciusornis sanctus* did not have an alula and (2) digit I was still functional as a prehensile organ.

Shafts and barbs are visible in many flight feathers (fig. 47). In several of the flight feathers of GMV-2130 and GMV-2146—primarily in the outermost primaries—there is clear evidence of asymmetric vanes, with a thin outer vane and a much wider inner vane

Fig. 46. Detail of the right foot of *Confuciusornis sanctus* (GMV-2133), plantar view. See Anatomical Abbreviations for definition of labels.

(fig. 47). The primary feathers are remarkably long; in GMV-2130 they could be over 210 mm, that is, approximately 3.5 times the length of the hand (figs. 30, 70). This proportion between the longest primaries and the length of the hand is maintained in other specimens (e.g., GMV-2131, GMV-2146, and GMV-2151). In GMV-2130, sparse covert feathers are preserved covering the primaries and secondaries. Contour feathers have also been reported by Hou et al. (1995c, 1996).

Despite Hou et al.'s (1996) claims, the general shape of the feathered tail of *Con-*

fuciusornis sanctus is strikingly different from that of the long, frondlike tail of *Archaeopteryx lithographica* (Gatesy and Dial, 1997). In GMV-2131, a narrow tuft of feathers surrounds the pygostyle, delimiting the shape of the rectricial bulb—nothing indicates the presence of rectrices forming the fanlike tail of more advanced birds (Gatesy and Dial, 1997) (fig. 9). In many specimens (e.g., GMV-2131, GMV-2146, GMV-2147, and GMV-2150), two very long, ribbonlike tail feathers project caudally from the area of the rectricial bulb (figs. 9, 48). In GMV-2150, these feathers are complete, measuring approximately 27 cm—slightly longer than the total skeletal length of this specimen (fig. 48). The width of these feathers is basically the same throughout its length—roughly 6 mm in GMV-2150 and GMV-2131. In GMV-2150, approximately 60 mm before the feathers' end, the feathers gradually increase in width, and two-thirds toward the distal end, they taper to a round edge (fig. 49). In all studied specimens for which a pair of long tail feathers is well preserved, neither the shaft nor the barbs are visible for most of the feathers' length. In GMV-2150, the rachis is visible in only the distal one-fourth of these feathers (fig. 49). In this portion, the rachis separates two distinct, symmetrical vanes in which barbs are well preserved. The absence of a shaft and barbs in the proximal three-fourths of these feathers is reminiscent of the ribbonlike condition of certain birds of paradise (e.g., *Paradisea ruber*). However, no extant bird with ribbonlike feathers shows a distal vaned differentiation (M. Lecroy, American Museum of Natural History, personal commun.).

Interestingly, whereas several specimens (e.g., GMV-2131, GMV-2146, GMV-2147, and GMV-2150) (figs. 9, 48) show a pair of long tail feathers, others (e.g., GMV-2130, GMV-2151, and GMV-2153) do not (fig. 8). This difference is clearly not due to preservational factors because all these specimens have exquisitely preserved plumage. This pattern in plumage variation has been regarded as an indication of sexual dimorphism (e.g. Hou et al., 1996; Martin et al., 1998).

ANATOMY OF *CHANGCHENGORNIS HENGDAOZIENSIS*

SKULL AND MANDIBLE

The skull of the only known specimen (GMV-2129) of *Changchengornis hengdaoziensis* has been compressed and deformed (figs. 52, 53), and it does not provide much information. It is subtriangular with a slender rostrum, somewhat longer than one-third of the skull's total length. The rostrum curves prominently, ending in a sharp tip (fig. 53). The rostrum of *Changchengornis hengdaoziensis* clearly differs from that of *Confuciusornis sanctus*, which is straight and more than one-half the total length of the skull (figs. 52, 53). The side of the rostrum, at least on its rostralmost portion (the only one preserving the lateral surface), is intensely perforated by longitudinal to suboval nutrient foramina (fig. 53). As in *Confuciusornis sanctus*, the presence of a rhamphotheca is suggested by such an intense perforation.

The premaxillae are fused at their rostral end but separated by a straight suture caudally (fig. 53). The boundary of the premaxilla with either the maxilla or the nasal is unclear. Thus, the interpretation of the bones roofing the antorbital cavity is complex. On the counterslab, an elongate nasal with a prominent lateroventral process may have overhung the antorbital cavity (fig. 52). Another elongate ossification medial to the nasal is probably the frontal process of the right premaxilla. In the slab, in a position that appears to be ventral and medial to the nasal, and rostral to its ventrolateral process, there is an ample, vertical bone perforated by a round foramen (fig. 53). This bone appears to be the nasal process of the maxilla, which medially walls the antorbital cavity. The round foramen perforating this maxillary process compares well with that of *Confuciusornis sanctus*, representing either the promaxillary or maxillary fenestra of *Archaeopteryx lithographica* and nonavian theropods (Witmer, 1997). A slender, rostrocaudally compressed lacrimal is preserved in lateral view in the counterslab (fig. 52). It forms a rostroventrally directed bar that separates the orbit from a suboval fossa, presumably the dorsal portion of a narrow antorbital fossa. The lacrimal appears to be fused to the

frontals. The angle at which it joins the frontal indicates that the caudodorsal corner of the antorbital fossa extended caudally more dorsally than ventrally.

The counterslab exposes the left quadrate in medial view (fig. 52). Its caudal margin has a sigmoid outline, being concave proximally and convex distally. The proximal end expands in what appears to be its otic articulation, although it is unclear whether the quadrate articulated with the braincase. Its distal end forms a round, medial condyle (fig. 52). Most of the orbital process is missing, although it is clear that it had a broad base, as in other nonornithurine birds (Chiappe, 1996). Nowhere in the preserved surface of the quadrate is there an indication of a pneumatic foramen.

The mandible is preserved in dorsomedial view in the slab (right) and in medial view (left) in the counterslab (figs. 52, 53). It appears to be much shorter than the skull, contrasting with the mandible of *Confuciusornis sanctus*, which is roughly of the same length as the skull. At the symphysis, the two rami are fused to each other although their rostral ends are separated by a deep notch (fig. 53). This notch gives a forklike appearance in dorsal or ventral view to the mandibular tip. This rostral mandibular notch is also present in *Confuciusornis sanctus*. The caudal portion of the mandible, rostral to its articular region, is remarkably tall, decreasing abruptly in height toward the articular surface (fig. 52). In this respect, *Changchengornis hengdaoziensis* also differs from *Confuciusornis sanctus*, in which the mandible is lower and of subparallel dorsal and ventral margins. The medial side of the mandibular ramus is deeply excavated, forming a broad fossa auditus. A large, suboval mandibular fenestra perforates the center of the fossa auditus. More caudally, there is a tiny, round caudal mandibular fenestra (i.e., the surangular foramen of nonavian theropods), as in *Confuciusornis sanctus*. The articular surface is saddle shaped (figs. 52, 53). It has a slightly concave transverse ridge, with facets sloping from it rostrally and caudally. The caudal facet of this ridge forms the rostral portion

Fig. 47. Detail of distal ends of primary feathers of *Confuciusornis sanctus* (GMV-2130). Note the asymmetry of their vanes.

of a large, subcircular basin at the very end of the jaw. There is no indication of a pneumatic foramen penetrating the articular. The caudal margin of the jaw is transversely straight.

VERTEBRAL COLUMN

The cervical series is mostly disarticulated and poorly preserved (figs. 50, 51). A mid-cervical element in the slab appears to be heterocoelic, at least in its cranial articular surface. Little can be said about the thoracic vertebrae, which are also disarticulated and worn away. Each thoracic centrum appears to be excavated by a lateral, oval fossa (fig. 50), as in *Confuciusornis sanctus* and other birds (e.g., enantiornithines, ichthyornithiforms, charadriiforms).

5 cm

Fig. 48. Specimen of *Confuciusornis sanctus* (GMV-2150) preserving a complete set of the elongate tail feathers (see fig. 49 for a detail of tail feathers)
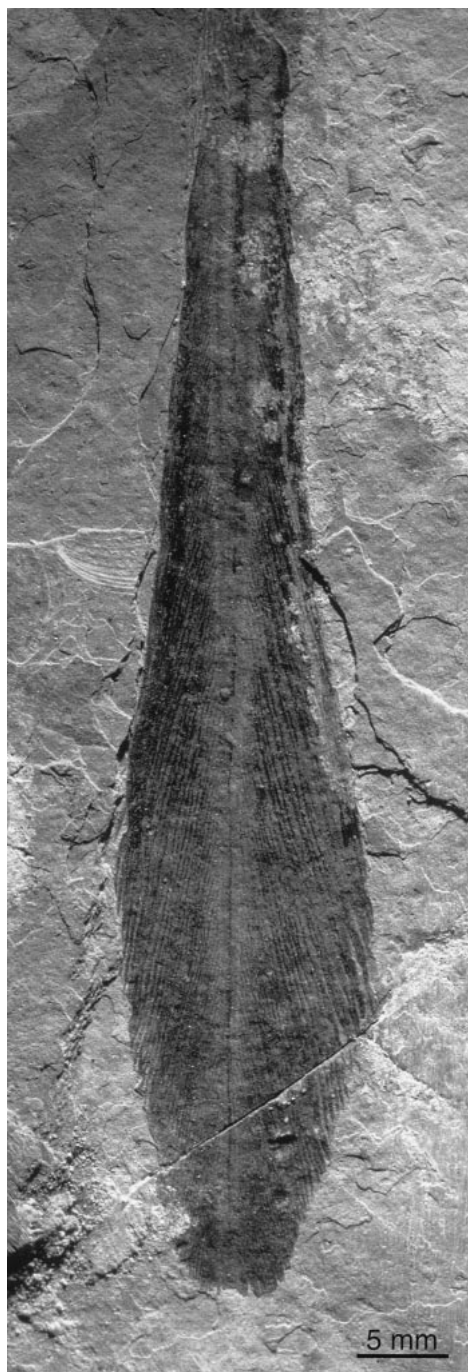
Fig. 49. Detail of distal end of the left elongate tail feathers of *Confuciusornis sanctus* (GMV-2150). Note the symmetrical rachis and barbed vanes.

The synsacrum is well exposed in ventral view in the counterslab (fig. 50). Judging by the number of transverse processes, the synsacrum is composed of seven elements completely fused to each other. Seven synsacral vertebrae also occur in *Confuciusornis sanctus*. The ventral surface of the synsacrum's caudal half bears a slight axial depression, although it is hard to say how much of this is a preservational artifact. The cranial articular surface is not well preserved, but the caudal one appears to be flat.

At least six free caudals are distinguishable. Their transverse processes are well developed and in some, small zygapophysial facets are preserved. The caudal series ends in a long, straight pygostyle with a round end (figs. 50, 51). The morphology of the pygostyle is comparable to that of *Confuciusornis sanctus*. This composite bone is as long or even longer than the combined lengths of the free caudals.

THORACIC GIRDLE

Most of the thoracic girdle is preserved in the slab (fig. 51); only impressions and fragmentary portions of the scapular blade are in the counterslab (fig. 50). The two coracoids are still in articulation with cranial portions of the sternum. The coracoid is elongate but only about half the length of the scapula (figs. 50, 51, 54). Comparable relative proportions of coracoid and scapula are present in *Confuciusornis sanctus*. The lateral margin of the coracoid is straight (fig. 54), unlike the convex margin of the Enantiornithes (Chiappe and Walker, in press). The dorsal surface of the left coracoid is exposed. It shows a dorsal, depressed area, which is most likely the result of a preservational artifact, as is indicated by a oblique crack toward its lateral margin (fig. 54). The enantiornithine dorsal coracoidal fossa (Chiappe, 1996) is not present. As in *Confuciusornis sanctus*, the coracoid and scapula fused to each other at their shoulder ends, forming a scapulocoracoid. At their junction, the scapulocoracoid bears a robust, tapering projection. The angle defined between the shafts of the two bones is roughly 90° (fig. 54). The scapular blade is slightly concave medially,

Fig. 50.   *Changchengornis hengdaoziensis* (GMV-2129a). See Anatomical Abbreviations for definition of labels.
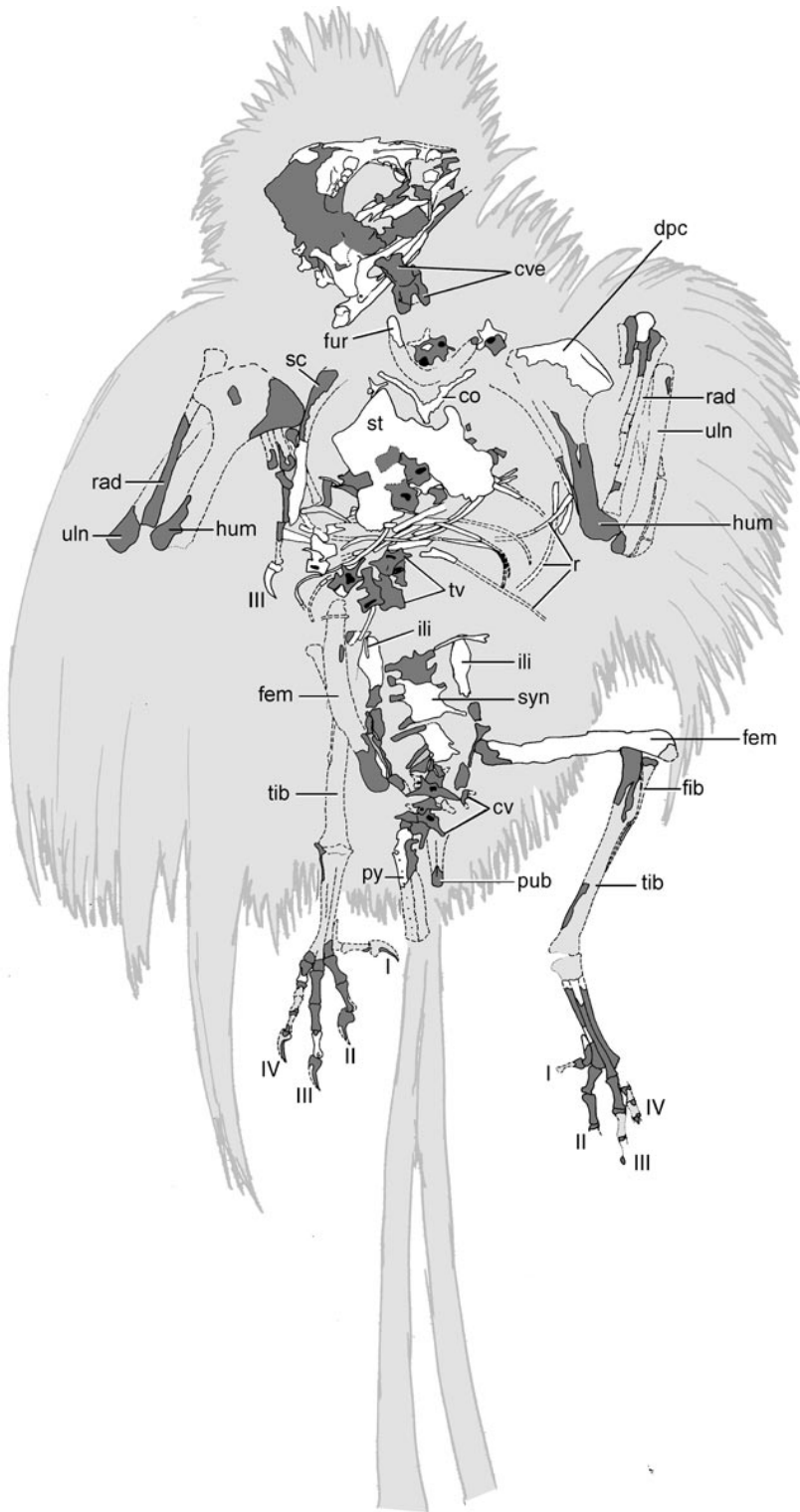
Fig. 50. Continued.

Fig. 51. *Changchengornis hengdaoziensis* (GMV-2129b). See Anatomical Abbreviations for definition of labels.
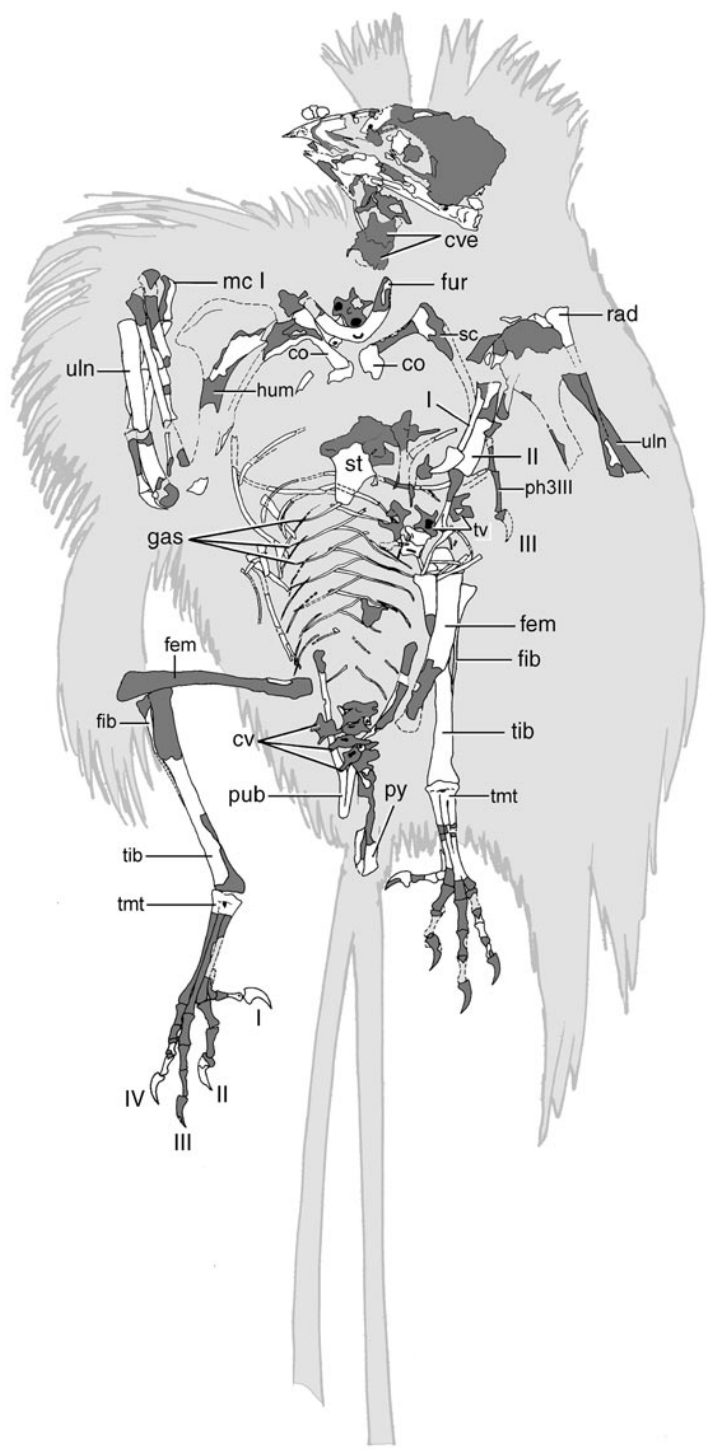
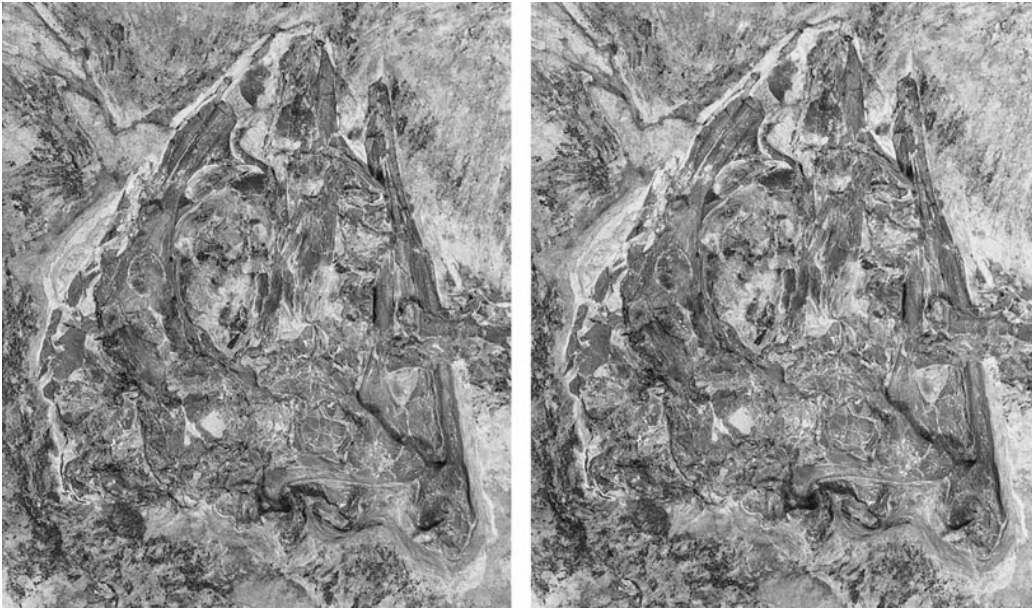Fig. 51. Continued.

Fig. 52.   Skull of *Changchengornis hengdaoziensis* (GMV-2129a). Stereopair. See Anatomical Abbreviations for definition of labels.
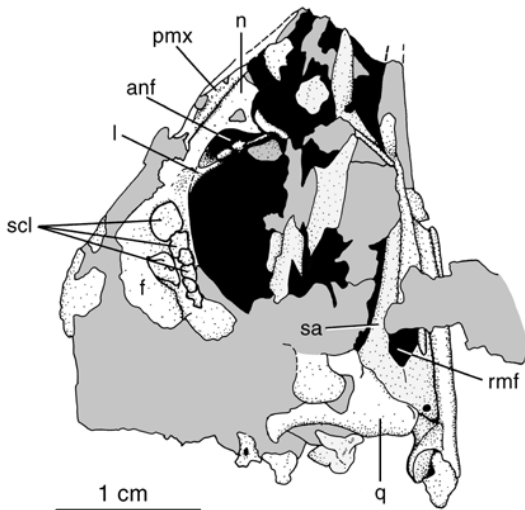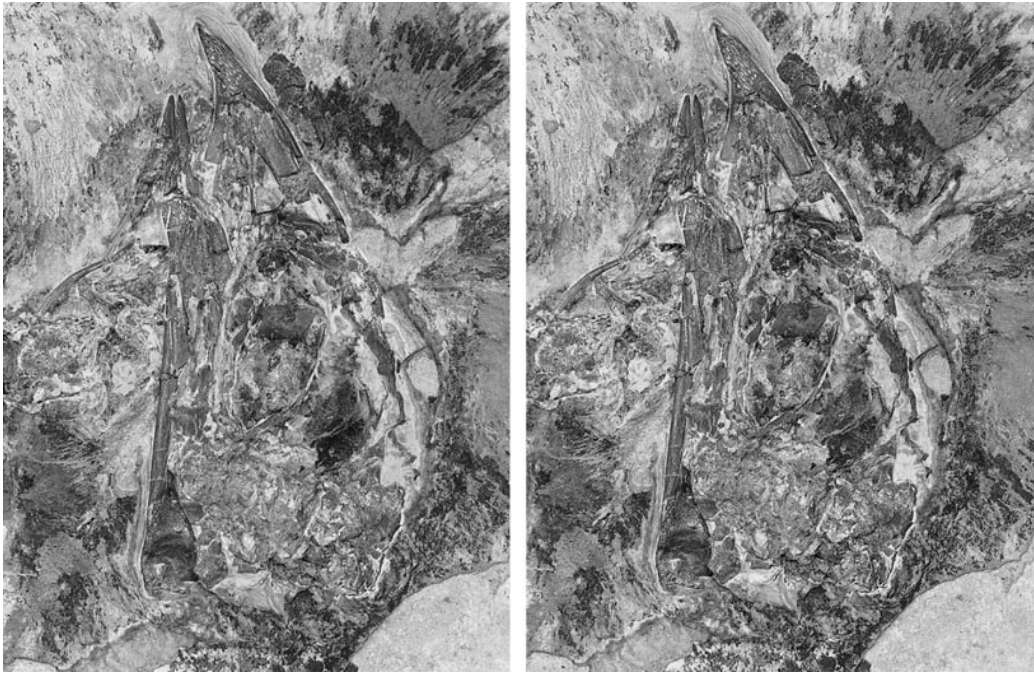

Fig. 52.   Continued.

presumably following the convexity of the rib cage.

As in *Confuciusornis sanctus*, the furcula is robust and boomerang shaped and has an interclavicular angle of about 85° (fig. 54). The cross section of the clavicular rami is in the shape of a horizontal 8, with shallow, central furrows both cranially and caudally.

This cross-sectional design appears to be different from that of *Confuciusornis sanctus*, which is essentially oval. At the junction of the two rami, the caudal surface of the furcula bears a weak but distinct tubercle (fig. 54). Nevertheless, this tubercle does not project ventrally, as does the hypocleideum of more advanced birds. This tubercle is absent in *Confuciusornis sanctus*, in which the caudal aspect of the rami's junction bears no more than a swell.

STERNUM, RIBS, AND GASTRALIA

The sternum was obviously large and long, even though its actual morphology is not clear due to its poor preservation. A large portion of it is preserved in the counterslab (fig. 50), and only its caudal end is present in the slab (figs. 50, 55). As in *Confuciusornis sanctus*, the sternum is virtually flat; in the only known specimen of *Changchengornis hengdaoziensis*, there is not even the incipient carina found in some specimens of *Confuciusornis sanctus*. In the slab, the caudal portion of the sternum preserves its natural margins. This portion indicates that the sternum ended in a median V-shaped body with a truncated end (fig. 55). The margins

Fig. 53.   Skull of *Changchengornis hengdaoziensis* (GMV-2129b). Stereopair. See Anatomical Abbreviations for definition of labels.
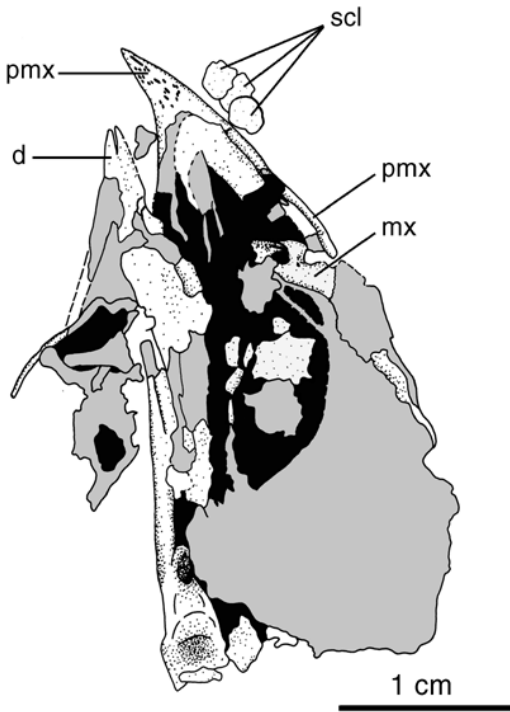

Fig. 53.   Continued.

of the sternum's caudal end are much steeper than the wider V-shaped caudal end of the sternum of *Confuciusornis sanctus*. The poor preservation of the sternal margins prevents the identification of rib facets, and even though some ribs are in contact with the sternum, it cannot be confidently stated whether ossified ventral ribs articulated with it.

Several disarticulated ribs and rib fragments are preserved on both the slab and counterslab. Nothing can reliably be identified as an uncinate process, although two tapering, short bones on the slab—left of the cranial half of the gastral basket—may be some of these processes (figs. 51, 55). The caudal end of the sternum dorsally overlaps two ribs (fig. 55). Because these bones are curved and compressed, instead of being straight and rodlike as are the gastral elements, they are interpreted as ribs, presumably the last floating ribs of the rib cage.

A well-developed basket of gastralia, comparable to that of *Confuciusornis sanctus*, is preserved in the slab (fig. 55). Eight rows of gastral elements follow caudally from the end of the sternum. As in *Confuciusornis*
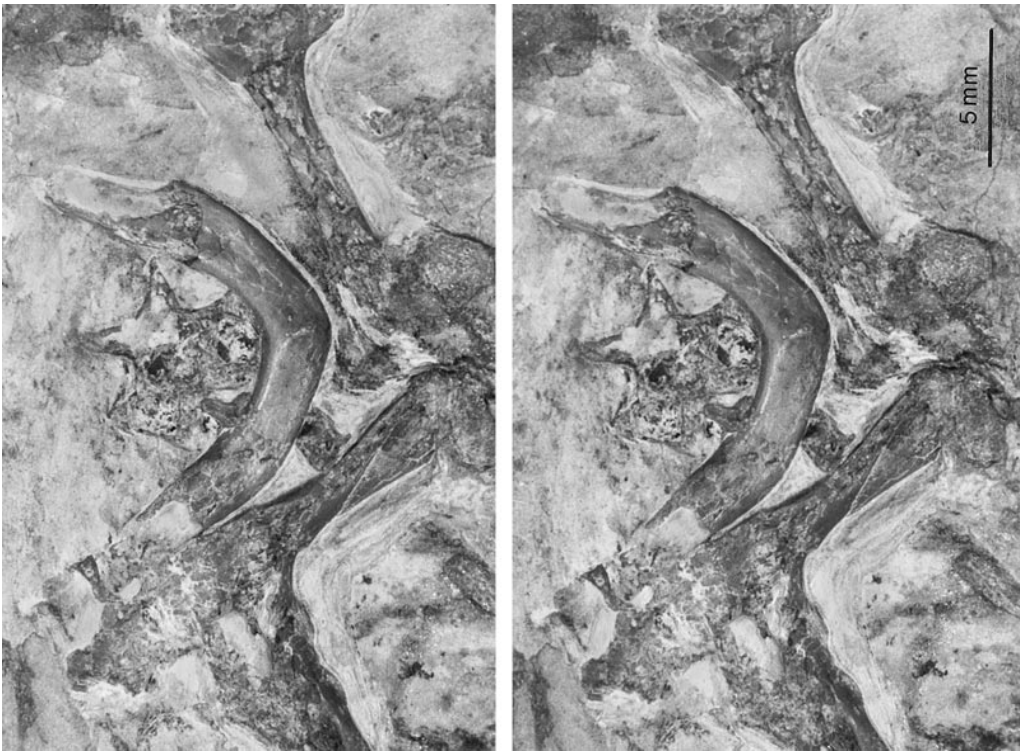
Fig. 54. Detail of the dorsal side of the furcula and scapulocoracoids of *Changchengornis hengdaoziensis* (GMV-2129b). Stereopair. See fig. 51 for labels.

sanctus, the gastral basket of *Changchengornis hengdaoziensis* is distinctly shorter than that of nonavian theropods (e.g., 12 rows form the gastralia of dromaeosaurid theropods; Norell and Makovicky, 1997). Each of these ribs is formed by two segments, a medial and a lateral one. Each row, thus, has four elements. In this respect, the gastral basket of *Changchengornis hengdaoziensis* differs from that of *Confuciusornis sanctus* in that the first row of gastralia in the latter is formed by a single pair of elements. Considering that the first row of the theropod gastralia is typically formed by a single pair of elements (Claessens, 1996; P. Currie, personal commun.), this difference may be a preservational artifact. The medial elements form a zigzag pattern in which an element of the left side contacts its preceding element of the right side, which is in contact with its preceding element of the left side, and so on (fig. 55). This zigzag pattern is typical of reptilian gastralia (Romer, 1956). The individual

elements decrease in length and thickness toward the pelvis, and, in general, the lateral elements are thinner and shorter than the medial ones. This latter condition is opposite to that of dromaeosaurids and troodontids, for which the lateral elements are longer than are the medial ones (Norell and Makovicky, 1997). As best seen in the right side of the fifth and sixth rows, lateral and medial elements overlap for quite an extended area (Fig. 55).

THORACIC LIMB

The wing morphology of *Changchengornis hengdaoziensis* compares well to that of *Confuciusornis sanctus*. The humerus is robust and with a subquadrangular-shaped proximal end (figs. 50, 51). The outer margin of the well-developed deltopectoral crest distally slants outward, ending in a truncated, short hook. On the cranial surface, the margin of the deltopectoral crest forms a distinct

Fig. 55.   Detail of sternum, gastralia, and manual fingers of *Changchengornis hengdaoziensis* (GMV-2129b), sternum and gastralia in dorsal view. See fig. 51 for labels.

ridge. The deltopectoral crest appears not to be perforated by a foramen, as it is in *Confuciusornis sanctus*. Unfortunately, neither of the two humeri is complete enough to be sure of this, and the bony sheet forming the central portion of the counterslab's left humerus becomes so thin that it may have been perforated. In the impression left on the slab by the left humerus, however, there is no indication of such a fossa (fig. 51), whereas in all observed specimens of *Confuciusornis sanctus*, this impression is always distinct. If a fossa perforated the humerus proximally, the position of it was somewhat different from that of *Confuciusornis sanctus*, in which it was located closer to the deltopectoral crest's outer margin. The proximal margin of the humeral head is straight in a nearly perpendicular plane to the shaft. Little can be

said about the ulna and radius; these bones are somewhat shorter than the humerus (figs. 50, 51; table 3). The ulnar shaft is significantly thicker than the cylindrical radial shaft: the diameter of the latter is roughly 50% of the former, a condition shared with *Confuciusornis sanctus* and more advanced birds (Chiappe, 1996).

As in *Confuciusornis sanctus*, the manual digital formula is 2-3-4-x-x. Metacarpal I is long and subrectangular, with a length of almost half the length of metacarpal II (figs. 50, 51; table 3). In this respect, *Changchengornis hengdaoziensis* differs from most other birds (including *Confuciusornis sanctus*), in which metacarpal I is one-third or less the length of metacarpal II. As in *Confuciusornis sanctus*, the proximal margin of metacarpal I is concave, suggesting the presence of a

Fig. 56. Detail of synsacrum and pelvis of *Changchengornis hengdaoziensis* (GMV-2129a) in ventral view. See fig. 50 for labels.

small cranial carpal fossa. The proximal phalanx of this digit is long and cylindrical. Its claw is large and robust, with deep lateral grooves and a well-developed flexor tubercle. It is unclear whether the metacarpals are fused to each other proximally, but metacarpals II and III remain unfused distally (figs. 50, 51). Metacarpal II is somewhat longer than metacarpal III. The proximal phalanx of digit II is robust, but in contrast to *Confuciu-*

sornis sanctus, it is longer than its intermediate phalanx. The latter is straight and not bowed (fig. 55) as in *Confuciusornis sanctus*. *Changchengornis hengdaoziensis* shares with *Confuciusornis sanctus* the presence of a claw of digit II that is much smaller than those of the other manual digits. As in *Confuciusornis sanctus*, digit III has a short proximal phalanx and two subequal intermediate phalanges that are roughly twice as long as

TABLE 3
Measurements (mm) of Forelimb and Hind-limb of *Changchengornis hengdaoziensis*

Maximum length measurement	Left	Right
Forelimb		
Humerus	33.53	—
Radius	31.07	30.35
Ulna	31.97	—
Metacarpal II[b]	17.07[a]	—
Metacarpal I	7.76	—
Digit III	—	21.76
Digit II	26.68	—
Phalanx 1-II	10.67	10.91
Phalanx 2-II	10.71	10.89
Hindlimb		
Femur	33.46	33.02
Tibiotarsus	36.59	36.86
Fibula	20.93	19.90[a]
Tarsometatarsus	20.64	20.34
Metatarsal I	5.21	5.13
Digit I	9.98	10.40
Digit II	16.59	15.88
Digit III	18.51	18.70
Digit IV	17.51	16.75

[a] Estimated value.

[b] Includes semilunate carpal.

the proximal phalanx. The ungual phalanx of this digit is strongly curved (approximately 180° of arc, including its horny sheath) and bears a distinct flexor tubercle. The ventral portion of this phalanx expands laterally below the phalanx's lateral groove.

PELVIC GIRDLE

Only portions of the ilia and pubes are preserved (figs. 50, 51), and there is not much that can be said about them. The preacetabular wings of both ilia are preserved in the counterslab, exposed in ventral view (fig. 56). They are elongate, extending rostrally beyond the cranial end of the synsacrum. The cranial half of the preacetabular wing shows moderate expansion. Its ventral surface is flat, although this may be a preservational artifact.

The shafts of the pubes are preserved in the slab (figs. 51, 57), although the impression of their distal ends is imprinted in the counterslab (figs. 50, 56). The pubic shafts form a V, and from the V's apex extends a

Fig. 57. Detail of right foot, pubes and pygostyle of *Changchengornis hengdaoziensis* (GMV-2129b); foot in plantar view. See fig. 51 for labels.

short, straight symphysis in which the pubes are fused only at its very end. The pubic apron is no more than one-third, and probably much less, the length of the pubis. It is uncertain whether there was a distal foot.

PELVIC LIMB

The femora are poorly preserved in both the slab and the counterslab. They are slight-

Fig. 58. Detail of flight feathers (right wing) and body feathers of *Changchengornis hengdao-ziensis* (GMV-2129a).
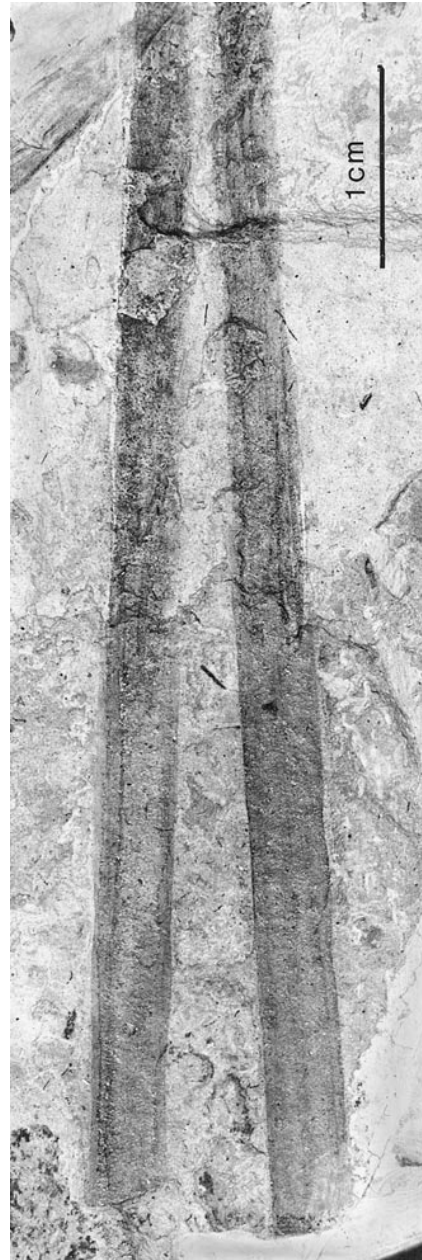

Fig. 59. Detail of the middle portion of the long tail feathers of *Changchengornis hengdao-ziensis* (GMV-2129a).

ly bowed and somewhat shorter than the ti-biotarsus (figs. 50, 51; table 3). The tibiotarsus is straight. Its fibular crest is weak, extending over the proximal third of the tibiotarsus. The fibula has a rodlike spine that does not seem to reach the proximal tarsals.

Metatarsals II–IV are fused at the proximal end of the metatarsus (fig. 57), and metatarsals III and IV also fuse to each other along their distal fourth; this is best seen in the right foot of the slab, which is exposed in plantar view (fig. 51). In contrast, in all the

observed specimens of *Confuciusornis sanctus*, metatarsals II–IV fuse only proximally. There is no evidence of a hypotarsus, although the proximal end of the plantar surface is formed by a thick ridge. This ridge is

Fig. 60. Composite specimen of *Confuciusornis sanctus* (GMV-2148). A slab containing several long and vaned feathers was glued to another slab including a small individual of *Confuciusornis sanctus* to simulate the long tail feathers seen in other specimens. The feet (inside box) are sculpted (see detail in fig. 61).

Fig. 61. Detail of the sculpted feet of a composite specimen of *Confuciusornis sanctus* (GMV-2148). Note the contact of the fossilized bone and the forgery in the upper portion of the photograph.

elevated and inflated in its central position. A long, distally tapering, splintlike metatarsal V is preserved on the right foot of the counterslab (fig. 50). As in nonavian theropods and those basal birds retaining a fifth metatarsal (e.g., *Archaeopteryx lithographica* and *Vorona berivotrensis*), this metatarsal abutted the plantar surface of metatarsal IV. Although its distal half is broken and displaced proximally, overlapping its proximal end, it is clear that metatarsal V extended for nearly one-third the length of metatarsal IV. Thus, metatarsal V of *Changchengornis hengdaoziensis* is proportionally longer than that of *Archaeopteryx lithographica* (25–30% the length of metatarsal IV, depending on the specimen; Wellnhofer, 1974, 1992) and somewhat shorter than that of *Confuciusornis sanctus* (approximately 36% the length of metatarsal IV in GMV-2133). Metatarsal III is the longest, followed by metatarsal IV and then metatarsal II. In the
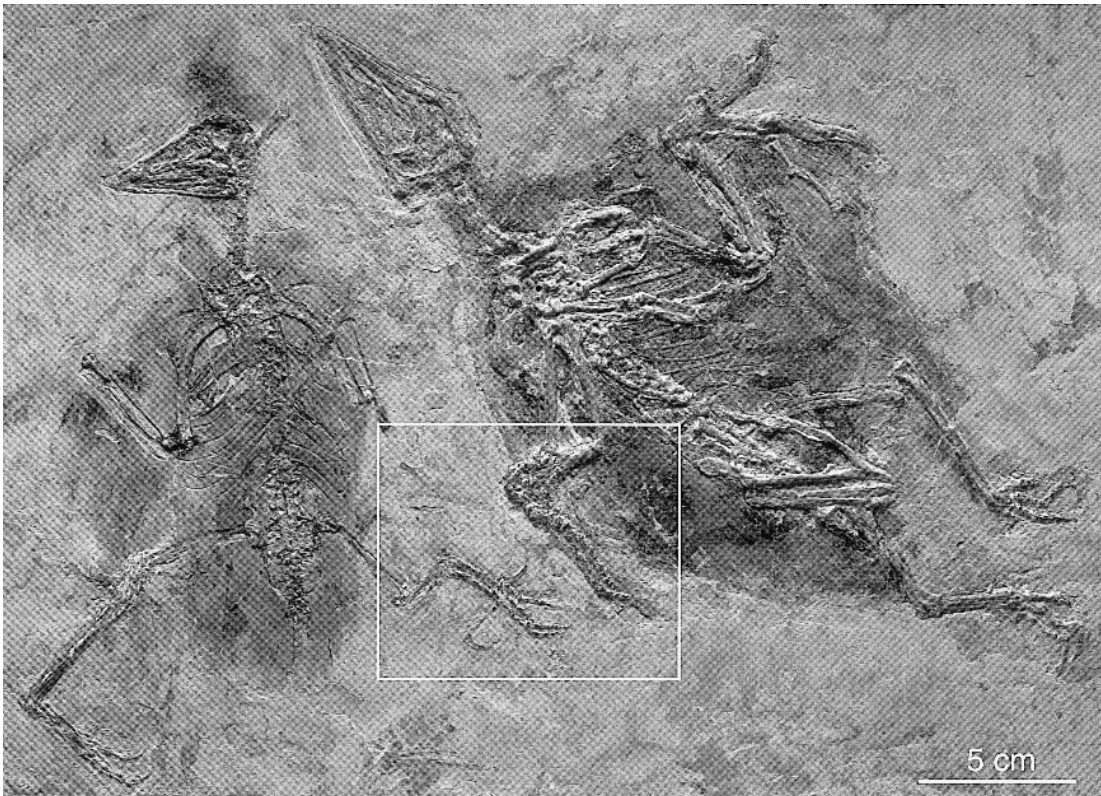
Fig. 62. Specimens of *Confuciusornis sanctus* (GMV-2153; two individuals) with sculpted additions (inside box; see detail in fig. 63).

Fig. 63. Detail of fake portions of the specimens of *Confuciusornis sanctus* (GMV-2153; two individuals) shown in fig. 62.

proximal half of the metatarsus, the widths of metatarsals II–IV are approximately the same, but in the distal half of the metatarsus, metatarsal III becomes thinner.

The trochleae of metatarsals II–IV are approximately of the same width (fig. 57). Metatarsal I is compressed laterally and, as in *Confuciusornis sanctus*, it has a round articulation for the hallux that projects perpendicularly from the metatarsal shaft. This gives the metatarsal a J-like appearance in dorsoplantar views (fig. 57). Metatarsal I closely adheres to the medial surface of metatarsal II, extending for about one-fourth the length of the latter. Distally, the trochlea of metatarsal I is only slightly more proximal than that of metatarsal II. Aside from their general outlines, details of the remaining trochleae are not distinguishable.

The phalangeal formula of the foot is typical of theropod dinosaurs: 2-3-4-5-x (figs. 50, 51, 57). Digit III is the longest, followed by digit IV, which is slightly longer than digit II. Digit I is fully reversed. Its length is approximately two-thirds the length of digit II (fig. 57). In this respect, *Changchengornis hengdaoziensis* differs from *Confuciusornis sanctus*, in which digit I is slightly less than half the length of digit II. The two phalanges of digit I are of subequal length. Its ungual phalanx is strongly arched, more than any

other pedal claw, and it bears a large, round flexor tubercle. The first two phalanges of digit II are of roughly the same length, and the claw is slightly longer. This claw also has a well-developed, round flexor tubercle. As in *Confuciusornis sanctus*, digit II does not exhibit the sickle-shaped claw of dromaeosaurids and troodontids (Gauthier, 1986; Currie and Padian, 1997) and the Malagasy bird *Rahonavis ostromi* (Forster et al., 1998a, b). In digit III, the first phalanx is longer than the following two, which are of subequal lengths. The flexor tubercle of the claw is well developed and the length of its bony portion is at least as long as the penultimate phalanx. The first and penultimate phalanges of digit IV are of subequal length and slightly longer than the two intermediate phalanges. The claw of this digit also bears a well-developed flexor tubercle.

PLUMAGE

The plumage forms a dark halo around the skeleton in both slabs (figs. 50, 51). As in *Confuciusornis sanctus*, feathers appear mostly to be preserved as carbonizations, but in some instances they are preserved as impressions. Barb and calami are visible in some of the flight feathers (fig. 58). As in some specimens of *Confuciusornis sanctus*, the only known specimen of *Changchengornis hengdaoziensis* bears a pair of long tail feathers that were probably as long as the body, although their distal ends are missing (figs. 50, 51). These ribbonlike feathers gradually increase in width distally. No barbs or calamus are distinguishable within the preserved sections of these feathers (fig. 59). This agrees with the morphology of *Confuciusornis sanctus*, in which barbs and calami are distinguishable in only the most distal portion of the tail feathers. Aside from these two feathers, the tail is short. As in *Confuciusornis sanctus*, there is no evidence of rectrices fanning from the rectricial bulb. Several isolated patches of short feathers are preserved in both the slab and counterslab. These appear to be contour feathers.

FORGERIES

Examination of several apparently complete skeletons of *Confuciusornis sanctus* reveal that entire portions have been carved or that multiple, incomplete specimens have been glued together to create composite ''complete'' specimens. Identification of the forgeries sometimes requires careful examination. Examples are shown in figures 60 and 62. The specimen of figure 60 (GMV-2148) is a composite made of a small specimen of *Confuciusornis sanctus* to which several long flight feathers have been glued near the pelvic region to imitate the long tail feathers of many other *Confuciusornis sanctus* specimens. The feathers are clearly not the tail feathers of *Confuciusornis sanctus*, because they are vaned and close examination reveals that there are more than two. These feathers

are comparable in length to the longest primaries of some of the largest specimens of *Confuciusornis sanctus*, although they could belong to some other feathered animal. The feet of GMV-2148 have been sculpted (fig. 61). The two specimens shown in figure 62 (GMV-2153) also exhibit sculpted portions. Both specimens are exposed in ventral view. The smallest specimen has the left foot and the right knee sculpted from a mix of sand and a binding mortar (fig. 63). The right hand and the left foot of the largest specimen have been sculpted in the same way (fig. 63).

The existence of these forgeries suggests that incomplete and disarticulated specimens of *Confuciusornis sanctus* may not be uncommon, indicating that many more specimens than previously believed may have been collected.

SYSTEMATICS OF THE CONFUCIUSORNITHIDAE

Hou (1997) assigned two specimens initially thought to be *Confuciusornis sanctus* to two new species, *Confuciusornis chuonzhous* and *Confuciusornis suniae*. *Confuciusornis chuonzhous* (IVPP-V10919) was based on a right foot articulated to a distal half of a tibiotarsus from the Chaomidianzi Formation (lower Yixian Formation of Hou [1997]) at the village of Huangbanji in the town of Shangyuan (Beipiao City, western Liaoning Province). Hou (1997) erected *Confuciusornis suniae* on the basis of a complete specimen (IVPP-V11308) from equivalent beds at the village of Sihetun (town of Shangyuan). Here we show that characters used by Hou (1997) to discriminate these two species have either been misinterpreted or are common to specimens of *Confuciusornis sanctus*. For example, *Confuciusornis chuonzhous* was believed to have three phalanges in its hallux; evidently, Hou (1997) misinterpreted metatarsal I as the proximal phalanx of this digit. Other differences between the hallux of *Confuciusornis chuonzhous* and *Confuciusornis sanctus* are clearly due to the incompleteness of the phalanges of this digit in the former species. Hou (1997) also argued for the presence of unfused proximal

tarsals in *Confuciusornis chuonzhous* compared with the fused astragalus and calcaneum of *Confuciusornis sanctus*. This interpretation, however, seems equivocal given the fragmentary nature of IVPP-V10919—the holotype of *Confuciusornis chuonzhous*. Moreover, even if correctly interpreted, this difference is most likely ontogenetic. The lesser curvature of the pedal claws claimed by Hou (1997) for *Confuciusornis chuonzhous* is not apparent to us.

Regarding *Confuciusornis suniae*, Hou (1997) pointed out several characters alleged to be different from *Confuciusornis sanctus*. Among these were the presence of a V-shaped notch at the tip of the snout, longer nasal processes of the premaxillae, and low and wide cervicals with reduced spinal processes. All these features, however, are not only common to IVPP-V11308, the holotype of *Confuciusornis suniae*, but to many specimens of *Confuciusornis sanctus* (all those for which the pertinent areas are preserved and well exposed). Other differences noted by Hou (1997) for *Confuciusornis suniae*— stronger long bones, smaller humeral opening, shorter tarsometatarsus, more recurved manual claws—are within the range of var-

iation observed among the large sample of specimens of *Confuciusornis sanctus* examined during the course of this study. The heart-shaped sternum noticed by Hou (1997) for *Confuciusornis suniae* cannot be confidently documented in IVPP-V11308; the lateral processes are identical to those of *Confuciusornis sanctus*. We find that the differences noticed by Hou (1997) between *Confuciusornis sanctus* and the two species erected by him are based on erroneous interpretations of the morphology of this species. *Confuciusornis suniae* and *Confuciusornis chuonzhous* are therefore considered to be junior synonyms of *Confuciusornis sanctus*. We have been unable to examine the recently described *Confuciusornis dui* (Hou et al., 1999) but at least some of the described characteristics of this species also fall within the morphological spectrum of *Confuciusornis sanctus*.

After examination of multiple specimens of *Confuciusornis sanctus* (see Referred Specimens in Systematic Paleontology, above) we were unable to find morphological characters that would confidently diagnose more than one species. As in the case of *Confuciusornis chuonzhous* and *Confuciusornis suniae*, some variation is clearly the result of preservational artifacts—most of the specimens are crushed and preserved in two dimensions—and the observed differences in plumage may be attributed to either sexual dimorphism or specific molting conditions (see Differential Plumage and Sexual Dimorphism, below). Aside from these presumably sex-correlated attributes, the only differences observed among the large sample of studied specimens are variations in size. None of the examined specimens, however, exhibit features characteristic of young ontogenetic ages. Based on the maximum length of their right humeri, GMV-2131 (one of the smallest studied specimens) is approximately 60% the size of GMV-2132 (one of the largest studied specimens); the relative proportions between the left femur of the smaller individual of GMV-2153 and the right femur of GMV-2154 suggest that the former individual was roughly 70% the size of the latter (table 4). Although most ornithologists working on living birds would argue that size differences of this magnitude

TABLE 4
Maximum Length (mm) of Humerus and Femur of *Confuciusornis sanctus*

Specimen	Humerus		Femur	
	Left	Right	Left	Right
GMV-2130	47.86	47.69	41.78	—
GMV-2131	41.01[a]	41.86	—	—
GMV-2132	68.10	69.15	—	—
GMV-2133	52.58	53.53	46.85	—
GMV-2146	41.95	42.69	—	—
GMV-2147	41.35	42.24	—	—
GMV-2149	53.52	—	45.45	44.48
GMV-2150	50.82[a]	51.54	44.96	—
GMV-2151	—	50.88	43.74	44.09
GMV-2153[b]	52.90	—	45.19	45.30
GMV-2153[c]	44.28	45.15	37.72	—
GMV-2154	63.14	64.19	51.72	53.08
GMV-2155	51.38[a]	52.16	44.51	45.79

[a] Estimated value.

[b] Larger specimen.

[c] Smaller specimen.

indicate specific differentiation, comparable size variations are not unprecedented among species of basal birds. The Eichstätt specimen of *Archaeopteryx lithographica* (Wellnhofer, 1974) is roughly half the size of the Solnhofen specimen (Wellnhofer, 1992), and these specimens are usually interpreted as the same species (e.g., Martin, 1991; Wellnhofer, 1992, 1993). Furthermore, a study of allometric scaling in six specimens *Archaeopteryx lithographica* (including both the Eichstätt and Solnhofen specimens) supports the idea that they all belong to the same species, interpreting the specimens of different sizes as members of a growth series (Houck et al., 1990). Although comparable studies have not been undertaken for *Confuciusornis sanctus* (most specimens still await further preparation), we believe that the observed size variation is the result of a growth series within a single species.

Hou et al. (1995b, 1996) were the first to propose a specific phylogenetic relationship for *Confuciusornis sanctus*. Hou et al. (1995b) placed this species within the Enantiornithes, as the sister-taxon of the Late Cretaceous, toothless *Gobipteryx minuta* from the Gobi Desert (fig. 64). Evidence for this systematic interpretation was disturbingly poor and based on a single character
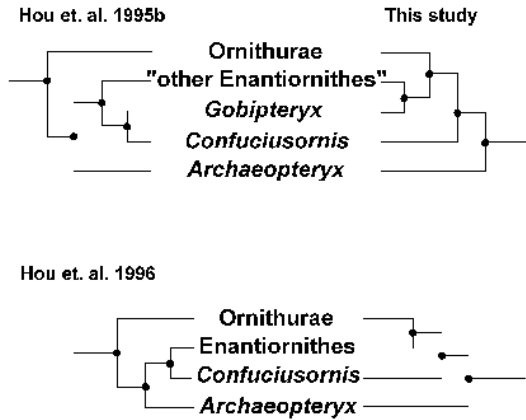
Fig. 64. Hou et al.'s (1995b, 1996) hypotheses of relationships of *Confuciusornis sanctus* as compared with that followed in this study.

(Chiappe, 1997a): the presence of an elongate coracoid—a condition common to all birds except for the most basal ones (e.g., *Archaeopteryx lithographica*). Furthermore, their support for a close relationship between *Confuciusornis sanctus* and *Gobipteryx minuta* was largely based on characters that are either not present in these two taxa (e.g., premaxilla elongated at the expense of the maxilla and well-developed nasofrontal hinge) or present in only one of them (e.g., the external nares are much smaller in *Gobipteryx minuta* than in *Confuciusornis sanctus*; the opposite is true for the antorbital fossa). Aside from the fact that these two taxa lack teeth—a condition independently evolved in other lineages of birds and nonavian theropods (fig. 65)—the only character common to these two species is the presence of a relatively robust mandible.

Hou et al.'s (1995b) view was slightly
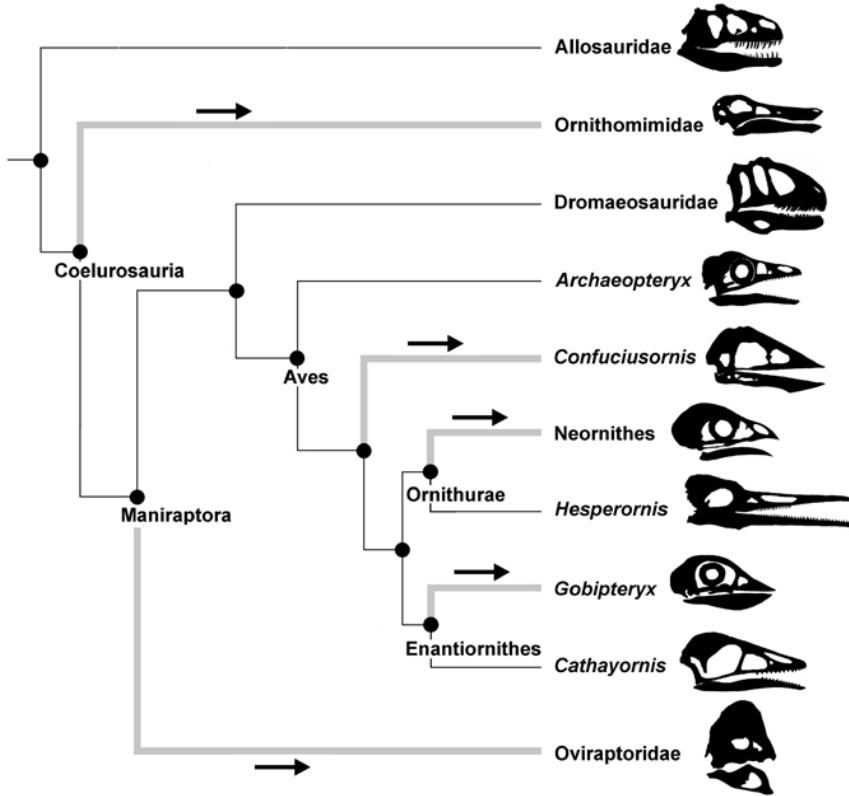
Fig. 65. Cladogram of major lineages of coelurosaurian theropods illustrating five independent cases of teeth loss. Within birds, teeth were lost independently at least in three lineages: in the confuciusornithids, the enantiornithine *Gobipteryx minuta*, and neornithine birds.

modified by Hou et al. (1996), who, after conducting a succinct cladistic analysis, supported the sister-taxon relationship between *Confuciusornis sanctus* and the Enantiornithes (fig. 64). Again, examination of the character evidence presented by these authors reveals that their phylogenetic argument is at best weak (Chiappe, 1997a). This time, the sister-group relationships between *Confuciusornis sanctus* and the Enantiornithes was based on the common possession of a short tail with a pygostyle and pleurocoels in their thoracic vertebrae (Hou et al., 1996). Nevertheless, a short tail with a pygostyle is present not only in Enantiornithes but in all birds other than some basal forms (e.g., *Archaeopteryx lithographica* and *Rahonavis ostromi*), and lateral excavations on the thoracic vertebral centra are also known for Ichthyornithiformes, Charadriiformes, Turniciformes, Procellariiformes, and to some degree in Hesperornithiformes.

Aside from the specific relationships between *Confuciusornis sanctus* and Enantiornithes proposed by Hou et al. (1995b, 1996), these authors followed Martin's (1983) initial claim that *Archaeopteryx lithographica* and Enantiornithes were more closely related to each other than to modern birds. Thus, Hou et al. (1995b, 1996) regarded *Confuciusornis sanctus* as an intermediate between *Archaeopteryx lithographica* and enantiornithine birds (fig. 64), placing all these taxa within the alleged clade ''Sauriurae.'' The paraphyletic status of ''Sauriurae'' has been discussed multiple times (e.g., Steadman, 1983; Olson, 1985; Chiappe, 1995a, b; Padian and Chiappe, 1998a) and has been documented by numerous cladistic analyses (e.g., Chiappe, 1991, 1995a, b, 1996; Chiappe and Calvo, 1994; Sanz et al., 1996, 1997; Forster et al., 1998a). Most characters regarded by Hou et al. (1995b, 1996) as shared by *Archaeopteryx lithographica* and *Confuciusornis sanctus* are either misinterpretations of the anatomy of the latter species (e.g., ''unfused'' distal carpals and metacarpals II and III), plesiomorphies (e.g., unreduced fingers), or poor descriptions (e.g., the ischia of these two taxa greatly differ except for the common presence of a proximodorsal process; the retroverted pubis of *Confuciusornis sanctus* is not like the vertical pubis of *Archae-
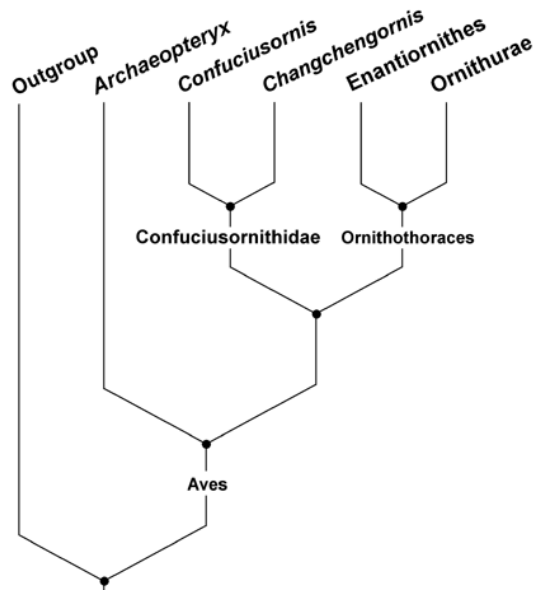
Fig. 66. Relationships of *Confuciusornis sanctus* and *Changchengornis hengdaoziensis* to other basal birds. See Chiappe (in press b) for cladistic analysis.

opteryx lithographica; the tails of these two species are completely different).

A cladistic analysis incorporating many basal bird species (Chiappe, 1997a, in press b) strongly supports the placement of *Confuciusornis sanctus* as the most immediate outgroup of the Ornithothoraces (fig. 66)—a clade encompassing the common ancestor of *Iberomesornis romerali* and modern birds plus all that ancestor's descendants (Chiappe, 1995a). This same cladistic analysis has supported the sister-taxon relationship between *Confuciusornis sanctus* and *Changchengornis hengdaoziensis*. These two taxa are placed within the Confuciusornithidae, here defined as the clade encompassing their common ancestor and all its descendants. Synapomorphies diagnosing the Confuciusornithidae include the presence of toothless jaws, a rostrally forked mandibular symphysis, a single foramen pneumatizing the maxilla's ascending ramus within the antorbital cavity, a pronounced and subquadrangular deltopectoral crest of the humerus, an ungual of manual digit II that is much smaller than those of manual digits I and III, and a V-shaped caudal end of the sternum.

IMPLICATIONS FOR THE EVOLUTION
OF AVIAN CRANIAL KINESIS

Extant birds all have kinetic skulls (Bock, 1964; Bühler, 1981; Zusi, 1993), permitting the independent protraction and retraction of the rostrum relative to the braincase (fig. 67). This type of movement is possible because the rostrum of living birds is connected to the braincase through only the movable articulations of the quadrate and palate and a flexible zone on the dorsal portion of the rostrum—the craniofacial hinge. The streptostylic quadrate is then able to swing rostrocaudally and, through the strut action of the jugal bar and palate, protract or retract the rostrum at the level of the dorsal flexion zone (Bock, 1964; Bühler, 1981; Zusi, 1993).

Two basic types of cranial kinesis occur among living birds (Bock, 1964; Bühler, 1981; Zusi, 1993) (fig. 67). In a prokinetic
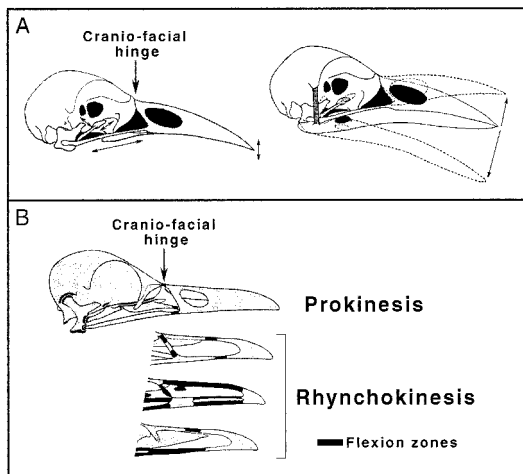
Fig. 67. Two basic types of cranial kinesis occur among living birds (Bock, 1964; Bühler, 1981; Zusi, 1993). In a prokinetic skull the rostrum acts as a single unit, maintaining the same shape during its protraction or retraction (A). Typically, there are three flexion zones between the rostrum and the orbital region (B): (1) a dorsal flexion zone (the craniofacial hinge), (2) flexion zones in each jugal bar, and (3) flexion zones in each palatine bar. In a rhynchokinetic skull (B), part of the rostrum changes shape during its protraction–retraction. The dorsal flexion zone of the rhynchokinetic skull is displaced somewhat rostrally than it is in the prokinetic skull. Figure modified from Bock (1964) and Bühler (1981).

skull, the rostrum acts as a single unit, maintaining the same shape during its protraction or retraction; typically, there are three flexion zones between the rostrum and the orbital region: (1) a dorsal flexion zone (the craniofacial hinge), (2) flexion zones in each jugal bar, and (3) flexion zones in each palatine bar. In a rhynchokinetic skull, part of the rostrum changes shape during its protraction–retraction. The dorsal flexion zone of the rhynchokinetic skull is displaced somewhat rostrally to that in the prokinetic skull. Unlike prokinetic skulls, rhynchokinetic skulls have two bending axes within the dorsal flexion zone. The movement between bony elements involved in either prokinesis or rhynchokinesis is essentially the same.

Several modifications of the basal archosaurian skull appear to be responsible for the development of the unique cranial kinesis of living birds. Sutural contacts between the jugal and postorbital, the quadratojugal and the squamosal, and the jugal bar and palate through the ectopterygoid would prevent, or strongly limit, the kinetic movements characteristic of the modern avian skull (Zusi, 1993). Thus, the loss of the postorbital or its contact with the jugal, the disappearance of the ectopterygoid, and the reduction of the squamosal process of the quadratojugal are important transformations for the development of the modern cranial kinetism of birds.

Hou et al. (1995b) described the skull of *Confuciusornis sanctus* as prokinetic. Nevertheless, considering the anatomical features here described, we find this proposal difficult to defend. As mentioned earlier, *Confuciusornis sanctus* is the only known bird with a primitive diapsid cranial design (fig. 20). The robust postorbital–jugal bar probably blocked any rostrocaudal movement of the jugal bar that may have been imparted by the streptostylic quadrate. Furthermore, no craniofacial hinge appears to be present (contra Hou et al., 1995b)—the caudal ends of the frontal processes of the premaxillae are thick and firmly attached to the frontals—and the jugal is remarkably tall at the rostral margin of the orbit, indicating the absence of a flex-

ion zone at the ventral base of the rostrum. In addition, the jugal bar of *Confuciusornis sanctus* may have been anchored to the palate by the ectopterygoid, if this is the ossification identified as such in the skull of GMV-2146 (fig. 19). All these features strongly suggest the absence of any modern type of avian kinesis, and probably of any kind of kinetism, in the skull of *Confuciusornis sanctus* (Chiappe et al., 1998b; Peters and Ji Q., 1998). Previous claims regarding the skull of this bird as prokinetic (Hou et al., 1995b) are not substantiated by the available anatomical data.

Interpretations of the kinetic properties of the skull of *Confuciusornis sanctus*, other basal birds, and their closest theropod relatives bear directly on our understanding of the evolution of the cranial kinesis of modern avians. Several studies have dealt with the kinetic properties of the skull of various primitive birds. The degree of confidence placed on these inferences depend not only on the quality of preservation (often poor) of the available fossils but also on the assumption of a close correlation between the observed morphology and the function associated with this morphology in extant organisms. Studies demonstrating that this assumption is sometimes unwarranted (see Lauder, 1995 for a review) indicate that these interpretations should be treated with caution. Certain conclusions, however, can be reached with a reasonable degree of confidence—for example, there is little doubt that the postorbital design of the skull of *Confuciusornis sanctus* would prevent any kind of prokinetic movement.

Is this essentially akinetic condition of the skull of *Confuciusornis sanctus* primitive? In other words, has it been inherited from ancestors with fully diapsid akinetic skull or has it evolved secondarily from forms with greater kinetic properties? In their discussion of the temporal construction of this bird, Peters and Ji (1998) suggested independent modifications of the diapsid bauplan within basal lineages of birds, implying that the temporal design of *Confuciusornis sanctus* must be primarily primitive. Assessment of this conclusion requires examination of the kinetic properties of other basal birds and of their phylogenetic interrelationships.

The skull of *Archaeopteryx lithographica* has been variably interpreted to be either akinetic (Simonetta, 1960; Whetstone, 1983), mesokinetic (Bock, 1964), or prokinetic (Bühler, 1985), with other authors supporting the presence of intracranial movement although without identifying a specific type (e.g., Wellnhofer, 1974, 1992). Studies on the braincase of the London specimen after its complete preparation in 1980 documented a tight sutural contact between the parietal and frontal, thus refuting earlier claims of a mesokinetic type of intracranial movement (Whetstone, 1983). Whetstone (1983) was also skeptical about the presence of either prokinesis or rhynchokinesis, instead arguing for the absence of intracranial mobility. Bühler (1985) argued for the presence of a primitive form of prokinesis, identifying a dorsal flexion zone at the base of the rostrum. This interpretation, however, was solely based on the presence of a streptostylic quadrate, flattened areas in the caudal margin of the nasals and the rostral portion of the frontals, and the supposed absence of a postorbital. The quadrate is streptostylic in a variety of nonavian theropods (e.g., Madsen, 1976; Currie and Zhao, 1993), in which rigid connections of the postorbital and squamosal to the jugal bar would prevent any kind of prokinetic movement—a streptostylic quadrate is necessary for, but not indicative of, the modern avian type of cranial kinetism. Other authors (e.g., Martin, 1983, 1985, 1991; Martin and Zhou, 1997) aside from Bühler (1985) have claimed that *Archaeopteryx lithographica* shared the modern avian condition of lacking the postorbital bone. This bone, however, is crushed but visible behind the orbit of the Berlin specimen (Heilmann, 1926; Wellnhofer, 1974; Walker, 1985; L. Chiappe, personal obs.). Furthermore, Walker (1985) identified several bone fragments located behind the orbit of the Eichstätt specimen as the postorbital, and the discovery in the Aktien-Vereins specimen (Elzanowski and Wellnhofer, 1996) of a squamosal with a forked postorbital process nearly identical to that of most nonavian theropods (Ostrom, 1969; Currie and Zhao, 1993; Clark et al., 1994; Currie, 1985, 1995) provides additional support to the presence of this bone in *Archaeopteryx lithographica*.

Heilmann (1926) and others (e.g., Thulborn and Hamley, 1985) illustrated the caudoventral margin of the postorbital in contact with a dorsocaudal process of the jugal; in these illustrations, the postorbital–jugal bar separates the orbit of *Archaeopteryx lithographica* from its infratemporal fenestra. Although a dorsocaudal process of the jugal is clearly present in *Archaeopteryx lithographica* (Wellnhofer, 1974; Elzanowski and Wellnhofer, 1996), its position is too caudal to abut the jugal process of the postorbital. Most likely, this process abuts the lateral side of the broad orbital process of the quadrate, as in the articulated skull of the enantiornithine hatchling from Catalonia (Sanz et al., 1997). Thus, only the presence of flattened areas in the nasofrontal area may support Bühler's (1985) interpretation of a prokinetic movement for *Archaeopteryx lithographica*. This condition, however, is not per se a clear indication of prokinesis, especially when other areas of the skull suggest very limited, if any, flexibility (Bühler, 1985). Even though the absence of a postorbital–jugal contact and the apparently sliding joint between the lacrimal and the maxilla hint at certain kinetic properties for the skull of *Archaeopteryx lithographica*, its particular type of cranial kinetism remains unclear.

Chiappe et al. (1998a) pointed out several features of the alvarezsaurid *Shuvuuia deserti* that suggested the presence of cranial kinesis. Although the postorbital is present in *Shuvuuia deserti*, its jugal process fails to reach the rodlike jugal, thus separating the orbit only incompletely. Lacking a contact between the postorbital and the jugal, the streptostylic quadrate of *Shuvuuia deserti* would have been able to swing rostrocaudally. Rostrally, the jugal becomes very thin and flat, suggesting the existence of a flexion zone immediately caudal to the antorbital cavity. The loose connection between the frontals and the preorbital bones also suggests the presence of a dorsal flexion zone. The apparent presence of flexion zones at the base of the rostrum, dorsally and ventrally, and evidence of a gap in the nasorbital septum ventral to the dorsal flexion zone, suggest that *Shuvuuia deserti* was able to protract and retract its rostrum much in the fashion of modern prokinetic birds. Specific differences

between *Shuvuuia deserti* and extant prokinetic birds exist in the location of the flexion zones and of their constituent bones. The ventral flexion zone of *Shuvuuia deserti* is caudal to the lacrimal, whereas in modern prokinetic skulls this is rostral to it, at the rostral end of the antorbital cavity. Likewise, the dorsal flexion zone of *Shuvuuia deserti* is between the frontals and the prefrontals/ectecthmoids (see Chiappe et al., 1998a for a discussion of the homology of the preorbital bones) and not between the frontals and the nasal–premaxillae, as in modern prokinetic birds. These differences suggest that although the inferred kinetism of *Shuvuuia deserti* is of a functional prokinetic type—with the rostrum moving as a single unit—it is not structurally identical to that of modern birds.

Martin and Zhou (1997) suggested the presence of prokinesis in the enantiornithine *Cathayornis yandica*, although without providing a detailed discussion of the anatomical support of this claim. These authors pointed to the absence of a postorbital and the flattened nature of the frontal process of the premaxilla and nasal. Little cranial material is known for the Enantiornithes (Chiappe and Walker, in press). *Cathayornis yandica* may not have a postorbital, but one is clearly present in an Early Cretaceous enantiornithine hatchling from Catalonia (Sanz et al., 1997), although in this specimen the postorbital does not contact the jugal bar. As in the case of other basal birds (e.g., *Archaeopteryx lithographica*), the absence of a postorbital–jugal contact in *Cathayornis yandica* and the Catalan enantiornithine hatchling suggests that their streptostylic quadrate may have been able to swing rostrocaudally, imparting movement to the jugal bar and rostrum. Whether this kinetism can be compared with the modern avian type of prokinetic movement requires further examination of the cranial morphology of the enantiornithine birds.

A peculiar type of kinesis, maxillokinesis, was proposed for *Hesperornis regalis* by Gingerich (1973). As postulated, maxillokinesis involves rostrocaudal movements along a dorsolateral groove of the maxilla into which processes of the premaxilla and nasal are received. Whetstone (1983) and Martin (1984) suggested the presence of mesokine-

sis in the skulls of *Hesperornis regalis* and *Parahesperornis alexi*. A restudy of the available material of these taxa rejected both maxillokinesis and mesokinesis as the kinetic mechanisms of the hesperornithid skull and pointed to prokinesis (Bühler et al., 1988). The complex frontoparietal joint of hesperornithids was interpreted as being essentially akinetic given its design and relations to other skull bones (Bühler et al., 1988). The presence of a streptostylic quadrate of fully modern aspect, a craniofacial hinge formed by the flat and thin frontal processes of the premaxillae and nasals rostral to their contact to the frontals (and dorsal to the rostral end of the mesethmoid), a flexible zone at the base of the rostrum on the rostral end of the jugal bar, and the existence of a gap between the nasal and interorbital septa led to the conclusion that the skull of these hesperornithids was prokinetic (Bühler et al., 1988), a view followed by Elzanowski (1991). The rigid connection between the bones of the rostrum and the apparent absence of flexion zones supported the view that the rostrum moved as a unit, rejecting the possibility of rhynchokinesis for the hesperornithid skull—although Zweers et al. (1997) suggested the presence of rhynchokinetic movements. As in *Shuvuuia deserti*, the lacrimal of the hesperornithids was included in the protraction–retraction movements of the rostrum, unlike most modern birds, in which this bone is not part of the rostrum (exceptions are in the nightjars and penguins). This again suggests that though functionally prokinetic, the skulls of the hesperornithids and alvarezsaurids are not structurally of the conventional modern prokinetic type.

Examination of the phylogenetic relationships among basal birds and their most in-mediate outgroups in light of the above functional inferences allows us to arrive at some basic considerations about the evolution of avian cranial kinesis. In spite of repeated arguments supporting the presence of prokinesis as the ancestral type of avian kinesis (e.g., Bühler, 1985; Bühler et al., 1988; Zusi, 1993; Chiappe et al., 1998a), evidence in support of prokinesis for both *Archaeopteryx lithographica* and the Enantiornithes is still very weak. The basically prokinetic skull of hesperornithids may be homologous to the prokinetic condition of basal neognaths (e.g., galliforms and anseriforms)—paleognath rhynchokinesis has consistently been interpreted as apomorphic (see Zusi, 1984)—although the historical relationships among basal neognaths are still a matter of debate. The basal avian relationship of the alvarezsaurids has been supported by several cladistic analyses (e.g., Perle et al., 1993; Chiappe et al., 1996, 1998a; Novas, 1996, 1997; Forster et al., 1998a) and disputed by others (e.g., Sereno, 1997; Chiappe, in press b; Novas and Pol, in press). In both instances, however, the prokinetic movement of the skull of the alvarezsaurid *Shuvuuia deserti* most likely evolved independently from that of hesperornithids and modern prokinetic birds. Character optimization of the postorbital–jugal contact, a feature strongly correlated with intracranial mobility, indicates that the presence of this contact in *Confuciusornis sanctus*, and, consequently, the essentially akinetic condition of its skull, is a reversal (fig. 68). The present knowledge of the interrelationships among basal bird lineages does not support the idea of multiple lines of independent evolution from ancestral forms with typical diapsid construction and an akinetic skull, as suggested by Peters and Ji (1998).

DIFFERENTIAL PLUMAGE AND SEXUAL DIMORPHISM

Of particular interest for the study of intraspecific variation is the existence of differential plumage among several well-preserved specimens of *Confuciusornis sanctus*. This difference is expressed in the presence of a pair of elongate feathers in the tail of some specimens versus only the tapering feathered tail surrounding the rectricial bulb in other specimens. Plumage differences may also have existed among individuals of *Changchengornis hengdaoziensis*, but in this case only the holotype is thus far known.

This difference in plumage has been regarded as a sexual characteristic (Hou et al.,
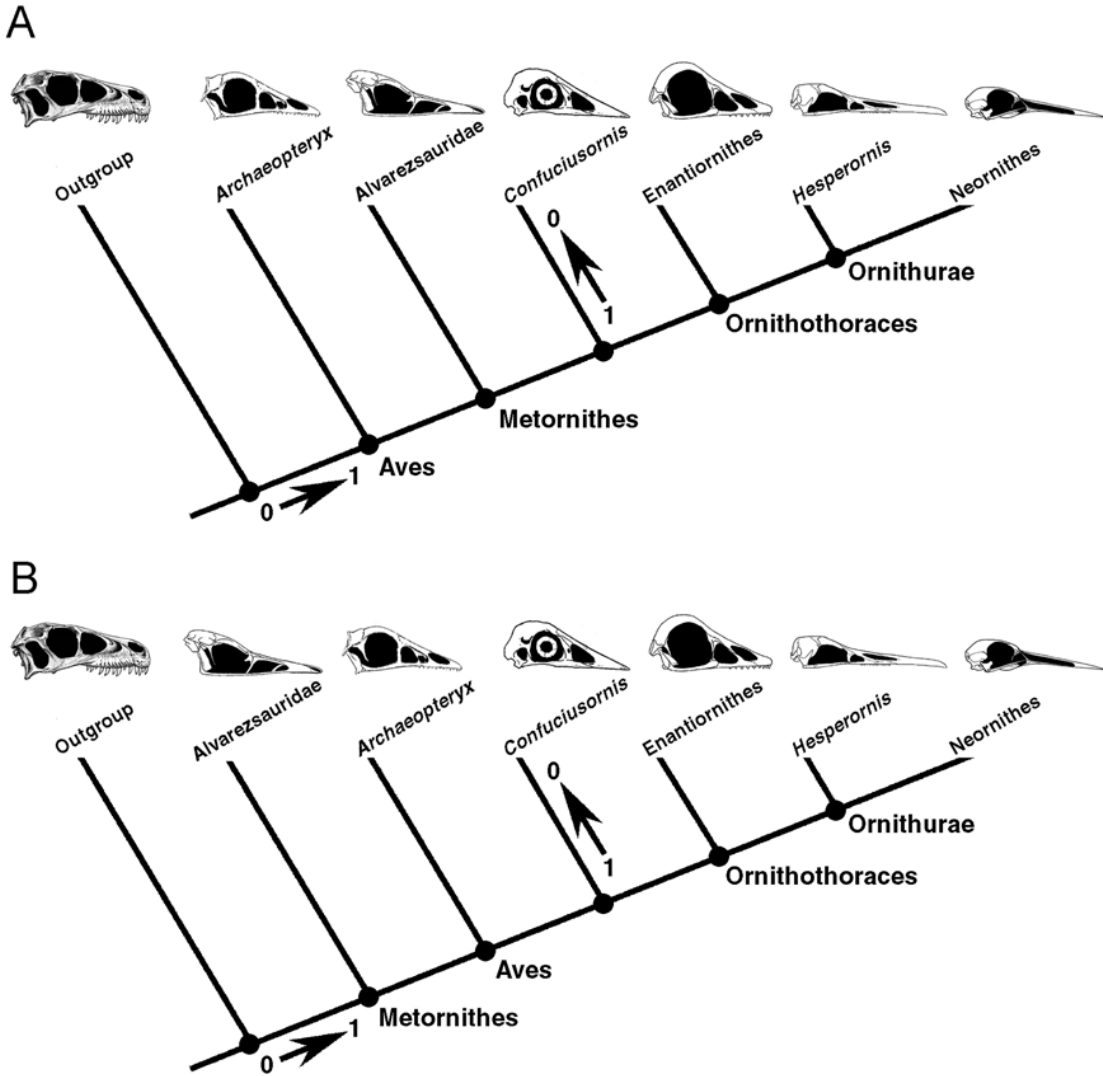
Fig. 68. Character optimization of the postorbital–jugal contact as indicated by the phylogenetic hypotheses supporting (A) the avian relationship of the Alvarezsauridae and (B) its sister-group relationship to Aves (see Chiappe [in press b] for a discussion of the cladistic analyses resulting in these two different topologies).

1996, 1999; Martin et al., 1998) because sexual dimorphism in modern birds often involves feather variation. Møller and Cuervo (1998) identified 70 lineages within extant birds for which ornamental feathers are regarded as independent evolutionary events. Although sexual dimorphism appears to be the most reasonable explanation accounting for the plumage variation among specimens of *Confuciusornis sanctus*, it may not be the only factor explaining the observed pattern.

Extant birds molt their entire plumage, or part of it, at least once a year (Campbell and Lack, 1985). Molting has not been documented for any basal bird, but the fact that the plumage of *Confuciusornis sanctus* and other primitive birds does not exhibit intense wear suggests that feathers were regularly replaced. All molt stages can be found within a population of living birds during its molting period—fully plummed males of certain birds of paradise have been collected on the

same day as other males just beginning to grow their display plumage (M. Lecroy, personal commun.)—and individuals do not develop their display plumage until they become sexually active adults. Furthermore, in some species of extant birds, the genders are known to molt asynchronically (Ginn and Melville, 1983).

Even if we were to accept the observed pattern as evidence of sexual dimorphism, correlating specific genders to individuals with or without long tail feathers is also not as evident as it may seem. Living birds typically exhibit the conventional model of sexual dimorphism in which males are larger and morphologically more ostentatious than females. In the males of the species included in the 70 lineages Møller and Cuervo (1998) identified as having evolved sexual dimorphism independently, sex-correlated feather lengths were at least 5% longer than those of females or sex-correlated feather traits were absent among females. Exceptions to this conventional model are known, however. Certain predatory groups of birds (e.g., Falconiformes, Strigiformes, and Stercorariidae) exhibit the reverse model, in which females are larger than males (Amadon, 1975). Polyandrous species also exhibit this reversed model. In these cases, females are the ones displaying ornate feathers. A reverse model has also been suggested for nonavian theropods, in which differential development of cranial crests, horns, and rugosities, the presence of robust and gracile forms, and the

identification of sex-specific characters have been used as evidence in support of sexual dimorphism (Chapman et al., 1997; Sampson, 1997). Thus, the fact that a reverse model of sexual dimorphism has been asserted for nonavian theropods and is known among certain extant birds would also complicate the specific identification of sexes among the specimens of *Confuciusornis sanctus*.

In summary, the existence of sexual dimorphism may be the simplest explanation to account for the observed differences in plumage within the available sample of *Confuciusornis sanctus*, but the variation in feather development of extant molting populations, the correlation between display plumage and sexual maturity of modern birds, and the occurrence of differential molting among genders of living birds can also account for this variation in plumage. Unlike the situation in nonavian theropod species in which only a handful of well-preserved specimens for a single species may be known, *Confuciusornis sanctus* presents an optimal case for the study of plumage variation in basal birds. Given our current knowledge, the hypothesis that the observed differences in the plumage of *Confuciusornis sanctus* are sex correlated (Hou et al., 1996; Martin et al., 1998) does not stand as the only explanation for the pattern present in the collection of specimens of this basal bird. Future morphometric analyses may help to test this hypothesis and to shed light on the plausibility of other, alternative explanations.

LIFE-STYLE OF THE CONFUCIUSORNITHIDAE

Hou and his associates (e.g., Hou et al. 1995c, 1996; Feduccia, 1996; Feduccia and Martin, 1996; Martin et al., 1998) have consistently argued that *Confuciusornis sanctus* was an enhanced tree climber. The anatomical rationale behind this claim stems primarily from the prominent development and curvature of the manual and pedal claws and the anisodactyl foot. This functional conclusion, coupled with assumptions about the pelvic structure of *Confuciusornis sanctus*, has led to its reconstruction in a squirrel-like posture (e.g., Hou et al., 1996; fig. 69)—a posture unknown for any other bird or nonavian di-

nosaur (Padian and Chiappe, 1998c). Despite the general design of the foot of *Changchengornis hengdaoziensis* suggesting a greater grasping ability than that of *Confuciusornis sanctus*, not a single feature of the morphology of these birds relates to climbing specialization (Peters and Ji, 1999). Features such as the pronounced curvature of the manual claws are primitive (Chiappe, 1997b), and evidence in support of the proposed correlation between the pelvis of *Confuciusornis sanctus* and its inferred climbing activities has never been provided by those supporting scansorial activities for this bird
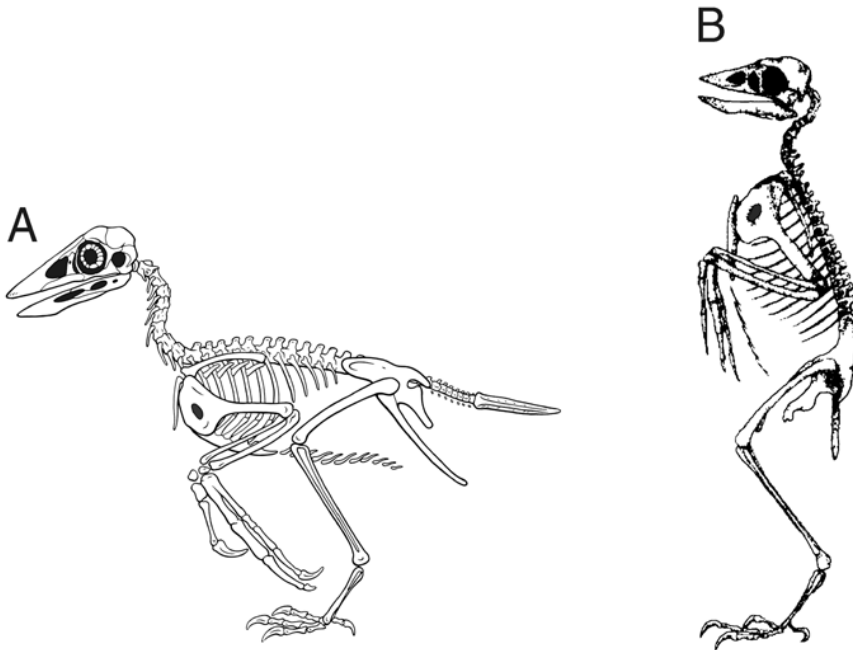
Fig. 69.   An avian posture reconstructed for *Confuciusornis sanctus* (A) is compared with the squirrel-like reconstruction of Hou et al. (1996) (B).

(i.e., Hou et al., 1995b, c, 1996). In addition, although the foot of *Confuciusornis sanctus* is anisodactyl, comparisons between its pedal anatomy and that of living birds suggest that this bird was not even a specialized percher. The relative lengths of the hallux and digit II of *Confuciusornis sanctus* (the hallux is approximately 50% the length of digit II) are dramatically different from those of extant perchers. For example, the hallux of perching passerine birds is usually longer than digit II (Bock and Miller, 1959). Furthermore, in extant species with feet specialized for grasping, the intermediate phalanx 3 of digit III is longer than either the intermediate phalanx 2 or the proximal phalanx (Hopson and Chiappe, 1998). In *Confuciusornis sanctus*, however, the proximal phalanx of digit III is consistently the longest. Relative lengths of the phalanges in the third pedal digit of *Confuciusornis sanctus* fall within the transition between birds that spend most of their time in trees and others that are predominantly terrestrial (Hopson and Chiappe, 1998). *Confuciusornis sanctus* may have occasionally perched in trees—animals often perform functions for which they are not specialized—but its relatively short and elevated hallux and the relative lengths of the nonungual phalanges of digit III suggest that the grasping capabilities of this bird were restricted, thus making dubious interpretation of it as a predominantly arboreal creature. A similar discussion is applicable for *Changchengornis hengdaoziensis*, although its somewhat longer hallux suggests better grasping ability.

There is little doubt that with their long, narrow wings with asymmetric feathers (Feduccia and Tordoff, 1979) and streamer-shaped tails (Balmford et al., 1993) both *Confuciusornis sanctus* and *Changchengornis hengdaoziensis* were capable of flight (Hou et al., 1995c, 1996; Peters and Ji, 1998). In spite of the primitive morphology of their skeletons, these taxa display a number of features (e.g., large sternum with incipient carina, strutlike coracoid, and pygostyle) that are more advanced than those of *Archaeopteryx lithographica* and that are usually correlated with aerodynamic functions. The question of whether *Archaeopteryx lithographica* was able to take off from a stand-still position has not been satisfactorily
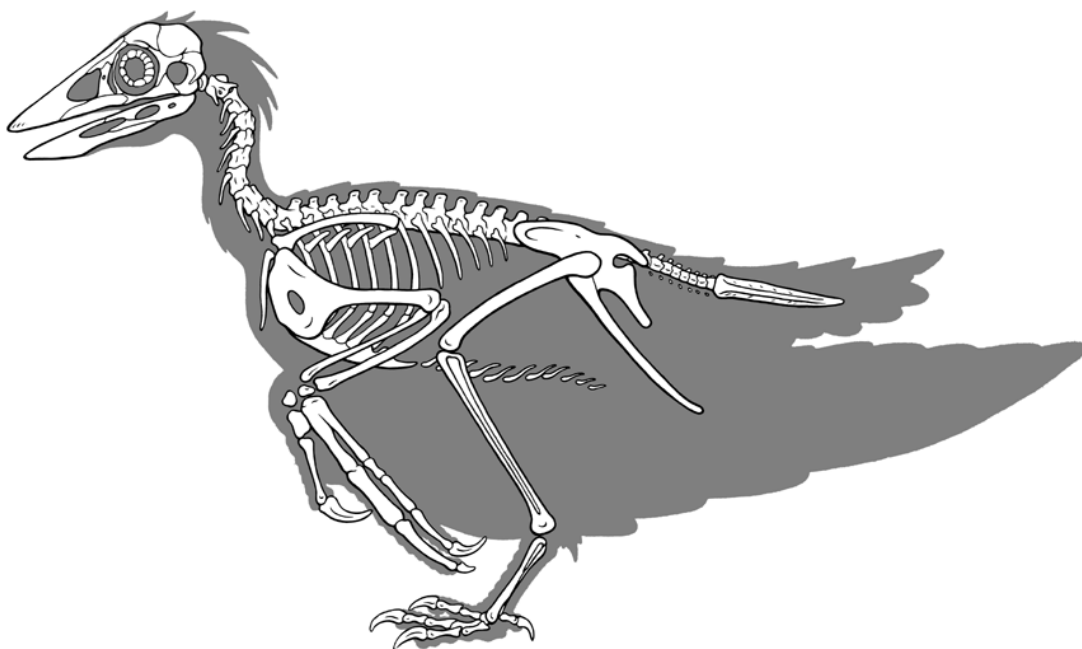
Fig. 70.   Skeletal reconstruction of *Confuciusornis sanctus*.

addressed, therefore most are reluctant to accept that it was able to perform this feat (e.g., Gauthier and Padian, 1985; Speakman, 1993; Burgers and Chiappe, 1999). Aerodynamic calculations, however, have suggested that *Archaeopteryx lithographica* was most likely able to take off after a short propulsive run (Burgers and Chiappe, 1999), in a fashion comparable to the take off of many extant large birds. Given that the confuciusornithids are more derived than *Archaeopteryx lithographica*, both in their flight-correlated skeletal features and in the morphology of their wings and tail, it would be reasonable to assume these birds were also able to lift off after a short take off run. This inference—one shared by Hou et al. (1995c, 1996)—bears on the issue of whether *Confuciusornis sanctus* was a tree climber. If it were capable of taking off from the ground, why would it have had to climb trees when it could have simply flown to them (Padian and Chiappe, 1998a, b)?

Several authors have argued that the abundance of specimens of *Confuciusornis sanctus* hint at colonial behavior for this species (e.g., Hou et al., 1996; Viohl, 1997; Martin

et al., 1998). Viohl (1997) postulated that the intense volcanism indicated by the nature of the fossil-bearing deposits may be a causal link to the existence of these apparent death assemblages. Indeed, the extreme abundance of some of the fossil taxa (e.g., *Confuciusornis sanctus*) in a relatively thin portion (approximately 84 cm) of the lower section at Sihetun suggests episodes of mass mortality (Wang et al., 1998). For example, our conversations with the local farmers indicate that more than 40 specimens of *Confuciusornis sanctus* were unearthed from a surface smaller than 100 m^2. Although the linking of catastrophic events of volcanic origin to the apparent death assemblages and linking of the possible existence of large colonies of *Confuciusornis sanctus* to the recovery of hundreds of specimens of this bird are both likely scenarios, detailed taphonomic studies and microstratigraphic studies of the fossil occurrences from the Jiulongsong and Hengdaozi members of the Chaomidianzi Formation have never been conducted. Corroboration of these hypotheses must await the results of these specific studies.

ACKNOWLEDGMENTS

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