

# A new carnosaur (Dinosauria: Theropoda) from the Lower Cretaceous of Japan

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**Abstract:** An associated skeleton from the Kitadani quarry of the Lower Cretaceous (Albian) strata in Fukui Prefecture, Japan, represents a new genus and species of carnosaur (Dinosauria: Theropoda). The immature specimen, which is about 4.2 m long, is well preserved and includes elements of the skull, vertebral column, front limbs, and hind limbs. The hands are relatively large and armed with strongly curved, sharp claws, suggesting that it was an active predator. Phylogenetic analysis indicates it is a basal allosauroid. An isolated astragalus from Australia may represent a closely related species.

**Résumé :** Un squelette provenant de strates du Crétacé inférieur (Albien) dans la carrière Kitadani, de la préfecture de Fukui, au Japon, représente un nouveau genre et une nouvelle espèce de carnosauure (Dinosauria : Theropoda). Le spécimen immature, d'une longueur d'environ 4,2 mètres est bien conservé; il comporte des éléments du crâne, de la colonne vertébrale ainsi que des membres antérieurs et postérieurs. Les mains sont relativement larges et munies de griffes acérées, fortement recourbées, suggérant qu'il était un prédateur actif. Une analyse phylogénétique indique qu'il s'agit d'un allosauroïde basal. Un astragale isolé de l'Australie pourrait représenter une espèce étroitement liée.

[Traduit par la Rédaction]

## Introduction

Over the last decade, many terrestrial vertebrate fossils (Hirayama 1996) have been recovered from the Tetori Group of the Hokuriku region of central Japan (Azuma et al. 1995; Azuma and Tomida 1997). The Tetori Group is divided into three subgroups (Kuzuryu, Itoshiro, and Akaiwa), which range in time from Bajocian to Albian (Maeda 1961) and in sedimentary environments from marine to fluvial.

The most productive Japanese dinosaur sites are found in Fukui and neighboring prefectures in the Kitadani Formation (Albian), which is the uppermost level of the Akaiwa subgroup. Rivers under a moist, temperate climate laid down the alternating sandstones, mudstones, and tuffs. The best Kitadani locality is on the Sugiyama River, within the city limits of Katsuyama in Fukui Prefecture (Fig. 1). The quarry was worked by the Fukui Prefectural Museum between 1988 and 1993 and from 1996 to 1998. Enough bones and teeth were recovered from the bottom of a narrow ravine to justify the expense of heavy equipment to take down the overburden. The back wall of the quarry is as much as 45 m high, making it one of the largest dinosaur quarries in the world. Fossils were recovered from several layers on the way down to the bonebed. Dinosaurs identified so far from the Kitadani Formation include at least one sauropod, an iguanodontian,

and a possible psittacosaurid. Footprints include those of theropods, birds, sauropods and iguanodontians (Azuma and Takeyama 1991). Indeterminate amphibian and small reptile tracks provide some indication of other types of animals that were living in the region with the dinosaurs. Fossil plants, freshwater mollusks, fish, turtles, and crocodiles have been found in the same beds, giving the most complete record of a dinosaurian ecosystem presently known in Japan. The recovery of a nearly complete crocodile skeleton and a partial skeleton of a theropod shows that articulated and associated skeletons can be collected at this site and gives the promise of more exciting discoveries in the future. Enough material has been recovered from the quarry to produce a composite skeleton of the iguanodontid. This and other major specimens can be seen on exhibit in the Fukui Prefectural Museum.

A variety of theropod teeth have been collected in the quarry. The larger ones are flattened and bladelike, and are reminiscent of the central Asian tyrannosaur *Alectrosaurus*.

Smaller teeth are similar in size and shape to those of dromaeosaurids, but do not have the peculiarities of denticulation found in either *Dromaeosaurus* or known velociraptorines. Nevertheless, teeth from the Katsuyama quarry are identified as dromaeosaurid on the basis of a characteristic twist in the anterior carina (Currie et al. 1990), and at least one dorsal vertebra (FPM 96082619) is suggestive of dromaeosaurid affinities.

In 1993, a right manual ungual (I-2), a right astragalus, and a right metatarsal III were found in a small area of the Kitadani quarry, and were recognized as part of an associated skeleton. Their discovery led to the reopening of that section of the quarry in 1996 and 1997, and many additional theropod bones were recovered.

To ascertain whether or not the elements were likely to belong to the same individual, a series of measurements

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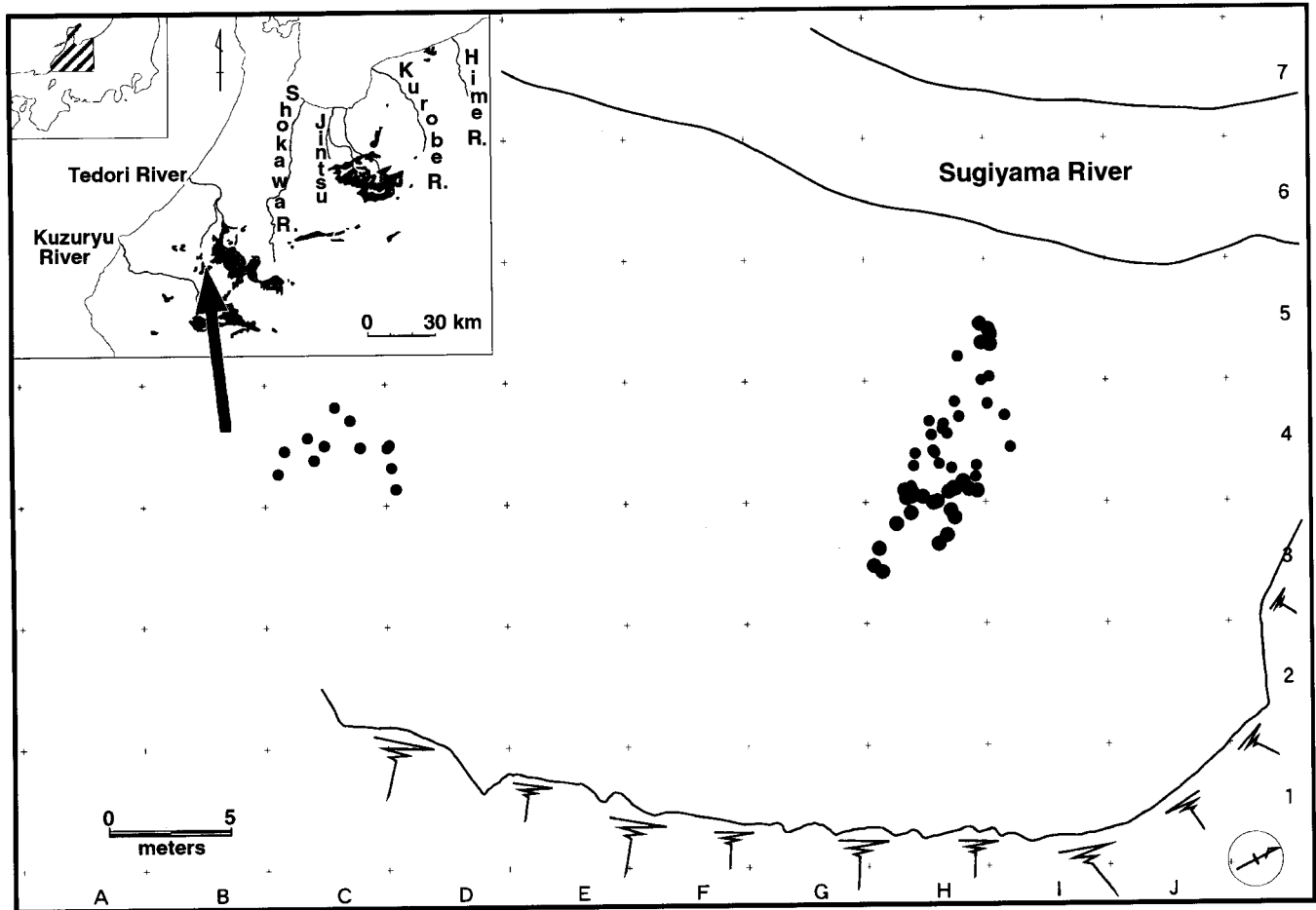
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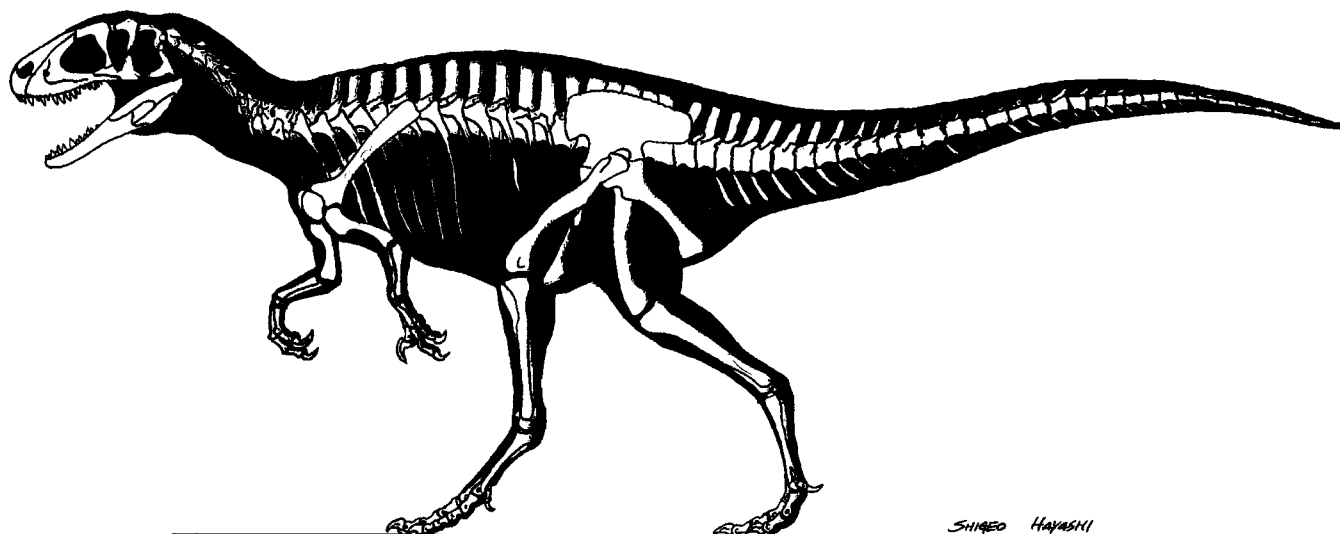
**Fig. 1.** Quarry map showing positions of theropod bones recovered. The cluster of bones centered on H-4 includes the material assigned to the holotype of *Fukuiraptor kitadaniensis*. Bones clustered around C-4 include juvenile *Fukuiraptor* material that is under preparation. The arrow in the first inset points to the location of the quarry west of Fukui City. The second inset shows the position of the second inset on the West Coast of the island of Honshu, Japan.



from this specimen were compared with the same measurements in a wide range of theropods. The femur (507 mm long) was used as the standard against which all other measurements were compared, because this bone is one of the least variable amongst theropod dinosaurs (Christiansen 1998). The length of the coracoid (which was found away from the main concentration of theropod bones) falls within the 95% confidence limits of a theropod with a 507 mm long femur, although it is at the lower extreme of the limits. Comparison of the humerus with femur length produced a figure that falls within the expected range of this measurement for all theropods. Although there is a considerable amount of variation in interspecific comparisons of theropod front limbs, the humerus compares closely in relative length with theropods like *Allosaurus*, *Eustreptospondylus*, and *Gasosaurus*. Ulnar length falls on the regression line for this measurement in *Allosaurus*, *Ceratosaurus*, compsognathids, coelophysoids, *Herrerasaurus*, and oviraptorosaurs. The relative length of this element is greater in *Deinonychus* and ornithomimids, but is significantly shorter in *Acrocanthosaurus*, *Carnotaurus*, and tyrannosaurids. Like other bones of the forelimbs, manual phalanges show a wide range of variability. Whereas the length of the second phalanx of the second

finger is close to what would be expected in an average theropod, the manual unguals (I-2, II-3) are larger than most and cluster with those of *Deinonychus*, *Allosaurus*, and *Alxasaurus*. Hind limb elements have more interspecific stability. The maximum width of the proximal head of the tibia, the shaft and distal widths of the fibula, the lengths of metatarsals II and III, the width of the astragalus, and the lengths of pedal phalanges III-1 and III-2 all fall within the 95% confidence limits for these measurements in theropods. Given the fact that the lengths of all elements fall within the expected range of size variability for a theropod 4.2 m in total length, that they were recovered from the same region of the quarry, and that no elements are duplicated, it is highly probable that they represent a single individual (Fig. 2). Bivariate analyses of theropod measurements are in the process of being refined and published by the second author.

The term Carnosauria was first used by von Huene (1920, 1926) to depict all large theropods excluding *Ceratosaurus* and tyrannosaurids. It has been used consistently since that time, although the taxa included have fluctuated. In this paper we follow Hutchinson and Padian (1997) in defining "Carnosauria" as all theropods closer to *Allosaurus* than to birds.

**Fig. 2.** Reconstruction of *Fukuiraptor kitadaniensis*.

### Systematic palaeontology

Dinosauria Owen, 1842  
 Theropoda Marsh, 1881  
 Carnosauria von Huene, 1920  
*Fukuiraptor* gen.nov.

### Etymology

"Fukui" refers to the prefecture in the central part of Honshu, Japan, where the specimen was found; "raptor" is Latin for robber.

### Genoholotype

FPMN 97122 (associated skull and limb bones) plus FPMN 96082443 (left humerus).

### Generic Diagnosis

Monospecific genus. See Species Diagnosis.  
*Fukuiraptor kitadaniensis* sp.nov.

### Etymology

The species is named after the Lower Cretaceous Kitadani Formation.

### Holotype

FPMN 97122 is an associated skeleton found in one small area of the Kitadani quarry. The lengths of all bones belong to an individual that was an estimated 4.2 m long when it was alive. The associated skeletal parts include (with their element numbers) a left maxillary fragment (FPMN 9712201), right dentary fragment (FPMN 9712202), four isolated teeth (FPMN 9712203, 9712204, 9712205, 9712206), dorsal centrum (FPMN 9712207), distal caudal (FPMN 9712208), both humeri (FPMN 96082443, 9712209), right ulna (FPMN 9712210), right manual ungual I-2 (FPMN 9712211), right manual phalanx II-2 (FPMN 9712212), left manual ungual II-3 (FPMN 9712213), fragments of the right ilium (FPMN 9712214), one pubis (FPMN 9712215 shaft, and possibly 9712216) and both ischia (FPMN 9712217, 9712218), the right femur (FPMN

9712219), the proximal half of the right tibia (FPMN 9712220), the distal half of the right fibula (FPMN 97080206), right astragalus (FPMN 9712221), right metatarsal I (FPMN 9712222), right metatarsal II (FPMN 9712223), right metatarsal III (FPMN 9712224) and pedal phalanges left I-1 (FPMN 9712225), right III-1 (FPMN 9712226), right III-2 (FPMN 9712227), and right IV-2 (FPMN 9712228).

### Referred specimens

FPMN 9712229 is a fragment of the left maxilla with two complete and one partial alveoli, whereas FPMN 9712230 is part of a dentary with three alveoli. FPMN 9712231, 9712232, 9712233, 9712234, 9712235, 9712236, 9712237, 9712238, and possibly 9712239 are isolated, shed teeth. FPMN 9712240 is a cervical centrum tentatively referred to *Fukuiraptor*. A partial cervical neural arch (FPMN 9712241) fits onto the centrum, and even though it was found in a different part of the quarry, it might be from the same individual. An almost complete dorsal neural arch (FPMN 9712242) may also belong to this genus. A theropod coracoid (FPMN 9712243) is the right size to belong to the holotype and was recovered from the same level as the main concentration of theropod bones, but was found five metres away in a different part of the quarry.

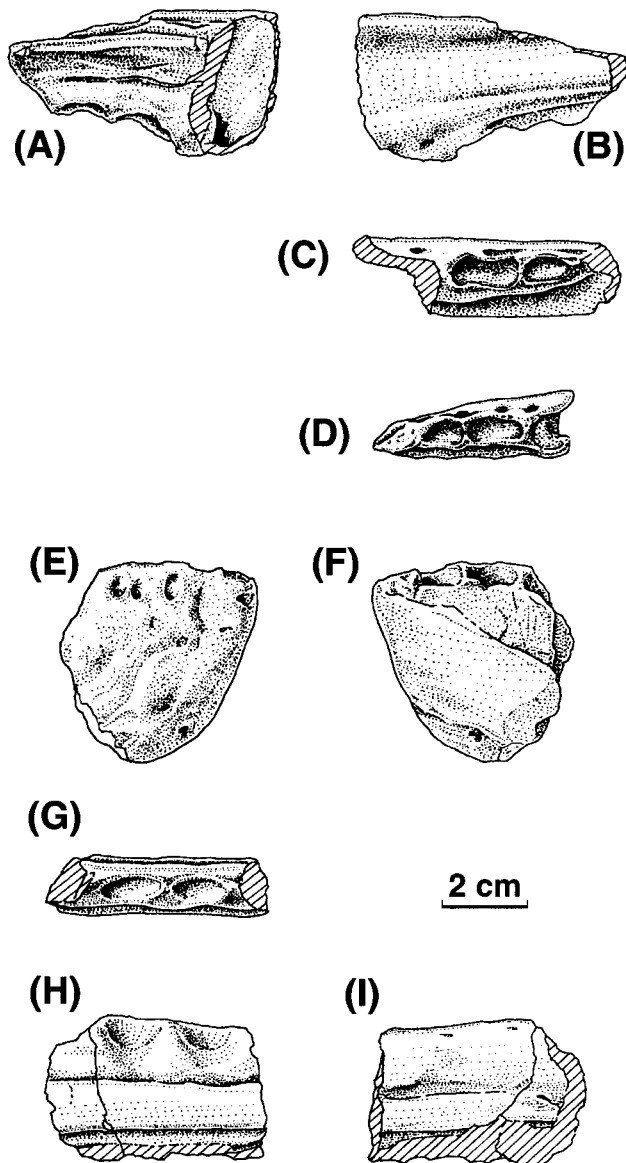
### Locality and age

The specimen was recovered from the Lower Cretaceous (Albian) Kitadani Formation (Akaiwa subgroup, Tetori Group). The Kitadani locality is on the Sugiyama River in the northern part of the city of Katsuyama, Fukui Prefecture (Latitude 36°7'N, Longitude 136°33'E).

### Diagnosis

Medium-sized theropod (holotype has an estimated length of 4.2 m, Fig. 2). Carnosaur with the following autapomorphies: fused interdental plates in maxilla and dentary (convergent with dromaeosaurids); narrow dentary; narrow bladelike teeth with oblique blood grooves (convergent with tyrannosaurids); ratio of ulna to humerus is 0.92, which is significantly higher than any other carnosaur, except

**Fig. 3.** *Fukuiraptor kitadaniensis*, maxillary and dentary fragments. Posterior fragment from left maxilla, FPM 9712201, in medial (A), lateral (B), and ventral (C) views. Symphyseal region of right dentary (FPM 9712202) in dorsal (D), lateral (E), and medial (F) aspects. Dentary fragment (FPM 9712229) in dorsal (G), medial (H) and lateral (I) views.



*Xuanhanosaurus*; relatively larger hands with better developed unguals than *Allosaurus*; pubic peduncle is lateromedially wider than anteroposteriorly long; relatively taller ascending process than other known carnososaurs.

#### Institutional abbreviations

FPMN, Fukui Prefectural Museum, Fukui, Japan; MOR, Museum of the Rockies, Bozeman, Montana, U.S.A.; USNM, National Museum of Natural History, Smithsonian Institution, Washington, U.S.A.

#### Description

The fragment of left maxilla (Figs. 3A–3C) includes the last two alveoli and part of a more anterior one. The sockets

are deep, and the interdental plates are fused. The lateral surface includes a well defined margin for the antorbital fossa, above which the lateral wall of the maxilla is smooth (Fig. 3B).

The symphyseal region of the right dentary (Figs. 3D–F) includes all or part of the first three alveoli. The jaw is relatively deep (48 mm), but mediolaterally narrow (15 mm). The width of the jaw and the angle of the poorly defined symphysis indicates that the jaws articulated at a highly acute angle. This in turn suggests that the skull was narrow in the snout region. There are interdental plates, the first of which is triangular and tapers anteriorly. The plates meet and fuse to each other, but in contrast with dromaeosaurids, there is a distinct inflection where they meet the dentary (Fig. 3F).

Another, more posterior fragment of the right dentary (FPM 9712229, Figs. 3G–I) includes portions of two alveoli. The lateral surface of the fragment is relatively smooth, although there is a pronounced longitudinal ridge, as in many carnososaurs (Currie and Zhao 1994). The presence of the ridge (Fig. 3I), above which is an anteroposteriorly long, but narrow, foramen (for nerves and blood vessels), suggests that this fragment came from the posterior half of the dentary. It can also be determined that the fragment is from a position anterior to where the foramina for branches of the inferior alveolar nerve penetrate the medial surface of most theropod dentaries. The preserved alveoli were, therefore, approximately the ninth and tenth in position. The jaw here would have been at least 48 mm high, with a mediolateral width of 17 mm.

The 9th alveolus (Fig. 3G) is 37 mm deep, 7 mm wide, and more than 12 mm long, while the 10th is 13.5 mm long. The 31 mm high crown of a developing tooth is present in the 10th alveolus. Although the base is not clearly exposed, the "fore-aft base length" (FABL of Farlow et al. 1991) can be estimated as 12 mm. The tooth has both anterior and posterior carina, but the anterior margin is covered by matrix and bone, so the nature of the anterior denticles cannot be determined. Posterior denticles extend along the midline to the base of the crown, and there are about 16 serrations per 5 mm.

Four other teeth from the same part of the quarry almost certainly came from the same individual. FPM 9712205 is a left premaxillary tooth (possibly the first right dentary tooth; although it is a little too big for the socket). The tip has been worn, but 11.5 mm of the root is preserved. The anterior carina is posteromedial in position, but is still farther forward than the posterior carina. In cross-section, the premaxillary tooth most closely resembles a premaxillary tooth of a dromaeosaurid (Currie et al. 1990). There are 16 denticles for every 5 mm on both the anterior and posterior carina. The cheek teeth are laterally compressed, bladelike, and curved, with the anterior and posterior carina lying on the midline. FPM 9712206 and 971220 clearly show oblique blood grooves (Figs. 4A, 4C) similar to those described for tyrannosaurids (Ablar 1992; Currie et al. 1990; Fiorillo and Currie 1994). Although useful for distinguishing tyrannosaurs from other theropods in Upper Cretaceous sediments of the Northern Hemisphere, the presence of oblique blood grooves may be more widespread than originally thought, and therefore have little taxonomic value.



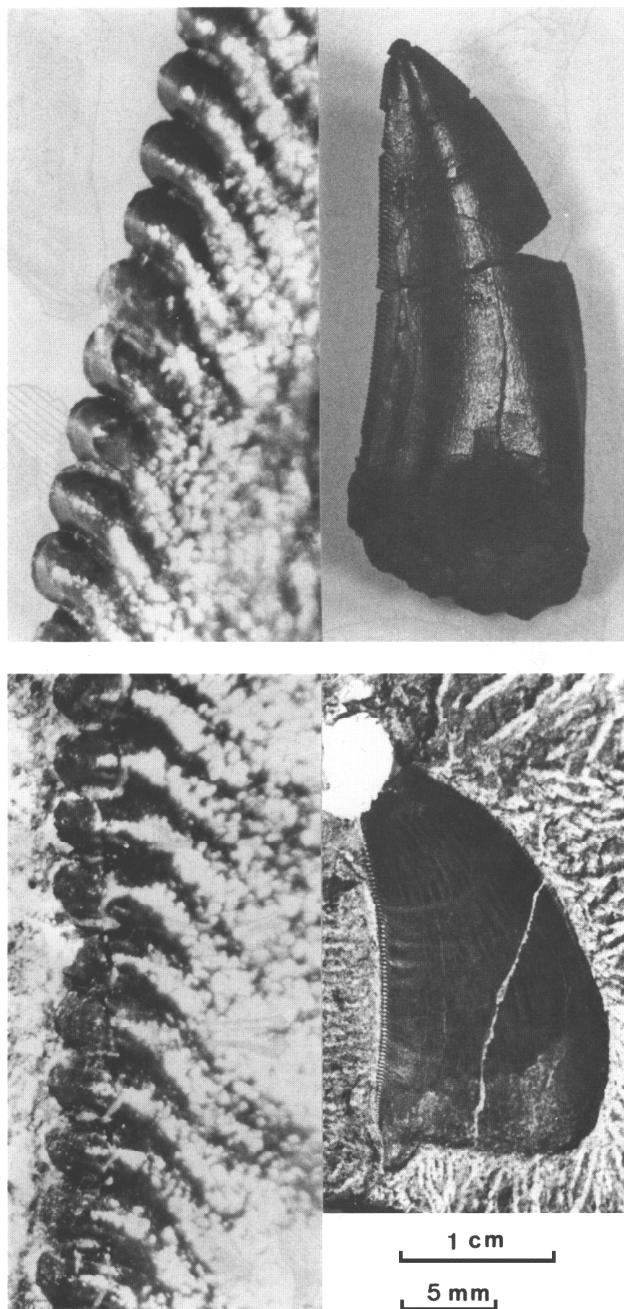
A partial centrum (FPMN 9712207) of a mid-cervical vertebra, possibly the fifth, is 58 mm long. This length does not include the convex anterior intervertebral articulation, which was not preserved. The posterior intervertebral articulation is deeply concave, which shows that the cervical centra were opisthocoelous. The parapophysis is preserved on the lower margin of the left side, and extends ventral to the lower edge of the anterior intervertebral articulation on the midline. The ventral surface of the centrum is concave between the parapophyses. The lateral surface of the centrum is concave dorsal to the parapophysis and is penetrated by one (possibly two) pneumatopores as in most theropods. The pair of sutures with the neural arch was still open at the time of death. A neural arch fragment (FPM 9712241) fits almost perfectly on the left side of the centrum. The suture on the arch fragment for the centrum is 52 mm long and has the same curvature and contours. Only the base of the transverse process is preserved, and its hollow interior clearly communicated with pneumatopores in the deep infradiapophysial fossa. Laminae anterior and posterior to the fossa supported the transverse process from below. The infraprezygapophysial fossa is present, but poorly preserved.

Dorsal neural arches can be assigned tentatively to *Fukuiraptor*. The almost complete arch (FPM 9712242) is from one of the last vertebrae of the presacral series. The transverse process bears both parapophysis and diapophysis, separated by 58 mm on the right side. It extends laterally, posteriorly, and dorsally about 60 mm from the longitudinal midline of the body. Each process is triangular in cross-section distally, with an anteroposterior length of 19 mm and a dorsoventral height of 13.5 mm. The base of the transverse process is excavated posteriorly by a deep infrapostzygapophysial fossa, in the floor of which several pneumatopores invade the interior of the neural arch. The width across the anterior zygapophyses is 35 mm, but the posterior zygapophyses are damaged enough to make such a measurement unreliable. The zygapophyses are inclined at an angle of about 45 degrees. The neural canal is large (minimum diameter is 12 mm). The neural spine is tall, laterally compressed (the distal end is only 7.5 mm thick), and platelike, and stood at least 10 cm above the roof of the neural canal. The anteroposterior length of the neural spine is 37 mm near the base, and more than 40 mm distally.

One dorsal centrum (FMPN 9712207, Figs. 5A–F) is long (77.5 mm), but the intervertebral articulation is 60 mm high and 56 mm wide. The centrum is narrow-waisted with a deep lateral depression ventral to the suture for the neural arch. Below the pair of lateral depressions, the width of the centrum is 23.5 mm. The neural arch was not fused to the centrum, which is another reason to believe the animal was immature at the time of death. The suture extends along the entire length of the centrum and is elevated 15 mm above the floor of the neural canal, which is 11 mm across at midlength. There is no pleurocoel.

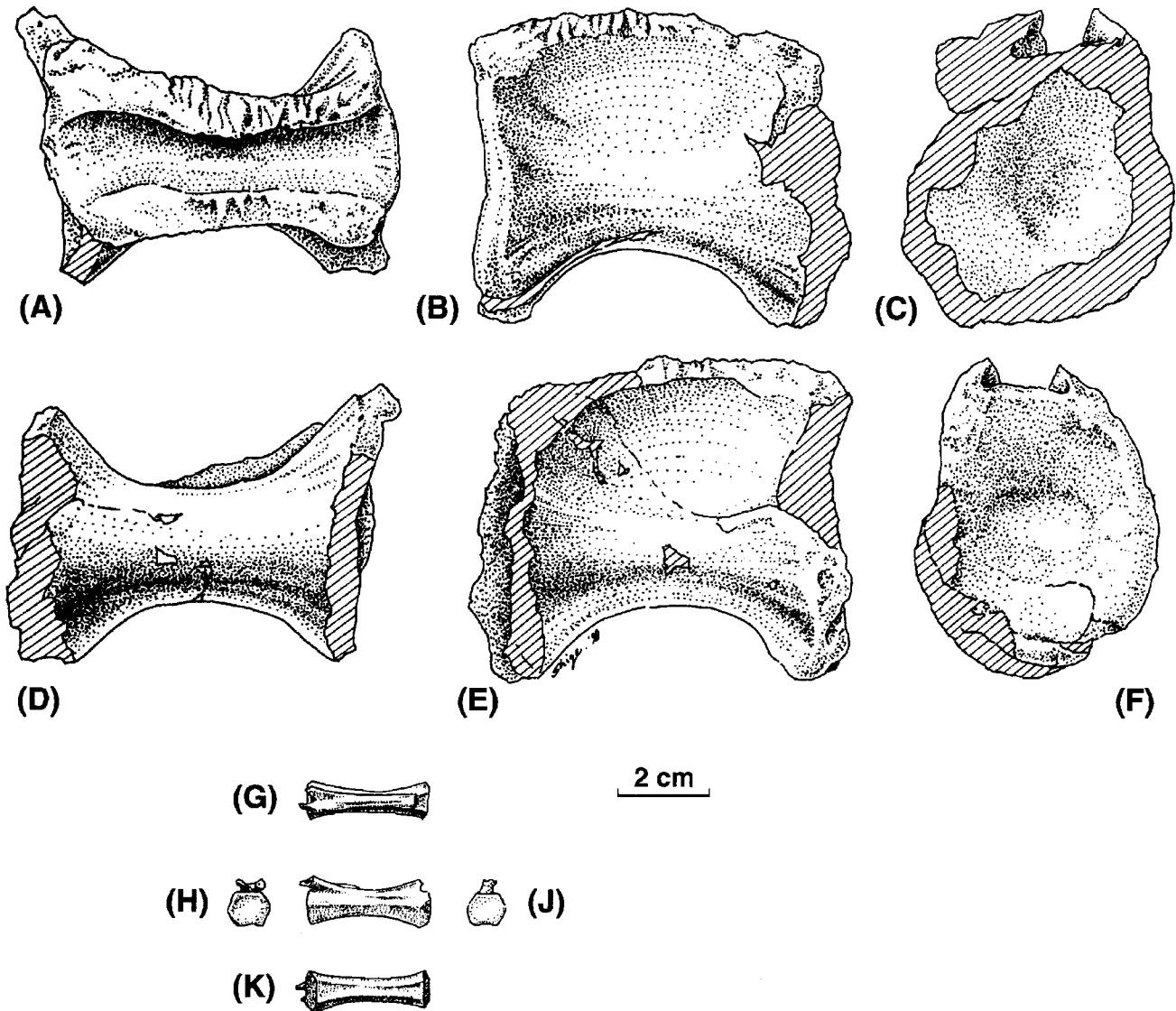
A distal caudal vertebra (FPMN 9712208, Figs. 5G–K) is 26.7 mm long and has a posterior intervertebral articulation that is 7.1 mm high and 8.3 mm across. The centrum has two longitudinal ventral ridges, and one on each side. Both the paired prezygapophyses and the medial postzygapophyses are broken, making it impossible to determine their extent.

**Fig. 4.** *Fukuiraptor kitadaniensis*, teeth (FPM 9712203 above, FPM 9712204 below) showing overall morphology (right) and enlargements of posterior denticles (left).

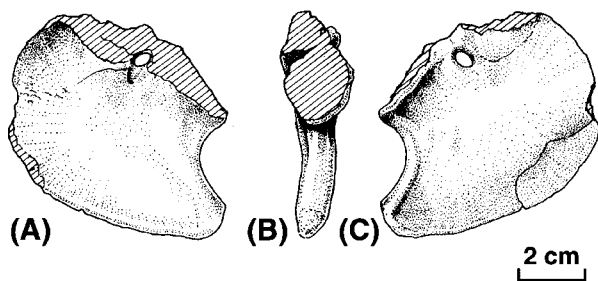


Three rib heads, all from the left side of the body, were found. Although they all resemble theropod ribs, there are enough differences to suggest that they might ultimately be shown to be from iguanodontids, which have similar steep-sided bodies (Norman 1986). The largest rib is 52 mm long between the lateral margin of the capitular articulation and the lateral margin of the capitular articulation, and has a shaft that narrows distally to 21.2 mm (anteroposterior shaft diameter) by 11.5 mm (mediolaterally). The feature that is least theropod-like is the capitular articulation, which is anteroposteriorly more elongate than it is wide. The

**Fig. 5.** *Fukuiraptor kitadaniensis*. Dorsal centrum (FPM 9712207) in dorsal (A), left lateral (B), posterior (C), ventral (D), right lateral (E), and anterior views (F). Distal caudal (FPM 9712208) in dorsal (G), anterior (H), lateral (I), posterior (J), and ventral (K) aspects.



**Fig. 6.** *Fukuiraptor kitadaniensis*. Coracoid (FPMN 9712243) in medial (A), posterior (B), and lateral (C) views.



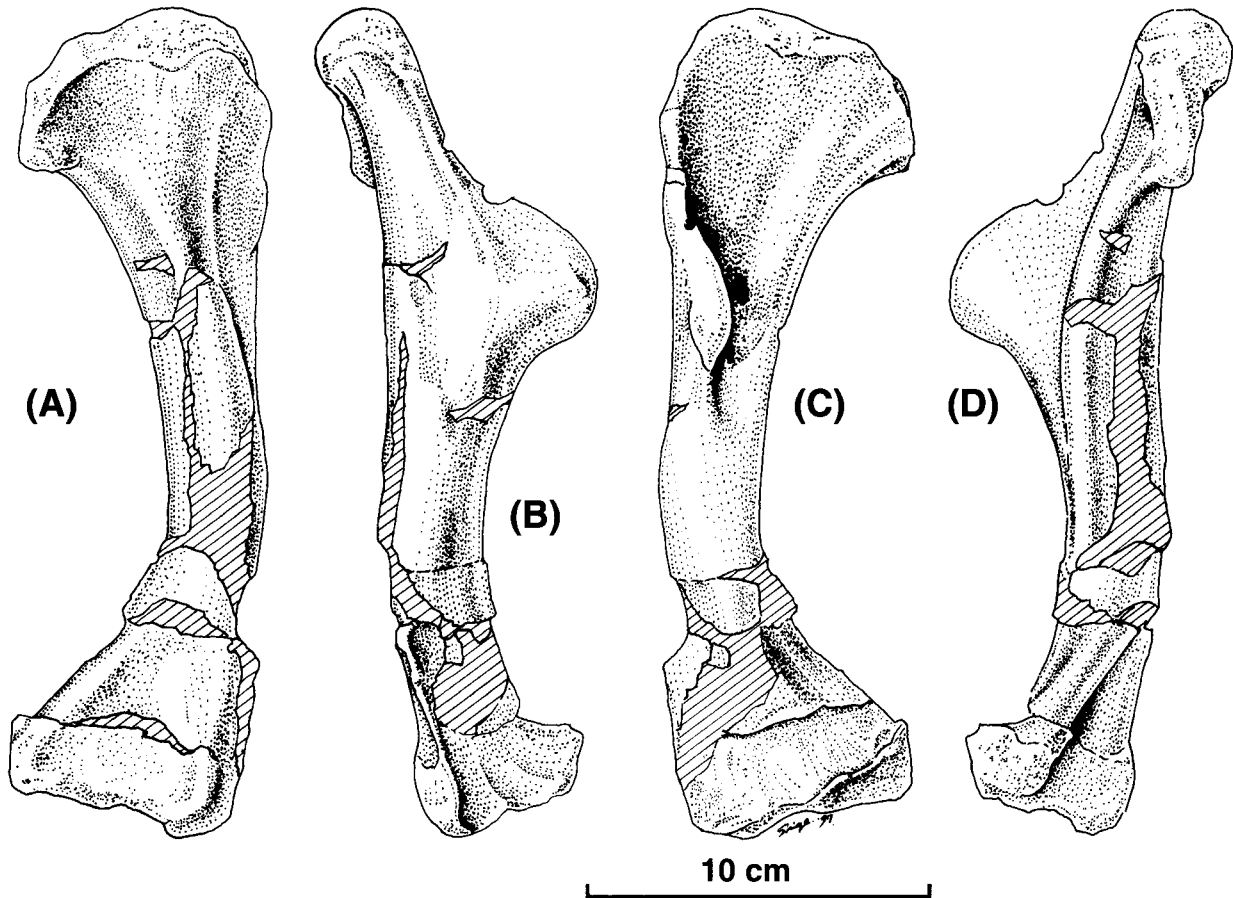
capitular articulation has a similar orientation in a posterior dorsal rib that has a capitular-tubercular length of 38 mm and a shaft diameter of 9.5 mm by 4.8 mm. The third rib is probably a mid-dorsal. It has a capitular-tubercular length of 57.3 mm, and the shaft narrows to 15 mm by 9 mm. The capitular articulation is different than in the other two ribs,

because its long axis has a mediolateral orientation. Furthermore, the margins of the articulation do not protrude much above the shaft of the rib, and the articular surface is deeply concave.

The coracoid (FPMN 9712243, Fig. 6) has an antero-posterior length of 73 mm, whereas the height is only 58 mm. It was not fused to the scapula, and the scapular suture is long (39 mm) and narrow (17 mm). The coracoid foramen (4.6 by 5.9 mm) is positioned high, and the internal extent of it almost reaches the scapular suture, as in *Allosaurus* (Madsen 1976). The glenoid articulation attains a maximum mediolateral width of 20.8 mm.

The preserved length of the right humerus (Fig. 7) is 230 mm, but the shaft is slightly telescoped. The left humerus is 242 mm long. The humerus is relatively robust with a maximum proximal width of 79.8 mm, and a distal expansion of 64. The deltopectoral crest extends into a conical process in the proximal half of the humerus. Its apex is 58 mm distal to the humeral head (Fig. 7B) and projects for-

Fig. 7. *Fukuiraptor kitadaniensis*. Humerus (FPMN 9712209) in dorsal (A), lateral (B), ventral (C), and medial (D) views.



ward approximately 26 mm from the shaft at an angle of almost  $90^\circ$  from the longitudinal axis of the head. It rises at an angle of approximately  $70^\circ$  to the plane of the distal end. Distal and lateral to the deltopectoral crest is a vertically elongate scar for the attachment of *M. humeroradialis*. The shaft is relatively short and robust and is subcircular in section. At midshaft, the bone has a diameter of 30 mm and a circumference of 89 mm. The distal end of the bone has a pair of condyles separated by a shallow intercondylar groove. The outer (radial) condyle is almost double the size of the ulnar condyle.

The right ulna (Fig. 8) measures 178 mm in length, excluding the olecranon, and 211 mm with it. The bone is robust, particularly the proximal end, which is 50.5 mm in maximum width. The proximal concavity that contacts the radius has neither articular facets nor strong ligamentous attachments. The curving shaft tapers to 27 mm in diameter, but the distal end expands again to 37.8 mm. Amongst described theropods, the ulna most closely resembles that of *Allosaurus* (Madsen 1976), although it is relatively longer (it is 92% the length of the humerus, compared with 85% the length in USNM 4734 and 80% in MOR 693). *Xuanhanosaurus qilixiaensis* is the only other carnosaur known with a similar ulnar to humerus ratio at 0.91 (Dong 1984). *Xuanhanosaurus* is a more primitive animal in most other characters

Several phalanges were recovered from the manus, including a 64.9 mm long (distance between the floor of the proxi-

Fig. 8. *Fukuiraptor kitadaniensis*. Right ulna (FPMN 9712210) in medial (A), anterior (B), posterior (C), and lateral (D) views.

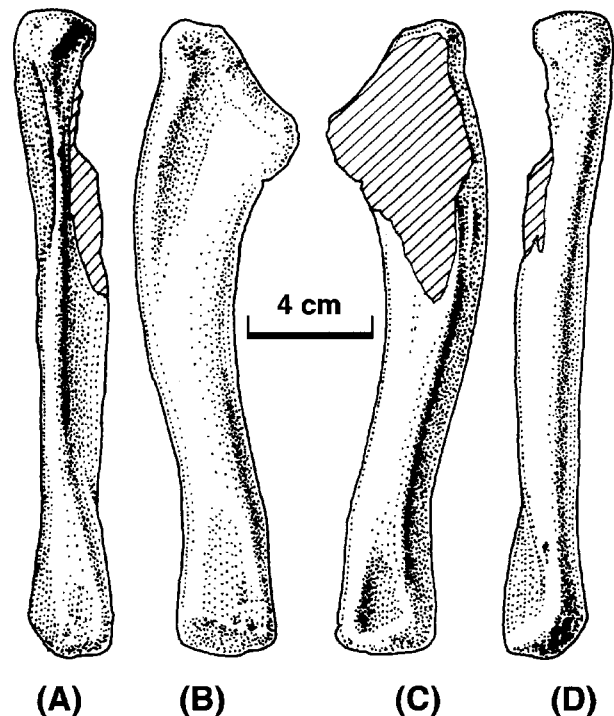
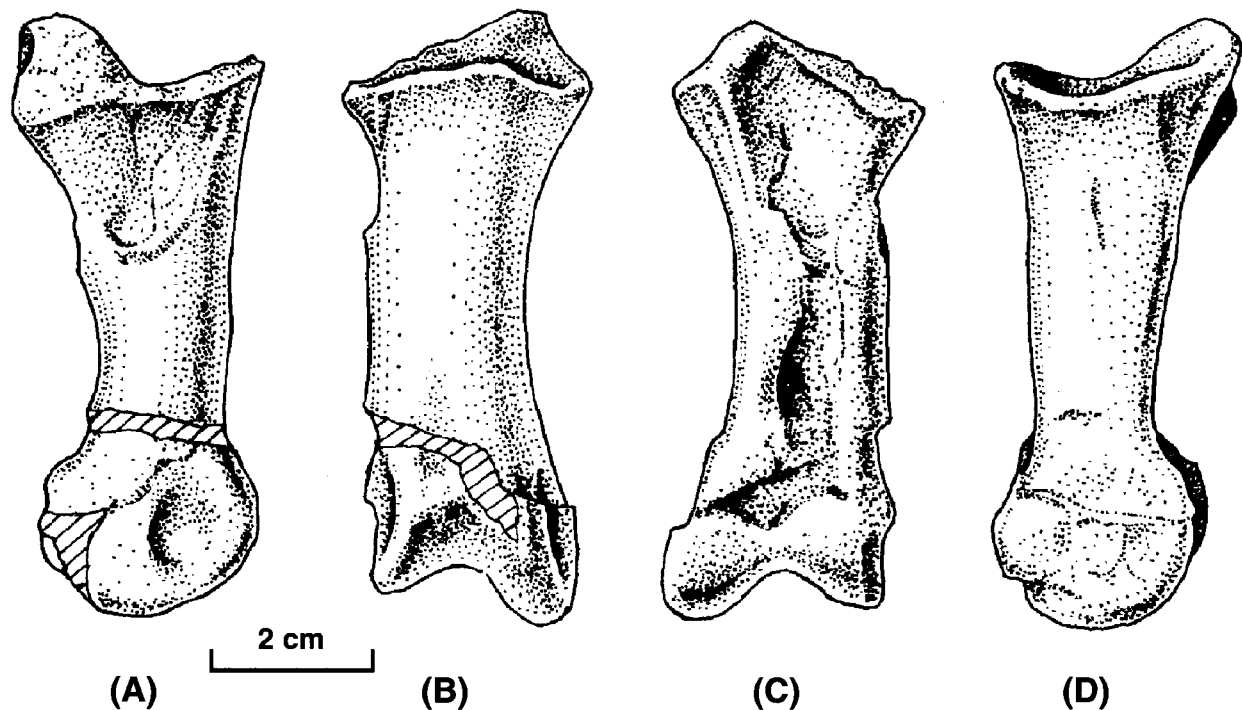


Fig. 9. *Fukuiraptor kitadaniensis*. Right manual II-1 (FPMN 9712212) in medial (A), anterior (B), posterior (C), and lateral (D) views.



mal articular concavity and the apex of the convex distal articular surfaces) II-1 from the right side (Fig. 9). The manual unguals (Fig. 10), which are probably from the first two digits, are laterally compressed, strongly curved, and taper to sharp points. The distance from the dorsal edge of the proximal articulation to the tip of I-2 is 121 mm measured in a straight line, and 154 mm measured along the outside curvature. The same measurements in manual unguual II-3 are 107.5 and 150 mm. The saddle-shaped articular facets are 29 mm high by 19 mm in both I-2 and II-3. In lateral view they are deeply concave, and are demarcated from the lateral and medial surfaces by sharp inflections with rugose margins. The flexor tubercles of the unguals are prominent, and extend 37 mm below the proximal articulation in I-2, and 33 mm in II-3. Five millimetre deep pits (with diameters of 7 mm) anterolateral and anteromedial to the tubercle of II-3 were for the attachment of powerful flexor ligaments. The vascular grooves on either side of each unguual are almost symmetrical.

A fragment of the right ilium (Fig. 11) includes the acetabular margin and the bases of the pubic and ischial peduncles. The incomplete acetabulum is 95 mm long (anteroposteriorly) as preserved. The lateromedial width of the acetabulum is 50 mm, less than half of the width of the proximal head of the femur. The pubic peduncle is broader mediolaterally than it is anteroposteriorly long. The preacetabular notch is relatively wide and open, and the ventral margin of the preacetabular blade is narrow and simple.

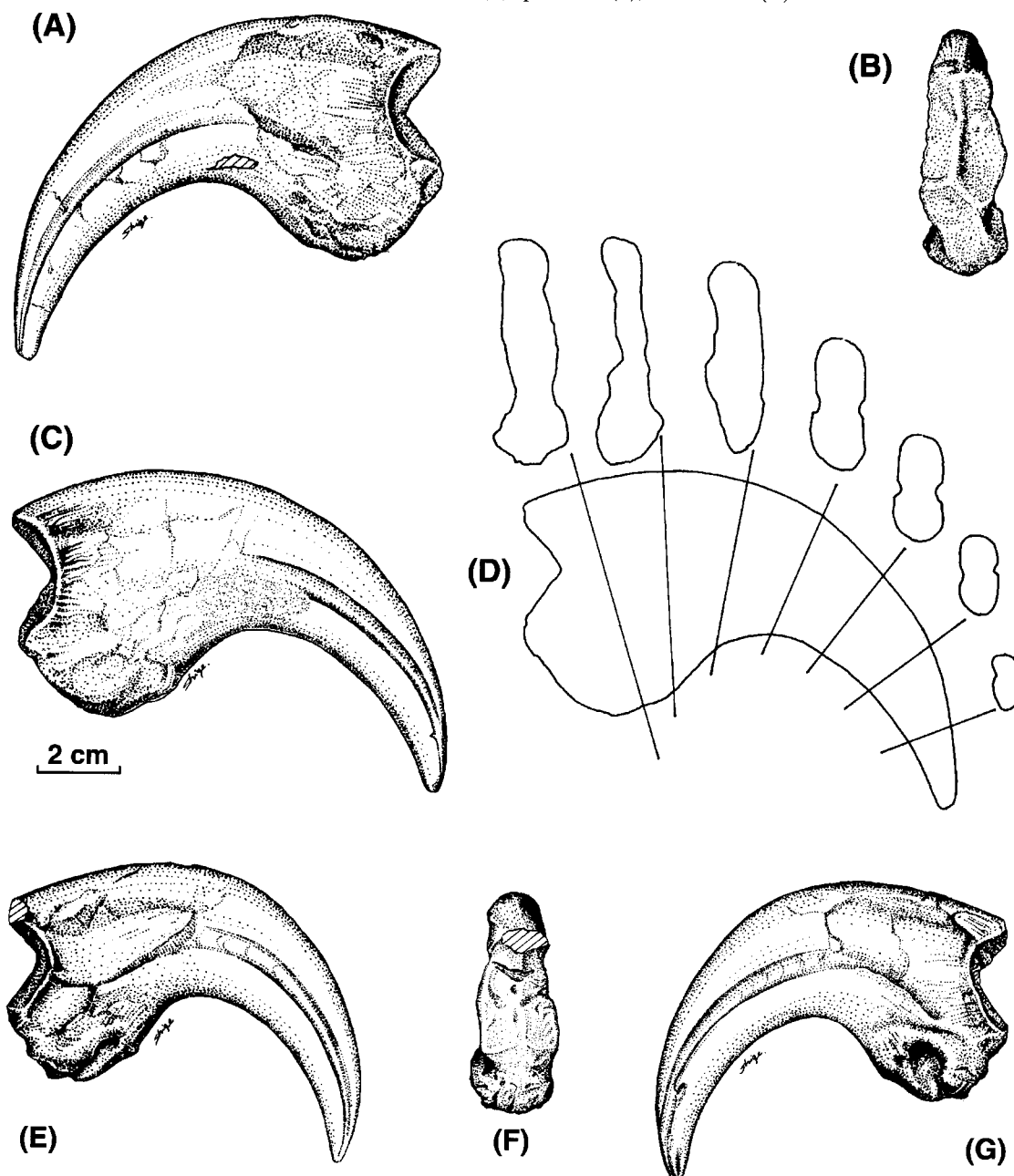
Several fragments, the largest of which is a section of the shaft, represent the pubis. Two fragments of the ischium, one representing the right side and the other the proximal margin of the left, provide little more information than the pubic fragment.

Calculation of the lengths of the missing elements (by using the known femur length of *Fukuiraptor* and comparing it with bivariate analyses done for these elements in other theropods) of the arm and leg suggests that the arm was about 72 cm long, and the leg was about 160 cm. This shows that the arm was less than half the length of the leg, even though the arm is relatively long compared to other carnosaurs.

The femur (Fig. 12) is 507 mm long, with a proximal width of 108.5 mm and a maximum distal width of 96.3 mm. The longitudinal axis of the proximal end is parallel to the transverse axis of the distal condyles. There is a distinct, winglike lesser (anterior) trochanter that is separated from the femoral head by a deep slot. The lesser trochanter is proximal in position, rising above the lower margin of the head as in other advanced carnosaurs. There is a poorly defined accessory wing rising from the base of the lesser trochanter, as in ornithomimids and some other theropods. Overall, the lesser trochanter is characteristic for a carnosaur, whereas the lesser trochanter of a dromaeosaurid is only separated from the head by a shallow depression (Ostrom 1976). As in *Sinraptor* (Currie and Zhao 1994) and carcharodontosaurids (R.A. Coria, personal communication, 1996), the medial surface of the femoral head is flattened and has a distinct ridge along the posterior margin. This extends distally into a lip that marks the ventromedial limit of the head itself. A distinct slot runs along the lateral margin of the ridge, as in *Giganotosaurus*. There is no evidence of a posterior trochanter nor of the plesiomorphic trochanteric shelf. Like most other theropods, there is a low moundlike process on the lateral surface at about the same level as the base of the lesser trochanter. The nutrient foramen enters the shaft of the femur distal to the base of the



**Fig. 10.** *Fukuiraptor kitadaniensis*. Manual unguals. Right I-2 (FPMN 9712211) in medial (A), posterior (B), and lateral (C) views, and in cross-sections (D). Left II-3 (FPMN 9712213) in lateral (E), posterior (F), and medial (G) views.

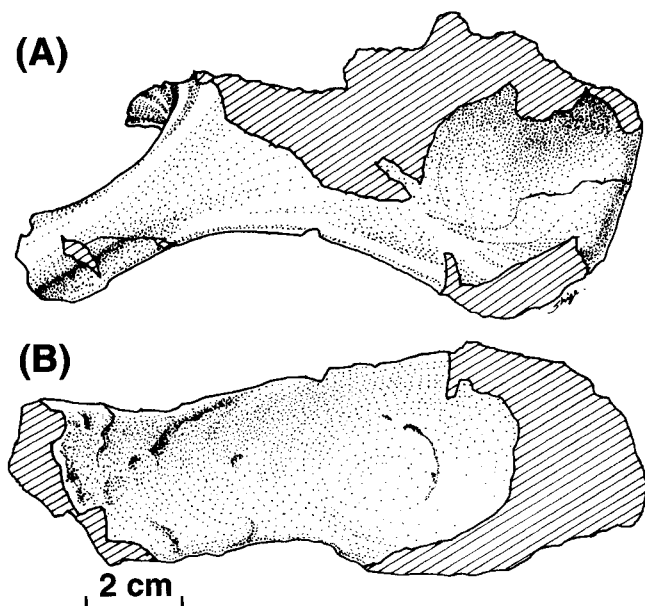


lesser trochanter on the anterodorsal surface. Deep, wide depressions proximal and distal to the foramen are preservational defects. The fourth trochanter, which is reduced or lost in dromaeosaurids, is a distinct ridge as in *Allosaurus*, *Sinraptor*, and other carnosaurids. The gently curved shaft has a minimum transverse width of 43 mm, an anteroposterior width of 53 mm, and a circumference of 164 mm, which suggest that the animal weighed 175 kg (Anderson et al. 1985). Distally, there is a sharp ridge (the mediolateral crest) along the medial margin of the anterodorsal surface of the distal end, as in *Sinraptor*, but in contrast to coelurosaurids, where this margin is low and rounded. The anterodorsal extensor groove is deeply concave (Fig. 12D) at the distal

end as in carnosaurids. Unlike *Sinraptor* (Currie and Zhao 1994) and other carnosaurids (Harris 1998), there is no ridge for cruciate ligaments in the flexor groove. The trochlea fibularis is deep and is overhung by a prominent crista tibiofibularis (Fig. 12D).

The right tibia (Fig. 13) is incomplete, but has all of the features expected in a carnosaurid. There is a well-developed cnemial crest on the proximal end. The fibular condyle is relatively large, positioned near the posterior margin of the tibia, and distinctly separated from the main body of the rest of the proximal end (Fig. 13C). The fibular crest is 9 cm long and pronounced (Figs. 13B, 13D, 13E). If it is assumed that the tibia was about the same length as the femur, then

**Fig. 11.** *Fukuiraptor kitadaniensis*. Lateral (A) and ventral (B) views of acetabulum of right ilium (FPMN 9712214).



the fibular crest is centered about one third of the distance from the proximal end. Although the full length of the tibia is unknown, alignment of the fibular crest with the tibiofibular ligament crest of the fibula confirms that the lower leg was at least as long as the femur.

The right fibula (FPMN 97080206) is preserved distal to the expansion for the interosseum tibiofibulare ligaments. The shaft tapers below this to 19 by 17 mm and then expands at the end to 31 mm. The distal end twists so that it terminates anterior to distal end of the tibia, where it also overlaps the lateral margin of the astragalus.

The right astragalus (FPMN 9712221) is almost complete, lacking only the medial margin of the condylar region and the dorsal edge of the ascending process (Fig. 14). In most features, the astragalus of *Fukuiraptor* is directly comparable with carnosaurs like *Allosaurus* (Madsen 1976) and *Sinraptor* (Currie and Zhao 1994). There is a horizontal groove across the faces of the condyles, which were oriented anteroventrally. The crescentic lateral, calcaneal suture (Fig. 14B) has a shallow notch for a process from the calcaneum, although it is not as well developed as it is in *Allosaurus* and *Sinraptor*. The astragalus has a distinct socket that embraced the mediolateral end of the fibula, which was otherwise supported mostly by the calcaneum. The fibular contact extends up the anterolateral margin of the ascending process of the astragalus. The morphology of the fibular contact shows that the distal end of the fibula was not significantly broader than the fibular shaft. The ascending process of the astragalus is relatively high. The ratio of the height of the astragalus to its width (breadth) is 1.39, which is higher than any known carnosaur, but is less than the same ratio in many coelurosaurs (Welles and Long 1974). Normally, the relative height of the ascending process is compared with the length of the tibia. However, the complete length of the tibia is unknown for *Fukuiraptor*, so we have compared it instead with the femur. Relative to femur length (0.22), the astragalus is significantly higher than those

of *Allosaurus* (0.18), *Ceratosaurus* (0.13), *Herrerasaurus* (0.10), and *Sinraptor* (0.13). However, the ascending process is significantly lower than those of coelurosaurs like *Caudipteryx* (0.28), dromaeosaurids (0.28), ornithomimids (0.26), oviraptorosaurs (0.28), therizinosaurids (0.27), troodontids (0.40), and tyrannosaurids (0.27).

Although the calcaneum is unknown, the calcaneal articulation and the fibular facet of the astragalus suggest that it must have been a rather small bone. The contact on the astragalus for the calcaneum shows that the latter bone would have been 46 mm high and 44.5 mm in antero-posterior length.

Metatarsals I, II, and III were recovered from the Kitadani quarry. The dorsal tip of the first metatarsal (Fig. 15) has been lost, but the preserved length of 67 mm would not have been much more than 10% longer during life. As determined by the contours of the second metatarsal, Metatarsal I was positioned on the posteromedial edge at least a third of the way from the distal end of the metatarsus. The lateral ligament pit has a diameter of 10.6 mm, whereas the medial one is only half the size.

Metatarsal II (FPMN 9712223, Figs. 16A–F) is 297.5 mm in maximum length, curves ventromedially, and has a shaft that is oval in cross-section. The proximal end is triangular in outline and is nearly planar. The distal end has a strongly asymmetrical ginglymus, in which the lateral condyle is much larger than the medial. The anterior part of the condyle is smoothly rounded, but the posterior region is divided by a deep groove. The articular surfaces of both condyles extend well up the flexor surface of the metatarsal. The lateral collateral ligament pit is larger and deeper than the medial one.

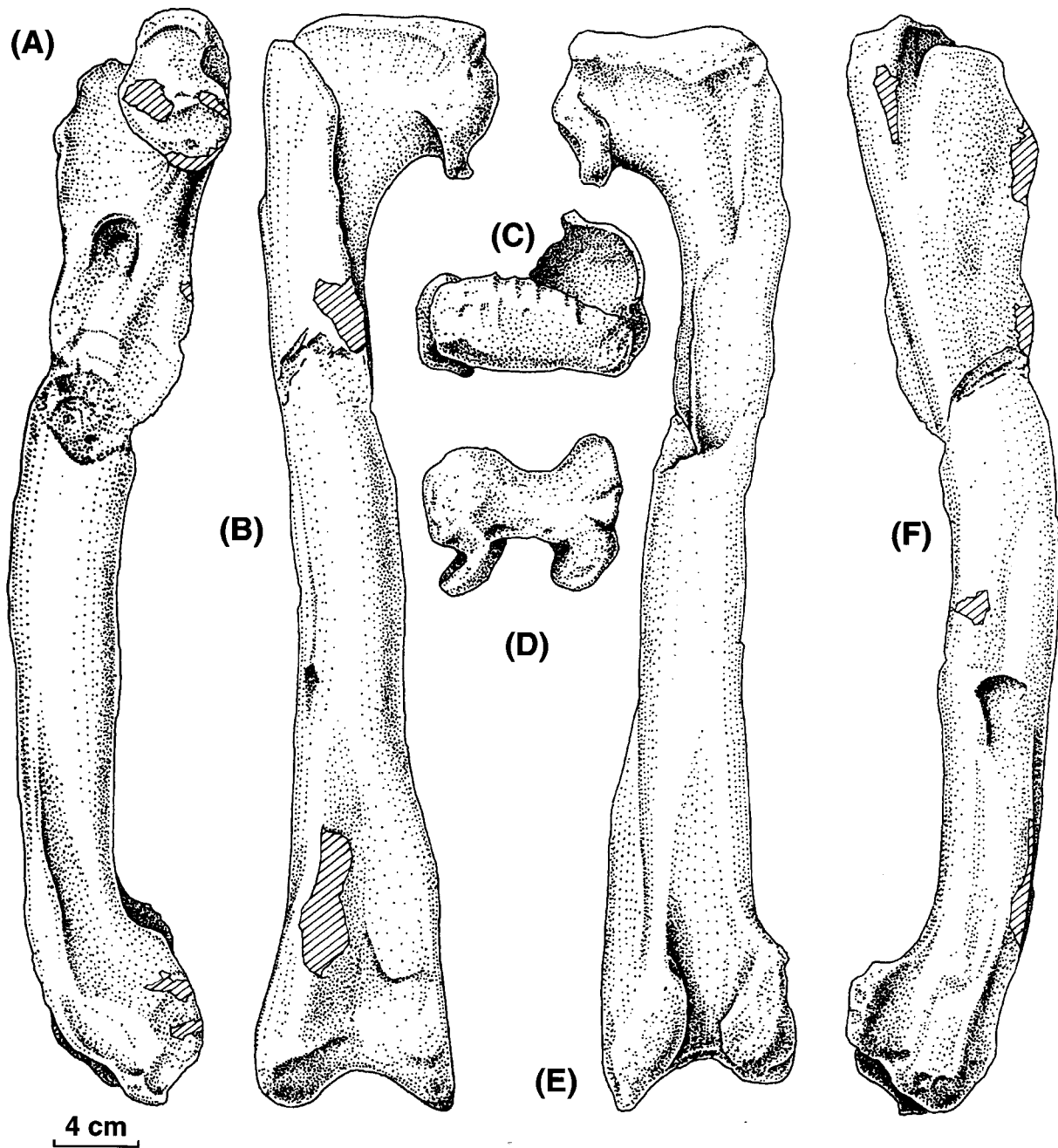
The 297.5 mm long third metatarsal (FPMN 9712224, Figs. 16G–L) is narrow proximally, but clearly separated metatarsals II and IV. In proximal aspect, the third metatarsal is roughly rectangular (Fig. 16L). The lateral surface of the shaft has a broadly concave surface, where it contacted the second metatarsal. Distally, the shaft expands into a wide, undivided articular condyle (Fig. 16L). The distal articulation extends well onto the posterior surface (Fig. 16 I). The distal ligament pits are equally developed on medial (Fig. 16G) and lateral (Fig. 16J) surfaces.

Only four pedal phalanges (Figs. 17, 18) have been recovered. Phalanx I-1 (FPMN 9712225, Fig. 17) has the typical theropod shape with a single concave proximal surface and collateral ligament pits close to the extensor surface. The first two of the third digit are 99.2 and 77.4 mm long and are relatively slender when compared with equivalent elements in large carnosaurs. This suggests that *Fukuiraptor* was a relatively lightly built animal, regardless of its size at maturity. Phalanx IV-2 is 38 mm long.

## Discussion

The theropod bones from the Kitadani quarry can be assigned with confidence to a single individual that was 4.2 m in length and weighed about 175 kg. This species is clearly a carnosaur, but also has some coelurosaurian characters. The dental shelves of the maxilla and dentary are narrow, and the interdental plates have fused to each other and to the margin of the jaw. These are characteristics that have previously

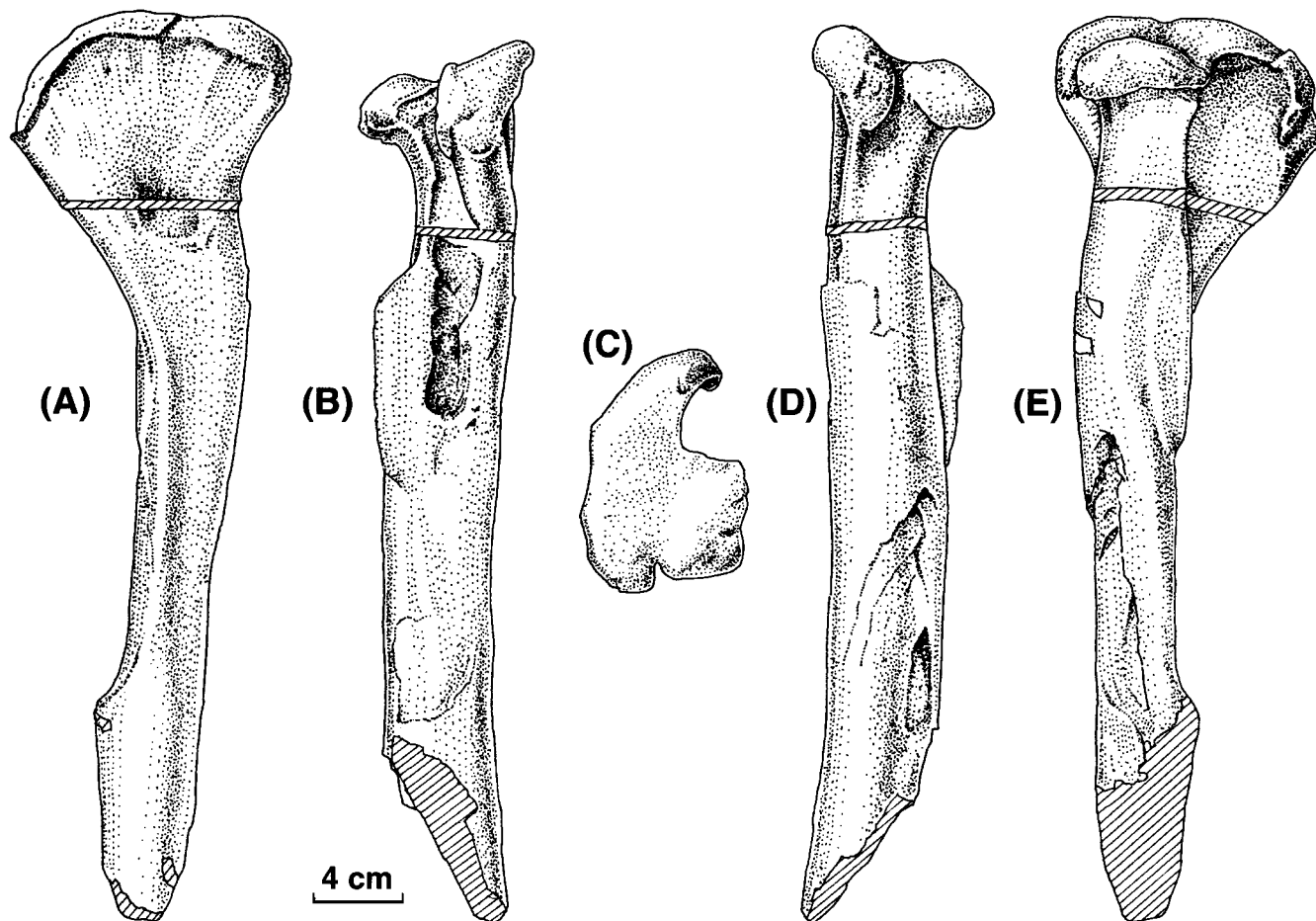
**Fig. 12.** *Fukuiraptor kitadaniensis*. Right femur (FPMN 9712219) in medial (A), anterior (B), proximal (C), distal (D), posterior (E), and lateral (F) views.



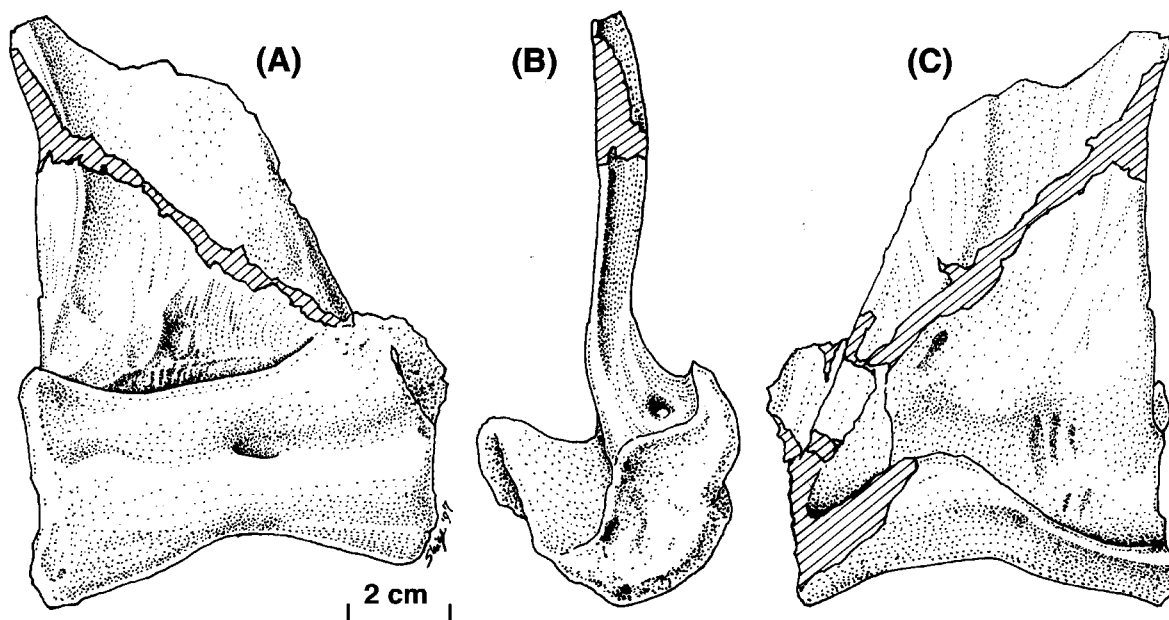
only been reported in dromaeosaurids. On the basis of these and the unguals, the specimen was originally assigned to the Dromaeosauridae (Azuma and Currie 1995). In all other characters, *Fukuiraptor* more closely resembles advanced carnosaur. The humerus is clearly long and slender. The ulna is shorter than the humerus and is stout and powerfully built. Manual phalanx II-2 is relatively shorter than the same element in *Deinonychus*, but the two preserved manual unguals (I-2, II-3) are almost as well developed. Both are powerfully built and strongly curved and are most reminiscent of carnosaur like *Allosaurus*. The fragment of ilium has an anteroposteriorly short pubic peduncle that appears to have been much larger than the ischial peduncle. The femur

is clearly that of a carnosaur and compares well with advanced allosauroid carnosaur like *Allosaurus* and *Sinraptor*. The head is perpendicular to the shaft, there is a deep cleft separating the aliform lesser trochanter, the fourth trochanter is well developed, and the distal end has a broad, shallow extensor groove. Although the distal end was not recovered, the tibia seems to have been at least as long as the femur. The astragalus has an ascending process that is relatively higher than those of any known carnosaur, but is somewhat shorter than those of coelurosaur like dromaeosaurids and tyrannosaurids. The three metatarsals recovered are relatively unspecialized and are similar to those found in carnosaur like *Acrocanthosaurus*, *Allosaurus*, and *Sinraptor*.

**Fig. 13.** *Fukuiraptor kitadaniensis*. Right tibia (FPMN 9712220) in medial (A), anterior (B), proximal (C), posterior (D), and lateral (E) views.

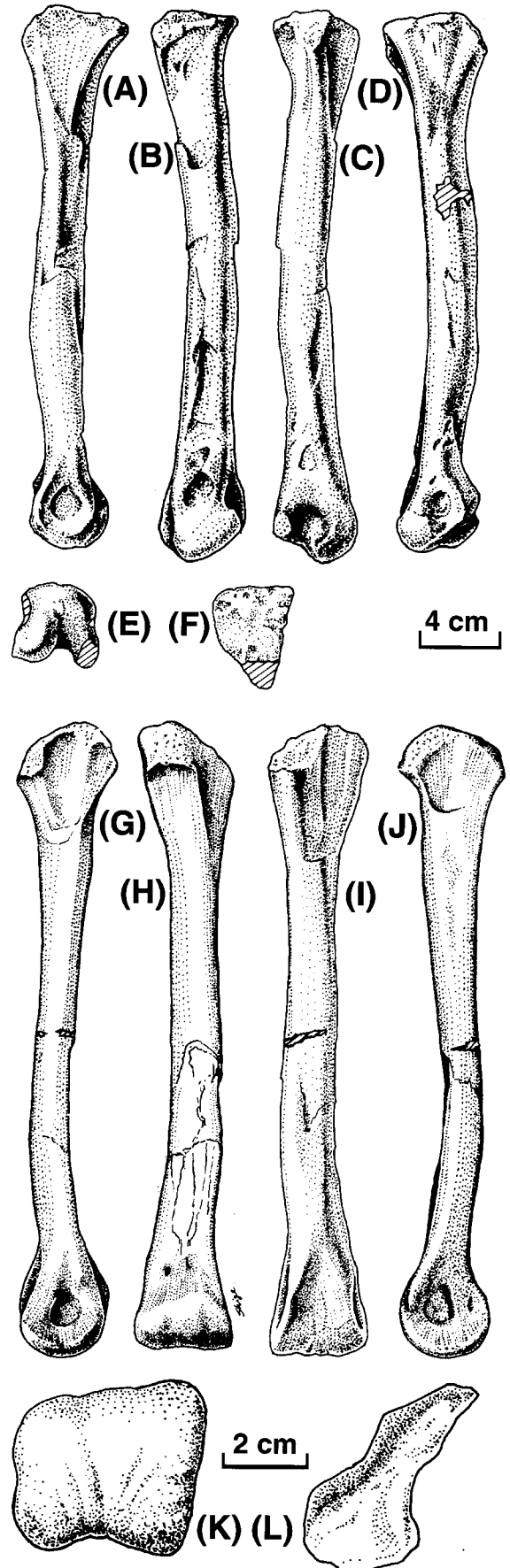
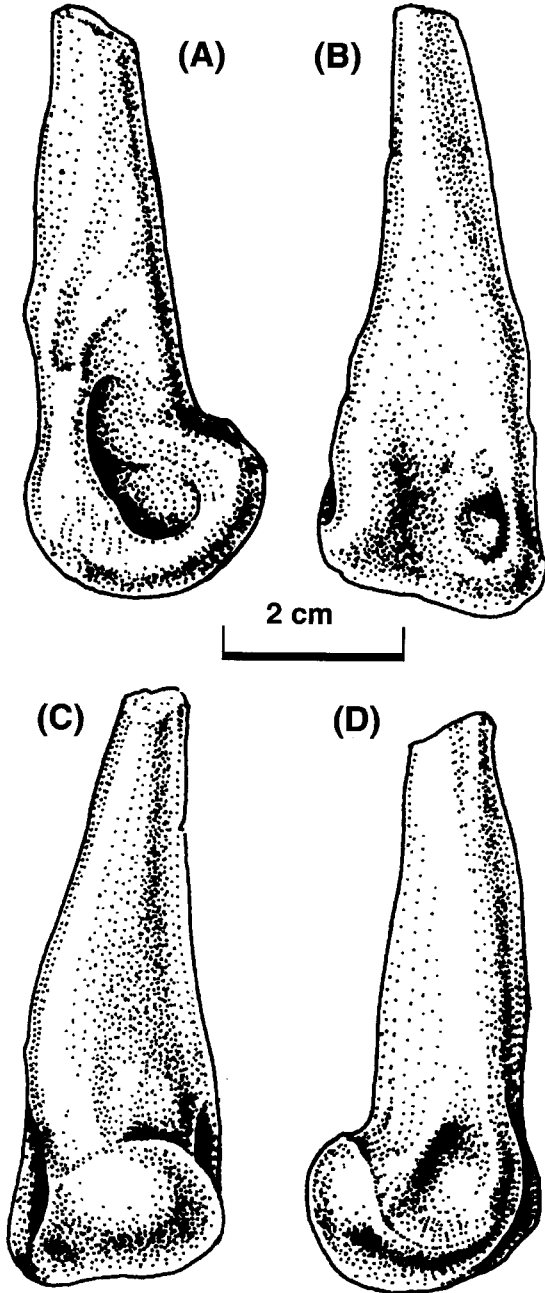


**Fig. 14.** *Fukuiraptor kitadaniensis*. Right astragalus (FPMN 9712221) in anterior (A), lateral (B), and posterior (C) views.



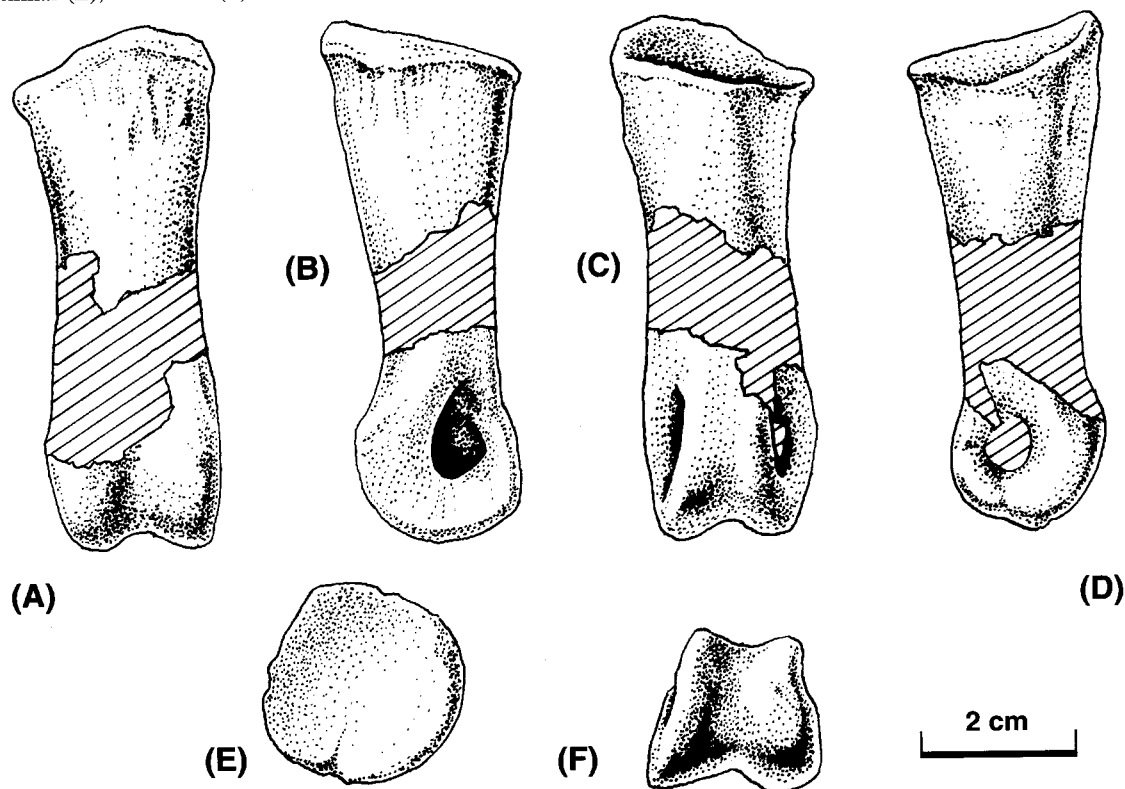
**Fig. 16.** *Fukuiraptor kitadaniensis*. Right metatarsal II (FPMN 9712223) in lateral (A), anterior (B), posterior (C), medial (D), distal (E), and proximal (F) views. Right metatarsal III (FPMN 9712224) in medial (G), anterior (H), posterior (I), lateral (J), distal (K), and proximal (L) aspects.

**Fig. 15.** *Fukuiraptor kitadaniensis*. Right metatarsal I (FPMN 9712222) in medial (A), anterior (B), posterior (C), and lateral (D) views.





**Fig. 17.** *Fukuiraptor kitadaniensis*. Left pedal phalanx I-1 (FPMN 9712225) of holotype in posterior (A), lateral (B), anterior (C), medial (D), proximal (E), and distal (F) views.



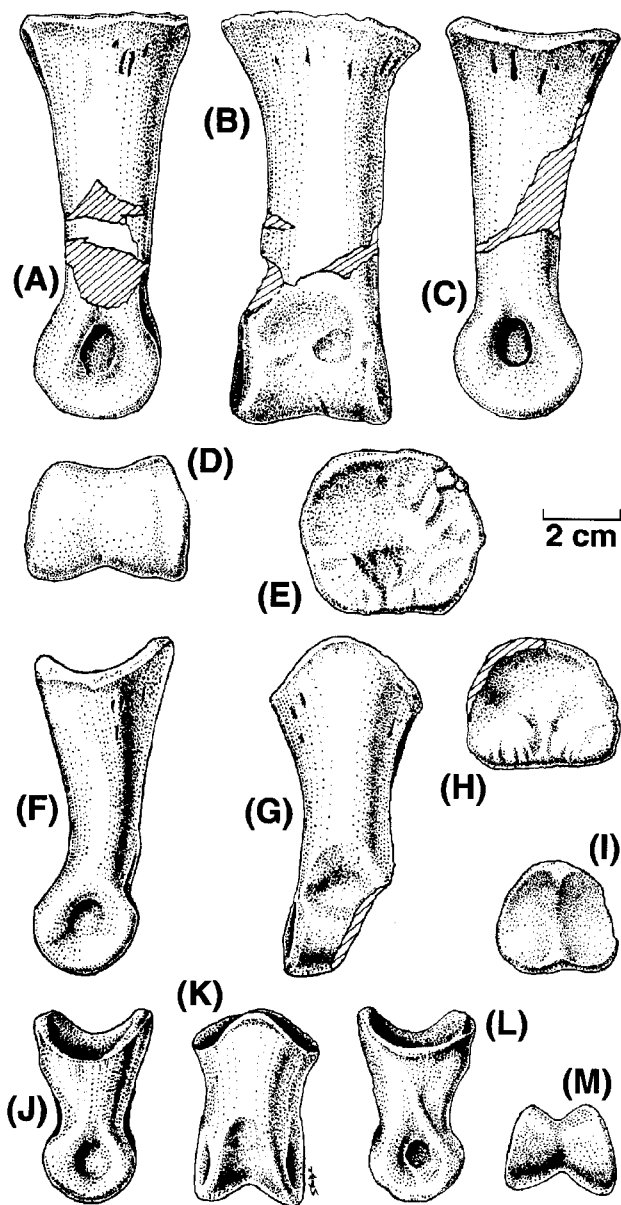
The third metatarsal is proximally slender, but still clearly separates the second and fourth metatarsals. In spite of a superficial similarity to dromaeosaurid metatarsals, the Fukui theropod is anatomically more conservative. In dromaeosaurs, the distal end of metatarsal III is wide between the flexor and extensor surfaces, and this also appears to have been the case in the Fukui specimen. However, the articular surface is more pulley-like in dromaeosaurs. The two pedal phalanges (III-1, III-2) are more elongate in appearance than they are in large theropods like tyrannosaurs and allosauroids, but fall within the 95% confidence intervals of all theropods in terms of length. The elongate appearance is, therefore, imparted by their slenderness, which suggests that the Fukui theropod never got to be as large and massive as most allosauroids and tyrannosaurids.

The morphology of the astragalus of *Fukuiraptor* is similar to an isolated astragalus from the Lower Cretaceous of Australia (Molnar et al. 1981). Identified originally as *Allosaurus*, Welles (1983) presented nineteen morphological differences from that genus, and Chure (1998) removed it from the Allosauridae. The Australian specimen seems to have had a high ascending process. Welles (1983) estimated the height to breadth ratio as 1.11, but Molnar et al. (1985) felt the ratio was closer to 0.93. Although breakage prevents determination of an accurate height to breadth ratio, it is clearly a higher ascending process than that found in *Allosaurus*. The differences between this specimen and *Allosaurus* that were cited by Welles (1983) are also differences that exist between *Fukuiraptor* and *Allosaurus*. These include a higher ascending process, a distinct vertical ridge

marking the medial margin of the fibular contact with the ascending process, a deeper upper horizontal groove with a sharper anterior edge above the condyles, a shallower lower groove across the condyles, and a stronger crescentic groove on the posterior surface of the ascending process. We agree with Molnar et al. (1985) that the tentative referral of the Australian specimen to the Ornithomimosauria by Welles (1983) is incorrect. The *Allosaurus* autapomorphies used by Molnar et al. (1985) are also found in *Fukuiraptor* and other carnosaur. The morphology of the Australian specimen suggests that it may be from an animal related to *Fukuiraptor*.

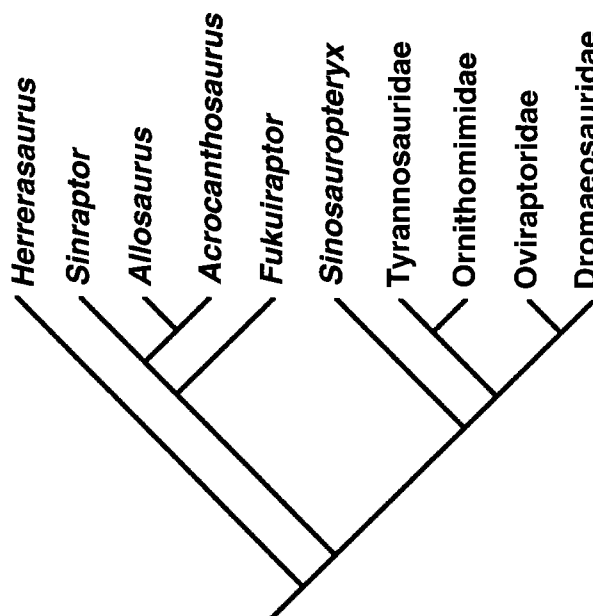
With its mosaic of character states, there is no doubt that the theropod from Fukui represents a new taxon. We compiled a data matrix based on other matrices (Holtz 1994; Sereno et al. 1994; Harris 1998) that included carnosaur, and performed a phylogenetic analysis using the beta version of PAUP 4.0 (Swofford 1998). The analysis included 32 cranial and dental characters, and 78 postcranial characters, 59 of which could be coded for *Fukuiraptor*. All of the characters were parsimony-informative, and six (numbers 5, 21, 28, 36, 45, 76) were ordered. *Herrerasaurus* was used as the outgroup. The coelurosaurian Dromaeosauridae, Ornithomimidae, Oviraptoridae, *Sinosauropteryx*, and Tyrannosauridae were included in the analysis, because in some characters *Fukuiraptor* looks more like a coelurosaur than a carnosaur. The Branch-and-Bound search method produced a single most parsimonious tree (tree length = 238, C.I. = 0.58, R.I. = 0.59, R.C. = 0.34), under both *Acctran* and *Deltran* transformations. *Fukuiraptor* sorted with *Acrocantiosaurus*, *Allosaurus*, and *Sinraptor* (Fig. 19), suggesting that the

**Fig. 18.** *Fukuiraptor kitadaniensis*. Pedal phalanges of holotype. Right III-1 (FPMN 9712226) in lateral (A), extensor (B), medial (C), distal (D), and proximal (E) views. Right III-2 (FPMN 9712227) in medial (F), extensor (G) and proximal (H) views. Right IV-2 (FPMN 9712228) in proximal (I), lateral (J), flexor (K), medial (L), and distal (M) views.



Carnosauria can be defined by six unambiguous characters (numbers 6, 28, 38, 42, 49, 50), and several more ambiguous ones (including numbers 12, 29, 35, 36, 37, 39, 51, 58, 65, 66, 84, 89, 91 and 96). Carnosauria can, therefore, be distinguished from Coelurosauria by the presence of a horizontal groove across the anterior face of the condyles; by the strongly opisthocoelous cervical vertebrae; by having pleurocoels on cervical centra and sometimes on the anterior dorsals as well, in the presence of the adductor fossa on the distomedial surface of the femoral shaft and a sharply defined mediolateral crest; and by ridge for the cruciate ligaments in the flexor groove of the femur.

**Fig. 19.** Most parsimonious tree generated in restricted analysis of phylogenetic relationships of *Fukuiraptor*.



## Conclusions

Most of the theropod bones recovered from the Kitadani quarry belong to a single individual 4.2 m in length and 175 kg in weight. *Fukuiraptor kitadaniensis* was a carnosaur that had some coelurosaurian characters and proportions. The jaw fragments have fused interdental plates as in the Dromaeosauridae. The humerus and ulna are long and slender like those of most coelurosaurs other than compsognathids and tyrannosaurids. Phalanx II-2 of the hand is basically the size expected for most theropods, but is shorter than those forms with elongate hands (dromaeosaurids, ornithomimids) and is longer than those with reduced forelimbs (*Acrocanthosaurus*, *Carnotaurus*, compsognathids, tyrannosaurids). The claws on the hand were well developed, however, and the one on the first digit in particular compares well with large clawed forms like dromaeosaurids, oviraptorosaurs, and *Allosaurus*. The astragalus has a tall ascending process, intermediate in height between carnosaur and coelurosaurs. Pedal phalanges are rather generalized, but suggest that mature animals were medium-sized at maturity. Comparison with an astragalus from Australia suggests that there may have been a related form in the Southern Hemisphere.

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of the Australian theropod astragalus. The illustrations were skillfully rendered by Mr. Shigeo Hayashi. We would like to thank all members of the Dinosaur Project of the Fukui Prefectural Museum and the Fukui Prefectural Government for their efforts and support over the last ten years. Support from the Natural Sciences and Engineering Research Council of Canada (203091-98) is gratefully acknowledged.

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## Appendix 1

Morphological characters used in this paper are as follows. Except where stated otherwise, characters are derived from Holtz (1994). "0" represents the primitive state. Unless specifically indicated, character states are unordered.

1. Antorbital fossa: 0, less than 25% of anteroposterior length of antorbital cavity; 1, greater than 40%.
2. Antorbital rim: 0, rim reduced or absent; 1, well-developed (Sues, 1997).
3. Astragalus: 0, condyles shallow; 1, deep and separated by deep sulcus (Welles and Long, 1974).
4. Astragalus: 0, condylar portion confluent with base of ascending process; 1, dorsal groove separates condyles from ascending process (Welles and Long, 1974).
5. Astragalus, height of ascending process: 0, less than a sixth of tibial length; 1, one sixth to one quarter; 2, more than a quarter (ordered).
6. Astragalus, pronounced horizontal groove across anterior face of condyles: 0, absent; 1, present.
7. Astragalus, round external fossa at base of ascending process: 0, absent; 1, present.
8. Astragalus, ascending process: 0, parallel to tibial shaft; 1, curves dorsolaterally toward fibular shaft (Russell and Dong, 1994).
9. Atlas, neurapophysis in lateral view: 0, not triangular; 1, triangular.
10. Axis, ventral keel: 0, absent; 1, present.
11. Basioccipital participates in basal tuber: 0, yes; 1, no, separated from tuber by a notch.
12. Basioccipital, distance across basal tubera: 0, greater than transverse width of occipital condyle; 1, less than the transverse width of condyle.
13. Basisphenoid: 0, unmodified; 1, strongly expanded and pneumatized (Sues, 1997).
14. Braincase, endocranial cavity: 0, typical size; 1, enlarged but temporal musculature extends onto frontals; 2, much enlarged but temporal musculature does not attach to frontals.
15. Braincase, internal carotid artery, pneumatized opening: 0, no; 1, yes.
16. Braincase, trigeminal nerve, separation of ophthalmic branch within the bone: 0, no; 1, incipient with trough in lateral surface of laterosphenoid; 2, complete with ophthalmic branch enclosed in a tube within laterosphenoid.
17. Calcaneum: 0, large; 1, small and possibly fused to astragalus (Welles and Long, 1974).
18. Carpus, semilunate carpal block fully developed with transverse trochlea: 0, absent; 1, present.
19. Caudal vertebrae, transverse processes: 0, present beyond caudal XV; 1, restricted to first 15 caudals.
20. Caudal vertebrae, double ventral keel: 0, absent; 1, present.
21. Caudal vertebrae, number of caudals: 0, 45 or more; 1, 30–44; 2, less than 25 (ordered).
22. Caudal vertebrae, proximal caudal zygapophyses: 0, short; 1, elongate.
23. Cervical ribs, anteroventral process at base of anterior rib shafts: 0, no; 1, yes.
24. Cervical vertebrae, epipophyseal shape: 0, rugosity on posterior zygopophysis; 1, powerfully developed.
25. Cervical vertebrae, interior of centrum: 0, apneumatic; 1, simple camerate; 2, complex camellate.
26. Cervical vertebrae, posterior view of centrum: 0, round or oval; 1, reniform and at least 20% broader than tall.
27. Cervical vertebrae, prezygapophyses: 0, planar; 1, flexed.
28. Cervical vertebrae: 0, not opisthocoelous; 1, weakly opisthocoelous; 2, strongly opisthocoelous (ordered).
29. Coracoid, posteroventral (acroracoid) process placement with respect to glenoid diameter: 0, same level; 1, protrudes markedly posteroventral to the glenoid.
30. Coracoid: 0, anteroposteriorly elongate to subcircular; 1, subrectangular and deeper than long.
31. Dentary: 0, straight in dorsal view; 1, medially inflected symphyseal region (Clark et al. 1994).
32. Dentary: 0, thick when compared to height, deep Meckelian groove: 1, thin and high with shallow Meckelian groove and dental shelf (Currie 1995).
33. Dentary, lateral view: 0, tapers conspicuously anteriorly; 1, upper and ventral margins subparallel (Currie 1995).
34. Dorsal vertebrae, several anterior dorsals opisthocoelous: 0, no; 1, yes.
35. Dorsal vertebrae, dorsal centrum shape: 0, cylindrical, central section thickness greater than 60% height of anterior face; 1, "hourglass" shaped, central section thickness less than 60% height of anterior face.
36. Dorsal vertebrae, neural spines of dorsals: 0, less than or equal to centrum height; 1, equal to twice centrum height; 2, more than twice centrum height (ordered).
37. Dorsal vertebrae, posterior dorsal neural spines: 0, oriented vertically or posteriorly; 1, oriented anteriorly.
38. Dorsal vertebrae, pleurocoels in centrum: 0, none; 1, on anterior dorsals; 2, on all dorsals.
39. Ectopterygoid, pneumatic recess: 0, not present; 1, elongate; 2, subcircular (modified from Gauthier, 1986).
40. Exoccipital-opisthotic, paroccipital process: 0, no pneumatization; 1, pneumatized in proximal part.
41. Exoccipital-opisthotic, paroccipital processes downturned: 0, no; 1, yes.
42. Femur, adductor fossa on distomedial surface of shaft: 0, absent; 1, present.
43. Femur, anterior trochanter: 0, separated from greater trochanter by cleft; 1, fused to it to form the trochanteric crest.
44. Femur, extensor groove on distal end: 0, absent; 1, shallow and broad; 2, deep and narrow.
45. Femur, fourth trochanter: 0, distinct crest; 1, low crest; 2, absent (ordered, Gauthier 1986).
46. Femur, greater trochanter: 0, anteroposteriorly short, 1, anteroposteriorly elongate, so it is anteroposteriorly as wide or wider than caput.
47. Femur, head shape: 0, bulky; 1, transversely elongate; 2, rounded.

48. Femur, head: 0, directed anteromedially; 1, directed medially (Bonaparte 1991).
49. Femur, mediolateral crest: 0, absent or weakly developed; 1, pronounced, extends one quarter or more the length of the shaft.
50. Femur, popliteal fossa (flexor groove), ridge for cruciate ligaments: 0, absent; 1, present.
51. Femur: 0, trochanteric shelf well developed; 1, trochanteric shelf absent; 2, replaced by rugosities; 3, low prominence with sharp upper margin; 4, low prominence grades into posterior trochanter.
52. Forelimb (humerus + radius + manus) / hindlimb (femur + tibia + pes) length ratio: 0, less than 50%; 1, greater than 50%.
53. Forelimb, radius/humerus length ratio: 0, less than 75% but greater than 50%; 1, less than 50%; 2, greater than 76%.
54. Frontal-parietal: 0, transverse dorsal suture; 1, frontals separated on midline by parietal wedge.
55. Humerus, deltopectoral crest: 0, low; 1, expanded and offset from humeral shaft (Makovicky & Sues, 1998).
56. Humerus, ends: 0, little if not expanded; 1, expanded more than 150% midshaft diameter.
57. Humerus, ulnar facet: 0, small or absent; 1, expanded (Russell and Dong, 1994).
58. Humerus/scapula length ratio: 0, greater than 65%; 1, less than 65%.
59. Humerus shaft: 0, straight; 1, sigmoidal.
60. Ilium orientation: 0, vertical blades well lateral to lamina formed by coalesced neural spines of sacrum; 1, blades medially inclined towards each other.
61. Ilium, pubic peduncle proportions: 0, more developed mediolaterally than anteroposteriorly; 1, more developed anteroposteriorly than mediolaterally.
62. Interdental plates: 0, present and separate; 1, fused to each other and dentary; 2, absent.
63. Ischium, distal expansion: 0, absent; 1, present but not boot-shaped; 2, boot-shaped.
64. Ischium: 0, more than 0.75 length of pubis; 1, less than three-quarters (modified from Gauthier, 1986).
65. Jugal, pneumatic: 0, no; 1, yes.
66. Lacrimal, horn: 0, nonexistent; 1, low ridge; 2, high and pointed.
67. Lacrimal, recess: 0, absent; 1, single opening; 2, multiple.
68. Mandible, external mandibular fenestra: 0, large; 1, reduced; 2, enlarged.
69. Manual phalanx I-1: 0, less than or subequal to length of metacarpal II; 1, greater than length of metacarpal II.
70. Manual unguals cross-section: 0, generally oval, two to three times deeper than wide; 1, blade-like, more than three times deeper than wide; 2, subtriangular, as wide or wider than deep.
71. Manual ungual curvature: 0, moderate; 1, strongly curved; 2, straight.
72. Manual ungual length: 0, moderate; 1, extremely long; 2, relatively short.
73. Manual ungual I-2: 0, subequal to unguals II-3 and III-4; 1, larger than other manual unguals.
74. Manual unguals: 0, dorsal margin convex in lateral view; 1, posterodorsal lip above articular surface (Currie and Russell, 1988).
75. Manual ungual, region palmar to ungual grooves: 0, wider than region dorsal to ungual grooves; 1, palmar and dorsal regions subequal in width.
76. Manus, digit count: 0, more than three digits; 1, three; 2, two (ordered, Gauthier 1986).
77. Manus/(humerus + radius) length ratio: 0, less than 66%; 1, greater than 66%.
78. Maxilla, palatal shelf: 0, narrow; 1, broad shelf contributing to secondary bony palate.
79. Metacarpal III, long and slender: 0, no; 1, yes.
80. Metatarsal III, proximal surface: 0, similar in area to metatarsals II and IV; 1, clearly smaller than metatarsals II and IV (ordered).
81. Metatarsal III, proximal view: 0, not hourglass-shaped; 1, hourglass-shaped; 2, barely visible (arctometatarsalian).
82. Metatarsus cross-section at mid-length: 0, subequal or wider mediolaterally than anteroposteriorly; 1, wider anteroposteriorly than mediolaterally.
83. Metatarsus, proportions: 0, moderate; 1, elongate relative to most other theropods of same femur length; 2, shortened relative to most other theropods of same femur length.
84. Nasal, participates in antorbital fossa: 0, no or slightly; 1, broadly, with nasal recesses.
85. Palatine, recesses: 0, absent; 1, present.
86. Palatine, subsidiary fenestra between pterygoid and palatine: 0, absent; 1, present (Sues, 1997).
87. Pedal phalanges 1-1 plus 1-2: 0, longer than III-1; 1, shorter than III-1.
88. Pelvis, pubic-ischial contact: 0, dorsoventrally deep shelf; 1, only narrow region.
89. Postorbital prominences: 0, absent; 1, present.
90. Postorbital-lacrimal contact: 0, none; 1, broad.
91. Prefrontal-frontal, peg in socket joint: 0, no; 1, yes.
92. Premaxilla, symphysis: 0, V-shaped; 1, U-shaped.
93. Pubis, distal view of conjoined pubic boots: 0, not triangular; 1, triangular.
94. Pubis, obturator process: 0, trapezoidal or quadrilateral in lateral view; 1, triangular in lateral view (Sereeno et al. 1996).
95. Pubis, pubic apron: 0, long and extending for more than 50% of pubic length; 1, short (Makovicky & Sues, 1998).
96. Pubis, pubic boot: 0, posterior portion same length as anterior portion; 1, posterior portion longer than anterior portion; 2, anterior portion absent.
97. Quadrate articulation position: 0, slightly posterior to occipital condyle in dorsal view; 1, well posterior to back of occipital condyle; 2, anterior to condyle.
98. Quadrate: 0, tall; 1, short with head at mid-orbital height.
99. Sacral pleurocoels on centra: 0, none; 1, present (Russell and Dong, 1994).
100. Sacral neural spines fuse to form lamina: 0, absent; 1, present.
101. Surangular, anterior ramus: 0, shallow; 1, deep.
102. Surangular, posterior surangular foramen: 0, small foramen; 1, large opening.



103. Teeth, anterior and posterior denticles: 0, subequal in size; 1, anterior denticles, when present, much smaller than posterior ones.

104. Teeth. 0, present; 1, absent.

105. Tibia, incisura tibialis: 0, occupies less than 50% of medial surface of proximal end; 1, occupies more than 66% of medial surface of proximal end.

106. Tibia, length; 0, not elongate relative to femur; 1, elongate (Sues, 1997).

107. Tibia, fibular (outer, lateral) condyle on proximal end: 0, large and posteriorly situated; 1, small and medially situated.

108. Tibia, fibular (outer, lateral) condyle: 0, outer margin of condyle is smoothly convex; 1, conspicuous waisting between body of condyle and main body of tibia, and has small, triangular prominence anteriorly, sometimes with low ridge extending to crista fibularis; 2, conspicuous waisting between body of condyle and main body of tibia, deep anterior trough.

109. Ulna, shaft: 0, straight; 1, visibly bowed (Gauthier, 1986).

110. Ulna/femur length ratio: 0, less than 27%; 1, more than 28%.

## Appendix 2

Data matrix used for phylogenetic analysis. 0 = primitive state; 1, 2, 3, 4 = derived character states; ? = missing data.

### *Acrocanthosaurus*

00001 10111 10001 00001 ?0112 10210 00011 21210 01020  
01111 10001 10110 10201 1111? 00?00 11000 1001? 01111  
10100 10111 10000 00100

### *Allosaurus*

01011 10110 11001 20001 00101 00210 00011 11110 11020  
01111 20001 10110 10101 22110 00100 11000 10010 00110  
10100 10111 10000 00100

### *Dromaeosauridae*

11112 00101 00010 11111 11011 11001 01100 00221 00112  
12100 41211 00011 11010 00101 10010 10110 10201 10100  
00011 22111 11101 10111

### *Fukuiraptor*

?0011 101?? ????? ?0??1 ????1 ??210 011?? ?1?? ?1010  
01111 102?1 10?1? 01??? ????1 10100 110?0 101?? ?00??  
?0??? ????? ?0000 00101

### *Herrerasaurus*

?0000 00001 00000 00000 00?00 00000 00000 00000 00000  
00000 01000 0?000 00000 0000? 00000 00000 00000 00?00  
00000 00000 00000 00001

### *Ornithomimidae*

10112 01110 00111 21011 10111 11010 10100 00201 01021  
02100 21200 00001 12100 00112 21001 10101 21101 11100  
01011 02111 10?11 11200

### *Oviraptoridae*

11112 00101 00011 11101 20001 11001 10100 00221 10112  
12100 21211 11011 12010 02211 10111 11110 10011 10100  
01111 02111 00?11 10110

### *Sinosauropteryx*

10112 0011? ???0? ?111? 00?01 ??01? 00000 000?? ?0011  
0110? 200?1 1101? 10110 01111 01100 11010 1100? ?1000  
00?11 20100 0010? 11?01

### *Sinraptor*

01000 11010 01000 10?01 ?0101 002?? 00001 11110 11020  
01011 1?00?  
????0 10101 120?0 00?00 0?000 10011 00110 10100 11000  
00000 000??

### *Tyrannosauridae*

11112 01110 00111 21010 11102 11001 00001 00221 01020  
01100 20110 00001 10011 22112  
22001 21011 21101 10111 11111 02111 11001 10201