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A NEW IGUANODONTIAN (DINOSAURIA: ORNITHOPODA) FROM THE LOWER CRETACEOUS KITADANI FORMATION OF FUKUI PREFECTURE, JAPAN

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ABSTRACT—The skull material of a new iguanodontian dinosaur, *Fukuisaurus tetoriensis* gen. et sp. nov., discovered from the fluvial deposits of the Lower Cretaceous Kitadani Formation, Tetori Group, Fukui Prefecture, Japan, is described here. Some features of *Fukuisaurus* show affinities with *Iguanodon*, *Ouranosaurus*, and *Altirhinus*, referred to as Iguanodontidae by some. A phylogenetic analysis using mainly cranial characters shows that *Fukuisaurus* is a definitive derived non-hadrosaurid iguanodontian and implies that *Fukuisaurus* is more derived than the clade of *Iguanodon* + *Ouranosaurus* and more basal to the clade of *Altirhinus*, *Probactrosaurus*, *Eolambia*, *Protohadros*, *Bactrosaurus*, *Telmatosaurus*, and hadrosaurids. It also supports that Iguanodontidae is paraphyletic by the exclusion of *Altirhinus* as suggested previously. The presence of *Fukuisaurus* indicates a wider geographical distribution of the group in eastern Asia. The occurrences of derived non-hadrosaurid iguanodontians from the Kitadani Formation and other formations in Japan support a dispersal of this group into eastern Asia by the Early Cretaceous and its temporal range extension in Japan. *Fukuisaurus* possesses a strong maxilla-vomer articulation, indicative of the independent acquisition of a non-pleurokinetic skull (not present in *Hypsilophodon*, *Iguanodon*, and hadrosaurids).

INTRODUCTION

The first iguanodontian tooth from the Kitadani Quarry, Fukui Prefecture, Japan, (Fig. 1) was discovered in 1989. Since the discovery, abundant iguanodontian remains, including material described here, have been recovered from a bone-rich horizon at the quarry. The quarry exposes the fluvial Kitadani Formation, part of the upper Akaiwa Subgroup of the Tetori Group. The iguanodontian-bearing horizon has also yielded a number of other remains belonging to *Fukuiraptor kitadaniensis* (Azuma and Currie, 2000), as well as fish scales, turtle remains (Adocidae, Nanhsiungchelyidae, and Sinemydidae?; Hirayama and Azuma, 1996), a goniopholidid crocodyliform skeleton (Kobayashi, 1998), and sauropod teeth (Azuma and Tomida, 1997). Most of the iguanodontian material is disarticulated and occurs over an area of 50 square meters.

The Tetori Group is subdivided into Kuzuryu, Itoshiro, and Akaiwa subgroups (Fig. 1). The Akaiwa and Itoshiro subgroups are mainly freshwater and brackish-water deposits, respectively (Maeda, 1961), and the ages of the formations, belonging to these subgroups, are not well resolved. Although the ages of the upper and lower boundaries of the Kitadani Formation are not defined clearly, the Kitadani Quarry, representing a portion of the Kitadani Formation, is suggested to range from the Late Hauterivian to Barremian based on a freshwater molluscan assemblage (Tashiro and Okuhira, 1993).

Altirhinus, *Iguanodon*, *Lurdusaurus*, and *Ouranosaurus* are considered to be members of the Iguanodontidae (Taquet, 1976; Norman and Weishampel, 1990; Taquet and Russell, 1999), whose monophyly (*Iguanodon*, *Ouranosaurus*, and *Altirhinus*) was proposed by Norman (1998). Iguanodontia of Norman (1998) differs from that of others (Forster, 1990; Sereno, 1999) in placing *Tenontosaurus* as a sister taxon of Hypsilophodontidae exclusive of *Dryosaurus* and *Camptosaurus*. The term, Iguanodontia, is used for a group that includes *Tenontosaurus*, *Dryosaurus*, *Camptosaurus*, *Iguanodon* and higher ornithopods (Forster, 1990; Winkler et al., 1997; Sereno, 1999) in this study.

Derived non-hadrosaurid iguanodontians from Asia include *Altirhinus* and *Iguanodon orientalis* from Mongolia (Rozhdestvensky, 1952; Norman, 1996, 1998), *Probactrosaurus* from China and Mongolia (Rozhdestvensky, 1967; Lü, 1997), *Nanyangosaurus*, *Jinzhousaurus*, *Bactrosaurus* from China (Gilmore, 1933; Godefroit et al., 1998; Xu et al., 2000; Wang and Xu, 2001) and some indeterminate material (identified as Iguanodontidae) from Thailand (Buffetaut and Suteethorn, 1998). Possible iguanodontid dinosaur teeth were reported from Japan (Hasegawa et al., 1995; Morozumi et al., 1995). However, the reliability of identification of an ''iguanodontid'' based on tooth morphology needs to be determined with additional material. The Fukui iguanodontian is significant because it preserves skull elements with teeth and provides more comparative information.

Institutional Abbreviations—**FPDM-V**, Fukui Prefectural Dinosaur Museum, Vertebrates, Japan; **SMU**, Southern Methodist University, Dallas.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
ORNITHISCHIA Seeley, 1888
ORNITHOPODA Marsh, 1871
IGUANODONTIA Dollo, 1888
Fukuisaurus, gen. nov.

Type and Only Known Species—*Fukuisaurus tetoriensis*, sp. nov.

Etymology—Referring to its occurrence in Fukui, and Greek *sauros*, lizard.

Diagnosis—Non-hadrosaurid iguanodontian differing in having the following combination of characters: narrow rostrum with posteriorly restricted primary palate, shallow maxilla with twenty alveoli, strong articular surface with the vomer associated with horizontal ridges and grooves in anterior fourth of the medial surface of the maxilla, a foramen on the lateral surface of the anterior process of the jugal, straight posterior border of the posterior process of the jugal with a squared posteroventral corner in lateral view, deep dentary with nineteen alveoli and a short coronoid process, anteroventrally projecting process extending from the anterior edge of the glenoid of the surangular, and straight lateral border of the sternal plate.

Fukuisaurus tetoriensis, sp. nov.
(Fig. 3)

Holotype—A right maxilla (FPDM-V-40-1) and a right jugal (FPDM-V-40-2).

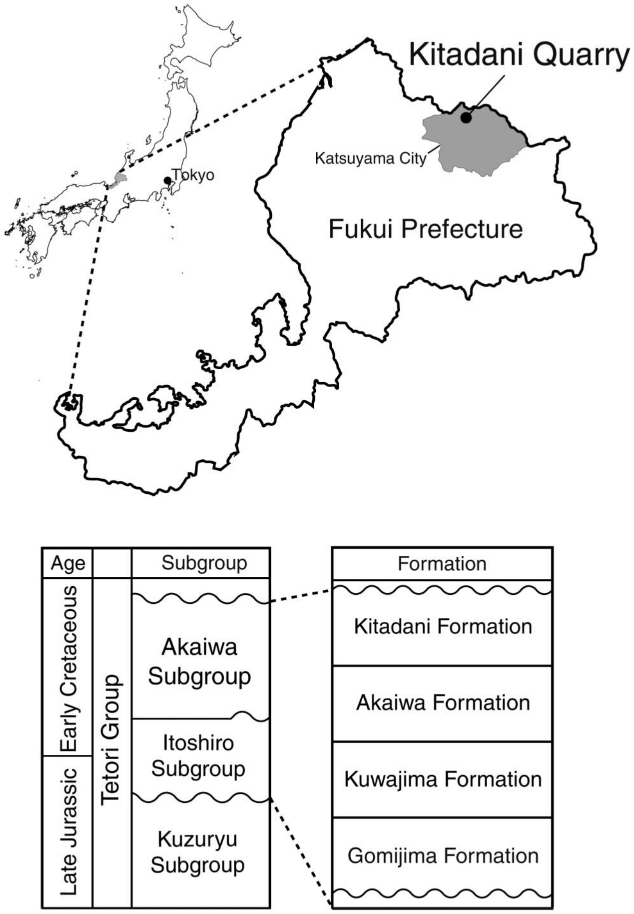

FIGURE 1. Locality map of the Kitadani Quarry in Katsuyama City, Fukui Prefecture, Japan, and the stratigraphic position of the Kitadani Formation in the Tetori Group along the Tetori River, following Maeda (1961). The ages of the Kitadani Formation and the Kitadani Quarry are discussed in text.

Paratypes—Disarticulated skull, mandible elements, and a sternal plate: premaxillae (left, FPDM-V-40-3; right, FPDM-V-40-4), a left maxilla (FPDM-V-40-5), quadrates (left, FPDM-V-40-6; right, FPDM-V-40-7), predentary (FPDM-V-40-8), dentaries (left, FPDM-V-40-9, right, FPDM-V-40-10), surangulars (left, FPDM-V-40-11; right, FPDM-V-40-12), an isolated left maxillary tooth (FPDM-V-40-13), two isolated left dentary teeth (FPDM-V-40-14, FPDM-V-40-15), and a right sternal plate (FPDM-V-40-16).

Etymology—Referring to its occurrence in the Tetori Group.

Diagnosis—As for the genus.

Locality—Kitadani Quarry (Late Hauterivian to Barremian), Katsuyama City, Fukui Prefecture, Japan (36° 7′ N, 136° 33′ E). Kitadani Formation (Early Cretaceous), the upper part of the Akaiwa Subgroup, the Tetori Group.

DESCRIPTION

Premaxilla

The premaxillae (Fig. 2A, B) are missing the posterodorsal and posteroventral processes, but the left premaxilla (FPDM-V-40-3) preserves a partial anterior border of the narial opening. The premaxillae are relatively unexpanded transversely at the oral margin. The primary palate is more posteriorly restricted than in *Iguanodon*. The periphery of the premaxillary beak is rugose with pits and grooves and lacks denticulation. A large, oval-shaped foramen (9.6 × 4.9 mm in FPDM-V-40-3) is present on the ventral surface midway between the anterior tip of this element and the primary palate. This foramen is connected to foramina at the anterodorsal surface and the anterior edge of the ventral surface of the premaxilla (Figs. 2A, 6). There is another small foramen positioned between the large foramen and the anterior border of the primary palate.

Maxilla

The maxillae (Figs. 2C–E, 3A) from both sides are preserved. The left maxilla (FPDM-V-40-5; Fig. 2C–E) is smaller than the one from right side (FPDM-V-40-1; Fig. 3A) (Table 1) but is more complete, missing the anterior tip. The left maxilla has twenty alveoli. It is triangular-shaped in lateral view and its dorsal apex (lacrimal process) is positioned roughly mid-length of the element. The dorsolateral surface of the anterior portion bears a groove for the premaxillary articular surface. Anteriorly, the groove faces laterally and widens (28.6 mm at maximum). It narrows posteriorly as in *Camptosaurus* and *Ouranosaurus* (Weishampel, 1984) and ends at the dorsal tip of the lacrimal process. The medial surface of the anterior portion (anterior to the sixth alveolus) has a rugose surface, which is at least 70 mm long, with horizontally running ridges and grooves for the maxilla-vomer articulation (Fig. 2D). In dorsal view, a medial border, posterior to the posterior end of the rugose surface, curves sharply medially (Fig. 2E). The lateral surface of the lacrimal process is vertical and there is no indication of the laterally exposed antorbital fenestra margin or fossa (Figs. 2C, 3A, 6), as seen in *Altirhinus* (Norman, 1998). The articular surface with the jugal extends to the apex of the lacrimal process, and a small rugose sutural surface with the lacrimal is present on the posterior side of the lacrimal process. The antorbital fenestra is medial to the jugal process as in *Protohadros* (Head, 1998) (Fig. 2E). The jugal process lacks a long posterolateral projection as occurs in *Iguanodon* (Norman, 1986), *Altirhinus* (Norman, 1998), and *Ouranosaurus* (Taquet, 1976). The articular surface for the ectopterygoid and palatine, medial to the jugal articular surface, is convex and rugose.

Jugal

The right jugal (FPDM-V-40-2; Fig. 3A, B) is nearly complete but missing the anterior tip of the anterior process, not preserving the articular facet with the lacrimal. The anterior process is dorsoventrally compressed, indicating there is no development of a jugal flange. There is a small foramen on its lateral surface below the ventral border of the orbit (Figs. 3A, 6). The medial surface of the process is concave and rugose, forming a sutural surface for the jugal process of the maxilla. The sutural surface for the ectopterygoid forms a pit on the anterior process and is separated from the maxillary articular surface by a ridge (Fig. 3B). The lateral surface of the postorbital process has a weakly ridged but planar articular facet (scarf joint) with the jugal process of the postorbital. The dorsal tip of the process is missing, but the facet is 18.1 mm wide and 19.9 mm long. The posterior process has a straight, vertical posterior border where it meets the quadratojugal and a convex ventral border, forming a squared corner at the posteroventral end. The medial surface of the posterior process is smooth, and the suture or facet for the anterior process of the quadratojugal is not clear.

Quadrate

Both quadrates (Fig. 3C–E) are preserved, and the right quadrate (FPDM-V-40-7) is more complete than the left (FPDM-V-40-6), but is missing most of the jugal wing. The left element is missing its dorsal and ventral ends but preserves the

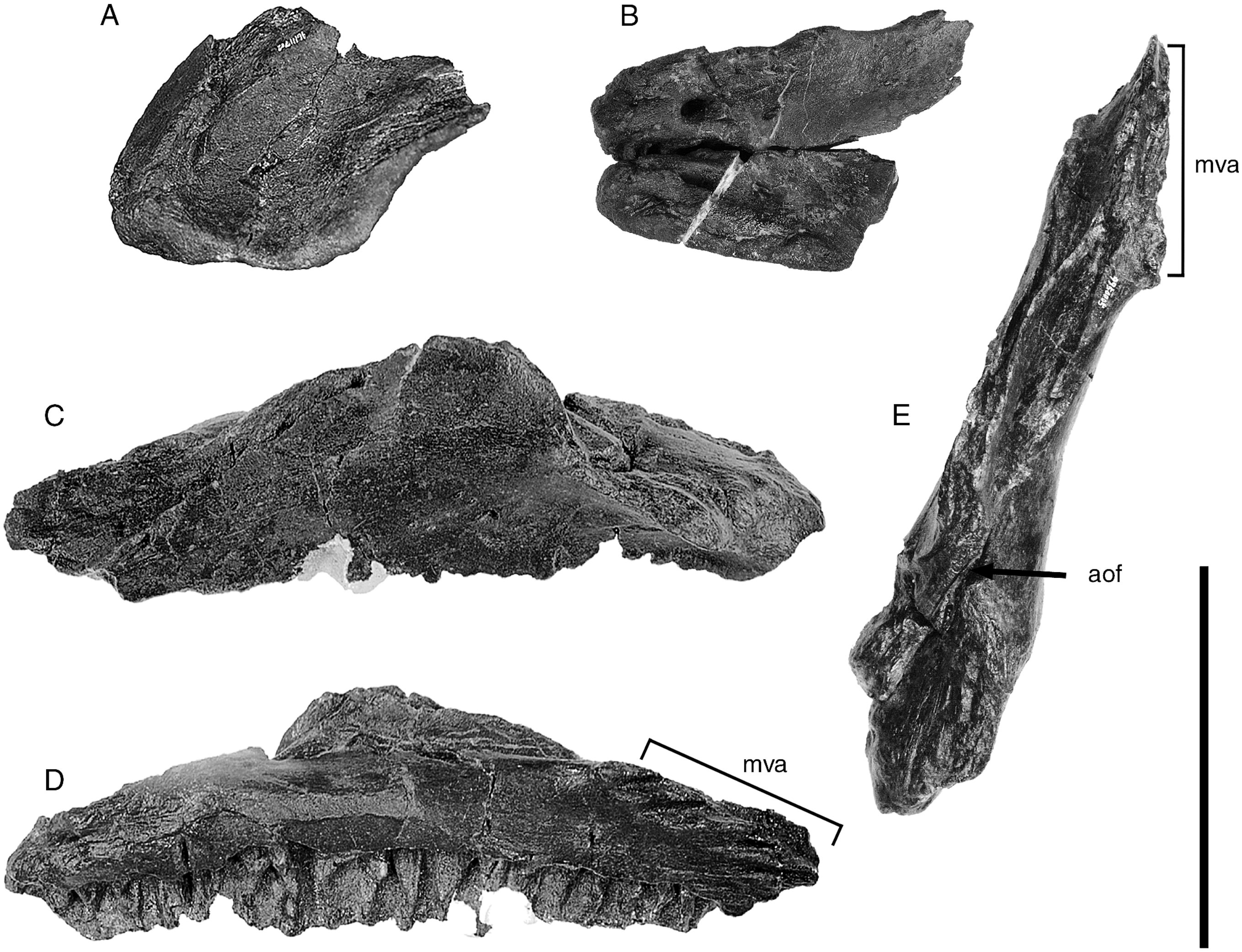

FIGURE 2. *Fukuisaurus tetoriensis* gen. et sp. nov. Premaxillae (left, FPDM-V-40-3; right, FPDM-V-40-4) in lateral (**A**) and ventral views (**B**). Left maxilla (FPDM-V-40-5) in lateral (**C**), medial (**D**), and dorsal (**E**) views. **Abbreviations: aof**, antorbital fenestra; **mva**, maxilla–vomer articulation. Scale bar equals 10 cm.

jugal wing. There is a notch at the middle of the jugal wing (Fig. 3E). The notch is circular in outline and is 29 mm in dorsoventral diameter. A dorsal quadratojugal facet is preserved in FPDM-V-40-6; it is vertical and straight, and the surface of the notch is smooth. Despite the lack of the quadratojugal, the element probably forms a straight posterior border, suggesting that the notch probably had a paraquadratic foramen (Fig. 6). The mandibular condyle is transversely expanded and divided into two condyles by a shallow sulcus (Fig. 3D). The lateral condyle is larger than the medial one (22.7 mm and 13.3 mm respectively in anteroposterior direction). The posterior edge of the main body is vertical relative to the dorsal head for one fourth of the total height. For the other three fourths of its length, the posterior edge is shifted anteriorly and is straight down to the mandibular condyle.

Predentary

The predentary (FPDM-V-40-8; Fig. 4A, B) is missing the anterior end and U-shaped in dorsal view and has three processes: a pair of lateral processes and one ventral process. The lateral processes have a denticulated ridge along the lateral margin. The ventral process is transversely flattened and is missing its ventral tip. The articular facet of the dentary with the ventral process (Fig. 4E) suggests that the distal end of the process is bifurcated and the total length of the process is estimated to be 37 mm. The lingual surface of the predentary body is smooth and lacks a median ridge. The articular surfaces for the dentaries are separated by a ridge on the lingual surface of the ventral process.

Dentary

The left dentary (FPDM-V-40-9, 78 mm in height at the deepest dentary body; for other measurements see Table 1) is complete and has nineteen alveoli (Fig. 4C–E). It is relatively deep and massive with a slightly concave ventral border. There is no diastema between the first dentary alveolus and the articular surface for the premaxilla. The posterior-most tooth extends just posterior to the midline of the coronoid process. The coronoid process is vertical relative to the anteroposterior axis of the dentary body, and its height above the tooth row is low. Dorsally, the coronoid process is slightly expanded and rather square-shaped. Anteriorly, the articular surface with the ventral process of the predentary is a shallow fossa on the ventral surface, as mentioned earlier (Fig. 4E). The straight posterior edge of the dentary indicates that the postdentary bones (especially

FIGURE 3. *Fukuisaurus tetoriensis* gen. et sp. nov. Right maxilla (FPDM-V-40-1) and jugal (FPDM-V-40-2) in articulation in lateral view (**A**) and the right jugal in medial view (**B**). Right quadrate (FPDM-V-40-7) in medial (**C**) and ventral (**D**, left is anterior side and bottom is lateral side) views and the left quadrate (FPDM-V-40-6) in lateral view (**E**). Scale bar equals 10 cm.

surangular and angular) were probably positioned posterior to the midline of the coronoid process in lateral view.

Surangular

The right surangular (FPDM-V-40-12; Fig. 4F, G) is nearly complete, but missing the retroarticular process. It is gracile and roughly triangular in lateral view with the apex of the element at its anterior border. An anteroventrally projecting tongue-like process (13 mm long and 12 mm wide) arises from the medial edge of the glenoid (Fig. 4G). Laterally, a small surangular foramen is present below the glenoid, and an accessory foramen (external mandibular foramen in Gilmore, 1909; second foramen in Norman, 1998) is close to the dentary-surangular suture (Fig. 4F). The ventral surface of the surangular, anterior to the level of the glenoid, has a shallow depression, divided into two sulci by an anterior-posterior running ridge, for the articular surface with the angular. The posterior third of the medial surface of the ventral portion is preserved and has a deep groove for the articular surface with the articular.

Maxillary Dentition

Articulated maxillary teeth in a right maxilla (FPDM-V-40-1) and an isolated tooth from the left side (FPDM-V-40-13; Fig. 5A, B) are preserved. They are narrower anteroposteriorly than dentary teeth. The labial surface of the tooth crown has a strong and mesially offset primary ridge. One subsidiary ridge is weakly developed in most of the preserved teeth (one tooth in

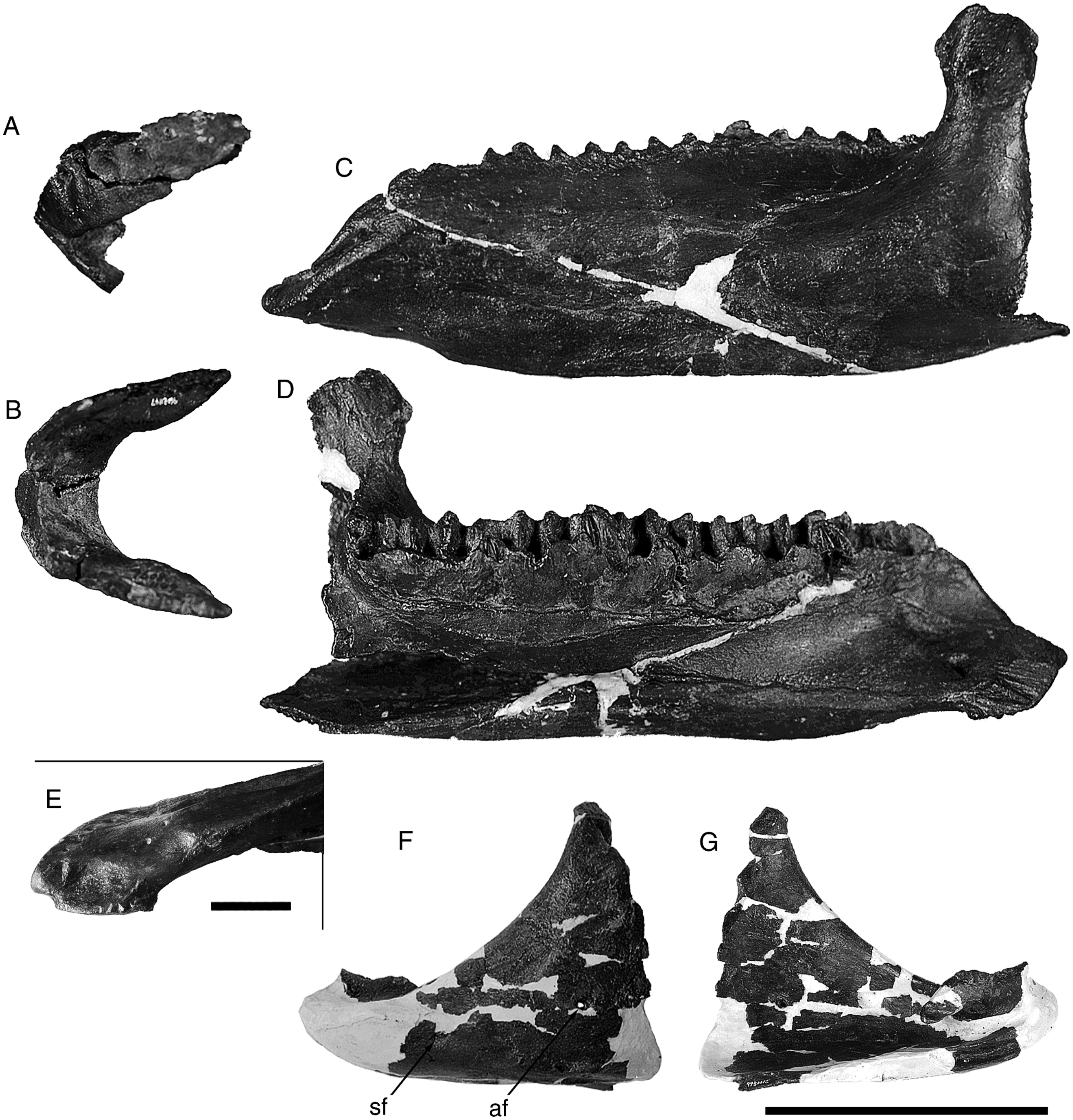

FIGURE 4. *Fukuisaurus tetoriensis* gen. et sp. nov. A predentary (FPDM-V-40-8) in lateral (**A**) and dorsal (**B**) views. Left dentary (FPDM-V-40-9) in lateral (**C**) and medial (**D**) views, and its anterior end in ventral view (**E**), showing an articular facet with the ventral process of the predentary. Right surangular (FPDM-V-40-12) in lateral (**F**) and medial (**G**) views. Scale bar below G is for all except for E and equals 10 cm, and one below E equals 3 cm. **Abbreviations: sf**, surangular foramen; **af**, accessory foramen.

FPDM-V-40-1 lacks the subsidiary ridge as in *Altirhinus*; Norman, 1998). Denticles are present on the tooth margin.

Dentary Dentition

Five teeth are present in the left dentary (FPDM-V-40-9), and two complete isolated left dentary teeth (FPDM-V-40-14, FPDM-V-40-15; Fig. 5C, D) are also known. Lingually the crown is diamond-shaped. The crown is higher than wide (width/height ratio is 0.50 and 0.63 in FPDM-V-40-14 and FPDM-V-40-15, respectively). Dentary teeth possess a mesially offset primary ridge, less prominent than that in maxillary teeth. A single secondary ridge (some teeth have two ridges) is distally positioned and nearly parallel to the primary ridge. Distal to the primary ridge, tertiary ridges arise from the base of the marginal denticles. The denticles on the distal margin are larger than the ones on the mesial margin

TABLE 1. Measurements of *Fukuisaurus* elements in millimeters: Length, maximum anterior-posterior length; Height, maximum dorsal-ventral length; and Width, maximum transverse thickness in all cranial elements except teeth. Asterisk represents the incompleteness of an element, but measurements of the preserved portion. Note: The widths of the maxillae are at the level of the posterior end of the jugal process. The height of the jugal is at the posterior border of its posterior process, and its width is anterior to the ectopterygoid articular surface. The length of the quadrate is that of the pterygoid wing, and its width is that of the mandibular condyle (not preserved in the right quadrate). The height and width of the dentary is measured at the level of the coronoid process. The height of the sternum is the maximum thickness at the distal end, and the width is at the posterior end of the expanded anterior portion (minimum width of the shaft of the posterior process is in parentheses). The tips of all preserved teeth are missing or worn out indicated by asterisk. The height of tooth is its enamel height, and one in parentheses is with its root.

Element	Specimen number	Length	Height	Width
Left premaxilla	FPDM-V-40-3	97.5*	71.8*	28.0
Right premaxilla	FPDM-V-40-4	87.8*	84.3*	31.2
Left maxilla	FPDM-V-40-5	205.2*	61.7	41.3
Right maxilla	FPDM-V-40-1	160.9*	68.0	44.0
Right jugal	FPDM-V-40-2	145.4*	91.1	26.0
Left quadrate	FPDM-V-40-6	57.4*	188.5	48.1
Right quadrate	FPDM-V-40-7	52.2*	143.4*	—
Predentary	FPDM-V-40-8	75.2*	48.1*	76.8
Left dentary	FPDM-V-40-9	259.4	115.8	46.7
Right surangular	FPDM-V-40-12	99.5*	89.1	31.4
Right sternum	FPDM-V-40-16	198.1	20.7	61.2(27.2)
		Height	Width	Thickness
Maxillary tooth	FPDM-V-40-13	15.5*(29.7*)	11.1	11.1
Dentary tooth	FPDM-V-40-14	31.2*(42.5*)	15.7	10.1
Dentary tooth	FPDM-V-40-15	23.4*	14.7*	8.5

(4.5 mm and 3.2 mm per four denticles, respectively, close to the mid-length of serrated margins in FPDM-V-40-15) although the size of denticles is larger towards the tip of the crown. The root has shallow vertical grooves distally and mesially for adjacent teeth. The angle between the crown surface and the root axis is approximately 120°.

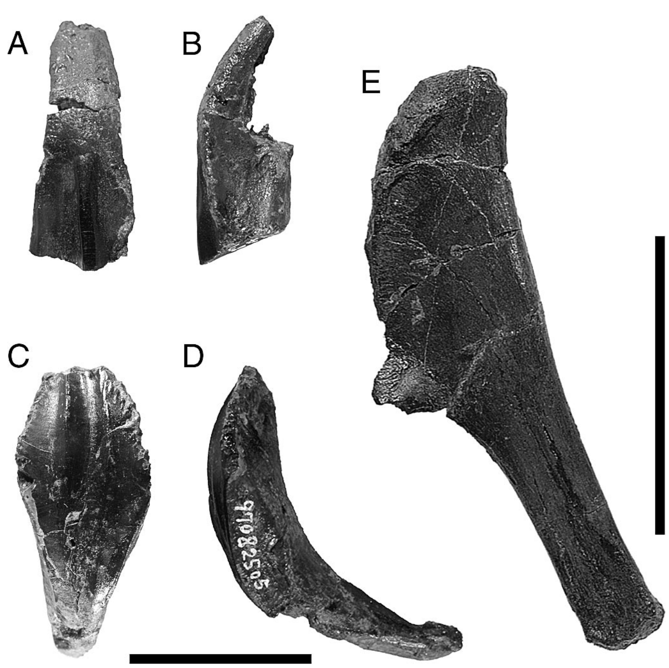

FIGURE 5. *Fukuisaurus tetoriensis* gen. et sp. nov. A left maxillary tooth (FPDM-V-40-13) in labial (**A**) and mesial (**B**) views and a left dentary tooth (FPDM-V-40-14; 97082505 written on the tooth is field number) in lingual (**C**) and distal views (**D**). Right sternal (FPDM-V-40-16) in dorsal view (**E**). Scale bar below a dentary tooth equals 2 cm for A–D, and one next to the sternal equals 10 cm for E.

Sternum

The right sternal plate (FPDM-V-40-16; Fig. 5E) is preserved. It has a mediolaterally expanded anterior portion and a posterolateral process (=posteroventrally projecting shaft in Weishampel and Horner, 1990), similar to *Iguanodon*, *Ouranosaurus*, *Altirhinus*, *Probactrosaurus*, and hadrosaurids (Weishampel and Horner, 1990; Norman, 1998). The lateral border of this element is straight. Its distal end is roughly same thickness of its shaft and lacks a transverse expansion.

DISCUSSION

Fukuisaurus cranial elements from the Kitadani Quarry were found disarticulated, and it is difficult to determine how many individuals are represented by the material described here. All elements probably belong to sub-adult to adult individuals, and the size difference in the maxillae (the height of the left maxilla is 90.7% of that of the right maxilla) shows that the composite

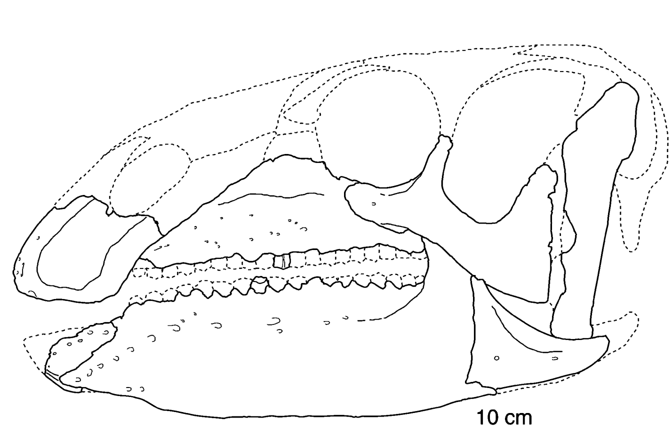

FIGURE 6. *Fukuisaurus tetoriensis* gen. et sp. nov. Reconstruction of the composite skull. Missing regions are indicated by dashed lines. Scale bar is the holotype material (a right maxilla, FPDM-V-40-1; a right jugal, FPDM-V-40-2) as a reference.

skull belongs to at least two individuals and two different ontogenetic stages.

Two characters indicate that *Fukuisaurus* is more derived than *Camptosaurus* and probably belongs to the Styracosterna (a monophyletic group including *Probactrosaurus*, *Iguanodon*, *Ouranosaurus*, *Protohadros*, and hadrosaurids; sensu Sereno, 1999) which bear a posterolateral process of the sternum (as seen in *Fukuisaurus*). More primitive forms (i.e., *Hypsilophodon*, *Tenontosaurus*, *Dryosaurus*, and *Camptosaurus*) have a kidney-shaped sternal plate (Dodson and Madsen, 1981). The posterior-most dentary tooth is positioned medial to the coracoid process of the dentary, suggesting that the phylogenetic status of *Fukuisaurus* lies with the Hadrosauriformes (Styracosterna with the exclusion of *Probactrosaurus*; Sereno, 1999). Although this character is listed a synapomorphic at the node of Hadrosauriformes, it is unknown in *Probactrosaurus*. *Fukuisaurus* appears not to be a hadrosaurid based on numerous characters (e.g., narrow rostrum, paraquadratic foramen present, asymmetrical maxillary teeth, and no miniaturization of maxillary teeth; Head, 1998). Based on the previous phylogenetic analyses by Kobayashi and Azuma (1999) and Head and Kobayashi (2001), *Fukuisaurus* is basal to *Probactrosaurus*, *Eolambia*, *Protohadros* and higher taxa, but its relationships with *Iguanodon*, *Ouranosaurus*, and *Altirhinus* remain unresolved.

A phylogenetic analysis was carried out with an emphasis on resolving relationships with derived, non-hadrosaurid iguanodontian dinosaurs because there are some characters indicating that *Fukuisaurus* is closely related to more derived iguanodontians. The accessory foramen on the surangular is present in *Fukuisaurus* as well as *Altirhinus* (Norman, 1998), *Ouranosaurus* (Taquet, 1976:fig. 32), and *Eolambia* (Head, 2001). The paraquadratic foramen is present in *Altirhinus*, *Iguanodon*, *Ouranosaurus* (Norman, 1998), and *Fukuisaurus* (paraquadratic foramen in *Hypsilophodon* is enclosed in the quadratojugal; Galton, 1974). The tooth morphology resembles that of *Altirhinus* especially in the lack of the secondary ridges in some maxillary teeth. The premaxilla-maxilla sutural surface widens posterodorsally in *Iguanodon* but it narrows in *Camptosaurus* and *Ouranosaurus* as well as *Fukuisaurus* (Weishampel, 1984). Norman (1998) considers a long posterolateral projection of the jugal process of the maxilla as an iguanodontid character, whereas the *Fukuisaurus* maxilla lacks the projection. Elevation of the lacrimal process of the maxilla with medial displacement of the antorbital fenestra, as seen in *Fukuisaurus*, are hypothesized to be synapomorphic characters for *Protohadros* and higher (Head, 1998).

To determine the phylogenetic status of *Fukuisaurus* within Iguanodontia, 13 taxa and 23 characters (22 cranial and one postcranial characters) (Appendices 1 and 2) are used in this analysis with two taxa as outgroups (*Dryosaurus* and *Camptosaurus*). All characters are equally weighted and unordered. *Lurdusaurus* from Niger, *Nanyangosaurus* and *Jinzhousaurus* from China, and some species of *Iguanodon* are not included in this analysis because of their incompleteness or lack of exposed features. Most character states are obtained from the literature (e.g., Godefroit et al., 1998; Head, 1998, 2001; Norman, 1998; Sereno, 1999). A Branch-and-Bound analysis was carried on using PAUP*4.0Beta (Swofford, 2000), which produced three most parsimonious trees with the shortest tree length of 35 steps, C.I. = 0.6571, R.I. = 0.8033, R.C. = 0.5279. The topologies of these most parsimonious trees agree with each other except for the relationships of *Bactrosaurus*, *Telmatosaurus*, and hadrosaurids. The strict consensus tree shows that *Fukuisaurus* is more derived than the monophyletic group of *Iguanodon* + *Ouranosaurus*, and is basal to the other ingroup taxa (*Altirhinus*, *Probactrosaurus*, *Eolambia*, *Protohadros*, *Bactrosaurus*, *Telmatosaurus*, and hadrosaurids) (Fig. 7A). Each tree resulted in the same character distribution at all nodes except for those of *Protohadros* and higher. Only a single character supports each node of the successive taxa (*Fukuisaurus*, *Altirhinus*, and *Probactrosaurus*) in all trees (Fig. 7B), indicating that the robustness of these trees is weak and that additional elements of *Fukuisaurus* need to be found. Despite the weaknesses, this tree is congruent with a previous analysis (Head, 2001) in the exclusion of *Altirhinus* from the Iguanodontidae by Norman (1998) and the monophyletic relationship of *Iguanodon* and *Ouranosaurus* (Godefroit et al., 1998). It also shows that all Early Cretaceous Asian forms (*Fukuisaurus*, *Altirhinus*, and *Probactrosaurus*) have paraphyletic relationships and are more derived than the clade of *Iguanodon* and *Ouranosaurus* and basal to *Eolambia* and higher.

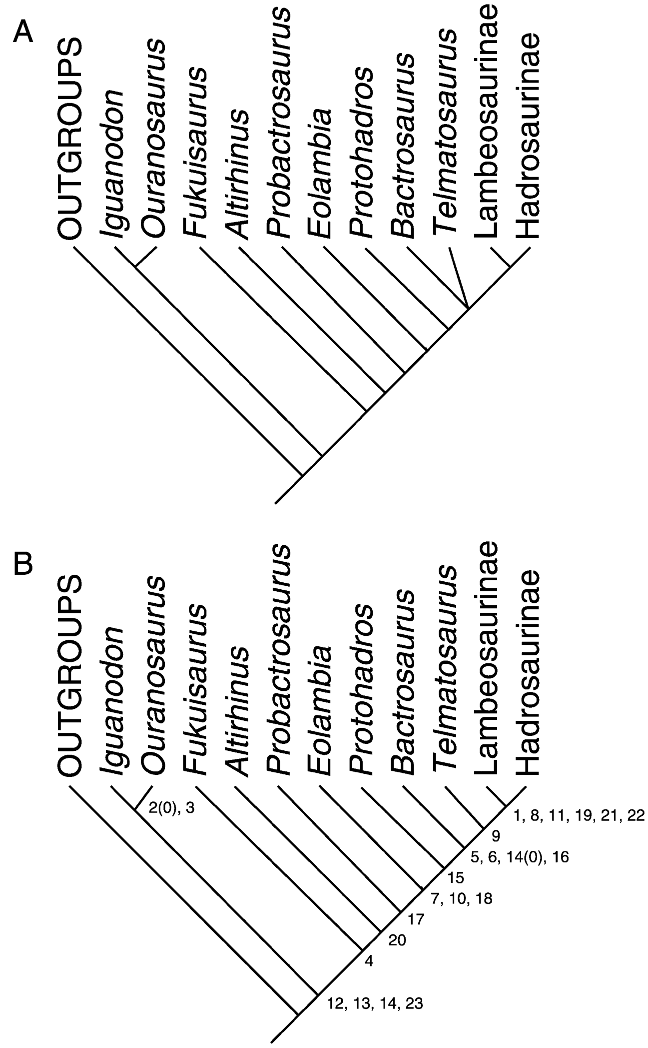

FIGURE 7. (**A**) Strict consensus tree of three most parsimonious trees with the shortest tree length from the phylogenetic analysis in this paper. (**B**) One of the most parsimonious trees with character distribution. Synapomorphies were determined by ACCTRAN character-state optimization (for character description, see Appendix 1).

The topology of the phylogenetic tree indicates that derived non-hadrosaurid iguanodontians established a Laurasian distribution with an independent dispersal to Africa for *Ouranosaurus* (or originated in Africa and dispersed into the Laurasian region). During the Early Cretaceous, the iguanodontian distribution extends to the eastern Asian continent for *Fukuisaurus* (Late Hauterivian–Barremian), *Altirhinus* (late Aptian–early Albian; Norman, 1998), *Probactrosaurus* (Aptian–Albian; Rozhdestvensky, 1967), and *Iguanodon orientalis* from Mongolia (?Cenomanian; Rozhdestvensky, 1952, 1967) and dispersed into North America. However, the occurrence of *Iguanodon lakotaensis* (Weishampel and Bjork, 1989) from North America and a possible close relationship of *Probactrosaurus* with *Eolambia* (Head, 2001) suggest a more complicated biogeographic history for derived iguanodontians during the Early Cretaceous (Head, 2001).

Fragmentary materials of iguanodontians from the Lower Cretaceous deposits of other formations in Japan have been reported (Azuma and Tomida, 1997), and some teeth were identified as Iguanodontidae. An iguanodontian tooth was found from the Tatsukawa Formation (the late Hauterivian–Barremian) of the Monobegawa Group, Tokushima Prefecture (Morozumi et al., 1995). Isolated teeth were discovered from outcrops in Ishikawa Prefecture, belonging to the Kuwajima and Okurodani formations of the Tetori Group (Hasegawa et al., 1995). The possible maximum range of the Okurodani Formation is considered to be between Tithonian to Hauterivian (Gifu-ken Dinosaur Research Committee, 1993). Although the age of the Kuwajima Formation is unclear, it is stratigraphically lower than the Kitadani Formation (Maeda, 1961) (Fig. 1). It suggests that derived non-hadrosaurid iguanodontians had dispersed into Japan at least by the early Early Cretaceous. Additionally, the occurrences of *Fukuisaurus* from the Kitadani Formation and ''iguanodontid'' fossils from the Kuwajima and Okurodani formations suggest an actual time range for the existence of the iguanodontians during the Early Cretaceous in the Tetori Basin of Japan.

Pleurokinesis (the transverse rotation of the maxilla with respect to the medial dermal skull roof) in the iguanodontian skull is present in *Iguanodon* and more derived iguanodontians as an adaptation for more efficient mastication (Norman, 1984). Although the loose premaxilla-maxilla and postorbital-jugal articulations have been argued as significant in providing rotation of the maxilla, the connection of the maxillae through articulation with the vomer must also allow freedom of movement. Norman (1984) suggested that *Hypsilophodon* as well as *Iguanodon* and hadrosaurids lack any inter-maxillary bracing, indicating that these taxa had pleurokinetic skulls, and the presence of the pleurokinetic skull may be a plesiomorphic state in iguanodontians. The robust, interdigitated, articular surface of the maxilla with the vomer in *Fukuisaurus* suggests the absence of pleurokinesis, despite similarities between *Fukuisaurus* and other iguanodontians in premaxilla-maxilla and jugal–postorbital articular morphologies. Thus, the strong medial bracing of the maxilla by the vomer in *Fukuisaurus* suggests the uniquely derived absence of pleurokinesis in the taxon.

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APPENDIX 1

Character states used for a phylogenetic analysis in this paper. Taxa used in this analysis are *Dryosaurus* (*D. altus* and *D. lettowvorbecki*; Galton, 1983), *Camptosaurus disper* (Gilmore, 1909), *Iguanodon* (*I. bernissartensis* and *I. atherfieldensis*; Norman, 1980, 1986 respectively), *Ouranosaurus nigeriensis* (Taquet, 1976), *Altirhinus kurzanovi* (Norman, 1998), *Probactrosaurus* (*P. gobiensis*, *P. alashanicus*, and *P. mazongshanensis*; Rozhdestvensky, 1967; Lü, 1997), *Eolambia caroljonesa* (Kirkland, 1998; Head, 2001), *Protohadros byrdi* (Head, 1998), *Telmatosaurus transsylvanicus* (Weishampel et al., 1993), *Bactrosaurus johnsoni* (Godefroit et al., 1998), Lambeosaurinae and Hadrosaurinae (Weishampel and Horner, 1990; Godefroit et al., 1998; Head, 1998; Sereno, 1999).

1. Laterally expanded rostrum (0) absent (1) present, (Sereno, 1986).
2. Denticulation (ventrally directed projections) at oral margin of premaxilla (0) present (1) absent, (Modified from Weishampel et al., 1993).
3. A long jugal process, projecting posteroventrally, of the maxilla (0) absent (1) present, (Norman, 1990).
4. High dorsal process of maxilla with the migration of the antorbital fenestra to the posterodorsal surface of the maxilla (0) absent (1) present, (Weishampel et al., 1993).
5. Dorsoventrally expansion of anterior part of jugal (0) absent (1) present, (Sereno, 1986).
6. Articulation between jugal and ectopterygoid (0) present (1) absent, (Head, 1998).
7. Paraquadratic foramen (0) present (1) absent, (Weishampel et al., 1993). The presence of the paraquadratic foramen is determined based on the morphology of the quadratojugal or the presence of quadratojugal facets dorsal and ventral to a notch of the jugal wing.
8. Narrow mandibular condyle of the quadrate (0) absent (1) present, (Weishampel et al., 1993).
9. Denticulation (dorsally/anterodorsally directed projections) at oral margin of predentary (0) present (1) absent, (modified from Weishampel et al., 1993).
10. Median ridge on the lingual surface of the predentary (0) absent (1) present, (Sereno, 1999).
11. Diastema of dentary (0) short or absent (1) long, (Sereno, 1986).
12. Posteriormost dentary tooth position is (0) anterior to the midline of the coronoid process (1) medial or posterior to the coronoid process of the dentary, (Sereno, 1999).
13. Postdentary bones are (0) extended anterior the midline of the coronoid process of the dentary (1) positioned posterior to the midline of the coronoid process of the dentary, (Sereno, 1986).
14. Surangular foramen (0) absent (1) present, (modified from Weishampel et al., 1993). The surangular foramen in this study is defined as a foramen on the lateral surface of the surangular below the glenoid.
15. Accessory foramen in the surangular (0) present (1) absent, (Kobayashi and Azuma, 1999). A foramen close to the dentary-surangular suture is defined as an accessory foramen, which is distinguished from the surangular foramen based on its position.
16. Position of angular on mandible (0) exposed laterally (1) not exposed laterally, (Weishampel et al., 1993).
17. Accessory ridges on maxillary tooth crown (0) present (1) absent, (Weishampel et al., 1993).
18. Symmetrical maxillary teeth with respect to the medial carina (0) absent (1) present, (Norman, 1990).
19. Miniaturization of maxillary teeth (0) absent (1) present, (Weishampel et al., 1993).
20. Number of teeth per tooth position in dentary (0) one or two (1) three or more, (Weishampel et al., 1993).
21. Symmetrical dentary teeth with respect to the medial carina (0) absent (1) present, (Norman, 1990).
22. Miniaturization of dentary teeth (0) absent (1) present, (Weishampel et al., 1993).
23. Ventrolateral process of the sternum (0) absent (1) present, (Dodson and Madsen, 1981).

APPENDIX 2

Data matrix applied in this paper for determination of the phylogenetic relationship of *Fukuisaurus* with iguanodontians. Characters are listed in Appendix 1. Missing or unknown characters are represented by "?".

Taxa	Characters				
	5	10	15	20	23
Dryosaurus	0?000	000?0	000??	00000	000
Camptosaurus	01000	01000	00000	00000	000
Iguanodon	00100	00000	01111	00000	001
Ouranosaurus	10101	00000	11110	00000	001
Fukuisaurus	01010	000?0	01110	?0000	001
Altirhinus	01110	00000	11110	00001	001
Probactrosaurus	0???0	?00?0	0?1??	?1001	0??
Eolambia	010?0	0?0??	01110	0110?	00?
Protohadros	11010	01001	11111	01101	00?
Bactrosaurus	01011	10001	01101	11101	001
Telmatosaurus	00?11	110??	01101	11101	00?
Lambeosaurinae	11011	11111	11101	11111	111
Hadrosaurinae	11011	11111	11101	11111	111