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NEW SPECIMENS, INCLUDING A GROWTH SERIES, OF *FUKUIRAPTOR* (DINOSAURIA, THEROPODA) FROM THE LOWER CRETACEOUS KITADANI QUARRY OF JAPAN

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Abstract: In addition to the holotype skeleton of *Fukuiraptor kitadaniensis*, isolated teeth and bones of the same taxon have been collected from the Kitadani Quarry of the Lower Cretaceous (Barremian) strata in Fukui Prefecture, Japan. These provide additional information that help determine its phylogenetic position, and also represent a growth series. The holotype is an immature specimen, which was about 4.2 meters long. Other fossils from the same quarry are all from smaller individuals. Some of the juvenile bones are less than a third the linear length of equivalent bones in the holotype.

Key words: *Fukuiraptor*, growth series, Kitadani, Japan

INTRODUCTION

The Kitadani Quarry is on the Sugiyama River within the city limits of Katsuyama in Fukui Prefecture, Japan. It is the largest dinosaur excavation that has been done in Japan, and is arguably one of the largest dinosaur quarries in the world. Worked originally by the Fukui Prefectural Museum between 1988 and 1993, and from 1996 to 1998, the excavation is being continued by the Fukui Prefectural Dinosaur Museum, which opened in 2000.

The excavation has produced bones, eggshell and footprints of theropods, sauropods and ornithischians. Other fossils recovered from the site include plants, freshwater mollusks, fish, turtles, crocodiles and birds (Azuma *et al*., 1995). The best specimens from the quarry include a nearly complete goniopholidid crocodyliform (Kobayashi, 1998), the iguanodontians *Fukuisaurus tetoriensis* (Kobayashi and Azuma, 2003) and the carnosaurian theropod *Fukuiraptor kitadaniensis* (Azuma and Currie, 2000).

The type material of *Fukuiraptor kitadaniensis* represents an immature individual that was about 4.2 meters long at the time of death. Most of the other theropod teeth and bones from the same quarry are from smaller individuals of the same taxon. Some of the juvenile bones are less than a third the linear length of equivalent bones in the holotype. In this paper, we have focused on teeth, humeri and femora because these are the most diagnostic elements that are well represented by multiple specimens. There are additional bones from the quarry that probably represent *Fukuiraptor*. However, they lack diagnostic *Fukuiraptor* characters, and/or they do not add significant information to the previous description (Azuma and Currie, 2000), and/or they do not provide information about growth in this taxon.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842

THEROPODA Marsh, 1881

CARNOSAURIA von Huene, 1920
Fukuiraptor kitadaniensis Azuma and Currie, 2000

Specimens used in this study (Teeth are listed in Table 1)
FPDM-V97122 (holotype), associated skeleton (includes humeri and right femur)
FPDM-V97122BNA3, femur, right, individual 3 (size class 2)
FPDM-V97122BNA12, femur, right, individual 5 (size class 3)

Table 1. Teeth of *Fukuiraptor kitadaniensis*. Abbreviations: AD1, number of anterior denticles per 5 mm; AD2, basal width of posterior denticle as seen in labial or lingual view; BW, labial-lingual basal width of tooth; CH, crown height; FABL, fore-aft base length; d, dentary; mx, maxillary; pm, premaxillary; PD1, number of posterior denticles per 5 mm; PD2, basal width of posterior denticle as seen in labial or lingual view; Pos, tooth position; TH, total height of crown and root of tooth.

#	Pos	CH	TH	FABL	AD1	AD2	PD1	PD2	BW
96080810	mx	50	xx	18.0	12.5	0.40	12.5	0.40	7.5
96081134	?	xx	xx	xx	xx	xx	12.5	0.40	xx
97080208	mx	xx	xx	9.5	20.0	0.25	20.0	0.25	xx
97081128	d	33.4	xx	17.4	16.5	0.30	16.5	0.30	7.5
97082330	mx	17	41.4	9.0	17.0	0.29	17.0	0.29	5.1
97082367	mx	23++	xx	14+	17.0	0.29	14.0	0.36	6.5+
97082574	mx	33	xx	11.9	17.5	0.29	17.5	0.29	5.7
97082728	mx	41+	xx	15.6	15.0	0.33	12.5	0.40	7.4
9712201	mx	37+	Xx	14	19.0	0.26	16.1	0.31	5.5
9712203	mx	31.3	xx	15.4	14.0	0.36	14.0	0.36	6.1
9712204	d	34	xx	13.2	15.0	0.33	15.0	0.33	8.2
9712205	pm	17+	31+	8.2	15.0	0.33	16.5	0.30	6.0
9712206	mx	26	xx	14.6	20.0	0.25	16.5	0.30	xx
9712229	mx	xx	xx	xx	xx	xx	17.0	0.30	xx
9712231	?								
9712232	?								
9712233	d	18.8	xx	11.5	19.0	0.26	16.0	0.30	5.6
9712234	mx	12.6	xx	10.4	16.5	0.30	16.5	0.30	4.6
9712235	mx	25	xx	13.0	17.0	0.29	14.0	0.36	xx
9712236	d	18.5	xx	12.0	19.0	0.26	16.0	0.31	5.0
9712237	?								
9712238	?								
9712239	?	18+	xx	7.4	20.0	0.25	20.0	0.25	4.9
980721002	d	18	xx	9.9	19.5	0.26	18.0	0.28	4.2
980724112	d	xx	xx	16.5	15.0	0.33	xx	xx	7.8
980801101	?	xx	xx	xx	15.0	0.33	xx	xx	xx
980803001	pm	xx	xx	8.0	20.0	0.25	19.0	0.26	5.5
980803120	mx	24+	xx	12.0	20.0	0.25	18.0	0.28	5.3
980803123	?	xx	xx	xx	17.0	0.29	15.0	0.33	xx
980804135	mx	17.6+	xx	8+	17.5	0.29	16.0	0.32	4.9
980804144	?	xx	xx	xx	xx	xx	11.0	0.45	xx
980805101	mx	33+	xx	xx	19.0	0.26	16.0	0.31	3.5+
980806009	?	27+	xx	xx	14.0	0.36	14.0	0.36	xx
980810141	mx	34	xx	15.9	14.0	0.36	13.0	0.38	5.6
980813008	mx	23	xx	10.5	16.0	0.31	16.0	0.31	5.6
980815020	d	27.5+	xx	12.0	16.0	0.31	15.0	0.33	9.5
980815176	d	25+	xx	13.4	17.5	0.29	17.5	0.29	6.5
98081540	mx	54.8	xx	22.0	14.0	0.36	12.5	0.40	7.5
980819055	mx	32+	xx	13.5	16.5	0.30	15.0	0.33	5.4
980819173	?	xx	xx	xx	15.0	0.33	xx	xx	xx
981200001	d	39+	xx	17.9	xx	xx	15.0	0.33	9.4
981200012	d	6	xx	5.0	25.0	0.20	22.0	0.23	2.3

FPDM-V970730003, femur, proximal two thirds of right,
FPDM-V97080623, femur, left (probably an ornithopod so do not include in measurements or on final of this list)
FPDM-V97080937, femur, left (size class 1)
FPDM-V97081115, humerus, right
FPDM-V97081201, femur, right, individual 4 (size class 2)
FPDM-V97081317, tibia, right
FPDM-V97081330, femur, right, individual 1 (size class 1)
FPDM-V970813046, femur, right,
FPDM-V970814001, tibia, right
FPDM-V970820060, tibia, right
FPDM-V970821039, femur, right,
FPDM-V97082120, humerus, right
FPDM-V97082553, humerus, left
FPDM-V98072302, femur, left (size class 1)
FPDM-V980723005, humerus, right
FPDM-V980801141, manual ungual with proximodorsal lip
FPDM-V980805018, femur, right
FPDM-V9708102884, femur, right (shaft only)
FPDM-V980813017, femur, right, individual 2 (size class 1)
FPDM-V980815162, elongate, relatively straight manual ungual.
FPDM-V98082026, pedal phalanx III-2
FPDM-V990410001, manual phalanx I-1
FPDM-V99090901, femur, distal end of left,
FPDM-V9912141, tip of small manual ungual
FPDM-V97120001, femur, proximal head of left
FPDM-V98120001, femur, shaft only of left
FPDM-V98120002, femur, shaft only of left
FPDM-V9812638, femur, shaft only of right

Locality and Age

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). Lower Cretaceous (Barremian) Kitadani Formation (Akaiwa Subgroup, Tetori Group).

Institutional abbreviations

FPDM-V, Fukui Prefectural Dinosaur Museum, vertebrate collection, Katsuyama, Fukui.

DESCRIPTION

TEETH

Five teeth were associated with the holotype skeleton of *Fukuiraptor kitadaniensis* (Azuma and Currie, 2000), including one in the socket of a dentary fragment. In addition to these, there is a tooth in one of the sockets of a posterior fragment from a left maxilla (FPDM-V9712201) of the holotype. The posterior left maxillary fragment figured by Azuma and Currie (2000, Figs. 3A-C) was incorrectly labeled as this specimen, but is actually that of a referred specimen (FPDM-V9712229).

Two premaxillary teeth are known for *Fukuiraptor* (Table 1), the best (Fig. 1) of which belongs to the holotype. The distal tip of the tooth is missing, partly because of wear and partly because of minor damage. The posterior carina forms the posterolateral edge of the tooth, and extends from below gum-line at the beginning of the enameled crown to the broken tip of the tooth. The anterior carina is posterolingual to the anterior longitudinal midline of the tooth, which gives the crown a J-shaped cross section (Fig. 1D). The carina extends distally from the enamel-dentine contact at the base of the crown (below gum-line) to the broken tip of the tooth. The first denticle is about 1.5 mm distal to the proximal end of the anterior carina, and was probably just above gum-line. The anterior denticles are low and rounded, but their basal diameters are the same or slightly more than those of posterior denticles at equivalent heights in the tooth. The posterior denticles are about twice the height of the anterior denticles, even though they have equivalent basal diameters, and are distally hooked (Fig. 1B). The root is incomplete, but there was clearly no constriction between root and crown.

A maxillary crown from the holotype (Fig. 2A, and fig. 4 in Azuma and Currie, 2000) shows that *Fukuiraptor* had narrow, blade-like cheek teeth. This crown is 31.3 mm high, and based on size comparisons with other teeth in the type, it is probably one of the last maxillary teeth. The denticulate anterior

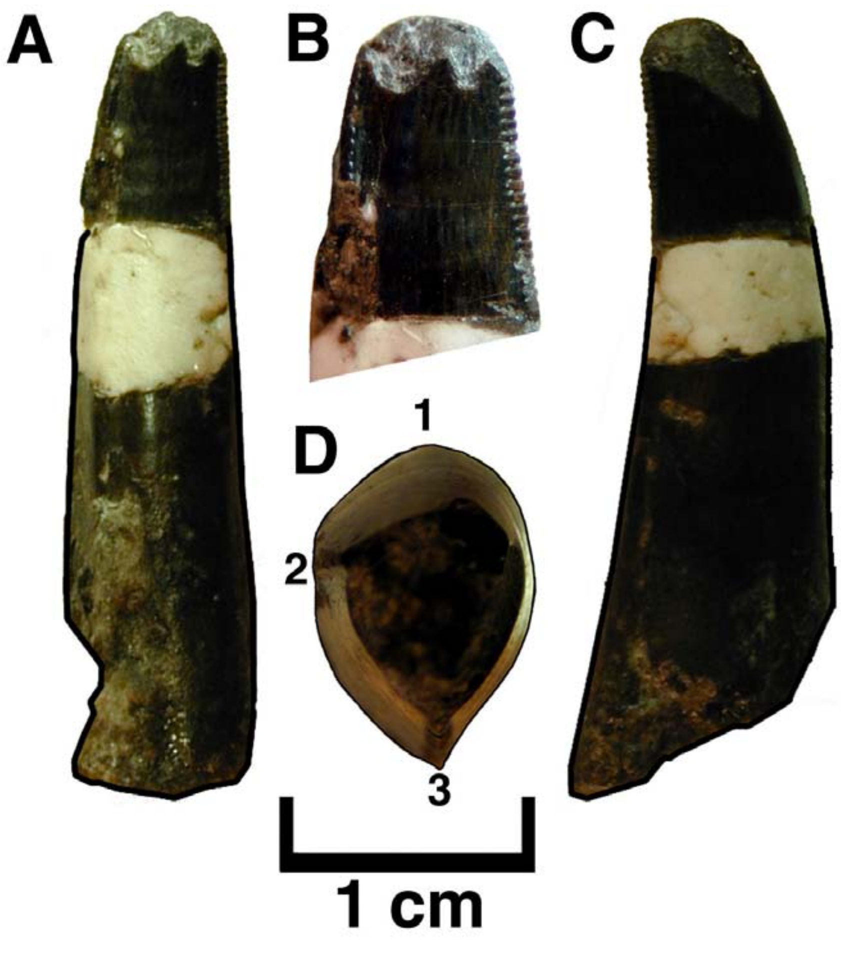


Fig. 1. *Fukukiraptor kitadaniensis*, left premaxillary tooth of the holotype in posterior (A, B), labial (C) and distal (D) views. The plaster fills an impression in the rock of the missing part of the tooth, and includes a cast of the anterior carina. 1, midline of anterior surface; 2, anterior carina; 3, posterior carina.

carina extends from just above gum-line to the tip of the tooth, whereas the denticulate posterior carina starts just below gum-line at the enamel-dentine interface. Denticles are small near the tip, but went right across the top of the pointed end. Anterior denticles are subequal with posterior denticles in terms of bas-

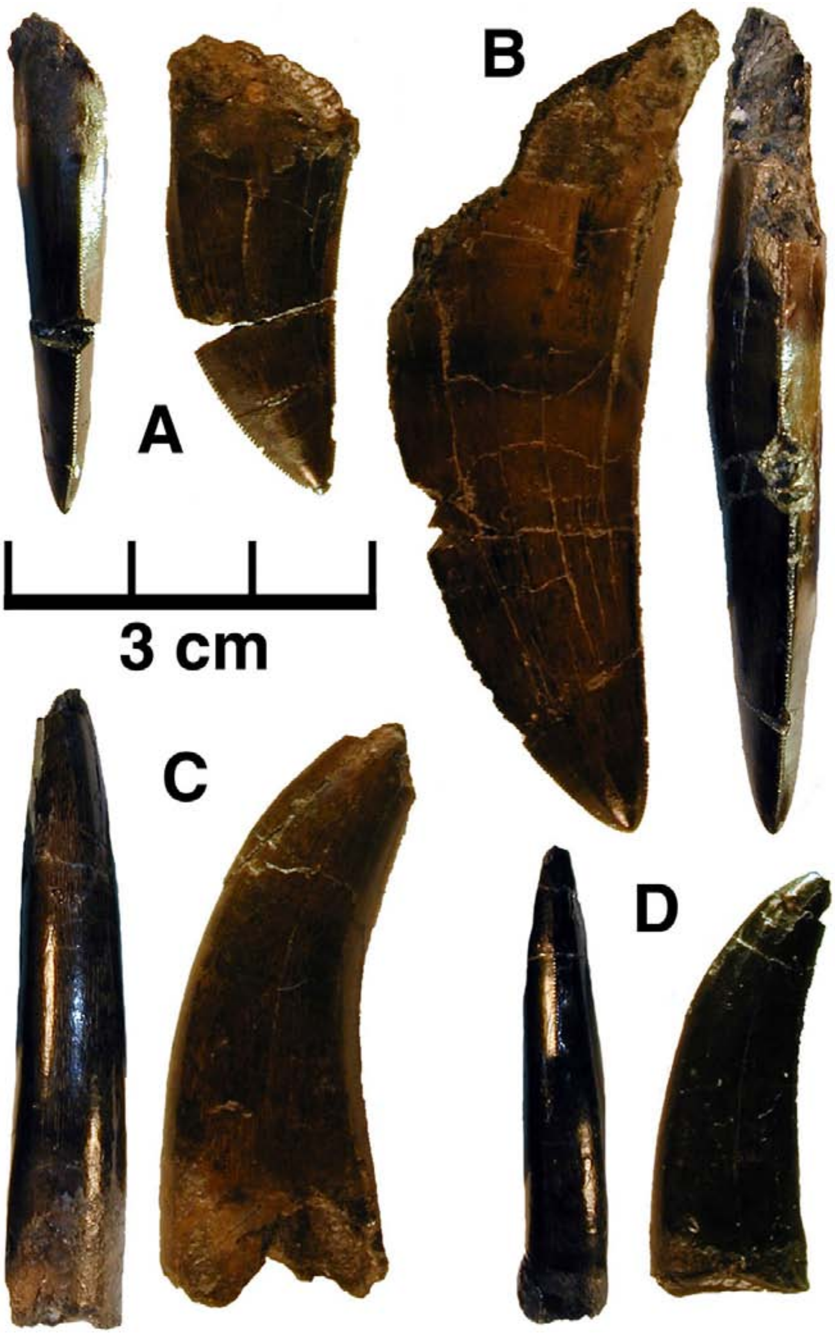


Fig. 2. Maxillary (A, B) and dentary (C, D) teeth of *Fukuiraptor kitadaniensis*. A, right maxillary tooth of holotype (FPDM-V9712203) in anterior and lingual views; B, left maxillary tooth (FPDM-V98081540) in labial and anterior aspects; C, left dentary tooth (FPDM-V98120001) in anterior and labial views; D, third right dentary tooth of holotype (FPDM-V9712204) displayed in anterior and lingual aspects.

al width, but are only about two-thirds the height. The posterior denticles are hooked towards the tip of the tooth. Oblique blood grooves trail away from between the bases of almost all denticles (fig. 4 of Azuma and Currie, 2000) on both labial and lingual sides.

The maxillary fragment from the holotype (FPDM-V9712201), which is coincidentally from the same position in the left maxilla of the other, slightly smaller individual (FPDM-V9712229), has been prepared to expose a germ tooth in the socket. Most of the crown (which is the second last maxillary tooth) is preserved, and shows that the teeth of *Fukuiraptor* were anteroposteriorly long but labial-lingually narrow. The crown lacks only the tip and is slightly more than 37 mm tall, with a basal cross-section of 14 x 5.5 mm. Most of the anterior carina is covered by bone so it is difficult to see how far it extends down the tooth, but like the posterior carina, it is denticulate. Although the basal diameter of each ante-

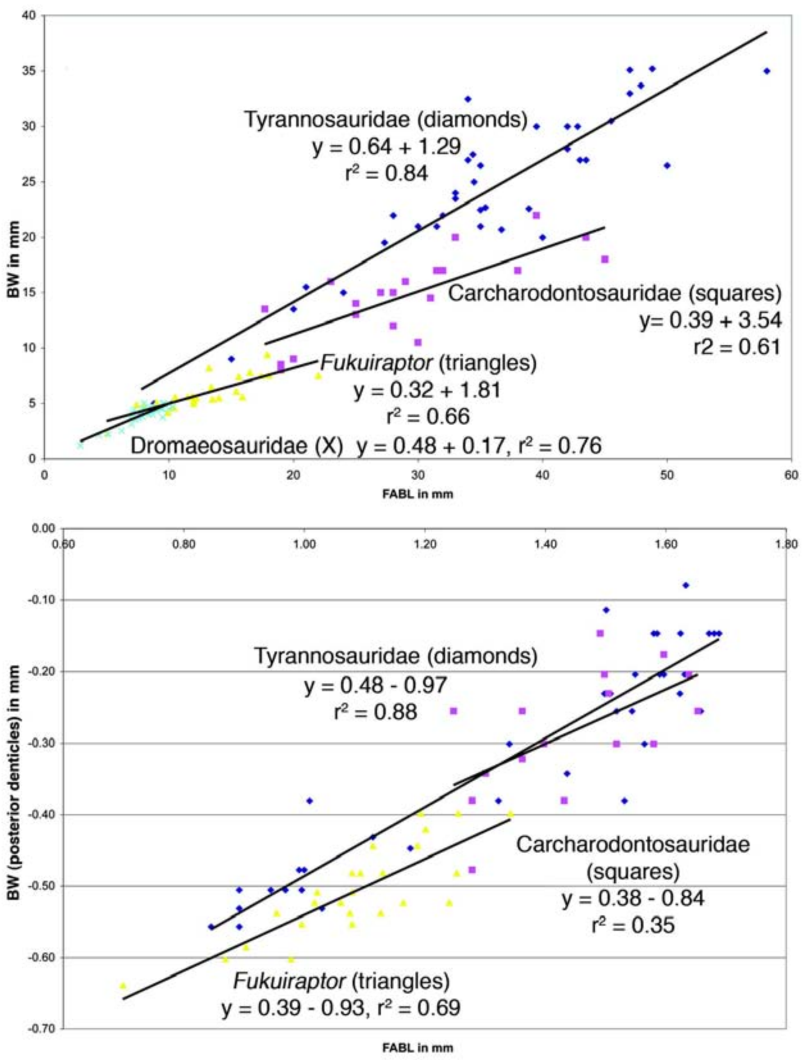


Fig. 3. Bivariate scatter plots comparing aspects of tooth dimensions with those of various theropods. A, FABL versus BW of tooth crowns in *Fukuiraptor* (triangles), dromaeosaurids (X), carcharodontosaurids (squares) and tyrannosaurids (diamonds). B,logarithms of FABL versus basal diameters of posterior serrations in *Fukuiraptor* (triangles), carcharodontosaurids (squares) and tyrannosaurids (diamonds).

rior serration is subequal to an equivalent posterior denticle, the anterior denticles are much shorter than the posterior ones. In this tooth, the maximum basal diameter of a serration (as seen in lingual aspect) is 0.31 mm, which works out to be about 16 denticles per 5 mm (=5 mm/0.31; a standard metric for theropod tooth comparison). There are problems with this measurement, however, because the carina in smaller theropods may be less than 5 mm long, and because denticle sizes are smaller at the proximal and distal ends of a carina. The minimum number of denticles per millimeter would be a better standard for comparison between theropods, although we recommend that the most useful measurement is probably the average basal diameter of the largest denticles.

In the referred maxilla (FPDM-V9712229), there is a fragment of a germ tooth in the third last alveolus, and it preserves a 13 millimeter section of the posterior carina. The maximum basal diameter for a posterior denticle as seen in lingual view is 0.30. The third last alveolus is incomplete, but the second last one is 15 x 7 mm, confirming that the basal cross-section of a posterior maxillary tooth of *Fukuiraptor* was longer than wide. The last alveolus is smaller but has similar proportions (11.8 x 5.9).

Using the characteristics found in maxillary teeth of the holotype of *Fukuiraptor kitadaniensis*, isolated maxillary teeth (Fig. 4) of other individuals can be identified. These characteristics include relatively narrow, blade-like crowns in which the Fore-Aft Basal Length (FABL) is double the measurement of the basal width perpendicular to the level where FABL is measured. The carinae are positioned along the anterior and posterior vertical margins of the teeth, and the anterior carina is not significantly offset lingually. Unlike coelurosaur teeth, the longitudinal axis of the tooth is sinuous when viewed anteriorly (Fig. 4A) or posteriorly (Fig. 4D). The denticles are relatively small (Table 1, more than 12.5 denticles per 5 mm), but like most coelurosaurian teeth, the posterior denticles are distally hooked. Although not present on all teeth, blood grooves are another way to separate *Fukuiraptor* teeth from those of other theropods in the Kitadani quarry.

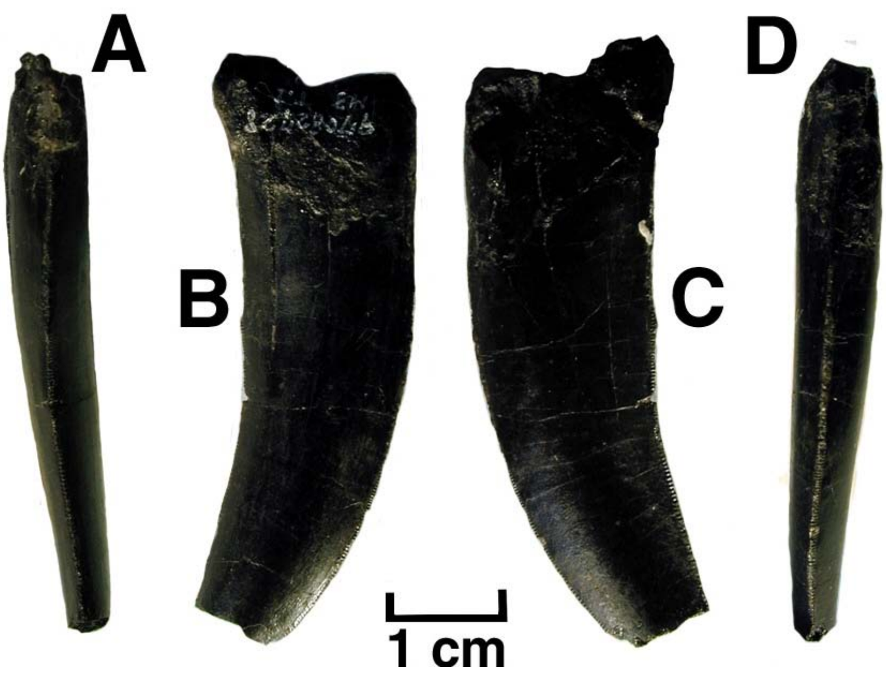


Fig. 4. Anterior maxillary tooth (FPDM-V97082728) of *Fukuiraptor*in anterior (A), lingual (B), labial (C) and posterior views.

The crown of one dentary tooth was recovered with the holotype, and it appears to be the third tooth from the right side (Fig. 2D). The crown is 34 mm high, and like anterior dentary teeth in most theropods, the base of the crown is relatively short (Table 1) anteroposteriorly compared to the basal width (BW/FABL ratio is 0.62). The proximodistal basal widths of anterior denticles are the same as those of equivalent posterior denticles. Although all of the anterior denticles are heavily worn, they were labiolingually narrower and appear to have been much shorter than the posterior denticles. The serrations of the dentary tooth are the same size as the anterior premaxillary denticles of the holotype, larger than the posterior premaxillary ones, similar to most of the maxillary ones, but larger than those from teeth of the posterior part of the maxilla (Table 1). The denticulate anterior carina only extends along the distal half of the anterior surface of the tooth, whereas the denticulate posterior carina forms the entire posterior margin of the tooth. Another tooth in the alveolus of a dentary fragment from the holotype was described briefly by Azuma and Currie (2000).

Teeth of *Fukuiraptor* are similar to those of many other carnosaurs. The cheek teeth are compressed labial-lingually, even more than the blade-like teeth of carcharodontosaurids (Fig. 3A, chart showing FABL vs BW). Serrations are smaller in comparison with FABL (Fig. 3B, chart showing FABLvs basal length of posterior denticle on a logarithmic scale) than in carcharodontosaurids and tyrannosaurids. Posterior denticles are relatively elongate with distally hooked tips. An anterior denticle has a comparable basal width, but is less than half the length of a posterior serration on the same tooth. Similar to tyrannosaurids, many *Fukuiraptor* cheek teeth have oblique blood grooves associated with the bases of the serrations (Azuma and Currie, 2000). The grooves tend to be found on both labial and lingual surfaces of the tooth, and are best-developed in association with the anterior denticles at the point of strongest curvature of the anterior edge of the tooth, and with the posterior denticles. Like carcharodontosaurid teeth (Sereno *et al*., 1996, Chure *et al*., 1999, Novas *et al*., 1999), the enamel on the labial and lingual surfaces of the teeth can have broad arcuate wrinkles that sweep down towards the root and away from the denticles. In some teeth, the anterior and posterior wrinkles extend right across the labial and/or lingual surfaces of the tooth to connect with each other (as in *Carcharodontosaurus* and *Giganotosaurus*). In anterior or posterior view, each cheek tooth has a flattened S-shaped curvature such as is also seen in carcharodontosaurids like *Giganotosaurus*. At the base of the crown, the tooth initially curves labially towards the outside of the jaw. This curve flattens, changes direction, and towards the tip of the tooth turns lingually. The anterior and posterior carinae of a cheek tooth are positioned on the midline, and follow the curvature of the tooth.

With the exception of five teeth (FPDM-V9812638, 96072901, 97082906, 980815181, 98092604) all of the teeth from the Kitadani Formation can be referred to *Fukuiraptor* (Table 1). There are 42 *Fukuiraptor* teeth, two of which are premaxillary, 19 are maxillary, 11 are dentary, and ten are too incomplete to determine. The ratio of labial-lingual basal width to FABL is 0.71 for the premaxillary teeth, 0.43 for the maxillary teeth, 0.64 for anterior dentary, and 0.46 for middle and posterior dentary teeth. This compares well with alveolar dimensions in preserved fragments of the maxilla (0.48) and dentary (0.69 for the anterior fragment, 0.43 for the posterior) in the holotype of *Fukuiraptor kitadaniensis*.

Many of the teeth are maxillary, and show the same characteristics as the maxillary teeth of the holotype. FPDM-V98081514 (Fig. 2B) is a large tooth that presumably occupied one of the third to fifth maxillary tooth positions. Like other maxillary teeth of *Fukuiraptor*, the denticulate anterior and posterior carinae extend from the gum-line to meet at the tip of the tooth. In addition to the presence of oblique blood-grooves, there are shallow arcuate wrinkles that span the labial and lingual surfacesof the tooth as in the holotype tooth FPDM-V9712206 (fig. 4 in Azuma and Currie, 2000), and in carcharodontosaurids and some tyrannosauroids. These wrinkles are deeper and better defined close to the oblique blood grooves that emerge from between the bases of adjacent denticles (both anterior and posterior). The wrinkles are much broader and less numerous than the blood grooves, but may have a served similar purpose in minimizing suction when the tooth was pulled out of flesh.

FPDM-V9712239 is a relatively small left, anterior dentary tooth with a BW/FABL ratio of 0.66. This is the same ratio as the width versus anteroposterior length of the first alveolus of the anterior dentary fragment (FPDM-V9712202) of the holotype. The anterior carina is lingual to the anterior longitudinal midline of the tooth. These two facts suggest the tooth may represent the first tooth of a left dentary.

A left dentary tooth FPDM-V9812001 (Fig. 2C) is similar to the anterior dentary tooth of the holotype (Fig. 2D) in most respects and can be assigned to *Fukuiraptor*. It is at least 15% larger than the holotype tooth, and supports the idea that the described skeleton (Azuma and Currie, 2000) was not full grown when it died. The posterior carina extends from the base of the crown to the tip, but the anterior carina is restricted to the distal third of the front surface of the tooth. It is not clear whether this represents individual variation, variation between dentary teeth in different positions along the tooth row, or ontogenetic variation. Looking at what happens in other taxa suggests that the latter may be the correct interpretation. As the teeth became larger in growing animals, the point of strongest anterior curvature (as seen in lingual or lateral views) seems to migrate more distally in theropods. In most cases, the denticulate anterior carina seems to extend from this inflection to the tip of the tooth, so it makes sense that as the strongly curved portion of the tooth gets pushed relatively farther from the base, the relative length of the denticulate anterior carina will also decrease.

A small (6 mm) tooth crown recovered from the Kitadani Quarry (Fig. 5) seems to be a posterior cheek tooth of *Fukuiraptor*. The proportions are similar to juvenile tyrannosaurid teeth from North America (Currie *et al.*, 1990) and the broad, "plump" appearance would not be expected in the cheek tooth of a small theropod species. Denticulation and faint crenulate wrinkles in the enamel are also consistent with this identification. Because the anterior carina is limited to the distal half of the tooth, it is probably from the dentary.

HUMERI

The holotype of *Fukuiraptor* included both humeri (Azuma and Currie, 2000). Four additional theropod humeri have been recovered from the Kitadani Quarry, all of which are smaller than the holotype humeri (Table 2, Fig. 6). Three are from the right side of the body, and one from the left. The deltopectoral crest of FPDM-V97082553 is less prominent than that of the holotype (Fig. 7), but is morphologically similar enough to tentatively identify this specimen as *Fukuiraptor*. The distal end of the crest is squared off in lateral aspect, and is oriented anteroventrally. In lateral aspect, the distal margin of the deltopectoral crest is thickened where it borders a shallow proximal depression on the lateral surface.

FPDM-V9808115 (Fig. 8) is the largest, most complete humerus other than the holotype. It is an elongate bone with a low deltopectoral crest that is intermediate in relative size between those of the holotype and FPDM-V97082553. It is evident from growth series of other theropods (Raath 1990) that crest height increases with positive allometry, so can only be used with caution for comparing humeri from individuals of different sizes. More significantly, FPDM-V98081115 has a more triangular deltopectoral crest than either the holotype or FPDM-V97082553, and in lateral view the ridge between the head of the humerus and the peak of the deltopectoral crest is straight rather than indented. The peak of the deltopectoral crest is 40% of the distance from the proximal to the distal end in the holotype of *Fukuiraptor*, whereas it is only 25% of the distance in FPDM-V9808115. These differences strongly suggest that FPDM-V98081115 represents a different taxon than *Fukuiraptor kitadaniensis*.

The remaining humeri (FPDM-V97082120, 980723005) are from small individuals (approximately 1.6 m long). The distal ends are similar to the holotype, to FPDM-V98081115, and to many other theropods. At this time they cannot be assigned with confidence to any theropod taxon.

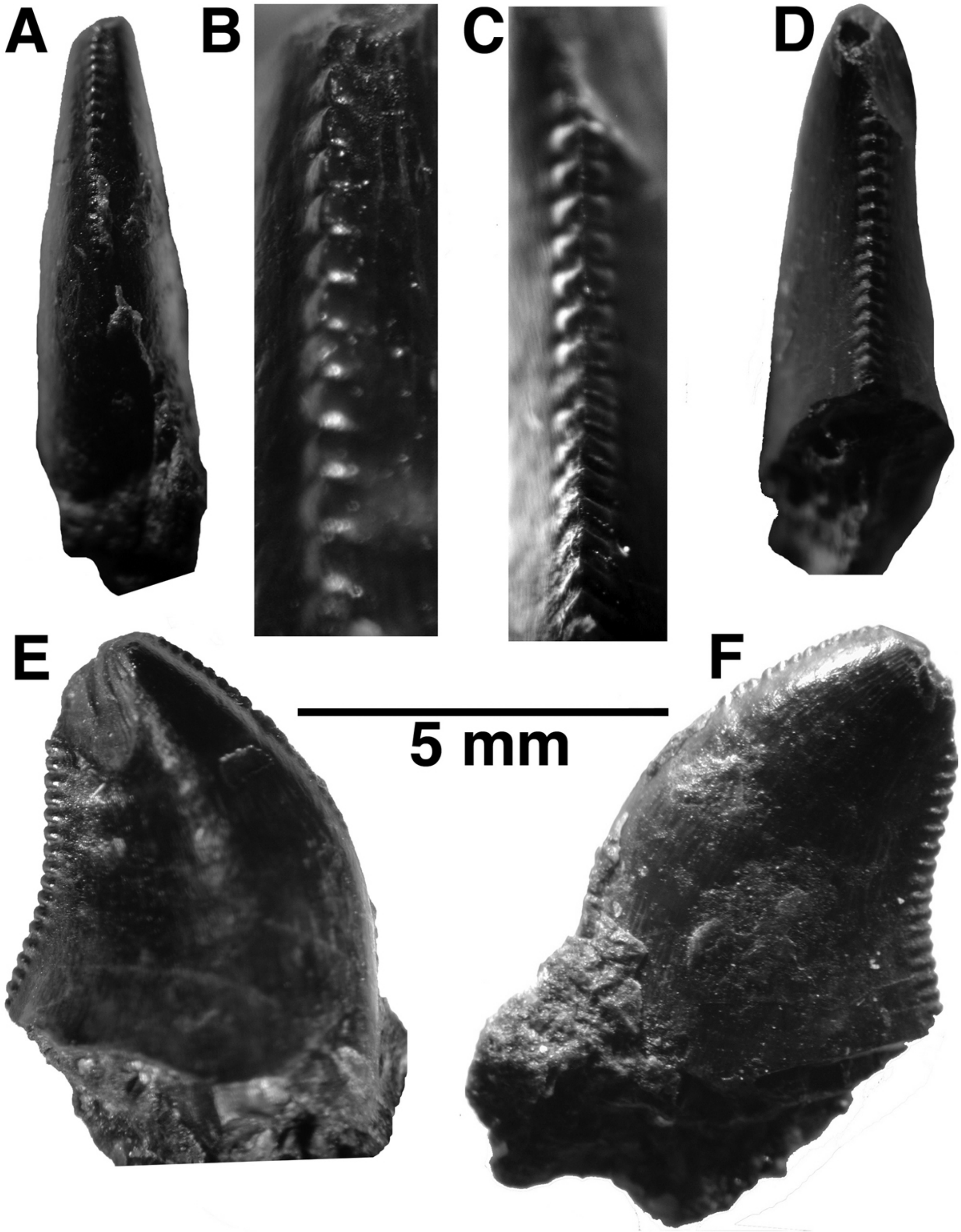


Fig. 5. Posterior dentary tooth (FPDM-V98120002) of a juvenile *Fukuiraptor* in anterior (A), posterior (D) and side (E, F) views. B and C are enlargements of the anterior and posterior denticles.

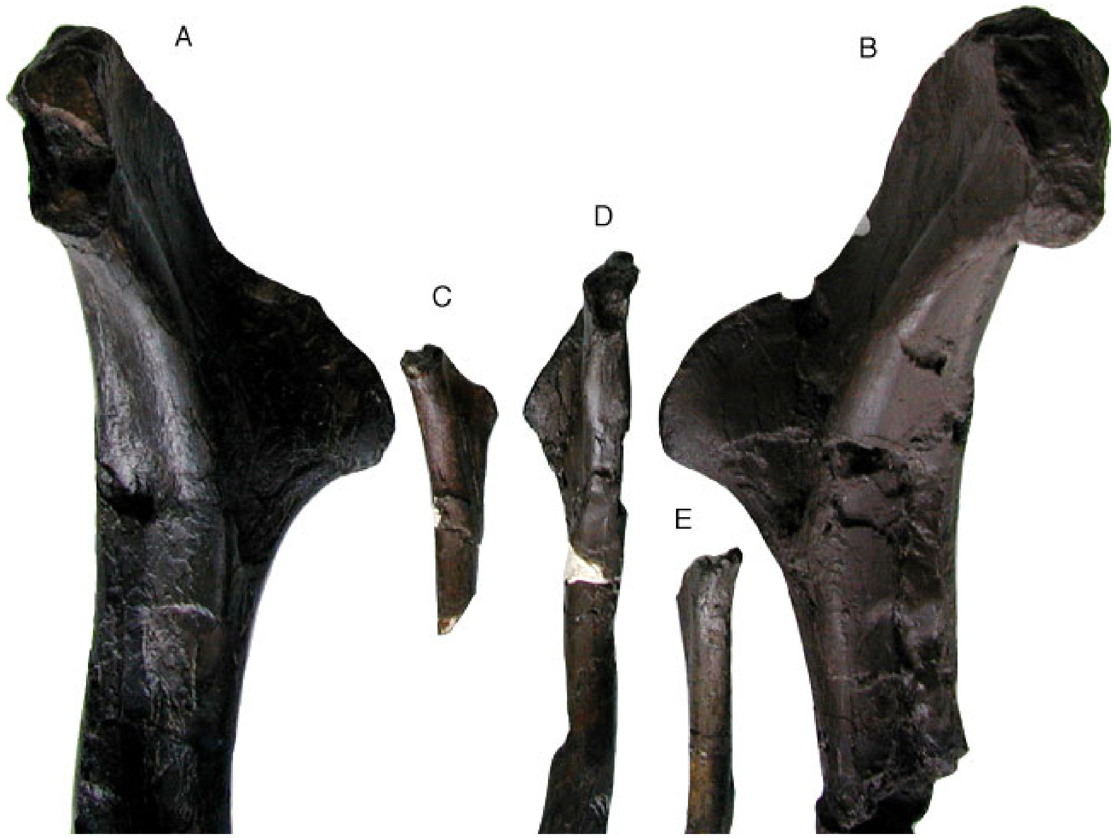


Fig. 6. Theropod humeri (medial views) from the Kitadani Quarry. A, B, holotype of *Fukuiraptor kitadaniensis*. C, FPDM-V97082553 (cf. *Fukuiraptor*). D, FPDM-V98081115, Dromaeosauridae incertae sedis. E, FPDM-V97082120.

Table 2. Measurements of theropod humeri from the Kitadani Quarry. Abbreviations: BL, estimated body length by comparison with the femora of other theropod taxa; DW, distal width; e, estimated; eL, estimated length of humerus; Femur, length of femur estimated from humerus length; PW, width of proximal end; SW AP, anteroposterior shaft width; SW C, minimum shaft circumference; SW T, transverse shaft width.

#	Type	97081115	97082120	97082553	980723005
L	242	144	Xx	Xx	Xx
PW	79.8	31.1	Xx	16+	Xx
SW T	27	12.5	9.9	8.5	11.2
SW AP	31.4	11.1	9.7	8.2	9.7
SW C	89	42	32	31	39
DW	64	29	20	xx	24.1
eL	245	145	105	83	115
Femur	507	284e	197e	151e	218e
BL	4.2e	2.3e	1.6e	1.2e	1.8e

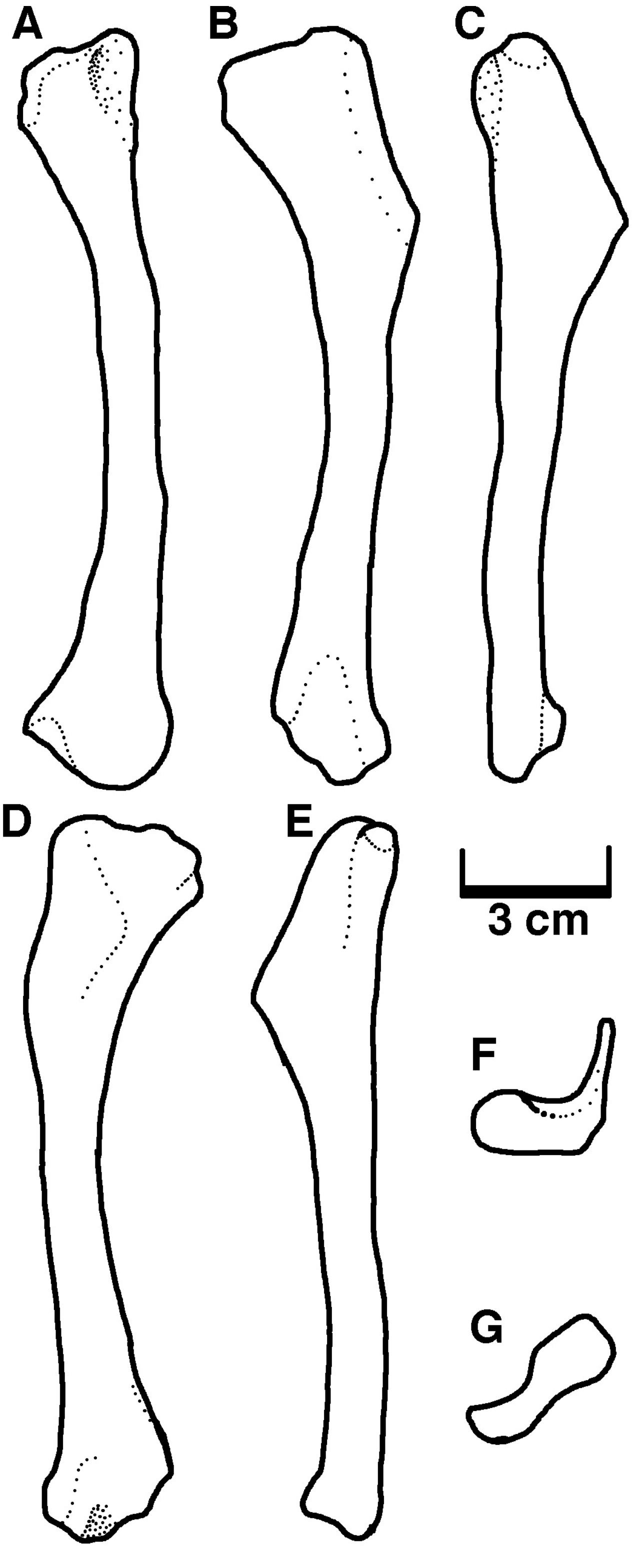


Fig. 7. Isolated right theropod humerus (FPDM-V9808115) in dorsal (A), dorsolateral (B), lateral (C), ventral (D), medioventral (E), proximal (F) and distal (G) views.

Fig. 8. Deltopectoral crests of right humerus (FPDM-V9808115) of unknown small theropod (A), and left humeri of *Fukuiraptor kitadaniensis* (B, FPDM-V97082553; C, holotype).

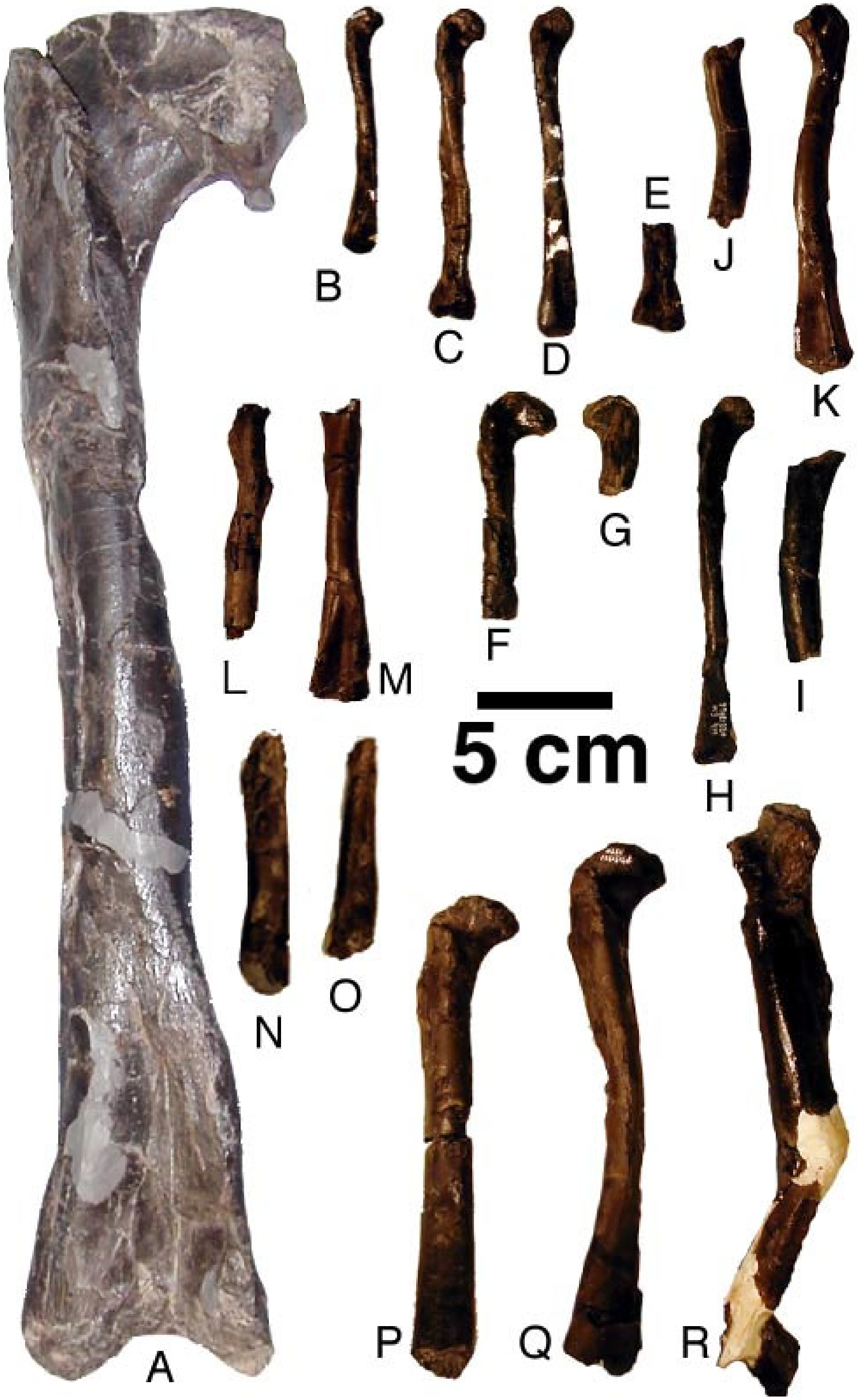
FEMORA

Eighteen partial and complete theropod femora have been collected from the Kitadani Quarry (Figs. 9, 10, Table 3). Thirteen of these are from the right side of the body, and the other five are from the left. Two of the incomplete left specimens (FPDM-97120001, 98120001) may be the same bone that became separated during collection. Although they are in the same size range (from an animal just over a meter in length), there is no good contact between the two pieces. No other possible connections exist between other incomplete femora. The fact that there are thirteen right femora, ten of which are complete or almost complete, indicates that a minimum number of thirteen individual theropods are represented in the collection. However, one left femur (FDM-V98072302) does not match the size of any right femur, so the minimum number of individuals represented by femora is fourteen.

Theropod femora are rich in features and are therefore diagnostic at the family level. Many of the Kitadani femora are incomplete, and show too few features to be identified more specifically than Theropoda. The smallest femur (FPDM-V980805018) is 18% the length of the holotype of *Fukuiraptor kitadaniensis*. However, like the femur of the holotype, it has a lateromedially elongate head (Fig. 10), an alariform lesser trochanter separated from the shaft by a deep slot, a low moundlike process on the lateral surface level with the base of the lesser trochanter, a distinct ridgelike fourth trochanter bounded anteromedially by a distinct oval muscle scar and posteriorly by a shallow depression, a gently curving shaft, and a sharp mediodistal crest. This suite of features is characteristic of carnosaurs, and suggests that the

Table 3. Minimum number of individuals of *Fukuiraptor* based on the femora from the Kitadani Quarry. Abbreviations: Body, estimated snout to tip of tail length of body; Class, size class; Ind. #, individual number; L, length; DW, distal width; eL, estimated length of femur; PW, proximal width; SW A-P, anteroposterior shaft width; SW Cir, circumference of shaft; SW T, transverse shaft width. Note that the size class is an arbitrary designation.

#	right or left	L	PW	SW A-P	SW T	SW Cir	DW	Class	Ind. #	eL	Body
980805018	right	92.2	15.1	9.2	7.4	32	13.2	1	1	93	735
970813046	right	116.3	17.4	11.7	6.6	35	17.5	2	2	116	925
970821039	right	122.7	18	11.4	9.6	36	17	2	3	123	978
99090901	left	xx	xx	xx	13.1	39	20.2	3	4	128	1021
980813017	right	xx	xx	10	12.3	40	xx	3	4	131	1046
98072302	left	134.2	21	10	13.7	40	20.5	3	5	134	1072
9812638	right	xx	xx	13.8	11.3	41	xx	4	6	134	1070
97080937	left	xx	xx	13.4	11.4	42	21.4	4	6	137	1095
970730003	right	xx	27.3	11.6	10.7	42	xx	4	7	137	1095
97120001	left	xx	21.1	13.7	12.6	42	xx	4	7	137	1095
97081330	right	134.9	20	xx	xx	43	xx	4	8	135	1078
98081028	right	xx	xx	14.2	12.3	46	xx	5	9	149	1194
98120001	left	xx	xx	16.4	11.5	46	xx	5	9	149	1194
98120002	right	xx	xx	17.2	15.5	55	xx	6	10	176	1416
97122BNA3	right	200	35	21.5	16.3	65	xx	7	12	204	1648
97081201	right	196	35	xx	xx	67	37.7	7	11	211	1707
97122BNA12	right	244	xx	26.4	21.4	80	xx	8	13	248	2015
97122	right	507	108.5	53	43	164	96.3	9	14	507	4200


A
B
C
D
E
J
K
L
M
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5 cm
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Fig. 9. Femora of *Fukuiraptor* showing range in size.
A, FPDM-V97122
B, FPDM-V980805018
C, FPDM-V970813046
D, FPDM-V970821039
E, FPDM-V99090901
J, FPDM-V980813017
K, FPDM-V980723002
L, FPDM-V9812638
M, FPDM-V97080937
F, FPDM-V970730003
G, FPDM-V9712001
H, FPDM-V97081330
I, FPDM-V98081028
N, FPDM-V98120001
O, FPDM-V98120002
P, FPDM-V97122BNA3
Q, FPDM-V97081201
R, FPDM-V97122BNA12

small femur is probably a juvenile *Fukuiraptor*. Five larger specimens (FPDM-V970813046, 970820039, 980723002, 97122BNA12, 97081201) show most of these characters, plus the presence of an accessory wing on the lesser trochanter, a deep anterodorsal extensor groove andan adductor fossa on the distomedial surface of the femoral shaft. Together with the smallest specimen and the holotype, they represent a growth series of *Fukuiraptor* femora. The remaining femoral specimens are not complete enough to be certain of their affinities, although none show characters diagnostic of Dromaeosauridae or any other coelurosaurian group.

DISCUSSSION

The theropod bones from the Kitadani Quarry can be assigned with confidence to two distinct taxa. Most of the teeth and bones can conservatively be attributed to juvenile *Fukuiraptor kitadaniensis*. Although this carnosaur has been the only theropod described so far from the Kitadani Quarry, there is at least one undescribed small theropod, possibly a dromaeosaurid from the site (Azuma and Currie, 2000). Manual unguals collected from the same quarry suggest that there may have been as many as three different types of small theropods in the fauna. Nevertheless, none of the preserved femora have any of the characteristic features of coelurosaurians. It can therefore be assumed that all of the better preserved femora in this collection are from *Fukuiraptor*.

Teeth that can be assigned to *Fukuiraptor* (based on tooth and denticle morphology, and positions of carinae) from the Kitadani Quarry show considerable variation in size. Variation in tooth size is high within most theropod individuals. However, identification of what jaw regions each of the teeth belong to demonstrates that the *Fukuiraptor* teeth came from individuals of different sizes. Some of those individuals were much smaller than the holotype specimen (Azuma and Currie 2000), and one was clearly larger.

Fukuiraptor teeth are distinctive amongst the teeth from the Kitadani Quarry. However, they are sim-

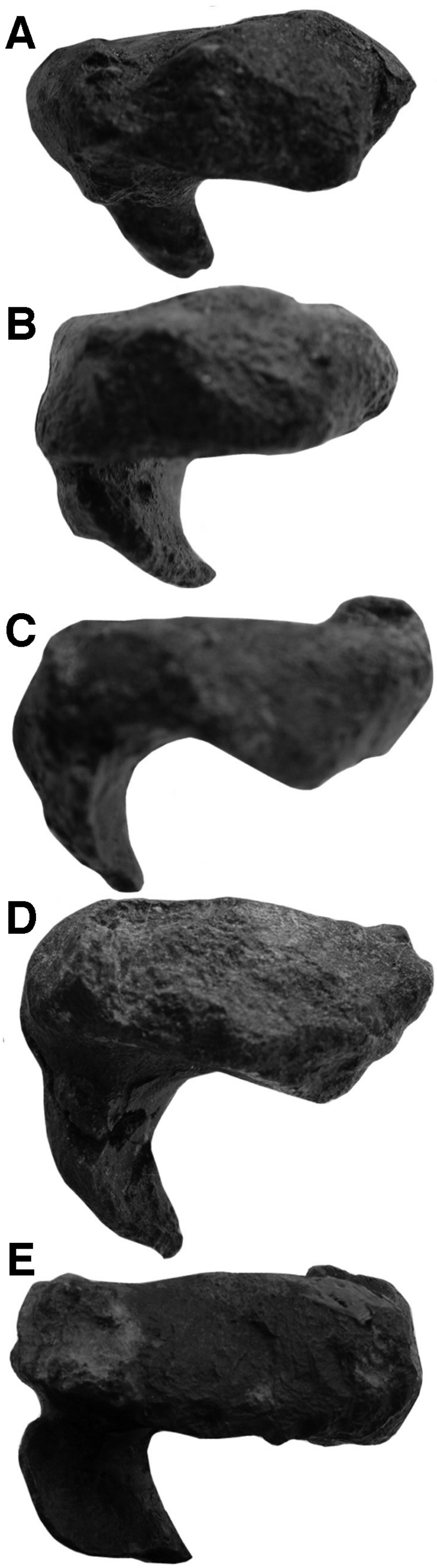

Fig. 10. Right femora of *Fukuiraptor kitadaniensis* in proximal view. A) FPDM-V980805018. B) FPDM-V970813046. C) FPDM-V970730003. D) FPDM-V97081201. E) Holotype (FPDM-V97122).

ilar to theropod teeth found in many localities in Japan and around the world. Like carcharodontosaurids from Africa and South America, they are narrow and blade-like, have relatively small serrations, and have arcuate wrinkles in the enamel on labial and lingual surfaces. Like carcharodontids as well, the interdental plates are fused to each other and to the margins of the jaws.

Chure *et al*. (1999) described a tooth from the late Cretaceous Mifune Group of Japan that is very similar in most respects (tooth size and shape, serration size, curved enamel wrinkles) to an anterior maxillary tooth of *Fukuiraptor*. They concluded that the Mifune tooth compares more closely with carcharodontosaurid teeth than with any other type of theropod tooth described. However, when the ratio of FABL is compared with BW (Fig. 3A) and posterior denticle size is compared with FABL (Fig. 3B), the Mifune tooth falls on the regressions for *Fukuiraptor* rather than Carcharodontosauridae.

Although *Fukuiraptor* teeth have oblique blood grooves similar to those of tyrannosaur teeth, neither they nor any of the other theropod teeth recovered from the Kitadani Quarry can be identified as tyrannosaurid. The only premaxillary teeth recovered so far have J-shaped cross-sections, like the premaxillary teeth of most theropod families (Currie *et al*., 1990). Manabe (1999) reported the discovery of an isolated tyrannosauroid premaxillary tooth from a nearby area in Fukui Prefecture, but from the underlying Jobu Formation (Itoshiro Subgroup, Tetori Group, Lower Cretaceous). The specimen was therefore recovered from an older formation, and represents a more ancient animal than *Fukuiraptor*. Premaxillary teeth of tyrannosauroids have also been reported from the younger Mifune Group of Japan (Anonymous, 1998), along with the carcharodontosaurid-like cheek teeth. Recent descriptions of tyrannosauroids from the Late Jurassic and Early Cretaceous of Europe and Asia (Hutt *et al*., 2001; Xu *et al*., 2004; Xu *et al*., 2006) confirm the likelihood of the Japanese tyrannosauroid records.

The smallest individual of *Fukuiraptor*in the Kitadani Quarry is less than a quarter the size of the holotype. A fourfold increase in size is reasonable for a growth series of an animal of this size, and probably does not represent a complete growth series. For example, Nile crocodiles grow to about the same length as *Fukuiraptor*, but are only 0.25 m long at birth (Cott, 1961).

It is difficult to study ontogenetic changes in limb proportions when dealing with unassociated specimens from bonebeds. However, using allometric equations developed for other theropods, such as tyrannosaurids (Currie, 2003), the approximate body lengths of each individual can be calculated (Table 3). These were arranged into arbitrary size classes, with the smallest individual being assigned to Class 1, and the largest to Class 9. *Fukuiraptor* size classes in the bonebed are nearly evenly distributed, with peaks of four individuals each for size classes 4 and 7. There are not enough specimens for this bimodal distribution curve to be statistically significant, but it provides weak evidence in support of this being an attritional death assemblage (Voorhies, 1969).

Fukuiraptor remains in the Kitadani Quarry are common in comparison with the fossils of herbivorous dinosaurs. Bonebeds dominated by theropods are very rare anywhere in the world, and the high number of carnivores in the Kitadani Quarry suggests that there were some unusual circumstances involved in the genesis of the site. Perhaps it was taphonomic, or perhaps it was more directly involved with the behaviour of *Fukuiraptor* itself. The concentration of juvenile *Fukuiraptor* teeth and bones may indicate that this was close to where the theropods were nesting, perhaps similar to the scenario described by Bakker and Bir (2004). There is a mixed faunal bonebed in Utah (USA) with a similar concentration of theropods. The Upper Jurassic Cleveland-Lloyd quarry is dominated by more than seventy individuals of *Allosaurus fragilis*, and has been interpreted as a predator trap (Madsen, 1976; Miller *et al*., 1996; Richmond and Morris, 1996), or as a drought-induced mass death assemblage (Gates 2005). *Coelophysis* (Colbert, 1989) and *Syntarsus* (Raath, 1990) are two examples of theropods that died en masse in Late Triassic to Early Jurassic times, whereas trackway sites (Ostrom, 1972) suggest that coelophysoids may have travelled in packs. The *Coelophysis* bonebed has also been interpreted as species-selectivity in drought conditions (Schwartz and Gillette, 1994). In Late Cretaceous times, bonebeds dominated by tyrannosaurids (Larson, 1997; Currie, 2000; Currie *et al*., 2004), carcharodontosaurids (Coria and Currie, 1997, 2006), dromaeosaurids (Ostrom, 1969; Maxwell and Ostrom, 1995) and troodontids (Varricchio and Currie, 1991) have been used to suggest that these animals hunted in packs. Unfortunately, there are no strong taphonomic signals in the Kitadani Quarry to eliminate any of these scenarios as possible explanations for the high concentration of *Fukuiraptor* specimens.

CONCLUSIONS

Most of the isolated theropod teeth and bones recovered from the Kitadani Quarry are from carnosaurs, although some of the teeth, a humerus and several unguals seem to be dromaeosaurid. One medium-sized carnosaur, *Fukuiraptor kitadaniensis*, has been described (Azuma and Currie, 2000) from the quarry. The type specimen had an estimated length of 4.2 m when it was alive. Azuma and Currie (2000) suggested that it was close to adult size when it died, and that the species never became as large as the majority of known carnosaurs. Amongst the isolated teeth and bones from the Kitadani Quarry, only one tooth is suggestive of a slightly larger individual, and the rest of the fossils are from much smaller individuals. Because it is more parsimonious to assume that they represent only one species of carnosaur from the Kitadani fauna, it is likely that they represent a growth series of *Fukuiraptor*. At least two other theropod taxa can be recognized in the fauna from teeth and manual unguals, but in the Kitadani Quarry these coelurosaurs are rare animals.

The theropod teeth and bones from the Kitadani Quarry represent a minimum number of 14 individuals based on femoral counts alone. The high concentration of juvenile carnosaurs at this one site may represent a breeding or nesting area, a predator trap, or the catastrophic demise of a social group. Taphonomic analysis of the bones in the quarry cannot resolve which of these three options (if any of them) is correct.

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일본 전기 백악기 Kitadani 채석장에서 산출된 *Fukuiraptor* (공룡, 수각류)의 개체발생을 포함한 새로운 표본들

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요 약: 모식표본 *Fukuiraptor kitadaniensis* 와 같은 종에 속하는 뼈와 이빨들이 일본 후쿠이현 전기 백악기(Albian) 지층인 Kitadani 화석지에서 발굴되었다. 이들 화석들은 계통발생학적 위치를 결정하는데 도움이 되는 여러 정보를 가지고 있을 뿐 아니라 일련의 개체발생을 나타내고 있다. 모식표본은 미성숙 표본이며 전체 길이는 4.2 m 였다. 같은 화석지에서 산출된 다른 화석들은 이 보다 더 작은 개체의 것이다. 새끼뼈의 일부는 모식표본의 것에 1/3 보다 작다.

주요어: *Fukuiraptor*, 성장단계, Kitadani, 일본

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