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ARTICLE

SPINOSAURID TEETH FROM THE LOWER CRETACEOUS KITADANI FORMATION OF THE TETORI GROUP, FUKUI, JAPAN

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ABSTRACT

Spinosaurids are large-bodied theropods exhibiting unusually narrow jaws with characteristic conical teeth commonly regarded as an adaptation for piscivorous diet. Despite rare occurrences of their bone materials, spinosaurids are widely known from the Jurassic to Cretaceous of both Gondwana and Laurasia mostly based on the teeth. Among them, Asian spinosaurids have been yielded from the Early Cretaceous deposits of Laos, Thailand, Malaysia, China and Japan. In the present study, 18 conical teeth from the Early Cretaceous Kitadani Formation of the Tetori Group cropping out in the Kitadani Dinosaur Quarry are identified as belonging to Spinosauridae based on the presence of unique morphological characters. These teeth also show some characters unique to Baryonychinae while lacking most denticles as in Spinosaurinae. Two of these teeth exhibit a limited distribution of denticles, which are larger than the minute denticles characteristic to Baryonychinae. Such an intermediate condition probably indicates that the spinosaurid from which these teeth were potentially derived represents a taxon closely related to the common ancestor of Baryonychinae and Spinosaurinae in the Early Cretaceous of East Asia. Therefore, further excavation at the Kitadani Dinosaur Quarry will provide important information for understanding spinosaurid evolutionary history.

Key words: Spinosauridae, Theropoda, Dinosauria, teeth, Early Cretaceous, Kitadani Formation, Tetori Group, Fukui, Japan

服部創紀・東 洋一（2020）福井県の下部白亜系手取層群北谷層から産出したスピノサウルス科の歯化石について．福井県立恐竜博物館紀要 19：1–9.

スピノサウルス科は，特徴的な円錐形の歯と顕著に狭い顎を持ち，一般的に魚食性であったと推定される大型の獣脚類である．その化石記録はジュラ紀〜白亜紀のゴンドワナ・ローラシア両大陸に広く分布しており，アジアでは前期白亜紀の化石記録が知られている．本研究では，北谷恐竜化石発掘現場に露出する下部白亜系手取層群北谷層から産出した円錐形の歯化石 18 本を，スピノサウルス科のものと同定した．これらはバリオニクス亜科の特徴を示す一方で，スピノサウルス亜科と同様に鋸歯をほとんど失っている．うち 2 本には限定的に鋸歯が分布するが，バリオニクス亜科特有の微細な鋸歯に比べてサイズが大きい．このような中間的な状態は，これらの歯の持ち主が，両亜科の共通祖先に近い分類群に属する可能性を示唆する．そのため，北谷恐竜化石発掘現場における更なる発掘調査が，スピノサウルス科の進化史を理解する上で重要な情報をもたらすと期待される．

INTRODUCTION

Spinosauridae is a clade of megalosauroid theropods closer to *Spinosaurus* than to *Torvosaurus* and is subdivided into Baryonychinae and Spinosaurinae (Sereno et al., 1998). Spinosaurids share a large body and unusual morphology such as narrow, elongated jaws with conical teeth probably adapted for a piscivorous diet (Taquet, 1984; Charig and Milner, 1986; Rayfield et al., 2007). Despite limited occurrences of their body fossils, spinosaurid remains are widely known from the Jurassic to Cretaceous of both Gondwana and Laurasia mostly based on their teeth with the morphologies unique among theropods (Hone and Holtz, 2017). Among them, Asian spinosaurids are known from the Early Cretaceous sediments of Laos (Allain et al., 2012), Thailand (Buffetaut et al., 2005; Samathi et al., 2019), Malaysia (Sone et al., 2015), China (Buffetaut et al., 2008) and Japan (Hasegawa et al., 2003; Kubota et al., 2017). Although the postcranial elements of *Ichthyovenator laosensis* were yielded in the Grès Supérieurs Formation of Laos (Allain

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FIGURE 1. Spinosaurid teeth from the Kitadani Dinosaur Quarry. From upper left to bottom right, FPDM-V-10237 (**A**), FPDM-V-546 (**B**), FPDM-V-10238 (**C**), FPDM-V-10000 (**D**), FPDM-V-9475 (**E**), FPDM-V-10239 (**F**), FPDM-V-10240 (**G**), FPDM-V-10241 (**H**), FPDM-V-10242 (**I**), FPDM-V-10243 (**J**), FPDM-V-10244 (**K**), FPDM-V-10245 (**L**), FPDM-V-10246 (**M**), FPDM-V-10247 (**N**), FPDM-V-10248 (**O**), FPDM-V-10249 (**P**), FPDM-V-9999 (**Q**) and FPDM-V-10251 (**R**).

et al., 2012) and an undescribed partial postcranial skeleton was recovered from the Khok Kruat Formation of Thailand (Buffetaut et al., 2005; Samathi et al., 2019), these specimens do not include any associated teeth. In contrast, isolated teeth are found in all these five countries and most of them share an unusual combination of characters unknown in either Baryonychinae or Spinosaurinae (Kubota et al., 2017), while some of them are tentatively referred to Spinosaurinae (Wongko et al., 2019).

In the present study, an assemblage of spinosaurid teeth from the Lower Cretaceous Kitadani Formation of the Tetori Group is reported for the first time. These specimens were recovered in the Kitadani Dinosaur Quarry (KDQ) during the first through fourth Dinosaur Excavation Projects from 1989 to the present and are housed at Fukui Prefectural Dinosaur Museum (FPDM). Among the abundantly-found conical teeth that mostly belong to crocodilians, a small number of specimens has been tentatively identified as spinosaurid teeth based on apparent differences in size and morphology. The Kitadani Dinosaur Quarry is located in the bank of the Sugiyamagawa River in the northern part of Katsuyama City, Fukui, central Japan (36° 7' 17.9" N, 136° 32' 41.4" E). The outcrop of the Kitadani Formation in KDQ is generally represented by alternating coarse to fine sandstone and siltstone, which have yielded abundant plant, invertebrate, vertebrate, and trace fossils (Goto et al., 2002; Azuma, 2003; Shibata and Goto, 2008). The Aptian age is inferred for this formation based on the co-occurrence of multiple species of charophyte gyrogonites (Sano, 2015) as well as on the suggested stratigraphic correlations of the formations within the Tetori Group (Sano and Yabe, 2016).

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1888
THEROPODA Marsh, 1881
TETANURAE Gauthier, 1986
MEGALOSAUROIDEA (Fitzinger, 1843) Walker, 1964
SPINOSAURIDAE Stromer, 1915
Spinosauridae indet.

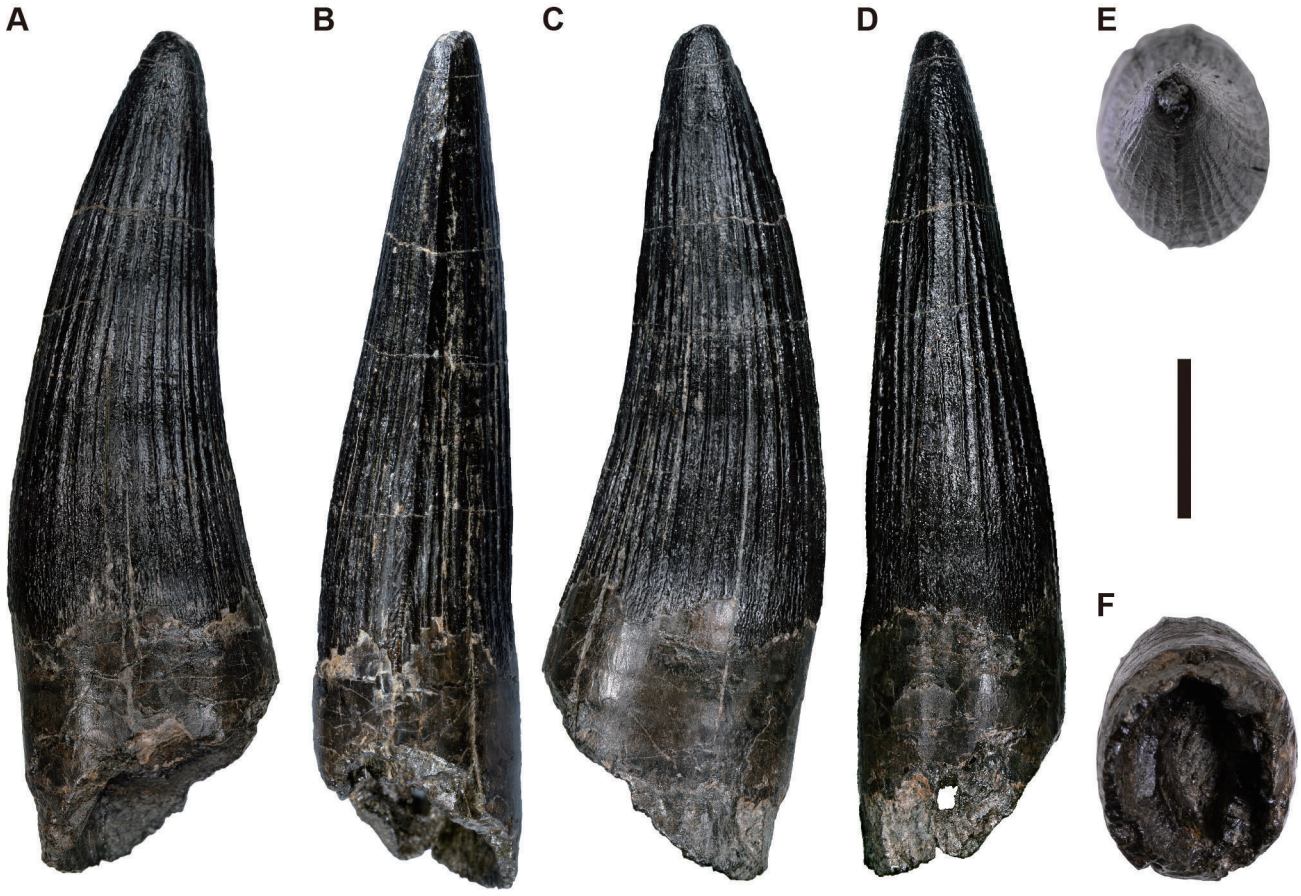

FIGURE 2. FPDM-V-9999 in labial (**A**), distal (**B**), lingual (**C**), mesial (**D**), apical (**E**) and basal (**F**) views. Scale bar equals 10 mm.

Material

Eighteen teeth in total with catalog numbers FPDM-V-546, 9475, 9999, 10000, 10237–10249, 10251 (Fig. 1).

Locality and horizon

The lowermost bonebed layer (Bonebed I sensu Shibata and Azuma, 2015) at KDQ in the northern part of Katsuyama City, Fukui, Japan; the Lower Cretaceous Kitadani Formation, Akaiwa Subgroup, Tetori Group (Aptian; Sano, 2015; Sano and Yabe, 2016).

DESCRIPTION

Among 18 teeth described here, 16 teeth are mostly composed of the crown, and FPDM-V-9475 and FPDM-V-10242 are mostly composed of the root (Fig. 1). All crowns are suboval in cross-section, nearly straight in lateral view, and slightly curved apicodistally (Fig. 2). In mesial view, the lingual margin of the crown is nearly parallel to the long axis of the tooth at the base whereas the labial surface inclines slightly lingually toward the apex.

The mesial carina is well defined throughout the crown in most specimens. However, it basally diminishes in FPDM-V-10238, basally disappears in FPDM-V-10239, and is completely absent in FPDM-V-10247 (Fig. 3). In FPDM-V-10248, the mesial carina inclines lingually and nearly reaches the cervix at the mesiolingual margin (Fig. 3). The distal carina is also well defined throughout the crown and further extends onto the root beyond the cervix in FPDM-V-9999 and FPDM-V-10243, whereas it diminishes basally in FPDM-V-10246 (Fig. 3). In FPDM-V-10247, the distal carina inclines slightly basolingually.

There are no denticles on the either carina, but with a few exceptions. There are about 20 denticles in basal 5 mm of the distal carina in FPDM-V-9999 and at least 10 denticles in the preserved apical 3 mm of the mesial carina in FPDM-V-10241. In both teeth, denticles are poorly developed and irregular in size (Fig. 4). In contrast, denticles are completely absent at least in other four specimens. The condition is only incompletely

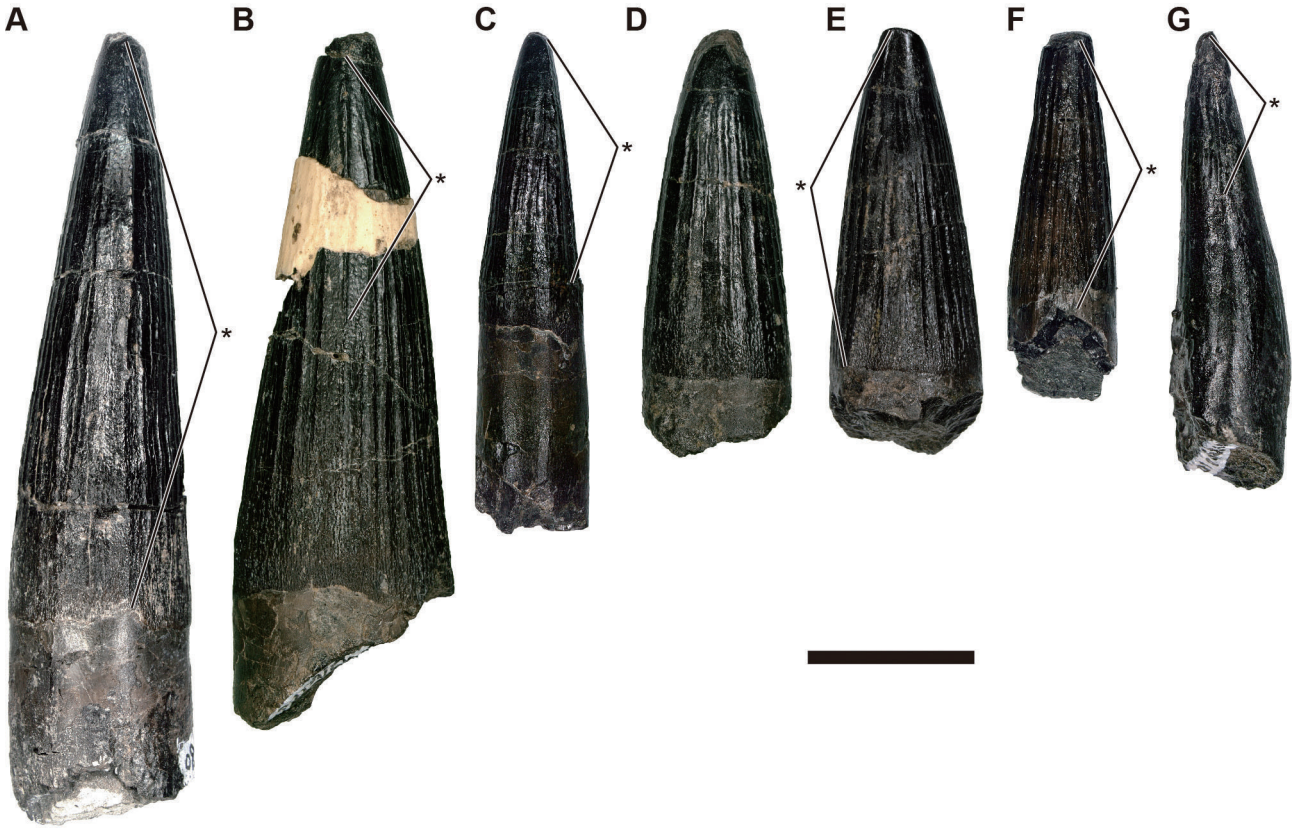

FIGURE 3. Mesial views of FPDM-V-10238 (**A**), FPDM-V-10239 (**B**), and FPDM-V-10248 (**C**), FPDM-V-10247 in mesial (**D**) and distal (**E**) views, and distal views of FPDM-V-10243 (**F**) and FPDM-V-10246 (**G**). Lines with an asterisk indicate the presence of a carina. Scale bar equals 10 mm.

observed in remaining 12 specimens because of damages on their carinae, nonetheless denticles are generally absent in the preserved part of each tooth.

All crowns bear distinct flutes and granules among them on the enamel surface (Figs. 1–6). All flutes diminish apically and disappear before reaching the apex. Although the flutes also disappear basally before reaching the cervix, the granules become better defined in the basal part of the crown. Granules are also well defined near both carinae to form many small ridges oriented somewhat apically toward each carina and forming an acute angle (Fig. 4) as on the teeth in Baryonychinae (Mateus et al., 2011).

The number of flutes varies from nine to 18 on each side among the specimens and regardless of the tooth size (Table 1). Several mesialmost and distalmost flutes disappear approximately at the midheight of the crown. For example, on both the labial and lingual sides of FPDM-V-9999, the masialmost and distalmost flutes apically approach each carina and disappear at the approximate midheight of the crown (Fig. 2), as in KDC-PV-0003, a purported spinosaurid tooth from the Lower Cretaceous Sebayashi Formation, Gunma, eastern Japan (Kubota et al., 2017). Furthermore, the first two or three flutes of both mesial and distal margins on both labial and lingual sides disappear on the way to the apex in a much smaller specimen, FPDM-V-546 (Fig. 5). In FPDM-V-10239, however, the mesialmost and distalmost flutes are present except in the apical part (Fig. 3).

There are also a small number of merges among flutes (Fig. 5). On the lingual side of FPDM-V-10000, the mesial third flute merges into the fourth one approximately at the midheight of the crown. On the labial side of FPDM-V-10000, the distalmost flute basally merges into the carina whereas the distal second one apically merges into the third one. On the labial side of FPDM-V-10238, the distal fourth flute merges into the fifth one.

The root is well preserved in FPDM-V-9475 with lacking most of the crown except for its base above the cervix exhibiting characteristic granules on enamel surface among flutes (Fig. 6). The root is not recurved through its length with only slightly swelled above its midlength and then tapers apically. Apically on the lingual side, there is a distinct fossa to receive a replacement tooth.

DISCUSSION

The 18 specimens described above are distinguished from the teeth of crocodilians by having a slight curvature only in the

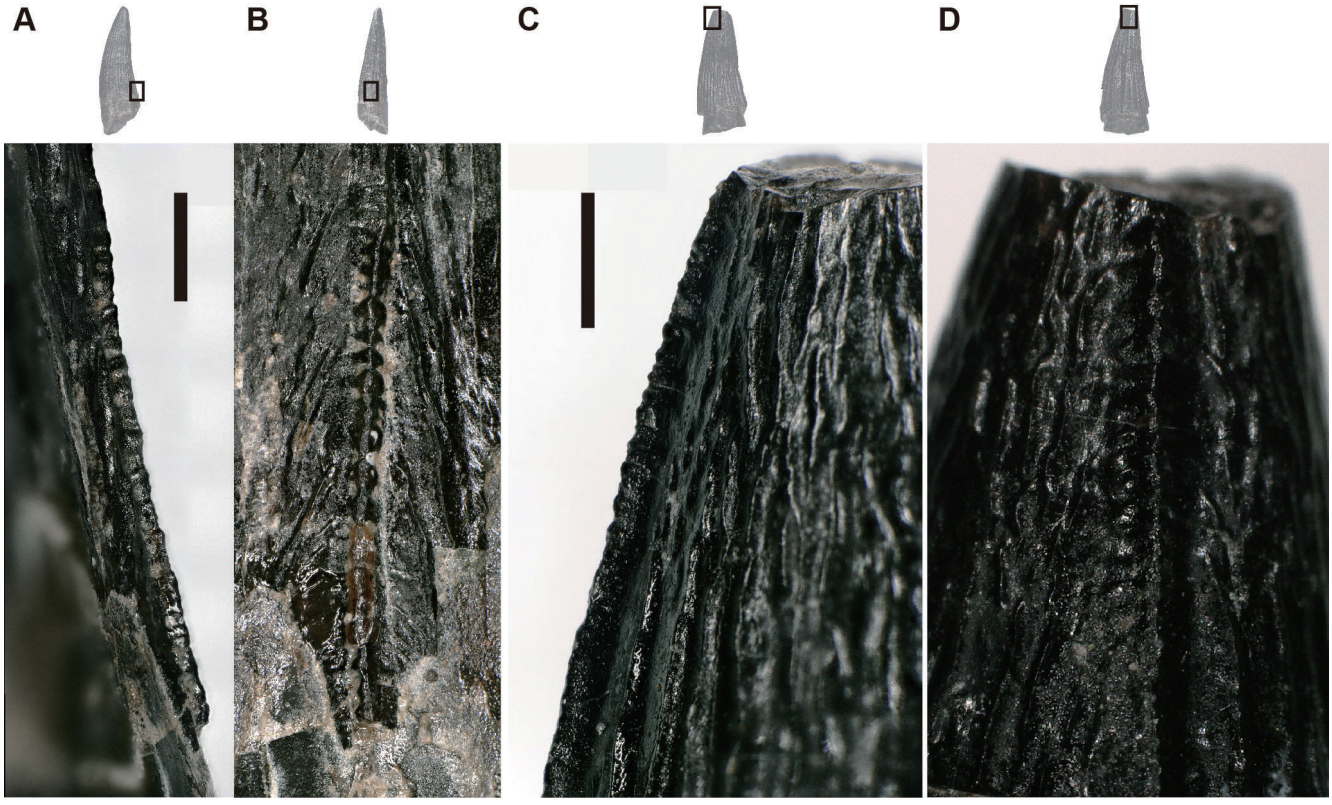

FIGURE 4. Denticles of FPDM-V-9999 (**A**, **B**) and FPDM-V-10241 (**C**, **D**) in labial (**A**), distal (**B**), lingual (**C**) and mesial (**D**) views. Squares on small views of whole teeth on the top indicate the areas magnified below. Each scale bar equals 1 mm.

mesiodistal plane and also from those of plesiosaurs by exhibiting a slight labiolingual compression of the crown and granules among the flutes as well as the flutes disappearing at the apex (Hasegawa et al., 2003; Naksri, 2007; Buffetaut et al., 2019). The specimens are tentatively called herein the KDQ spinosaurid to simplify the following discussions, although it may include several taxa.

Teeth of the KDQ spinosaurid are generally similar to those of Baryonychinae in having the granules curved basally adjacent to the carinae, and the denticles irregular in size (Mateus et al., 2011; Hendrickx et al., 2019). In addition, the partial absence of the carina observed in the KDQ spinosaurid has not been reported in other known spinosaurids and is distinct from the well-pronounced carinae characteristic to Spinosaurinae (Mateus et al., 2011). However, considering that denticles are absent in most teeth examined here except for the two with fairly limited distribution of denticles, the condition of KDQ spinosaurid is more similar to that of Spinosaurinae (Mateus et al., 2011; Hendrickx et al., 2019). In addition, the lack of a large number of minute denticles in the KDQ spinosaurid, i.e., only four or fewer denticles recognized per 1 mm, is apparently distinct from a baryonychine synapomorphy and rather likely to be a plesiomorphy for Spinosauridae (Mateus et al., 2011; Hendrickx et al., 2019). Therefore, the unique combination of characters seen in the KDQ spinosaurid can be regarded as an intermediate condition between Baryonychinae and Spinosaurinae, indicating a basal position within Spinosauridae that is close to the divergence of these two subclades. A similar intermediate condition characterized by larger denticles is also seen in at least one spinosaurid tooth from the Sebayashi Formation of Gunma, Japan (KDC-PV-0003) although its carinae are fully occupied by denticles (Kubota et al., 2017) and thus more similar to Baryonychinae than to the KDQ spinosaurid. While the partial absence of denticles is also known in a putative spinosaurid *Ostafrikasaurus*, it is interpreted as a result of wearing (Buffetaut, 2012), and a ceratosaurid affinity is suggested for its teeth (Rauhut, 2011; Hendrickx et al., 2019; Soto et al., 2020). Although Hendrickx et al. (2019) argues that the large number of minute denticles is a precursor of evolution of the unserrated carinae, the presence of a small number of large denticles with mostly unserrated carinae in the KDQ spinosaurid indicates that these characters may have developmental processes distinct from each other.

Finally, the presence of definitive spinosaurid teeth from KDQ reveals a previously-unknown aspect of the Katsuyama Dinosaur Fauna (Azuma and Tomida, 1995) and a greater theropod diversity within it than recognized before. In contrast to the carnivorous allosauroid *Fukuiraptor kitadaniensis*

TABLE 1. Dental characters and measurements of spinosaurid teeth from the Kitadani Dinosaur Quarry. Linear measurements were taken in the manner described by Hendrickx et al. (2019).

Specimen number	Number of labial flutes	Number of lingual flutes	Distribution of mesial carina	Distribution of distal carina	Distribution of denticles	Crown height (mm)	Crown-base length (mm)	Crown-base width (mm)	Preserved length (mm)
FPDM-V-546	18	18	whole crown	whole crown	?	14.4	8.7	7.8	19.8
FPDM-V-9475	?	15	?	?	?	?	6.4	5.9	26.2
FPDM-V-9999	17	17	whole crown	invading root	distobasal	38.2	16.5	13.3	53.5
FPDM-V-10000	12	12	?	whole crown	?	45.6	17.9	16.2	41.9
FPDM-V-10237	11	14	whole crown	whole crown	absent	?	9.2	8.0	36.3
FPDM-V-10238	15	12	apical	whole crown	?	34.5	12.4	11.1	47.8
FPDM-V-10239	15	14	apical	whole crown	absent	35.4	14.0	13.3	64.8
FPDM-V-10240	?	9	whole crown	whole crown	?	24.5	8.8	7.9	25.9
FPDM-V-10241	15	13	whole crown	whole crown	mesioapical	18.9*	7.5*	7.6*	18.9
FPDM-V-10242	18	18	whole crown	whole crown	absent	?	10.7	10.2	26.7
FPDM-V-10243	11	10	whole crown	invading root	?	16.0*	7.7	6.6	22.6
FPDM-V-10244	16	15	whole crown	whole crown	?	27.5	12.5	9.0	32.3
FPDM-V-10245	?	?	?	?	?	23.2*	13.3	11.1	35.0
FPDM-V-10246	14	12	?	apical	?	25.4	9.9	6.4*	27.6
FPDM-V-10247	13	14	absent	whole crown	?	22.0*	10.1	9.2	24.3
FPDM-V-10248	15	12	whole crown	whole crown	?	18.4	6.3	6.4	30.2
FPDM-V-10249	10	10	whole crown	whole crown	absent	23.5	8.9	8.0	29.9
FPDM-V-10251	?	15	?	?	?	?	?	?	21.4

*Specimen incomplete in measured dimension.

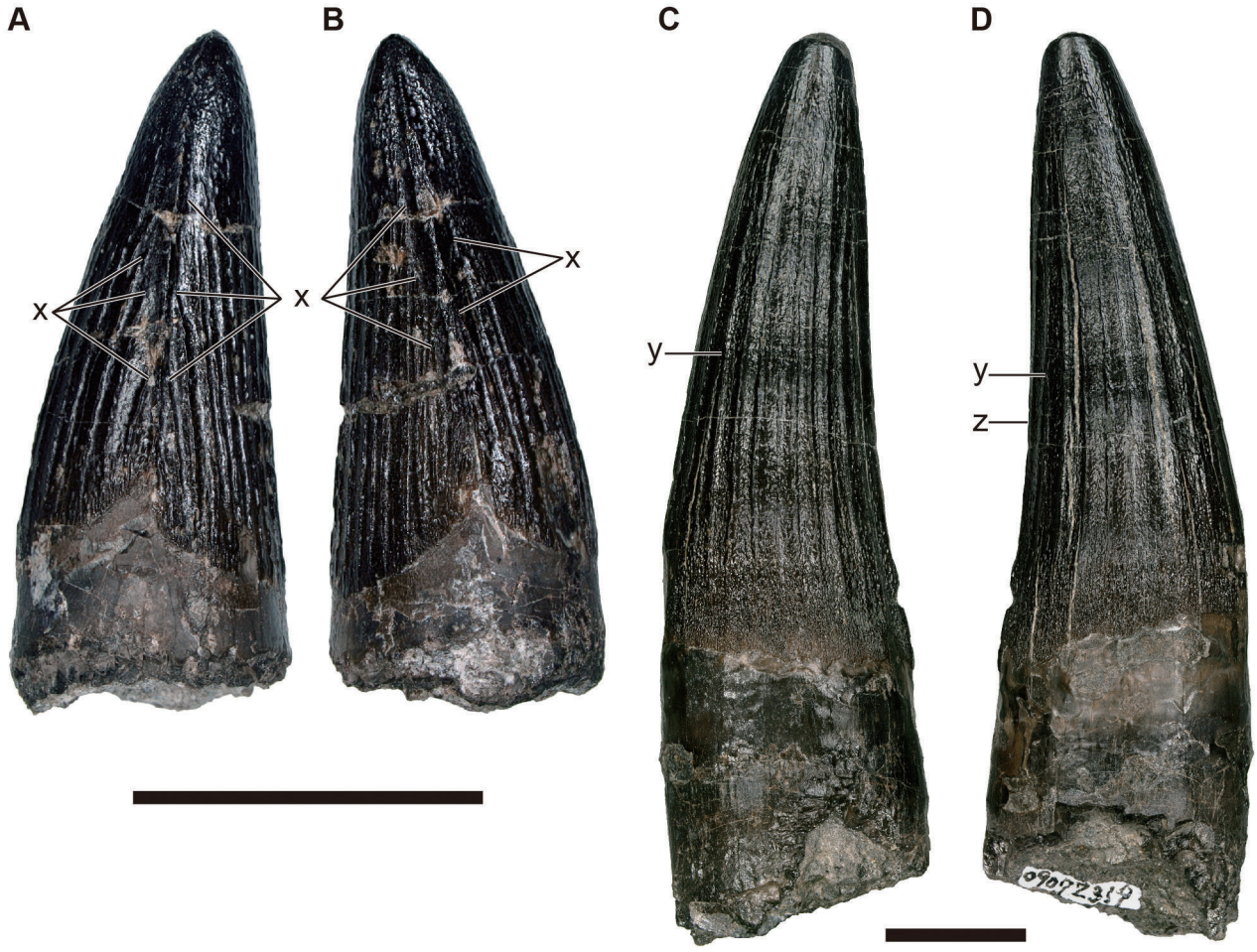

FIGURE 5. FPDM-V-546 in mesial (**A**) and distal (**B**) views, and FPDM-V-10000 in lingual (**C**) and labial (**D**) views. Lines with "x" indicate a disappearance of a flute, whereas a line with "y" indicates a merge of flutes and that with "z" indicates a merge between a flute and the carina. Each scale bar equals 10 mm.

(Azuma and Currie, 2000) and the omnivorous or herbivorous maniraptoriform *Fukuivenator paradoxus* (Azuma et al., 2016), the KDQ spinosaurid may have been a piscivorous predator as were other known spinosaurids (Taquet, 1984; Charig and Milner, 1986; Rayfield et al., 2007) and thus occupied niches different from those Kitadani theropods. Morphological variabilities among spinosaurid teeth from KDQ are possibly explained by the heterodonty within a jaw, as well as by intra- and/or interspecific variations. To clarify which of these phenomena primarily contributes to such an observed variation, remains of teeth-bearing skeletal parts of definitive spinosaurids are necessary. Such specimens will also allow us to reveal the position of the KDQ spinosaurid in still largely unresolved phylogeny of Spinosauridae. Therefore, further excavation in KDQ holds a key for clarifying spinosaurid evolution in East Asia.

CONCLUSIONS

Eighteen conical teeth from the Early Cretaceous (Aptian) Kitadani Formation at KDQ are identified as those of Spinosauridae based on the presence of morphological characters of their crowns unique to the clade such as the suboval cross section, presence of many flutes and granules and apical reduction of the flutes, as well as the apicodistal curvature in lateral view. These specimens also share some characters with the teeth of Baryonychinae, while they lack most of denticles as in the teeth of Spinosaurinae. Among these specimens, two of them exhibit a limited distribution of denticles, which are nonetheless larger than minute denticles characteristic for Baryonychinae. Such a combination of characters likely indicates the potential presence of a taxon closely related to the common ancestor of these clades in the Aptian of East Asia. Therefore, future fieldwork in KDQ will provide important information for understanding a controversial evolutionary history of Spinosauridae.

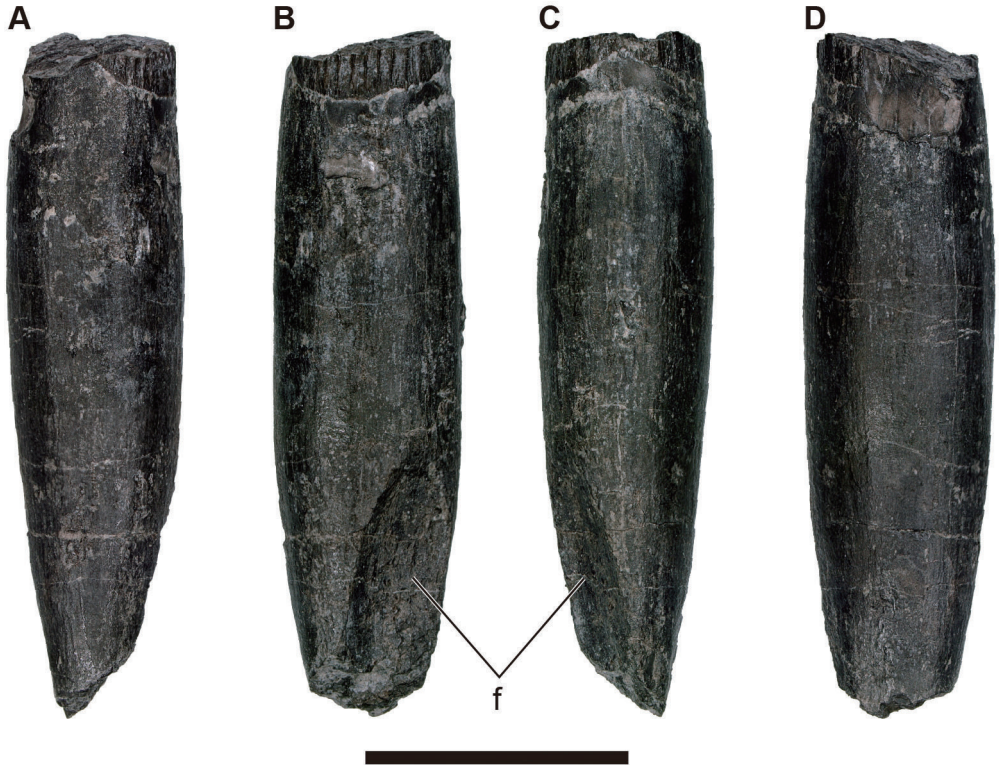

FIGURE 6. V-9475 in mesial (**A**), lingual (**B**), distal (**C**) and labial (**D**) views. "f" indicates a fossa for a replacement tooth. Scale bar equals 10 mm.

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