Important Features of the Dromaeosaur Skeleton: Information from a New Specimen

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ABSTRACT

A partial, but three dimensionally preserved skeleton of a dromaeosaurid (IGM 100/985) was discovered at Tugrugeen Shireh, Gobi Desert, Mongolia, by the 1993 MAS-AMNH expeditions. The specimen clarifies a number of anatomical issues that have been left unanswered in previous studies of dromaeosaurids. Paired sternal plates are present, with well-developed articular grooves for the coracoids. A fully articulated gastral basket was recovered with the specimen, revealing a complex imbricating structure, and possible sliding articular surfaces between segments. The articulated pelvis shows that the pubis was sharply retroverted in dromaeosaurs at an angle of 155° relative to the horizontal axis. Further similarities between dromaeosaurs and avialans, revealed in IGM 100/985, include reduction of the antiliac hook, loss of a shelf for M. cuppedicus, and distally unfused ischia. Both feet were recovered with all but distal phalanges in articulation, and demonstrate that the hallux was not reversed as in some previous reconstructions of dromaeosaurid pedes.

INTRODUCTION

Dromaeosaurs have figured prominently in discussions of bird origins (Ostrom, 1976a; Gauthier, 1986; Holtz, 1994). Several features impinging on this discussion are found in the postcranial skeleton of these animals. Unfortunately, well-preserved, articulated postcranial remains are rare and have not been adequately described. Instead, workers have for the most part been forced to rely on poor photographs of Mongolian materials or the reconstructed composite illustrated in Ostrom (1969a). Here we describe a few important aspects of dromaeosaur postcranial anatomy observable in a well-preserved, al-

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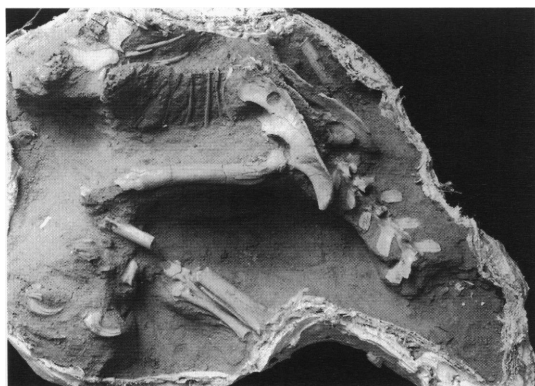
Fig. 1.   Dorsal view of partially prepared specimen IGM 100/985 in field jacket. Notice the three-dimensional articulation of the elements.

beit incomplete, dromaeosaur skeleton, IGM 100/985 (Institute of Geology Mongolia), from the Late Cretaceous Tugrugeen Shireh locality of Mongolia (Gradzinski and Jerzykiewicz, 1972). We will concentrate on five aspects of this anatomy: the sternal plates and gastral basket, the pes, and the pelvis and anterior caudal vertebrae. Additional evidence from a second dromaeosaur postcranium (IGM 100/986) will be presented where relevant to understanding the anatomy of IGM 100/985. The second specimen was collected by the MAS-AMNH field party in

1993 at a locality known as Chimney Buttes, Mongolia.

INSTITUTIONAL ABBREVIATIONS: AMNH—American Museum of Natural History, New York; IGM—Mongolian Institute of Geology, Ulan Bataar; TMP—Royal Tyrrell Museum of Paleontology, Drumheller; YPM—Yale Peabody Museum, New Haven.

DETAILS OF THE FIND

IGM 100/985 was discovered as a surface find. The specimen is preserved three dimensionally in a death position with the legs tucked up under the body (fig. 1). It was collected at Tugrugeen Shireh (Djadokhta Fm.) during the 1993 field season of the Mongolian Academy of Sciences–American Museum of Natural History Joint Expedition. It was close to the top of the section in the westernmost exposure (fig. 2). Much of the skeleton was eroded, although parts of the skull, forelimbs, ribs, and vertebrae were found in the downslope rubble. Although small rootlets had invaded and disturbed some of the elements, many of the bones are preserved in remarkable detail.

The specimen is referable to the Dromaeosauridae on the basis of the presence of a characteristic, highly modified second pedal digit, retroverted pubes, and the elongate pre-
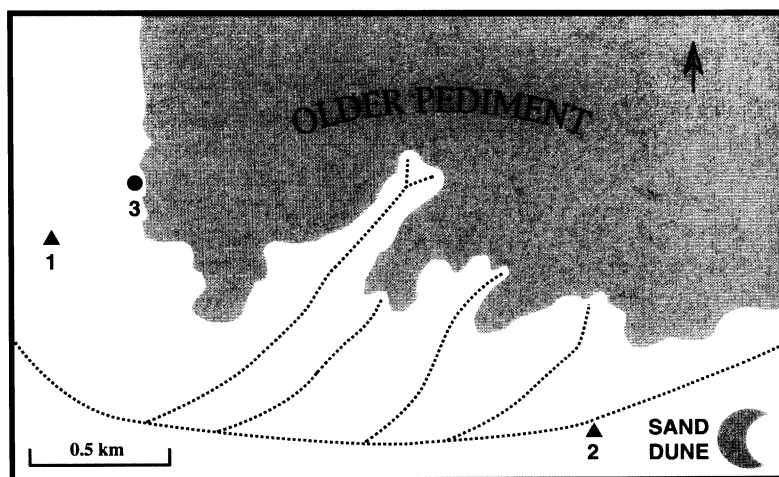

Fig. 2.   Map of Tugrugeen Shireh locality modified from Gradzinski and Jerzykiewicz (1972) showing site where IGM 100/985 was discovered (dot marked 3). Triangle 1 designates the campsite of the 1971 Polish–Mongolian Expedition and Triangle 2 shows the location of the 1993 MAS–AMNH Expedition campsite.

zygapophyses in the caudal vertebrae (Ostrom, 1990). The specimen is immature, as witnessed by the unclosed sutures between the centra and neural arches. Anatomical measurements are given in table 1.

Indication that IGM 100/985 was scavenged by burrowing arthropods following death comes from 1 cm holes bored through the sternal plates (fig. 3) and pelvis (fig. 12). Judging from burrow systems found at Tugrugeen Shireh (Fastovsky et al., 1997) and at other Djadokhta localities (Johnston et al., 1996), burrowing arthropods were ubiquitous in these areas. The burrows are similar to Fastovsky et al.'s (1997) Class 3, which are similar to the burrows in a *Pinacosaurus grangeri* specimen from Bayan Mandahu figured by Jerzykiewicz et al. (1993; fig. 9).

DESCRIPTION

STERNAL PLATES

Sternal plates have so far been reported only in *Velociraptor mongoliensis* (Barsbold, 1983) among Dromaeosauridae. Paired sternal plates are also present in the Tugrugeen dromaeosaurid (fig. 3). The two plates contact each other along a straight midline edge, but are not fused. They are broadest anteriorly. The lateral edges of the sternum are lost to erosion, but posteriorly the two plates taper to meet in an obtuse point at the posterior end of the sternum.

Each plate bears a sulcus along most of its anterior edge for articulation with the coracoid (fig. 4). The sulcus faces anterolaterally, although less laterally than in modern avian sterna. The surface of the sulcus is pitted and unfinished, which suggests the presence of a large pad of cartilage between sternum and coracoid, as in extant avian taxa. Posterior to the coracoid articulation, the sternal plate becomes very thin. A short distance behind the anterior rim of the sternum, the sternal plates form a small ventrally convex bulge at the midline. Posterior to this bulge each plate is almost planar, curving slightly dorsally at its lateral border. Unfortunately, because of erosion, it is impossible to determine the number of attachments for sternal ribs.

Besides Dromaeosauridae, paired sternal plates have been described only in oviraptorids among non-avialan Maniraptora (Barsbold, 1983). Dromaeosaur sternal plates are extremely similar to those of oviraptorids in both relative size and shape except for the aberrant condition in the holotype of *Ingenia yanshini* (IGM 100/30), where the sternal plates are fused into a single sternum. In another specimen assigned to this taxon (IGM 100/33) the plates are paired (Barsbold, 1983), however, confusion regarding the reference of specimens to the taxon *Ingenia yanshini* exists (H. Osmólska, personal commun.).

GASTRAL BASKET

In addition to the sternal plates, the Tugrugeen dromaeosaurid preserves an articulated gastral basket with 12 pairs of imbricated gastral segments (fig. 5). Within a pair, each gastral segment is composed of two rodlike elements that articulate end to end. The lateral element is tapered where it approaches the corresponding rib, and bears a longitudinal grooved articular facet medially. This facet lies in a vertical plane and contacts a similar facet on the medial element. These grooves are offset relative to each other, such that the raised border on one element fits into the sulcus of the other. Evidently, this configuration permitted some longitudinal sliding between the elements of a single gastral segment. Unlike such elements in many other theropods (Lambe, 1917; Maleev, 1974; Madsen, 1976; Sternberg, 1933), the medial element in each gastral segment is significantly shorter than the lateral one. Shorter medial than lateral gastral segments are also found in the troodontid *Sinornithoides youngi* (P. J. Currie, personal commun.).

An aberrant anatomical feature not reported previously in other coelurosaurs is the presence of a bifid proximal gastral element (fig. 5). This bifid bone is found in the seventh segment on the right side, and the bifurcation is directed dorsolaterally. There is no corresponding element in any of the other preserved gastral segments, and it is probably an individual abnormality.

Each gastral element is rod shaped and roughly circular in cross section. The first pair of gastralia is the most robust and is composed of one element on each side. These elements contact one another ventral

TABLE 1

Selected Measurements (in mm)
(* denotes slight breakage)

Pelvis

Sacrum length (anterior posterior)	89.2
Ilium length	137.0*
Diameter of acetabulum between peduncles	29.8*
Width of brevis shelf	16.5*
Pubis length	165
Length of pubic symphysis	85.4
Width of apron at beginning of symphysis	40.4
Ischium length	94.6*

Tarsals

Distal tarsal width	15.4*

	MT2	MT3	MT4	MT5*	MT1
Length	71*	84.2	79	29.9	22
Length	p1.1	p2.1	p3.1	p4.1	
	13.8	24.1	37.6	26.8	
	ungual	p2.2	p3.2	p4.2	
	20.3	24.2	25.1	21.3	
		ungual		p4.3	
		53.6		16.8	
				p4.4	
				16.2	
				ungual	
				30	

Caudal vertebrae	1st caudal	2nd caudal	3rd caudal	4th caudal	5th caudal	6th caudal	7th caudal	8th caudal
Maximum length	17	19.1	20.3	23.4	24.5*	24.1	23.9*	25.9*
Posterior width	15.4	15.1	13.4	13.7	14.4*	13	11.6	11.4
Width at transverse processes			49.4	48.9*	45.7	42.4		
Chevron length	33.6					26.4		

Sternum (right element)

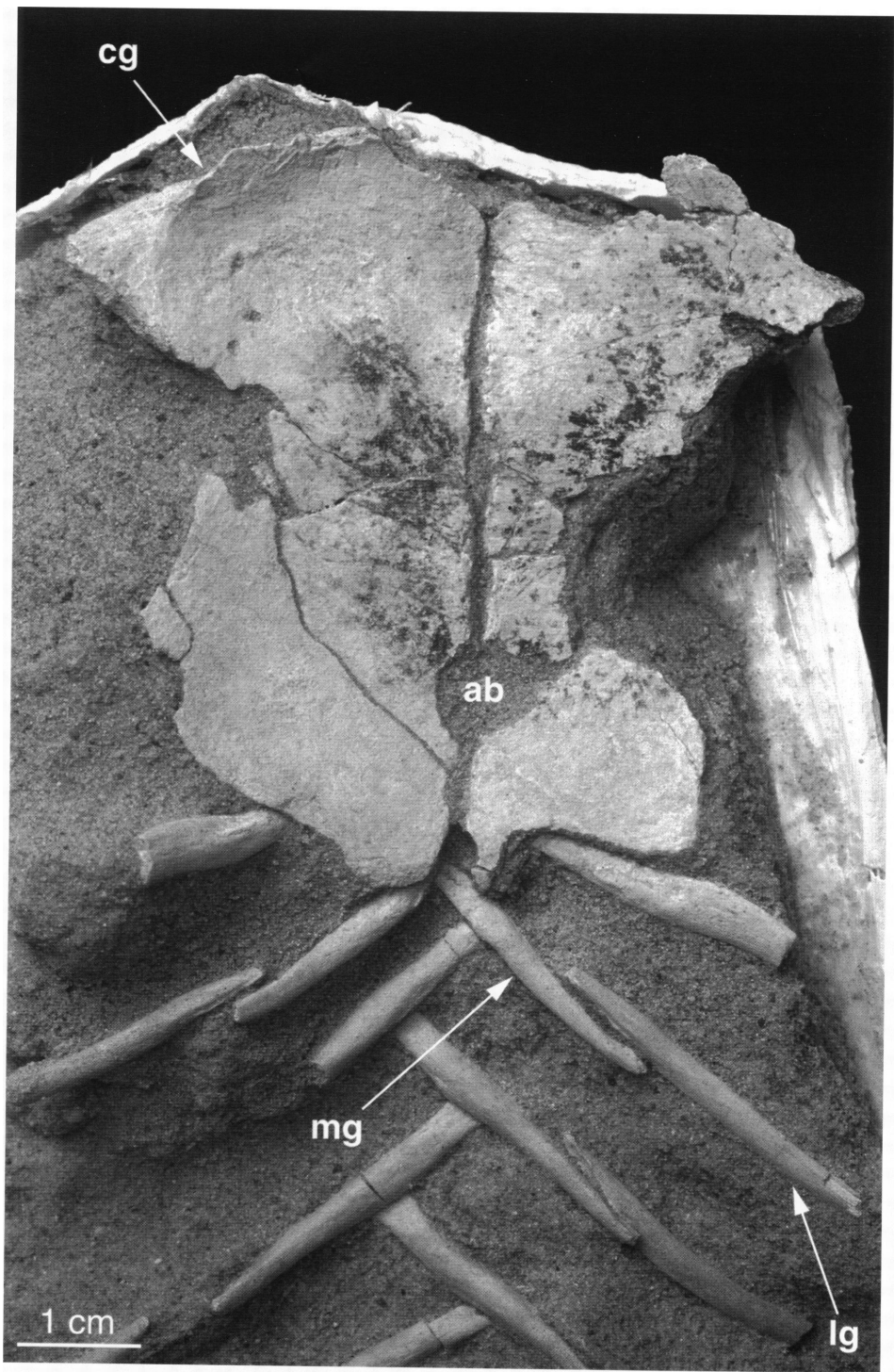|	
Maximum length	71.0
Maximum width	42.1
Length coracoid articulation	32.1

Fig. 3.   Dorsal view of paired sternal plates of IGM 100/985. ab = arthropod boring; cg = coracoid groove of sternal plate; mg = medial gastralia; lg = lateral gastralia.
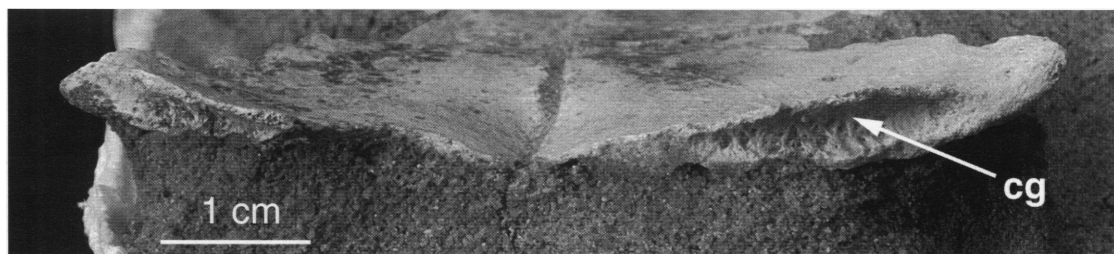
Fig. 4. Anterior view of anterior edges of paired sternal plates showing large grooves for reception of the coracoid. cg = coracoid groove.

to the posterior margins of the sternal plates, with which they articulate through antero-dorsally oriented grooves. The first two pairs of segments are aligned symmetrically on either side of the ventral midline, but other segments of the right side are offset posteriorly relative to the left in an imbricate meshwork. Each right segment tip articulates with its left counterpart behind the tapered tip of the latter, and is itself contacted by the tip of the posterior left segment slightly posterolateral to its terminus (fig. 5). This series of terminal articulations forms a zigzag pattern centered on the midline. The articular facets between medial elements are flattened and simple, unlike the saddle-shaped facets of tyrannosaurid gastralia (Lambe, 1917). This perpendicular coupling between the intrasegmental and intersegmental articulations suggests that longitudinal sliding in the segments was translated into a rotational movement between segments at their distal ends, which has been suggested as an important constituent of the theropod respiratory cycle (Claessens, 1996).

Gastral baskets of theropods are rarely well preserved. Consequently, this area has not been important in phylogenetic study.

PES

Since Ostrom's (1969a) description of *Deinonychus antirrhopus,* dromaeosaurs were known to have highly specialized feet. The ginglymoid shape of the distal end of metatarsal II and the derived aspect of the more distal phalanges, modified into a retractable sickle claw, are unique among dinosaurs, even though some other taxa (notably troodontids and some avialans) show incipient development of these features (Os-

mólska and Barsbold, 1990; Chiappe, 1996). However, one aspect of the foot has been implicated as a synapomorphy with Avialae: the supposed retroversion of the first digit, the hallux, into a position that is like that of modern birds (Ostrom, 1976a).

IGM 100/985 has both feet well preserved and articulated in three dimensions. The feet are in a death position. Digits III and IV of the right foot are contracted toward the plantar side of the appendage. Digit II is pulled back toward the top of the foot (fig. 6A, B). The left foot is folded tightly against the anterior face of the crus. Most of the phalanges were disarticulated except for I-1, II-1, and III-1. As in all Theropoda the foot is functionally tridactyl, although it may have been didactyl in locomotion, and metatarsal III is longest. Of the three primary metatarsals, II is the shortest while IV is intermediate in length but nearly as long as III; contra Holtz's (1994) scoring of this character in Dromaeosauridae (his character 122: "Metatarsal IV longer than II and closer to III in length").

Only one distal tarsal is preserved in the specimen, in articulation with the left metatarsus (figs. 7, 8). The tarsal is positioned over the posterior part of the proximal articular surface of metatarsals III and IV. It is a tabular, irregular bone that displays a zone of thinning above the border between metatarsals III and IV. A small notch on the posterior border of this bone is in line with the thin zone. Its increased size suggests that the tarsal may be composed of two fused tarsal elements (fig. 8). Topologically the constricted zone of the distal tarsal is in a position corresponding to the common border between distal tarsals III and IV as figured by Ostrom
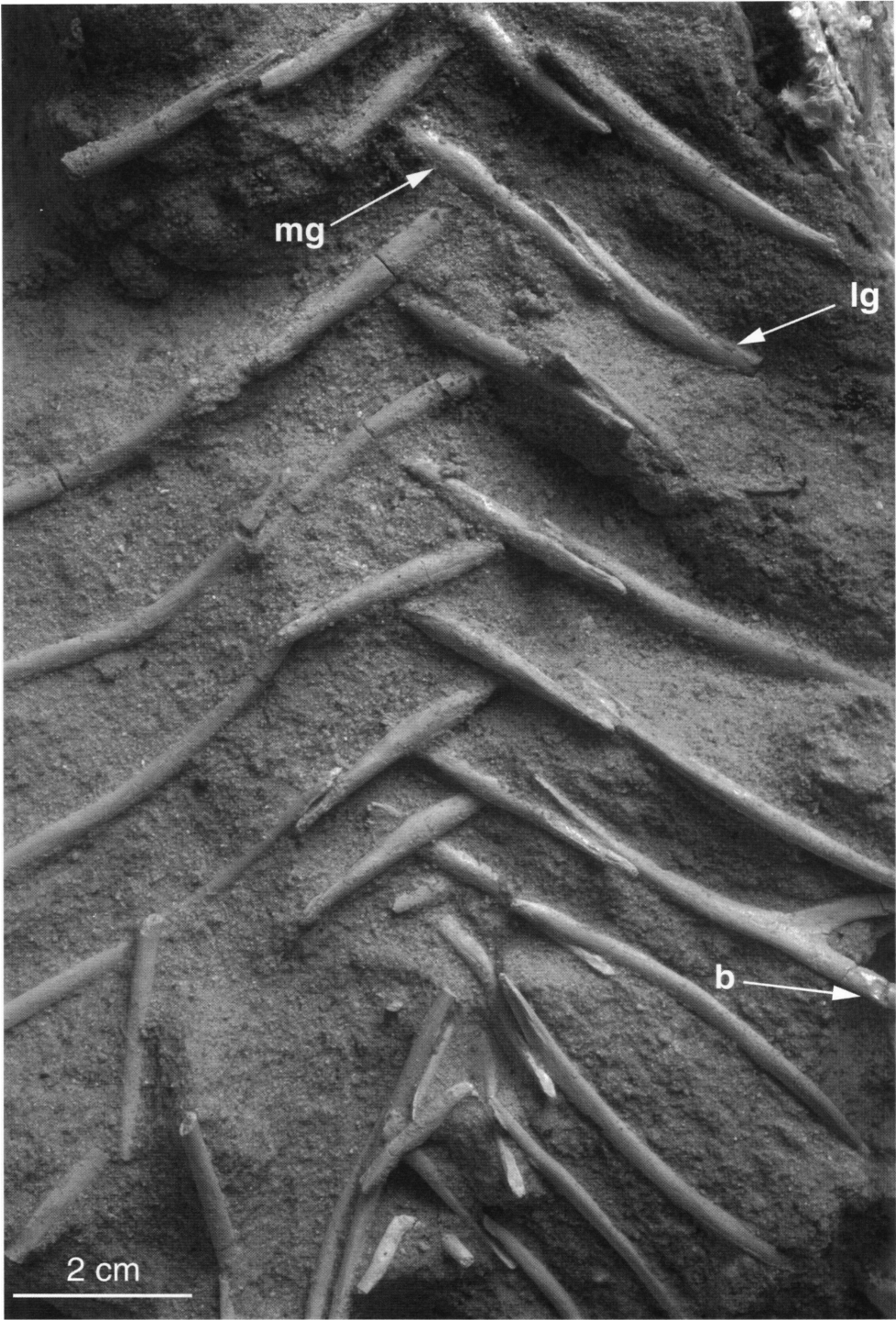
Fig. 5.   Articulated gastral basket of IGM 100/985 in dorsal view. Notice the bifid element in gastral segment 7 of the right side. b = bifid segment; mg = medial gastralia; lg = lateral gastralia.
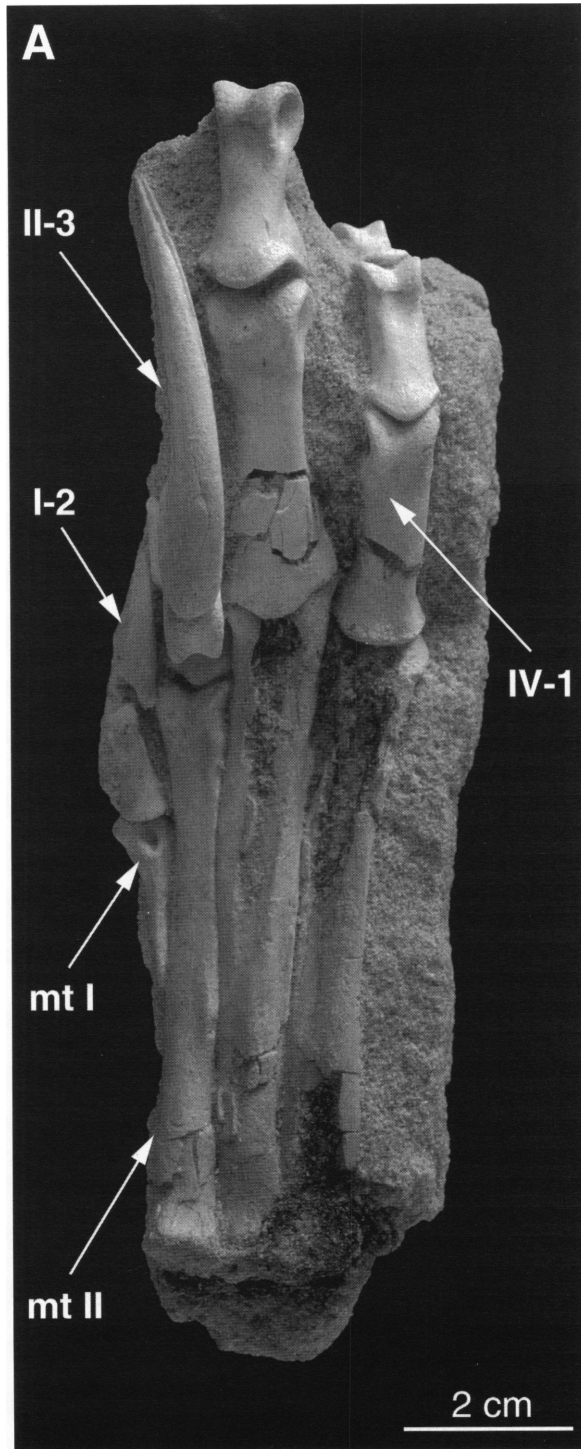
Fig. 6.   Right pes of IGM 100/985 in (A) anterior and (B) medial views. Notice the position of the hallux and the retracted condition of the second digit. mt = metatarsal; combinations of Roman and Arabic numerals designate positions of individual phalanges.
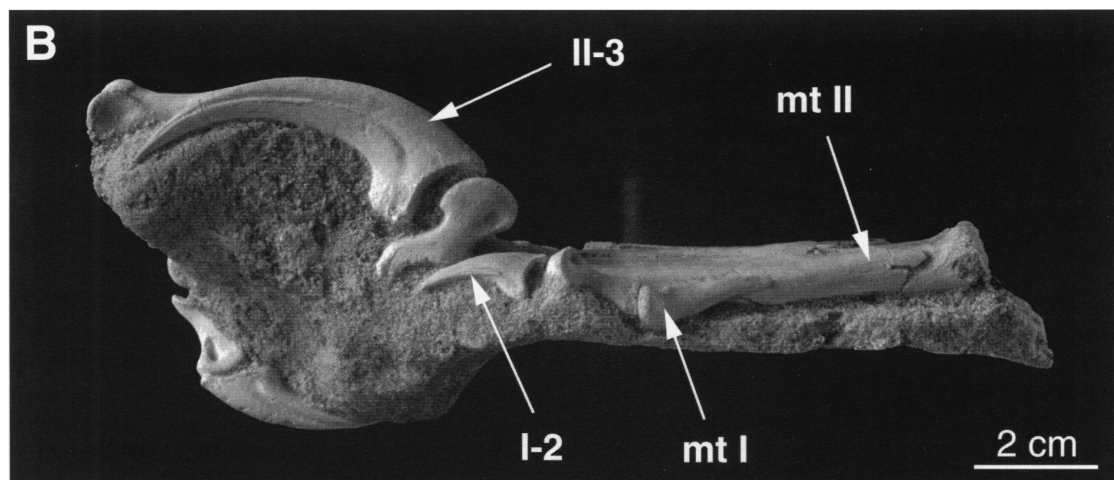
Fig. 6.   (*Continued*)

(1969a: fig. 70). Given the difficulty of homologizing the distal tarsals, it is also possible that the single preserved tarsal corresponds to distal tarsals II and III as suggested by Gilmore (1933). The proximal articular surface is inclined anteroventrally from the thickened posterior border. The distal tarsal is incompletely fused to metatarsal III, and possibly also to metatarsal IV. In IGM 100/986, the distal tarsals appear fused to each other as well as to the metatarsals. The incomplete fusion seen in IGM 100/985 may be related to the immaturity of the specimen. In some ceratosaurs (Raath, 1969; Rowe, 1989; Rowe and Gauthier, 1990), *Elmisaurus rarus* (Osmólska, 1981), troodontids (Barsbold, 1974), and some avialans such as *Archaeopteryx lithographica* (Wellnhofer, 1992) the distal tarsals fuse to the metatarsus to form a tarsometatarsus. Although this character probably had separate origins in Ceratosauria and Maniraptora, as shown by its absence among basal tetanuran and coelurosaurian lineages, the patchy distribution as well as ontogenetic nature of this character make it difficult to assess where and how many times it arose among maniraptorans.

Digit I lies not posterior, but rather medial, to the metatarsus (figs. 6A, B). The shaft of the first metatarsal tapers proximally and is subcrescentic in cross section. Its lateral face is longitudinally concave where it is appressed to the shaft of the second metatarsal. The medial face is gently convex. The distal articulation is medially offset from the shaft of metatarsal I, suggesting that the hallux was at a slight angle to the long axis of the metatarsus. There is no ligament pit on the medial face of the distal articular facet. The posterior surface of metatarsal I is triangular, and distally it bears a small concave fossa just above the trochlea. Posteriorly the articular surface is weakly divided by a median depression. The first phalanx of digit I is short and constricted at midlength. Its proximal articulation is simple (non-ginglymoid) and the distal one is weakly ginglymoid. A small lappet extends proximally from the plantar face of the proximal articulation overlapping the depression on the distal articulation of the metatarsal. The ungual of the first digit is weakly curved, and is triangular in cross section, with the medial face larger than the lateral one. A prominent groove lies along the distal two-thirds of each side of the claw (the claw sheath). The articulations between the first phalanx and metatarsal and the first phalanx and ungual are subparallel to those of the other toes.

In most reconstructions of theropod feet (Ostrom, 1969a, 1969b, 1990, but notably not in Barsbold, 1983), the presence of a scar on the posteromedial face of metatarsal II has been used to fix the position of the first metatarsal. IGM 100/985 shows that this is not the correct point of articulation, and that the scar is unrelated to the first digit.

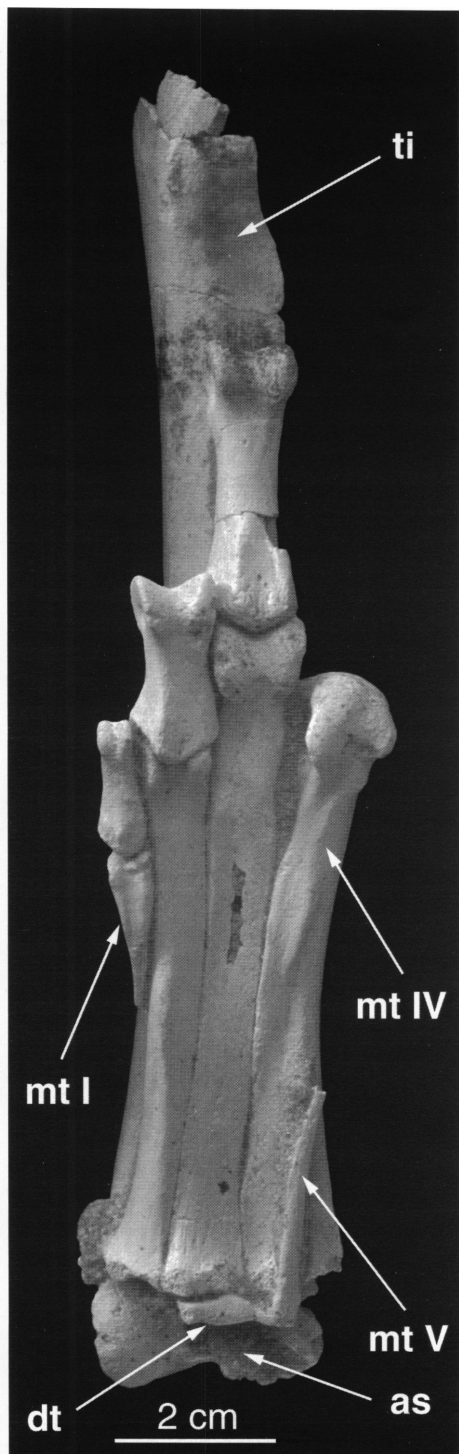Metatarsal II is medially convex, and the

Fig. 7. The left pes of IGM 100/985 in posterior view. as = astragalus; dt = distal tarsal; mt = metatarsal; ti = tibia.
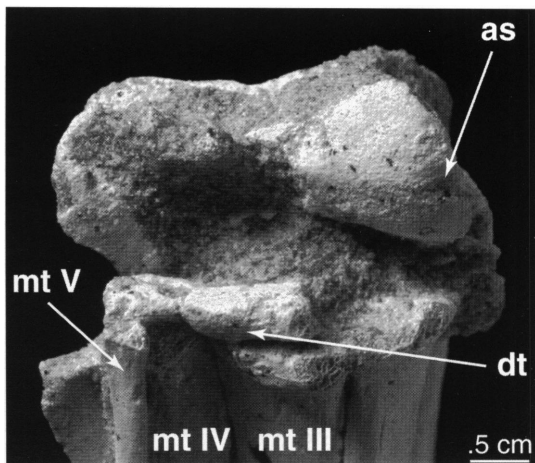

Fig. 8. Detail of preserved distal tarsal of left foot in posterodorsal view. Note the thin region of the bone above the contact between metatarsals III and IV. as = astragalus; dt = distal tarsal; mt = metatarsal.

lateral surface is flattened where it is appressed against metatarsal III. The proximal articulation with the distal tarsal is inclined anteriorly. Proximally on metatarsal II, the lateral surface curves around and contacts metatarsal III posteriorly. More distally a flat surface forms. Initially it is oriented posteromedially, but it expands laterally to form a posteriorly directed flat face on the metatarsal. About half way down the length of the shaft, a robust, longitudinal ridge is displaced slightly to the medial side (fig. 7). Topologically it resembles the medial plantar crest of the avian metatarsus (Baumel, 1979), and may have been the origin of flexors and adductors of digits I and II or a border that channels the flexor tendons as they extend the length of the metatarsus to the digits. This area is the feature that was interpreted as an attachment for metatarsal I in previous reconstructions of theropod feet. Such a ridge is also present on metatarsal II of *Deinonychus antirrhopus* (AMNH 2136) and *Velociraptor mongoliensis* (AMNH 6518) as well as *Sinornithoides youngi*. The proximal articular facet of metatarsal II is anteroposteriorly expanded and overhangs the anterior face of the metatarsal. There is an elongate tubercle on the anterolateral corner of the shaft just above its midlength. It overlaps the shaft of the third metatarsal slightly and probably

marks the insertion of the M. tibialis cranialis (George and Berger, 1966). Enantiornithine birds and *Syntarsus rhodesiensis* display a similar tubercle (Chiappe, 1992, 1993). Below the tubercle the second metatarsal marginally overlaps the third metatarsal to a point just above the distal ginglymus. Adjacent to the lateral articular ridge of the ginglymus is another laterally directed tubercle, although this one is much smaller than that for the M. tibialis cranialis. The distal articulation has a deeply incised ginglymus. This feature is known only in the Dromaeosauridae (Currie and Peng, 1993) among nonavialan theropods.

Digit II displays the diagnostic features of the Dromaeosauridae, including a penultimate phalanx with an extensively circumscribed distal trochlea and a large proximal heel, as well as a trenchant ungual. Phalanx II-1 is wider and flatter when compared to the phalanges of the other digits. A tongue-like process extends from the plantar border of the proximal articulation and overlaps the trochlea of metatarsal II. A ridge connects this tongue with the medial condyle of the distal trochlea defining the border between the ventral and lateral sides of the phalanx. The phalanx is markedly constricted dorsoventrally in lateral view, but has a hypertrophied trochlea with a wide range of articulation. The ligament fossae on the lateral and medial surfaces of the distal end are dorsal to the center of the circle described by the trochlea in lateral view, although this offset is not as extreme as in the penultimate ungual. Phalanx II-2 is distinguished by its elongate proximoventral heel, the sharp constriction of the shaft between the articular facets, and the tall, narrow distal trochlea. The heel is more robust medially and concave ventrally. The ridge dividing the proximal articular facets continues on to the heel. The dorsomedial corner of the margin of the articulation forms a small everted tubercle. In spite of its short length, the phalanx is constricted between the two articular ends; this character distinguishes the dromaeosaur foot from that of troodontids (Currie and Peng, 1993). The trochlea is very tall and narrow and the articular surface defines an arc slightly in excess of 180°, as in *Deinonychus antirrhopus* (Ostrom, 1969a) and *Ve-*

lociraptor mongoliensis (Osborn, 1924). The digit II ungual is hypertrophied, as in a majority of dromaeosaurids, but not in *Adasaurus mongoliensis* (Barsbold, 1983; Ostrom, 1990). It is strongly recurved, and has a tall, narrow cross section. A large flexor tubercle is positioned adjacent to the ventral border of the articular facet. The lateral groove for the claw sheath is positioned at a level dorsal to the medial one, as in other dromaeosaurids (Kirkland et al., 1993; Rauhut and Werner, 1995).

Holtz (1994; character 32) coded pedal digit II as longer than digit IV in dromaeosaurs, *Ornitholestes hermanni* (Osborn, 1903), and *Archaeopteryx lithographica*. The condition is clearly opposite to the state coded by Holtz (1994) in dromaeosaurs (fig. 6A), and is indeterminate in *Ornitholestes hermanni* where a number of phalanges are missing (AMNH 619; Ostrom, 1969a, 1976a: fig. 15). Furthermore, pedal digit IV is longer than digit II in the Berlin specimen of *Archaeopteryx lithographica* (personal obs.; Wellnhofer, 1974). Consequently, this character appears to be uninformative as presented by Holtz (1994).

Proximally, metatarsal III is constricted between metatarsal II and IV, but it does not display an arctometatarsalian condition (fig. 6A). Just below the proximal articulation, the anterior face is gently convex, but at a level even with the tubercle of metatarsal II the surface is raised into a low, longitudinal mound. This protuberance is also present in *Velociraptor mongoliensis* (AMNH 6518), *Deinonychus antirrhopus* (AMNH 2136), and an unnamed dromaeosaur from Khulsan collected by the Mongolian American Expeditions (IGM 100/981). It is not present in ornithomimids, oviraptorosaurs, and in so-called "arctometatarsalian" (Holtz, 1994) taxa. Below this mound, the anterior face of the metatarsal shaft flattens and expands mediolaterally. The proximal end of metatarsal III is anteroposteriorly expanded and the largest diameter of the articulation between the crus and metatarsus is across the articular facet of this bone. The medial face of metatarsal III is expanded in the anteroposterior plane and the contact with metatarsal II is robust. Metatarsal III thins laterally such that the flat posterior face is inclined posterola-

terally in the proximal third of the shaft. Distal to this, the posterior face of the shaft twists to become level with the posterior face of metatarsal II. The distal half of the shaft is gently concave. In contrast to the condition in other nonavialan theropods, the trochlea of metatarsal III is ginglymoid in dromaeosaurs. In IGM 100/985 the ginglymus is asymmetric and the medial condyle is larger than the lateral one. The anterodorsal terminus of the medial condyle is raised relative to the shaft of the metatarsal. A large, but shallow, ligament fossa is evident on the medial face of the trochlea, whereas the ligament fossa of the lateral face is smaller but deeper. The contact with metatarsal IV is anteriorly convex proximally, grading into concave distally. This contact terminates a short distance proximal to the distal trochleae. A small notch between the distal ends of metatarsal III and IV probably (figs. 6A, 7) corresponds to the distal vascular foramen (Baumel, 1979) of modern avians. In anterior view, the contact between metatarsal III and IV is recessed from the anterior surface of either bone, forming a sulcus along most of the length of the metatarsus. The contact between these bones on the plantar face of the metatarsus is more planar, however, and is only concave for a short distance just distal to the proximal articulation.

Phalanx III-1 is long and relatively slender (fig. 7). The proximal articulation is slightly skewed medially, causing the proximomedial part of the shaft to be vertical and the lateral face to slant ventrolaterally. Just proximal to the distal trochlea, the dorsal face of the phalangeal shaft is indented by a proportionately deep extensor pit. The trochlea is ginglymoid and the trochlear ridges are inclined dorsomedially. By contrast, phalanx III-2 is shorter, stouter, and has a more symmetrical distal articular facet. The proximal articulation is, however, skewed in a fashion similar to that of III-1. Phalanx III-3 generally resembles III-2 although the extensor fossa and ligament fossae are less distinctly developed. Digit III ends in a weakly curved ungual that bears a low flexor tubercle. The ungual is less curved than the corresponding element in *Troodon formosus,* and resembles those of other dromaeosaurs such as *Deinonychus antirrhopus* (Ostrom, 1969a, 1969b).

Metatarsal IV is markedly flattened anteroposteriorly. It is widest at the proximal articular surface but narrows distally and is thinnest just proximal to the distal trochlea. The lateral edge of the shaft is concave in anterior view. In lateral view, the lateral edge is raised proximally to form a short crest just below the proximal articular facet. Topologically, this structure compares to the lateral plantar crest of the modern avian tarsometatarsus (Baumel, 1979). For more than half of its length the posterior face of metatarsal IV is flat. The lower third of the posterior face is raised into a large, longitudinal ridge with a rugose finish that is characteristic of muscle insertions. In modern birds part of the gastrocnemius tendon inserts on the posterolateral aspect of the tarsometatarsus. Metatarsal IV terminates in a large simple articular condyle that is larger medially than laterally. This asymmetry diverts the axis of digit IV away from digit III. Anteriorly, just proximal to the articulation, the metatarsal shaft bears a shallow extensor pit. On the posterior face of the bone, the articulation divides into two tongues, the medial of which extends further proximally than the lateral one. A small ridge connects the lateral tongue to the shaft. In accordance with the overall asymmetry of the articulation, the medial ligament fossa is much larger than the lateral one.

There are five phalanges in digit IV including the ungual. These grade from larger to smaller distally. Phalanx IV-1 is bowed toward the medial side. It has a simple, concave proximal articulation that is skewed medially to accommodate the asymmetry of the distal articulation of metatarsal IV. Ventrally the phalanx bears two tubercles proximal to the proximal articulation. The distal articulation is ginglymoid and a pronounced extensor pit is positioned just proximal to it. Phalanx IV-2 is shorter than phalanx IV-1 and does not display the medial curvature of the latter. The proximal articulation is divided by a low vertical ridge, and the lateral portion of the articular facet displays a stronger distal slope than the medial one. This difference is also present in phalanges IV-3 and IV-4. The latter phalanges are both short and stout. As is typical for theropods, the penultimate phalanx has the ligament pits shifted dorsally relative to their location on more

proximal phalanges. All of the phalanges bear a proximally directed tongue at the dorsal extremity of the proximal facet that overhangs the articulation. Articular geometry of the phalanges of digit IV suggests that it diverged laterally from digit III at the articulation between metatarsal IV and phalanx IV-1, but because of the curvature of phalanx IV-1 and the asymmetry of the articulations of more distal phalanges, the digit turned medially distally. The ungual of digit IV is only weakly curved and has a small proximally situated flexor tubercle. A well-developed groove for the claw sheath is symmetrically present on each side of the ungual.

Metatarsal V is only preserved on the left foot, and is lacking the distal end (figs. 7, 8). It is a slender splintlike bone with a flat posterior face. It tapers gradually toward its distal end and is gently curved laterally. As in other dromaeosaurs, metatarsal V is almost half the length of metatarsal IV. In many other theropods, metatarsal V appears proportionately shorter. Metatarsal V articulates with the posterior edge of the preserved distal tarsal and the posterior face of metatarsal IV.

THE PELVIS AND ANTERIOR CAUDALS

Among dromaeosaurs, a fully articulated pelvis has only been described for *Adasaurus mongoliensis* (Barsbold, 1983), although the pelvis of *Velociraptor mongoliensis* (IGM 100/25) was discussed in a paper reconstructing theropod pelvic myology (Perle, 1985). The *Adasaurus mongoliensis* specimen comprises the fragmentary remains of a severely pathologic individual. IGM 100/985 preserves the sacrum, pelvis, and anterior caudals in lifelike articulation (figs. 1, 12). The right ilium and caudosacral vertebra have been eroded, but the elements themselves are otherwise in good condition. The fractured right ilium reveals that the surface bone is dense, but spongy just below the surface.

Five coossified sacral vertebrae, as reported in *Deinonychus antirrhopus* (Ostrom, 1976b), are fused by both their centra and neural arches (fig. 9). The ilia are longer than the sacrum, however, and they completely cover the last dorsal and first caudal in lateral view. The transverse processes of the first

caudal and last dorsal vertebrae do not contact the ilia. Rugose scars on the medial faces of the ilia, opposite transverse processes, suggest that there was a ligamentous connection between the elements involved (fig. 10).

The first four sacrals all have fused neural spines forming a continuous lamina (fig. 9). The fifth sacral is incompletely preserved, preventing determination of whether its neural spine was fused to this lamina. The zygapophyses of the sacral vertebrae are fused to form a sinuous ridge on either side of the neural spine lamina, as was described for *Ornithodesmus cluniculus* (Howse and Milner, 1993). In contrast to *Saurornitholestes langstoni* (TMP 67.20.36), the last dorsal vertebra and sacral vertebrae do not possess pneumatic foramina. Vertebral pneumatization occurs early in theropod ontogeny as witnessed in *Microvenator celer* (Makovicky and Sues, submitted), so it may represent a diagnostic feature of the Tugrugeen specimen. However, this condition needs to be reevaluated in other dromaeosaurs.

As in other maniraptors, the ventral faces of the midsacral centra bear a shallow, continuous sulcus. This is difficult to see in IGM 100/985 because most of the centra are damaged by erosion, and the sulcus is comparatively shallow in comparison to that in some specimens of *Saurornitholestes langstoni*, however, some variation occurs in the development of this sulcus in the latter taxon. Most of the sacral ribs and transverse processes are not preserved.

The ilium is dolichoiliac and the postacetabular portion is longer than the preacetabular one (fig. 11). The anterior end is not well preserved, but appears to have been convex, forming an acute angle at the anterodorsal corner of the ilium. Below this, the anterior rim descends posteroventrally and forms a small pointed process. This is proportionately much smaller than the anteroventral hook of the ornithomimid or tyrannosaurid ilium, and the dromaeosaur condition approaches that of Avialae where there is no trace of an anteroventral process. Another derived condition of the ilium shared by Avialae and dromaeosaurids is the absence of a medial antiliac shelf for origin of the M. cuppedicus muscle (Rowe, 1986). Such a shelf is primitive for tetanurans
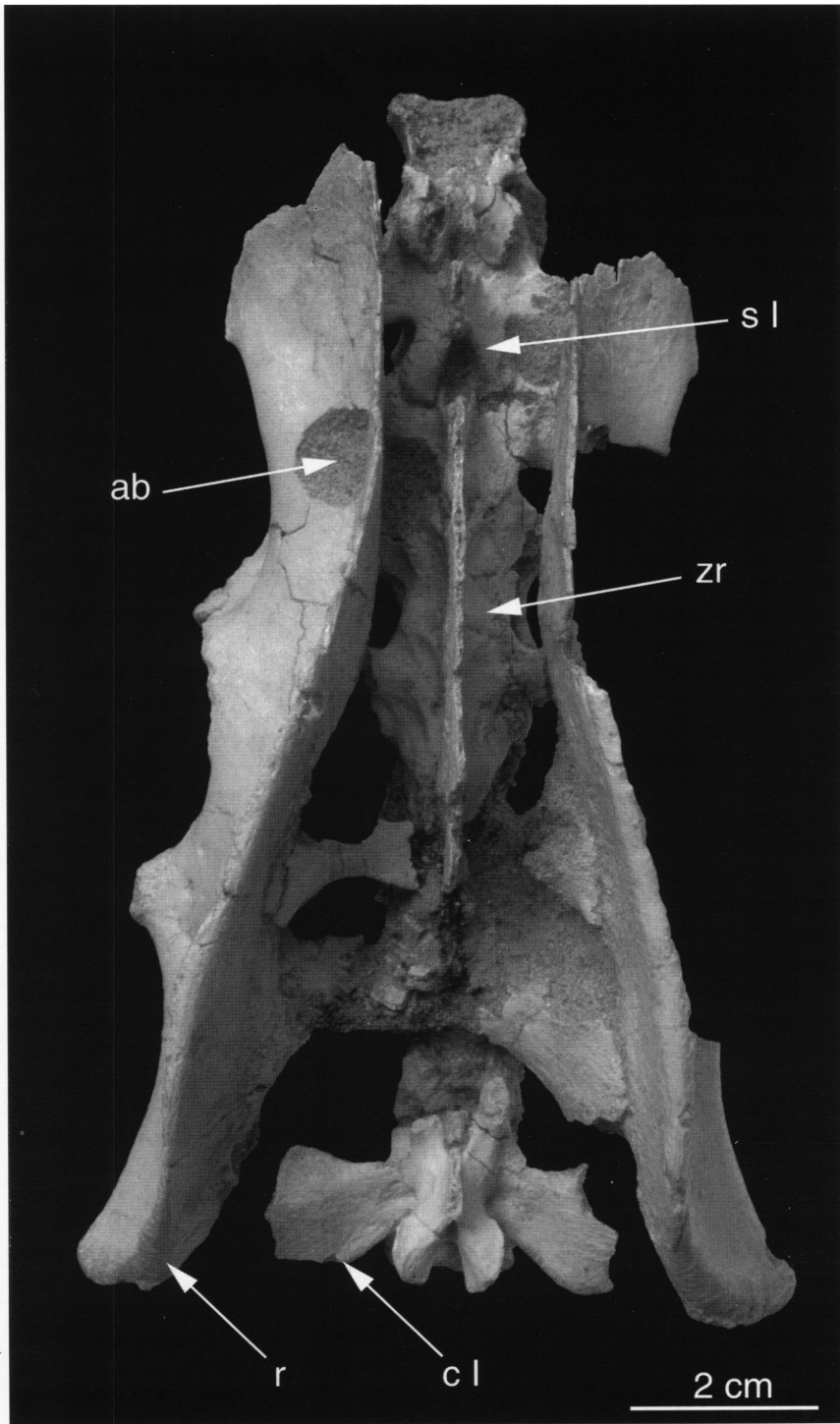
Fig. 9.   Articulated sacrum and ilia of IGM 100/985 in dorsal view. ab = arthropod borings; cI = caudal I; r = rugosity; sI = sacral I; zr = zygapophyseal ridge.
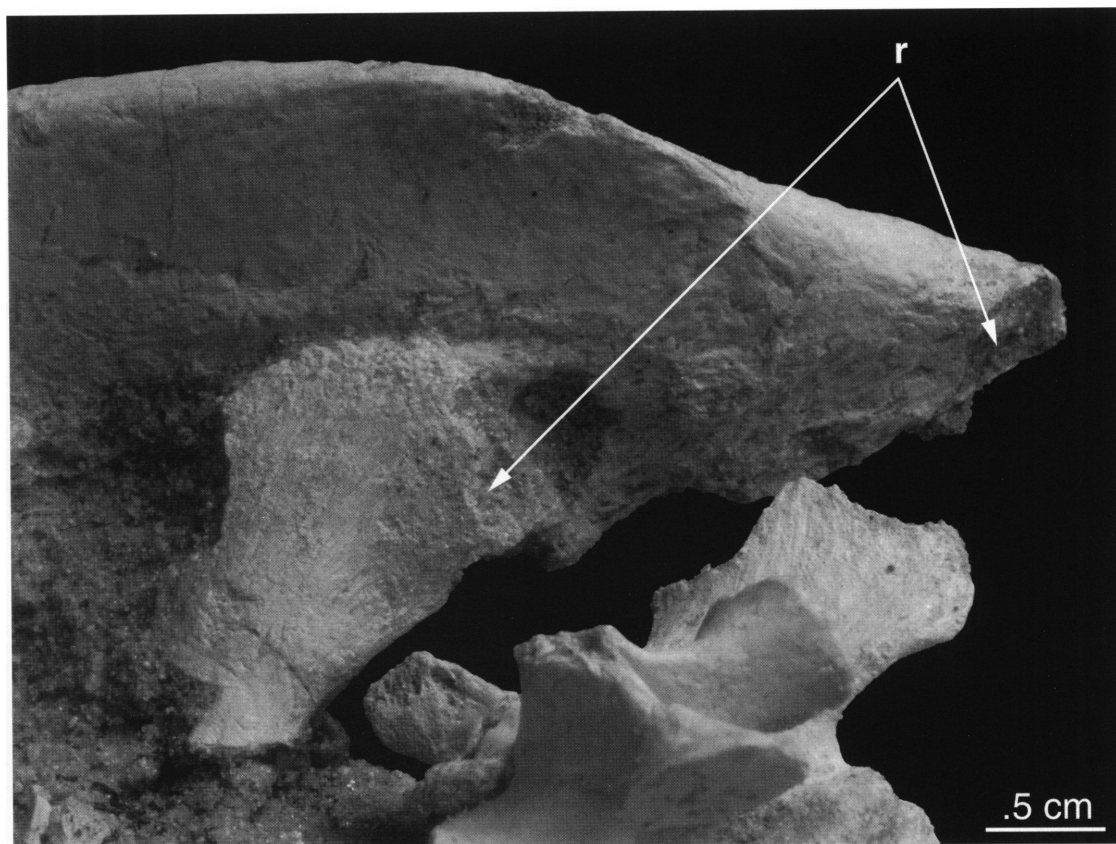
Fig. 10. Detail of rugose scars on medial face of right ilium opposite the transverse processes of the anteriormost caudal. r = rugosities.

(Rowe and Gauthier, 1990) and is present in other advanced, small theropods such as ornithomimids, troodontids, *Microvenator celer,* and *Unenlagia comahuensis* (Novas and Puerta, 1997). The ventral margin of the ilium slopes laterally and the everted rim continues as a ridge that overhangs the wide pubic peduncle. The pubic peduncle is anteroposteriorly much longer than the ischiadic peduncle as in other dromaeosaurs such as *Deinonychus antirrhopus* (AMNH 3015) and *Velociraptor mongoliensis* (IGM 100/25). The lateral face of the pubic peduncle is anterolaterally concave and is lightly striated, which suggests muscular insertion. The posterior face of the pubic peduncle forms the widest portion of the acetabulum. Posterodorsal to the pubic peduncle, the width of the acetabulum diminishes and is narrowest just behind the dorsal apex. As it descends onto

the anterior face of the ischiadic peduncle, the acetabulum becomes wider and twists laterally to form an anterolaterally facing antitrochanter. The ischiadic peduncle is shallow and subtriangular.

Posterior to the ischiadic peduncle, the lateral face of the ilium is concave and has a thickened dorsal rim (fig. 9). Ventrally, the postacetabular wing forms a wide and flat brevis shelf, a feature not previously described in dromaeosaurids, but present in a number of undescribed specimens collected by the MAS–AMNH expeditions, including IGM 100/981 and IGM 100/982. The postacetabular wings of the ilia diverge from the sacrum, and in dorsal aspect the rim of each ilium forms a sigmoid curve that is laterally concave anterior to the acetabulum and convex posterior to it (fig. 9). However, there is no contact between the iliac blades and neu-
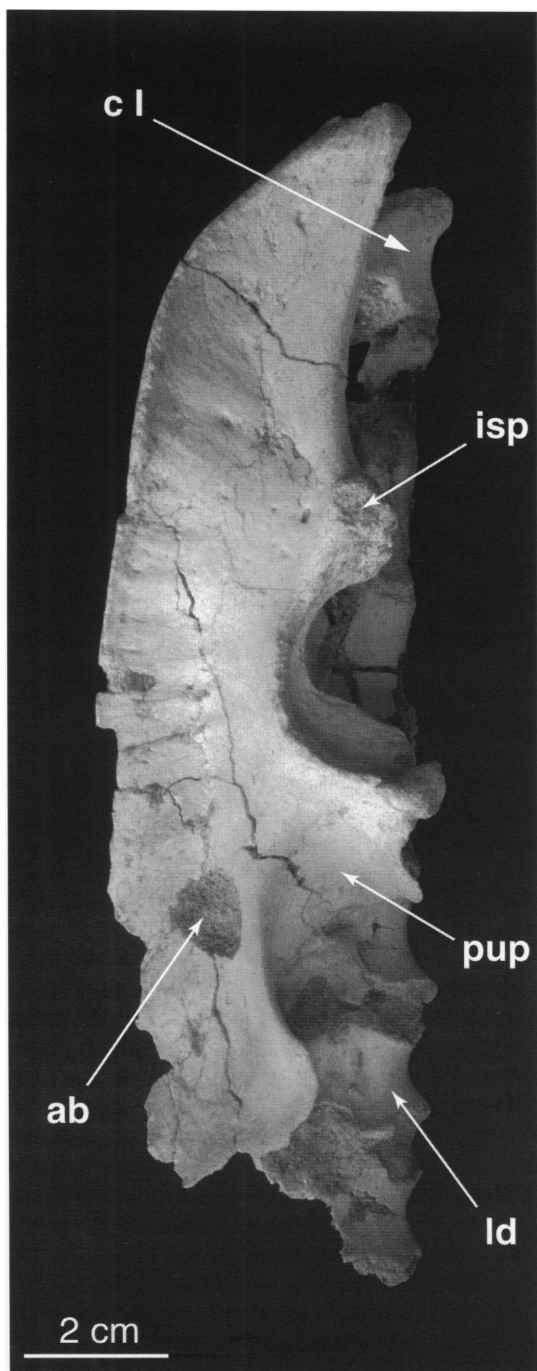
Fig. 11. Lateral view of left ilium in articulation with the sacrum. Anterior is toward bottom of page. ab = arthropod boring; ld = last dorsal vertebra; cI = caudal I; isp = ischiadic peduncle; pup = pubic peduncle.

ral spines as, for example, in ornithomimids and *Mononykus olecranus*. At the posterior terminus of the ilium the dorsal rim is very robust and rugose.

The most significant feature of the pelvis is the degree of pubic retroversion (fig. 12). There is an angle of 155° between the long axis of the pubis and a line passing between the anteriormost and posteriormost extremities of the ilium. This retroversion is far more pronounced than that seen in reconstructions of *Deinonychus antirrhopus* (Ostrom, 1976b) and more closely approximates the condition seen in the Berlin specimen of *Archaeopteryx lithographica* (personal obs.), *Mononykus olecranus* (Perle et al., 1993, 1994), and *Velociraptor mongoliensis* (Perle, 1985). The proximal end (fig. 13) is only preserved on the left pubis. It is anteroventrally expanded and laterally concave. The iliac articulation is long and narrow. Posterior to it is an equally long finished edge facing posterodorsally, which constitutes the pubic portion of the acetabulum. The posterior part of this articular face extends along the dorsal edge of the ischiadic peduncle of the pubis. Although not well preserved, the articulation with the ischium appears to have been subtriangular in axial view. Ventral and medial to the ischiadic process of the pubis, the shaft bears a small, posteriorly facing depression enclosed laterally by the ischiadic process and medially by a sharp ridge that descends ventrally to form the pubic apron. The anterior edge of the iliac process of the pubis is vertical, below which the pubic shaft kinks sharply backward. The corner formed by this kink bears a low tubercle that probably served as the origin of the M. ambiens, as suggested by the position of this muscle in some modern birds (George and Berger, 1966). Below this, the pubic shaft is very thin and teardrop shaped in cross section. The medial face bears a ridge that widens distally to form the pubic apron. The pubic apron is relatively short in IGM 100/985 and is only present for about half the length of the pubis (fig. 14). In general, the pubic canal in dromaeosaurs appears to be wider than previously reconstructed (Ostrom, 1976b). A wide pubic canal is also characteristic of other advanced small theropods such as ornithomimids, avimimids, oviraptors, troodontids, and Avialae,
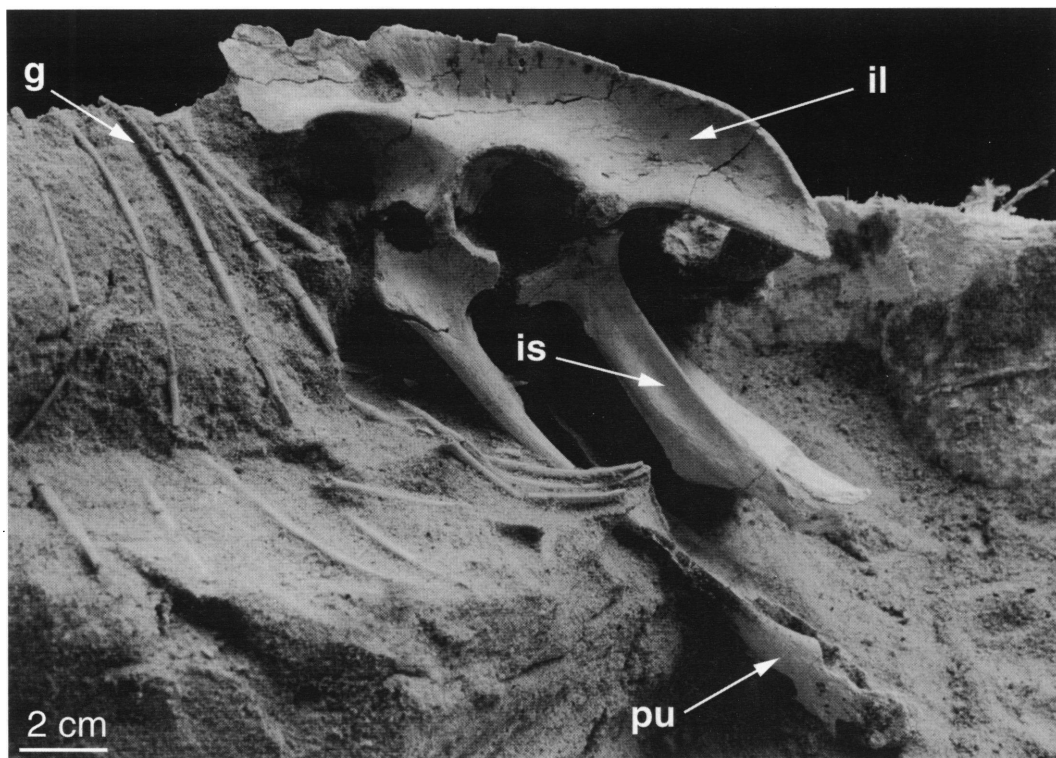
Fig. 12.   Left lateral view of the articulated pelvis of IGM 100/985. Notice the large degree of pubic retroversion. g = gastralia; il = ilium; is = ischium; pu = pubis.

but is not encountered in more primitive tetanurans. Proximally each flange of the pubic apron curves posteriorly as it approaches the midline such that the midline contact is directed posteriorly at its proximal border. The two sides of the apron do not meet below this contact, but are separated by a thin slit that extends up to a point where the pubic shafts broaden in an anteroposterior plane. This expansion commences just past two-thirds of the way down the preserved length of the pubes and terminates in the pubic boot. Unfortunately, most of the pubic boot was not preserved, yet the incipient angle of the boot indicates that the there was no anterior expansion, and furthermore that the boot was relatively short and deep.

Both ischia are preserved in the Tugrugeen dromaeosaurid, but as with the pubes, only the left element has the proximal end preserved (figs. 15 A, B). The ischia are only half as long as the pubes. As in *Archaeopteryx lithographica* and more advanced avi-

alan taxa, the ischia are unfused despite contacting each other distally. Fused ischia have not been reported in any dromaeosaur, but the lack of fusion in IGM 100/985 may be an ontogenetically immature feature. The proximal end is anteroposteriorly expanded, giving it a "T"-shaped profile in lateral view. The pubic process is longer than the iliac one, and is transversely expanded where it meets the pubis. The dorsal border forms the ischiadic contribution to the acetabulum and its narrow morphology shows that it had no weight-bearing function. Just below the pubic process, there is a prominent anteriorly directed tubercle. The iliac process is robust and has a large subtriangular articular facet for articulation with the ischiadic peduncle of the ilium. The main body of the ischium is constricted below the expansion of the articular processes but gradually widens distally and becomes flat and platelike. Hypertrophy of the obturator process to form a large triangular flange along the anterior border of
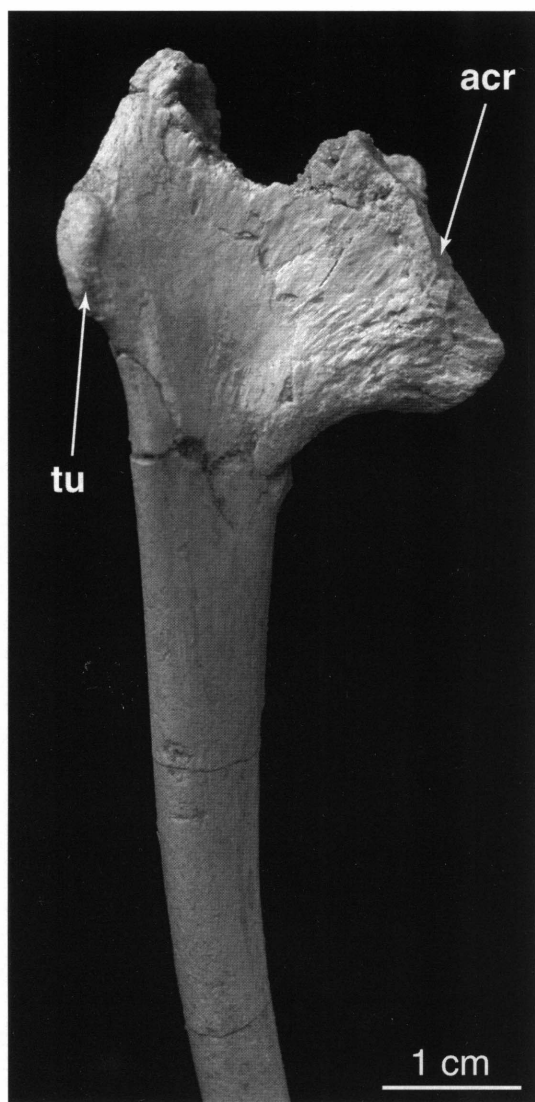
Fig. 13. Detail of the proximal end of the left pubis in lateral view. The large tubercle forming the corner of the anterior face is in the same position as the M. ambiens insertion of modern ratites. acr = acetabular rim; tu = tubercle.

the ischium is partly responsible for this morphology. The apex of the obturator process is situated about three quarters of the way down the length of the ischium. Distal to the obturator flange, the ischium terminates as a flattened spatulate process, with a rugose surface that may have been an attachment for a ligament connecting the distal ends of the ischia. These rugosities may also mark a zone where the ischia became fused in mature individuals. In axial view each ischium shows a medial curvature toward the distal end. A sharp ridge extends from the iliac process down the posterior edge of the ischium for a third of its length. Ventral to this the ridge is continuous with a shallow groove along the medial side of the posterior border of the ischium.

CAUDAL VERTEBRAE

A series of eight articulated caudals was found in articulation with the sacrum. The anteriormost is covered in lateral view by the postacetabular ala of the ilia (fig. 9). This vertebra has expanded transverse processes and it is evident from the rugose ventral surfaces of these processes that part of the M. caudifemoralis brevis originated there. The rugosities on the medial face of the ilia level with the transverse processes of the first caudal suggest a strong ligamentous bond, and it is evident that this element was functionally as much a part of the sacrum as of the tail. All the preserved caudals have short centra, with a roughly square cross section and a pronounced ventral sulcus (figs. 16A, B). Central length displays a marked increase distally, however (table 1). The ventral border of the intercentral articular facets are highly beveled to form large chevron facets.

The anterior caudals have medially inclined prezygapophyseal articular facets and the postzygapophyses display a corresponding inclination (figs. 16A, B). The neural spines of the first four caudals are axially short, moderately tall, and do not lean strongly toward the posterior. The transverse processes are short in the first two caudals, but become elongated in the more posterior parts of the series. The processes flare distally and have rounded terminations, unlike the squared-off reconstruction in Ostrom (1969a: fig. 38). The second caudal has a diverging ridge that extends from the base of the prezygapophysis posteriorly across the proximal part of the transverse processes, where it diverges into a branch toward the distal end of the transverse processes and one that turns medially toward the base of the postzygapophyses (fig. 16A). This latter ridge forms a small pocket on the lateral face of the neu-
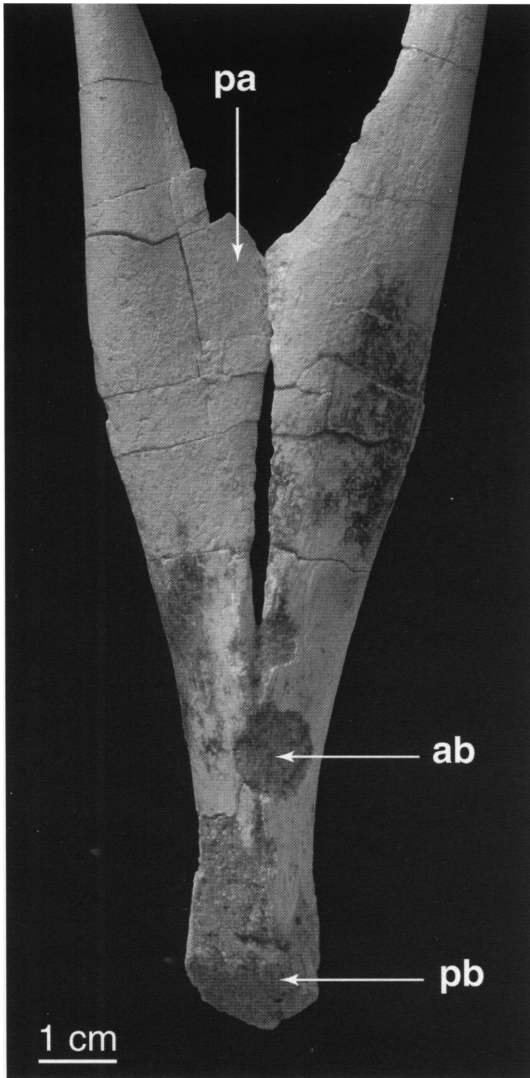
Fig. 14.   Anterior view of distal part of fused pubes. Notice the incomplete co-ossification of the pubic apron. ab = arthropod boring; pa = pubic apron; pb = pubic boot.

ral arch. The second caudal is the only vertebra to display this peculiar morphology.

In the three distalmost vertebrae in the series, the neural spine becomes elongated axially and stretches along the length of the neural arch. The neural spines display a concomitant decrease in spine height as well as a progressive angling toward the posterior. The last preserved caudal demonstrates incipient elongation of the prezygapophyses

and reduction of the postzygapophyses, features that become hypertrophied in the distal caudals of dromaeosaurs (Ostrom, 1969a, 1969b).

The first chevron is located between caudals 1 and 2 (fig. 16A). Larson (1994) suggested that, as in extant crocodilians, the position of the first chevron can be used to determine the sex of a specimen, with females having a more distal location of the first chevron. This would suggest that IGM 100/985 is a male. The first chevrons are elongate and slender, but from the third chevron back, they become abbreviated and expanded proximodistally to form a plate at the distal end (fig. 16B).

DISCUSSION

The articulated and three-dimensional preservation of the Tugrugeen specimen sheds light on several problematic points in the anatomy of advanced small theropods in general and dromaeosaurids in particular. Additionally it provides new phylogenetic information pertinent to maniraptoran phylogeny, as well as yielding some insights on the functional anatomy of dromaeosaurids.

In his seminal paper on theropod phylogeny, Gauthier (1986) considered the presence of fused sternal plates as diagnostic of Coelurosauria. He coded fused sterna as present in Ornithomimosauria based on his allocation of Ingenia yanshini to that clade. Avialae and Caenagnathidae (= Oviraptorosauria) were also scored as possessing fused sternal plates. No oviraptorosaur, with the exception of IGM 100/30, is known to have fused sternal plates. This condition is observed in several adult specimens (IGM 100/42 and specimens recently collected by MAS–AMNH expeditions) and does not appear to be related to ontogenetic age.

Sternal ossifications are absent in the only known articulated skeleton of a troodontid (Russell and Dong, 1993a). In Ornithomimosauria, sternal plates are reported only in the primitive form Pelecanimimus polyodon (Peréz-Moreno et al., 1994). Among theropods other than Coelurosauria (sensu Gauthier, 1986), sternal plates are known from a single, weakly keeled sternal element in Sinraptor dongi (Currie and Zhao, 1993), and as

paired elements in a tyrannosaurid (Lambe, 1917) and *Carnotaurus sastrei* (Bonaparte et al., 1990).

The disjunct distribution of ossified sternal plates, and of their fusion into a single sternal element may turn out to be diagnostic features of different clades within Theropoda. Furthermore, ossification of the sternal plates into a single element may be diagnostic of Avialae or Metornithes depending on the condition in *Archaeopteryx lithographica.* Clarity on this point requires further phylogenetic analysis, however, and neither of these features can easily be considered diagnostic of the Coelurosauria or clades within Maniraptora at present.

Very little attention has been paid to the gastralia of theropods. Comparison of the gastral basket of IGM 100/985 to other theropods demonstrates that dromaeosaurs, troodontids, and basal avialans differ from ornithomimids and more basal tetanurans in having shorter medial than lateral gastral segments. Furthermore, there may be differences in shape of the distal articulations between medial segments. In tyrannosaurs these articulations are saddle shaped (Makovicky and Currie, in press), whereas they are more spatulate in IGM 100/985. Ostrom (1969a) reconstructed the medial gastralia of *Deinonychus antirrhopus* as being L-shaped at the midline, but such a morphology is not visible in any of the gastralia in IGM 100/985. The anteriormost and distalmost pairs of medial gastralia are fused in some tyrannosaur specimens (Lambe, 1917; Makovicky and Currie, in press), and a fused gastral segment was recovered with one specimen of *Troodon formosus* (Russell, 1969). Fused gastral segments are known from juvenile tyrannosaurs (Makovicky and Currie, in press), so lack of fusion cannot be strictly interpreted as being an ontogenetic feature. Fusion of gastralia has also been recognized in some specimens of *Archaeopteryx lithographica* (Wellnhofer, 1974, 1992, 1993), but has yet to be reported in any dromaeosaur.

The dromaeosaur sacrum was only mar-ginally treated in previous descriptive works, in spite of being known for a number of taxa including *Deinonychus antirrhopus* (Ostrom, 1976b), *Saurornitholestes langstoni* (TMP 67.20.36), and *Velociraptor mongoliensis* (IGM 100/25). The dromaeosaurid sacrum consists of five coossified vertebrae, although the last dorsal vertebra may coossify with the first sacral in old individuals (Ostrom, 1976b). Five sacral vertebrae appears to be the primitive state for tetanuran theropods and is found in primitive avialians, primitive ornithomimosaurs (Barsbold, 1983), and probably *Ornitholestes hermanni* (AMNH 619) among coelurosaurian taxa. In view of the length of the ilium in the Tugrugeen dromaeosaurid, which covers the last dorsal and first caudal as well as the true sacrals, it is strange that incorporation of further vertebrae into the sacrum has not occurred as in troodontids, oviraptorids, avimimids, and some ornithomimids. Nevertheless, distinct scars on the medial face of the ilia opposite the transverse processes of the these two vertebrae indicate that the last dorsal and first caudal were functionally part of the sacrum.

From the second sacral back, the centra develop a shallow sulcus along the ventral midline. This is only weakly developed in the Tugrugeen specimen, but in old individuals of *Saurornitholestes langstoni* the sulci become confluent and deep. A similar, but less pronounced, sulcus is present on the sacrum of *Chirostenotes pergracilis* (TMP 84.167.44) and *Troodon formosus* (Varrichio, personal commun.) and this structure probably corresponds to the ventral synsacral sulcus (Baumel, 1979) of certain ornithothoracine birds.

Dromaeosaur sacra have a number of diagnostic features, which have not been appreciated previously. The zygapophyses are fused to form a sinuous ridge on either side of the fused neural spine lamina. This structure is only well developed in dromaeosaurs and the fragmentary type of *Ornithodesmus cluniculus* (Howse and Milner, 1993). The latter taxon was referred to the Troodontidae,

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Fig. 15.　Left ischium in (**A**) lateral and (**B**) medial views. dg = distal groove; ilp = iliac peduncle of ischium; op = obturator process; pup = pubic peduncle of ischium; tu = tubercle.
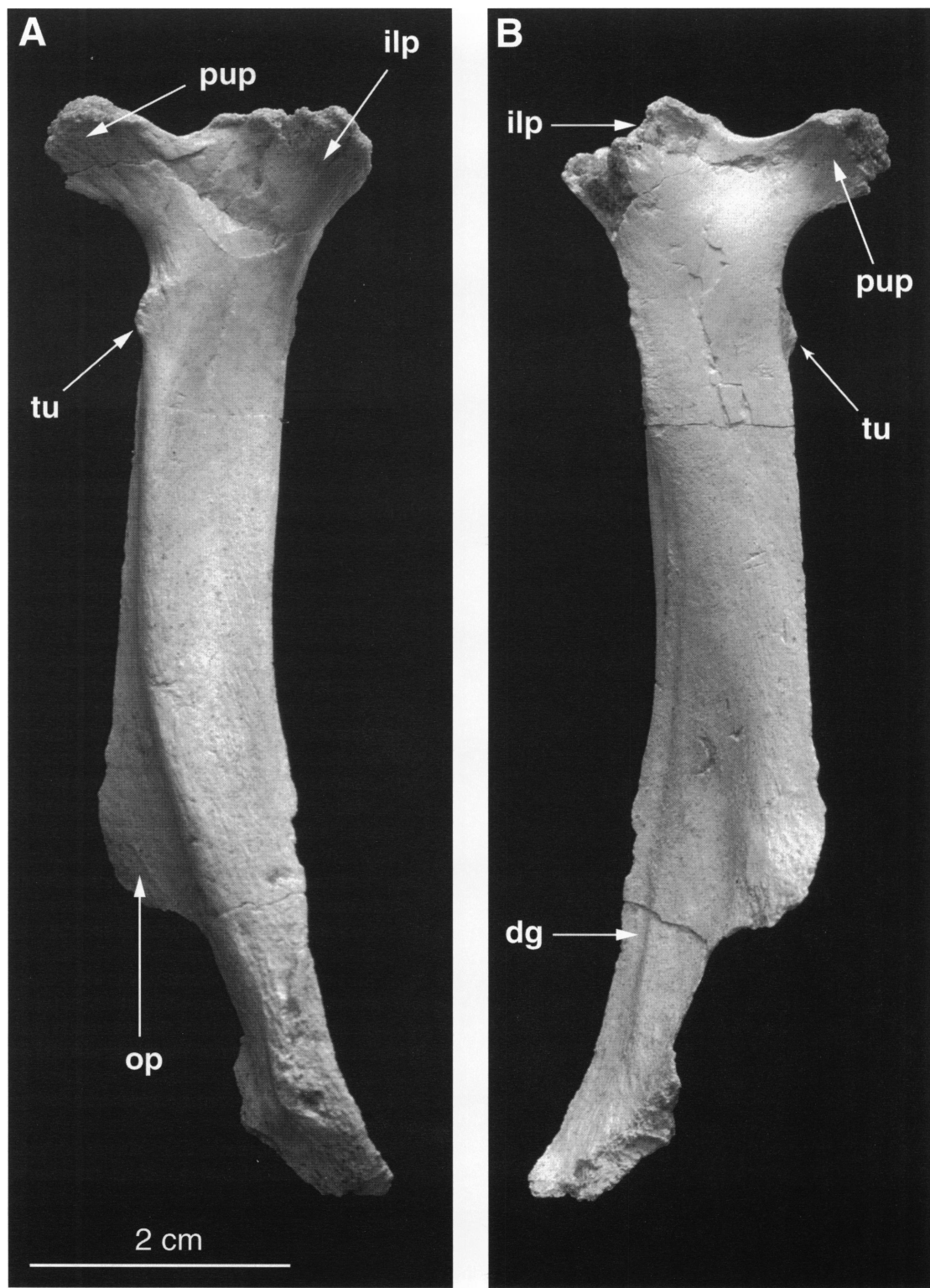
because of similarities with a *Saurornitho-lestes langstoni* sacrum, which Howse and Milner (1993) erroneously interpreted as being from a troodontid. In other coelurosaurian taxa the neural canal and zygapophyses coalesce more smoothly in the sacrum, without forming a distinct ridgelike structure as seen in dromaeosaurs. As in a number of other theropods, including tyrannosaurs, ornithomimids, and caenagnathids, the neural spines of the dromaeosaur sacral vertebrae fuse to form a lamina. In other theropods, notably ornithomimids (Gilmore, 1920; Osmólska et al., 1972), the formation of this feature displays ontogenetic variation, and this may well be the case in dromaeosaurs too. Dromaeosaurs are one of a few lineages that display pneumatization of the dorsal vertebral centra, and in at least *Saurornitholestes langstoni* this pneumatization is also developed on the first two sacral vertebrae. As stated above, the last dorsal and first sacrals of the Tugrugeen specimen do not have pneumatic foramina perforating the centra. Because vertebral pneumatization develops very early in ontogeny, this feature cannot be related to the immaturity of the specimen and is either an individual anomaly or of phylogenetic significance.

The ilium displays a number of features not previously discussed for dromaeosaurids. Of these, the absence of a medial shelf along the antiliac blade is an advanced character that is shared with birds, and is not present in other maniraptoran lineages (contra Novas and Puerta, 1997). This shelf is present in *Unenlagia comahuensis* (Novas and Puerta, 1997), in which respect this taxon is more primitive than dromaeosaurs. Likewise the length of the pubic peduncle markedly exceeds that of the iliac peduncle in both dromaeosaurs and basal avialan taxa such as *Archaeopteryx lithographica*, whereas the size difference of these processes is less pronounced in other maniraptorans.

The orientation of the pubis in dromaeo-saurs has received much attention in recent phylogenetic literature (Ostrom, 1976a; Gauthier, 1986; Holtz, 1994) because it has been judged to be a synapomorphy of a clade uniting this theropod taxon with the Avialae. In his description of the pubis of *Deinonychus antirrhopus,* Ostrom (1976b) suggested that the pubis and ischium were less divergent than in other theropods based on the orientation of these elements in a quarry and the orientation of the pubic peduncle. Nevertheless, because the pubes lacked the entire proximal end he could not accurately determine the exact orientation of the pubis, and judged that it may have a ventral to slightly retroverted position. The articulation seen in the Tugrugeen specimen, as well as an articulated specimen of *Velociraptor mongoliensis* (IGM 100/25; Perle, 1985), clearly shows that the pubis was retroverted at an acute angle in velociraptorine dromaeosaurs.

The presence of a kink in the anterior edge of the pubis in IGM 100/985 with the corner formed by the tubercle for the M. ambiens suggests that a similar kink in the Berlin specimen of *Archaeopteryx lithographica* (fig. 17) may be homologous, although the pubis is apparently rotated out of place in this specimen (Ostrom, 1976b; Wellnhofer, 1985). Walker (1980) suggested the presence of a "pectineal process" at the proximal end of the pubis in *Archaeopteryx lithographica* based on the morphology of the Berlin and London specimens, but his claim was refuted by Wellnhofer (1985) on the grounds that no comparable structure is present in other specimens of *Archaeopteryx lithographica.* Our identification of a pectineal process in IGM 100/985, however, substantiates the presence of a large M. ambiens origin on the pubis of dromaeosaurs and suggests a similar point of insertion in *Archaeopteryx lithographica.* A similar, but smaller, expansion of the proximal end of the pubis is present in *Confusciu-sornis santus* (personal obs.), and the M. ambiens may have originated on the expanded

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Fig. 16.   Second caudal (**A**) and series of caudals III–V (**B**) vertebrae in lateral and dorsal views. Note the proximal end of the first chevron at the anterior end of caudal II. cIII = caudal III (positions of vertebrae indicated by Roman numerals); ch = chevrons; ns = neural spine; prz = prezygapophysis; pz = postzygapophysis; trp = transverse process.
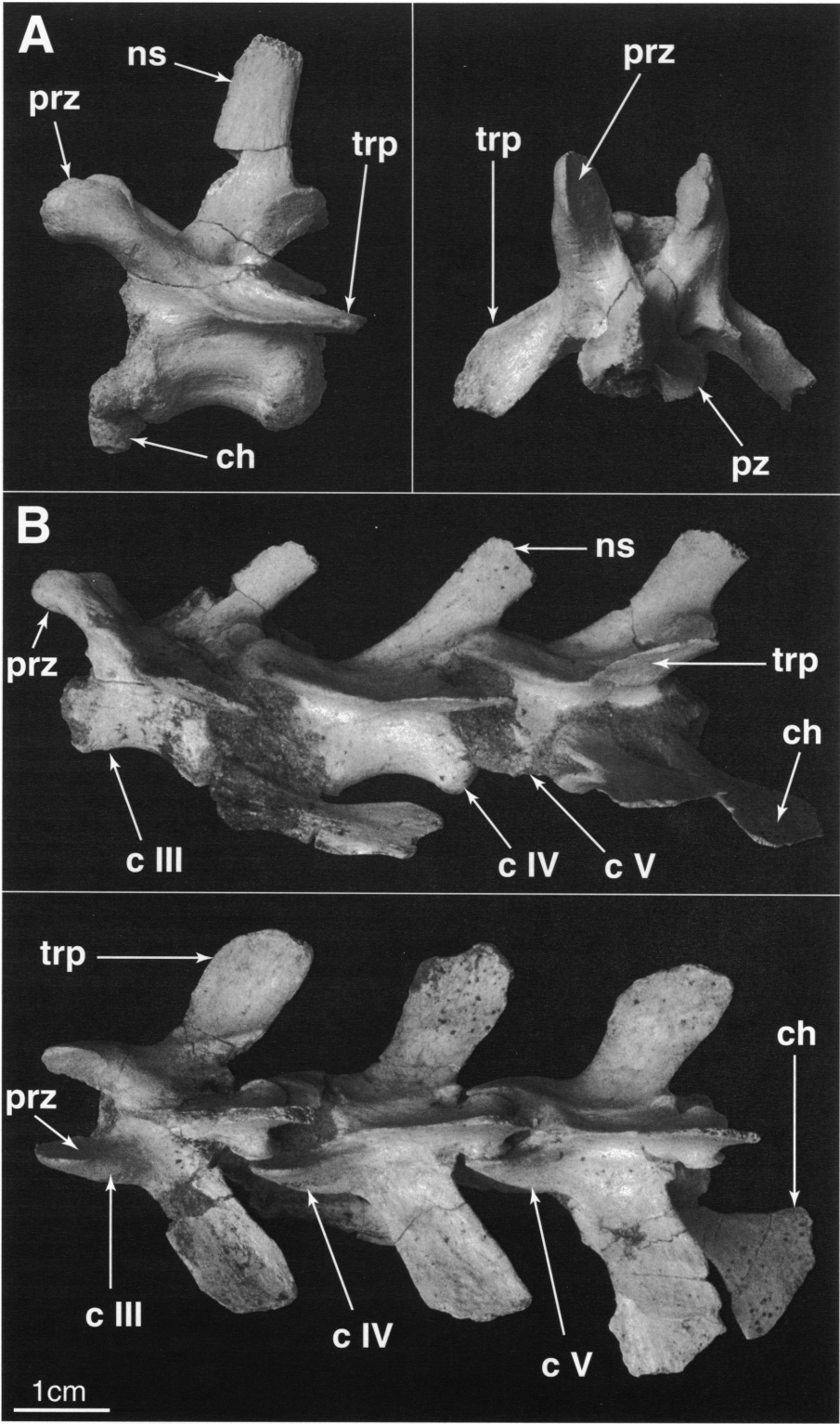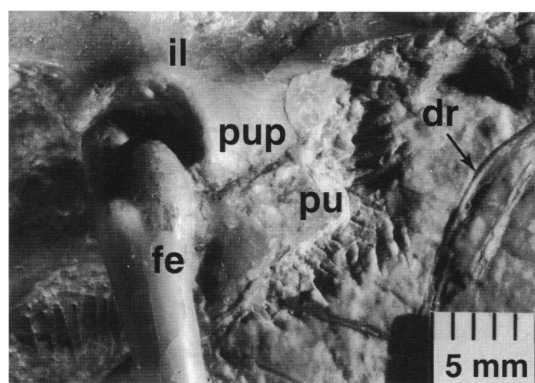
Fig. 17.   Detail of the proximal end of the pubis and iliac pubic peduncle of the Berlin specimen of *Archaeopteryx lithographica*. dr = dorsal rib; fe = femur; il = ilium; pu = pubis; pup = pubic peduncle of ilium.

anterior prong of the proximal end of the pubis in *Mononykus olecranus* (Perle et al., 1994; Chiappe et al., 1996). A large pectineal process is present on the proximal end of the pubis in ratites, but is situated on the pubic peduncle of the ilium in neognaths (Walker, 1980). If the pubic orientation seen in the Eichstätt, Aktienverein and Solnhofen specimens is correct (see Walker, 1980; Tarsitano and Hecht, 1980; and Howgate, 1985 for counterarguments), the pubis of *Archaeopteryx lithographica* is less retroverted than in dromaeosaurs. This larger angle between the pubis and femur in dromaeosaurs may account for the more prominent nature of the pectineal process.

Perle (1985) argued that the posterior orientation of the pubis in the Dromaeosauridae would lead to a marked increase in retractive muscular force on the femur, and that the animals may have progressed using saltatory locomotion. The anatomy of the more distal hindlimb elements, however, argues against such a conclusion. In mammals that are obligate saltators, the distal hindlimb elements, especially the metatarsus, are extremely elongate. Dromaeosaurids, by contrast, have one of the shortest metatarsus-to-tibia ratios among advanced small theropods.

Pubic retroversion has been considered to be an apomorphy of dromaeosaurs and avialans (Ostrom, 1976a; Gauthier, 1986; Holtz, 1994). Barsbold (1979) pointed out that pubic retro-

version was more widespread in theropods, and also occurred in therizinosaurs. However, until recently, the systematic position of therizinosaurs within Dinosauria has been hotly debated (Paul, 1984; Sereno, 1989; Barsbold and Maryanska, 1990; Russell and Dong, 1993b; Clark et al., 1994).

Detailed examination of this feature in IGM 100/985 indicates that pubic retroversion in dromaeosaurs and basal birds is composed of a suite of interrelated features rather than a single character. It can be distinguished easily from the therizinosaur condition by the lack of a flange for the insertion of the M. ambiens (pectineal process), a narrow pubic peduncle, and an ischium that is nearly as long as the pubis (~⅔) in therizinosaurs.

Nevertheless, the interdependence of some of these pelvic characters linking avialians and dromaeosaurs is difficult to judge, and many of these features may be related to the opisthopubic condition. More detailed information concerning the distribution of these individual features is required from other maniraptoran taxa, before we can justify coding this complex as anything more than a single character.

The lack of an anterior expansion of the pubic boot was cited as a maniraptoran apomorphy by Gauthier (1986: character 79). The presence of this feature cannot be confirmed for *Microvenator celer*, because the pubic boot is incompletely preserved (Makovicky and Sues, submitted). Although, this feature is present in *Coelurus fragilis* (YPM 2010), the pubic foot is proportionately enormous and elongate relative to that of most other theropods. Besides having no anterior expansion, the pubic boot of dromaeosaurids, *Unenlagia comahuensis,* and basal avialans such as *Archaeopteryx lithographica* (Berlin specimen, personal obs.) and *Sinornis santensis* (Sereno and Rao, 1992) is short and deep, and is readily distinguished from that of other maniraptorans.

The ischia are unfused in dromaeosaurs, most avialans—although *Noguerornis gonzalezi* appears to have an ischiadic symphysis, it is unclear whether it is fused or not (Chiappe, personal commun.)—the troodontid *Sinornithoides youngi,* and some oviraptorid specimens (IGM 100/30 and IGM 100/42). The type of *Saurornithoides mongoliensis* (AMNH 6516) and an adult oviraptorid

IGM 100/972 (Norell et al., 1995: fig 1) have fused ischia, however, and lack of fusion may be ontogenetic in a number of theropods. It is nevertheless a diagnostic character in birds and since fused ischia have not been reported in any dromaeosaur, it may possibly be a character uniting these two taxa. Most advanced maniraptoran taxa are characterized by a wide and flat ischium with a distally positioned obturator process (Gauthier, 1986), whereas the ischia of ornithomimids, *Ornitholestes hermanni,* and tyrannosaurs are slender and rodlike with a proximally situated obturator process.

In previous reconstructions of some theropods, the hallux was placed in a reversed or a semireversed position (see Ostrom, 1969a, 1969b, 1978). This reconstruction was based on three sources of evidence. First, the second metatarsal of many theropods bears a rugose patch or ridge on the posteromedial face of the shaft, which was interpreted as a point of attachment. Secondly, many footprints attributed to theropods display a short imprint pointing nearly opposite to the direction of the three main weight-bearing toes, and it has been suggested that this impression was made by a reversed hallux. Finally, by invoking phylogeny, a number of workers have suggested that the reversed condition of the first digit in the foot of avialan taxa was also present in at least some non-avialan theropods. For example, Ostrom (1978) stated that the orientation of the pedal ungual of digit I of *Compsognathus longipes* was oriented in parallel with those of the other toes, but then proceeded to argue that this was an artifact

of preservation and that the toe may have been reversed in the live animal. His reconstruction (Ostrom, 1978: fig. 14) shows the toe as reversed on one foot but in a normal orientation on the other.

In spite of the cumulative strength of these arguments, the Tugrugeen specimen demonstrates that the hallux was not reversed in dromaeosaurs, but articulated in parallel with the other toes. Articulated specimens show that this was also the condition in oviraptorids and other theropods. Recently, Gatesy and Middleton (1996) have shown that the imprint of a seemingly reversed hallux may be an artifact of the depth of substrate relative to the length of the foot, providing further evidence against the hypothesis of a reversed hallux. Thus, full reversal as seen in *Archaeopteryx lithographica* and ornithothoracine birds is only found within Avialae.

REFERENCES

Barsbold, R.
    1974. Saurornithoididae, a new family of small theropod dinosaurs from Central Asia and North America. Paleontol. Pol. 30: 5–22.
    1979. Opisthopubic pelvis and the carnivorous dinosaurs. Nature 279 (5716): 792–793.
    1983. Carnivorous dinosaurs from the Late Cretaceous of Mongolia. Joint Soviet-Mongolian Palaeontol. Exped. Trans. 19: 1–119. [In Russian]

Barsbold, R., and T. Maryanska
    1990. Segnosauria. *In* D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria, pp. 408–415. Berkeley: Univ. of California Press.
Barsbold, R., and H. Osmólska
    1990. Ornithomimosauria. *In* D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria, pp. 225–244. Berkeley: Univ. of California Press.
Baumel, J. J.
    1979. Osteologia. *In* J. J. Baumel, A. S. King,

A. M. Lucas, J. E. Breazile, and H. E. Evans (eds.), Nomina Anatomica Avium, pp. 53–121. London: Academic Press.

Bonaparte, J. F., F. E. Novas, and R. A. Coria
1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. Nat. Hist. Mus. Los Angeles Cty. Contrib. Sci. 416: 1–41.

Chiappe, L. M.
1992. Enantiornithine (Aves) tarsometatarsi and the affinities of the Late Cretaceous Avisauridae. J. Vertebr. Paleontol. 12(3): 344–350.
1993. Enantiornithine (Aves) tarsometatarsi from the Cretaceous Lecho Formation of Northwestern Argentina. Am. Mus. Novitates 3083: 27 pp.
1996. Late Cretaceous birds of Southern America: anatomy and systematics of Enantiornithes and *Patagopteryx deferrariisi*. Münch. Geowiss. Abh.(A) 30: 203–244.

Chiappe, L. M., M. A. Norell, and J. M. Clark
1996. Phylogenetic position of *Mononykus* (Aves: Alvarezsauridae) from the Late Cretaceous of the Gobi Desert. Mem. Queensland Mus. 39(3): 557–582.

Claessens, L. P. A. M.
1996. Dinosaur gastralia and their function in respiration. J. Vertebr. Paleontol. 16 (suppl. to 3): 28A.

Clark, J. M., A. Perle, and M. A. Norell
1994. The skull of *Erlicosaurus andrewsi*, a Late Cretaceous "segnosaur" (Theropoda: Therizinosauridae) from Mongolia. Am. Mus. Novitates 3115: 39 pp.

Currie, P. J., and J. H. Peng
1993. A juvenile specimen of *Saurornithoides mongoliensis* from the Upper Cretaceous of Northern China. Can. J. Earth Sci. 30: 2224–2230.

Currie, P. J., and X.-J. Zhao
1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. Can. J. Earth Sci. 30: 2037–2081.

Fastovsky, D. E., D. Badamgarav, H. Ishimoto, M. Watabe, and D. B. Weishampel
1997. The paleoenvironments of Tugrikin-Shireh (Gobi Desert, Mongolia) and aspects of the taphonomy and paleoecology of *Protoceratops* (Dinosauria, Ornithischia). Palaios 12: 59–70.

Gatesy, S. M., and K. M. Middleton
1996. Sinking dinosaurs: sub-surface preservation of foot kinematics in Greenland-

ic theropods. J. Vertebr. Paleontol. 16 (suppl to 3): 37A.

Gauthier, J.
1986. Saurischian monophyly and the origin of birds. In K. Padian (ed.), The origin of birds and the evolution of flight. California Acad. Sci. Mem. 8: 1–55.

George, J. C., and A. J. Berger
1966. Avian myology. New York: Academic Press.

Gilmore, C. W.
1920. Osteology of the Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. U.S. Natl. Mus. Bull. 110: 1–154.
1993. On the dinosaurian fauna of the Iren Dabasu Formation. Bull. Am. Mus. Nat. Hist. 67: 23–78.

Gradzinski, R., and T. Jerzykiewicz
1972. Additional geographical and geological data from the Polish-Mongolian palaeontological expeditions. Paleontol. Pol. 27: 17–30.

Holtz, T. R., Jr.
1994. The phylogenetic position of the Tyrannosauridae: implications for theropod systematics. J. Paleontol. 68(5): 1100–1117.

Howgate, M. E.
1985. Problems of the osteology of *Archaeopteryx*, is the Eichstätt specimen a distinct genus? In M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer (eds.), The beginnings of birds, pp. 105–112. Willibaldsburg: Freunde des Jura-Museums Eichstätt.

Howse, S. C. B., and A. R. Milner
1993. *Ornithodesmus*—a maniraptoran theropod dinosaur from the Lower Cretaceous of the Isle of Wight, England. Palaeontology 36: 425–437.

Johnston, P. A., D. A. Eberth, and P. K. Anderson
1996. Alleged vertebrate eggs from Upper Cretaceous redbeds, Gobi Desert, are fossil insect (Coleoptera) pupal chambers: *Fictovichnus* new ichnogenus. Can. J. Earth Sci. 33(4): 511–525.

Jerzykiewicz, T., P. J. Currie, D. A. Eberth, P. A. Johnston, E. H. Koster, and J. Zheng
1993. Djadokhta Formation correlative strata in Chinese Inner Mongolia: an overview of the stratigraphy, sedimentary geology, and paleontology and comparisons with the type locality in the pre-Altai Gobi. Can. J. Earth Sci. 30(10&11): 2180–2195.

Kirkland, J. I., R. Gaston, and D. Burge
   1993.   A large dromaeosaur (Theropoda) from the Lower Cretaceous of Eastern Utah. Hunteria 2(10): 1–16.
Lambe, L. M.
   1917.   The Cretaceous theropodous dinosaur *Gorgosaurus*. Geol. Surv. Can. Mem. 100: 1–84.
Larson, P. L.
   1994.   *Tyrannosaurus rex. In* G. D. Rosenberg, and D. L. Wolberg (eds.), Dinofest. Paleontol. Soc. Spec. Publ. 7: 139–155.
Madsen, J. H., Jr.
   1976.   *Allosaurus fragilis*: a revised osteology. Utah Geol. Min. Surv. Bull. 109: 1–163.
Maleev, E. A.
   1974.   Gigantic carnosaurs of the family Tyrannosauridae. Joint Soviet-Mongolian Palaeontol. Exped. Trans. 1: 132–191. [In Russian]
Makovicky P. J., and P. J. Currie
   In press. The presence of a furcula in tyrannosaurid theropods, and its functional and phylogenetic implications. J. Vertebr. Paleontol.
Makovicky, P. J., and H.-D. Sues
   Submitted. Anatomy and phylogenetic relationships of the theropod dinosaur *Microvenator celer* from the Lower Cretaceous of Montana. Am. Mus. Novitates.
Norell, M. A., J. M. Clark, L. M. Chiappe, and D. Dashzeveg
   1995.   A nesting dinosaur. Nature 378(6559): 774–776.
Novas, F. E., and P. F. Puerta
   1997.   New evidence concerning avian origins from the Late Cretaceous of Patagonia. Nature 387: 390–392.
Osborn, H. F.
   1903.   *Ornitholestes hermanni,* a new compsognathoid dinosaur from the Upper Jurassic. Bull. Am. Mus. Nat. Hist. 19: 459–464.
   1924.   Three new Theropoda, *Protoceratops* zone, Central Mongolia. Am. Mus. Novitates 144: 12 pp.
Osmólska, H.
   1981.   Coossified tarsometatarsi in theropod dinosaurs and their bearing on the problem of bird origins. Palaeontol. Pol. 42: 79–95.
Osmólska, H., and R. Barsbold
   1990.   Troodontidae. *In* D. B. Weishampel, P. Dodson, and H. Osmolska (eds.), The Dinosauria, pp. 259–268. Berkeley: Univ. California Press.
Osmólska, H., E. Roniewicz, and R. Barsbold
   1972.   A new dinosaur, *Gallimimus bullatus* n. gen., n. sp. (Ornithomimidae) from the Upper Cretaceous of Mongolia. Palaeontol. Pol. 27: 103–143.
Ostrom, J. H.
   1969a. Osteology of *Deinonychus antirrhopus,* an unusual theropod from the Lower Cretaceous of Montana. Peabody Mus. Nat. Hist. Yale Univ. Bull. 30: 1–165.
   1969b. A new theropod dinosaur from the Lower Cretaceous of Montana. Postilla 128: 1–17.
   1976a. *Archaeopteryx* and the origin of birds. Biol. J. Linn. Soc. 8: 91–182.
   1976b. On a new specimen of the Lower Cretaceous theropod dinosaur *Deinonychus antirrhopus.* Breviora, 439: 1–21.
   1978.   The osteology of *Compsognathus longipes* Wagner. Zitteliana 4: 73–118.
   1990.   Dromeosauridae. *In* D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria, pp. 269–279. Berkeley: Univ. California Press.
Paul, G.
   1984.   The segnosaurian dinosaurs: relics of the prosauropod-ornithischian transition. J. Vertebr. Paleontol. 4: 507–515.
Pérez-Moreno, B. P., J. L. Sanz, A. D. Buscalioni, J. J. Moratalla, F. Ortega, and D. Rasskin-Gutman
   1994.   A unique multitoothed ornithomimosaur from the Lower Cretaceous of Spain. Nature 370: 363–367.
Perle, A.
   1985.   Comparative myology of the pelvic femoral region in the bipedal dinosaurs. Paleontol. J. 1985(1): 105–109. [Translated from Russian]
Perle, A., M. A. Norell, L. M. Chiappe, and J. M. Clark
   1993.   Flightless bird from the Cretaceous of Mongolia. Nature 362: 623–626.
Perle, A., L. M. Chiappe, R. Barsbold, J. M. Clark, and M. A. Norell
   1994.   Skeletal morphology of *Mononykus olecranus* (Theropoda: Avialae) from the Late Cretaceous of Mongolia. Am. Mus. Novitates 3105: 29 pp.
Raath, M. A.
   1969.   A new coelurosaurian dinosaur from the Forest Sandstone of Rhodesia. Arnoldia 4: 1–25.
Rauhut, O. W. M., and C. Werner
   1995.   First record of the family Dromaeosauridae (Dinosauria: Theropoda) in

the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan). Palaeontol. Z. 69(3/4): 475–489.

Rowe, T.
1986. Homology and evolution of the deep dorsal thigh musculature in birds and other Reptilia. J. Morphol. 189: 327–346.
1989. A new species of the theropod dinosaur *Syntarsus* from the Early Jurassic Kayenta Formation of Arizona. J. Vertebr. Paleontol. 9(2): 125–136.

Rowe, T., and J. Gauthier
1990. Ceratosauria. *In* D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria: 151–168. Berkeley: Univ. of California Press.

Russell, D. A.
1969. A new specimen of *Stenonychosaurus* from the Oldman Formation (Cretaceous) of Alberta. Can. J. Earth Sci. 6: 595–612.

Russell, D. A., and Z.-M. Dong
1993a. A nearly complete skeleton of a new troodontid dinosaur from the Early Cretaceous of the Ordos Basin, Inner Mongolia, People's Republic of China. Can. J. Earth Sci. 30: 2163–2173.
1993b. The affinities of a new theropod from the Alxa Desert, Inner Mongolia. Ibid.: 2107–2127.

Sereno, P. C.
1989. Prosauropod monophyly and basal sauropod phylogeny. J. Vertebr. Paleontol. 9(suppl. to 3): 38A.

Sereno, P.C., and C. Rao
1992. Early evolution of avian flight and perching: new evidence from the Lower Cretaceous of China. Science 255: 845–848.

Sternberg, C. M.
1933. A new *Ornithomimus* with complete abdominal cuirass. The Can. Field-Nat. 46(5): 80–83.

Tarsitano, S., and M. K. Hecht
1980. A reconsideration of the reptilian relationships of *Archaeopteryx*. Zool. J. Linn. Soc. 69: 149–162.

Walker, A. D.
1980. The pelvis of *Archaeopteryx*. Geol. Mag. 117(6): 595–600.

Wellnhofer, P.
1974. Das fünfte Skelettexemplar von *Archaeopteryx*. Palaeontogr. An. 147(4–6): 169–216.
1985. Remarks on the digit and pubis problems of *Archaeopteryx*. *In* M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer (eds.), The beginnings of birds, pp. 113–122. Willibaldsburg: Freunde des Jura-museums Eichstätt.
1992. A new specimen of *Archaeopteryx* from the Solnhofen Limestone. *In* K. E. Campbell, Jr. (ed.), Papers in avian paleontology honoring Pierce Brodkorb: 4–23. Nat. Hist. Mus. Los Angeles Cty. Sci. Ser. 36.
1993. Das siebte Exemplar von *Archaeopteryx* aus den Solnhofener Schichten. *Archaeopteryx* 11: 1–48.