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Terminally Resorbed Iguanodontid Teeth from the Neocomian Tetori Group, Ishikawa and Gifu Prefecture, Japan

By

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Abstract Some teeth from Shiramine, Ishikawa Prefecture, were nicknamed "Shima-ryu." This enigmatic taxon was identified only as "ornithischian". These teeth are identified and described herein as terminally resorbed maxillary teeth of iguanodontids. The presence of iguanodonts in the Tetori Group suggests dispersal of the essentially European taxon to the East Asian Cratons, such as the Sino-Korean/Yangtze Cratons by Neocomian times and this also indicates a land connection via the Turgai Sea by then.

Introduction

Ever since the discovery of the tooth of a carnosaur and two dinosaur footprints in 1985 at Kasekiheki, fossil bluff, in Shiramine, Ishikawa Prefecture (MANABE *et al.*, 1989), many intensive prospecting for dinosaurs has resulted in the discovery of a more diverse dinosaurian fauna not only from the area but also from neighbouring Fukui and Gifu Prefectures (e.g. DONG *et al.*, 1990). An unidentifiable tooth was found by one of us (IY) in Kasekiheki in the spring of 1987 (Loc. 1 in Fig. 1). It was figured in DONG *et al.* (1990: 25) with similar teeth from the same locality previously collected by Mr. Mitsuo Kuwayama. These teeth were nicknamed as "Shima-ryu" (Shima = the local area; ryu = dragons in Japanese) and they were tentatively identified as Ornithischia family indet. Two of us (MO and IS) collected the similar teeth in Gifu Prefecture, the other side of the Hakusan divide (Loc. 2, 3, 4 in Fig. 1).

Despite the larger number of specimens, the identity of the taxon remained unknown. Some argued that it was unique among Dinosauria to have the root larger than the crown (some are preserved that way: e.g. SBEI 003). Eventually, one of us (MM) found almost identical teeth (e.g. BMNH 36503) in the collection of the Natural History Museum, London, in 1990. They were terminally resorbed *Iguanodon* teeth from the Tilgate Forest area of the Wealden of Sussex, England. The purpose of this paper is to identify the "enigmatic" Shima-ryu.

Repository Abbreviations

BMNH	formerly British Museum (Natural History), now the Natural History Museum, London, UK
IS	Private collection under the care of Mr. Ikoi Shibata, c/o Api Co. Ltd., 1–1 Kanou-sakurada-cho, Gifu-shi, Gifu, 500
MO	Private collection under the care of Mr. Masatoshi Ohkura, 86 Nanzan-cho-naka, Kounan-shi, Aichi, 483
NSM PV	Department of Palaeontology, National Science Museum, Tokyo, Japan
SBEI	Shiramine Village Board of Education, Ishikawa Prefecture, Japan
YNUGI	Geological Institute, Yokohama National University, Yokohama, Japan

Geological Setting

The Tetori Group is widely distributed in the eastern part of the Inner Zone of west Japan. The Tetori Group consists mainly of conglomerate, sandstone and mudstone, and is divided into three subgroups: Kuzuryu, Itoshiro and Akaiwa Subgroups in upward sequence (MAEDA, 1961). All the specimens described herein were obtained from the upper part of the Itoshiro Subgroup: Kuwajima Formation in the Shiramine area and Okurodani and Amagodani Formations in the Shokawa area (Fig. 1 & 2).

Locality 1

Specimens: SBEI-1, 2, 3, 4, 5 and NSM PV 20036.

Location: The outcrop exposed along the Tedori River at Kuwajima, Shiramine Village, Ishikawa Prefecture (Locality 1 in Fig. 1A, 1B, 36°12′N, 136°38′E).

Stratigraphic position: The uppermost of the Kuwajima Formation.

Lithofacies: Alternating beds of fine-grained sandstone, mudstone and thick coarse-grained sandstone. The dinosaur teeth were obtained from a muddy fine-grained sandstone bed.

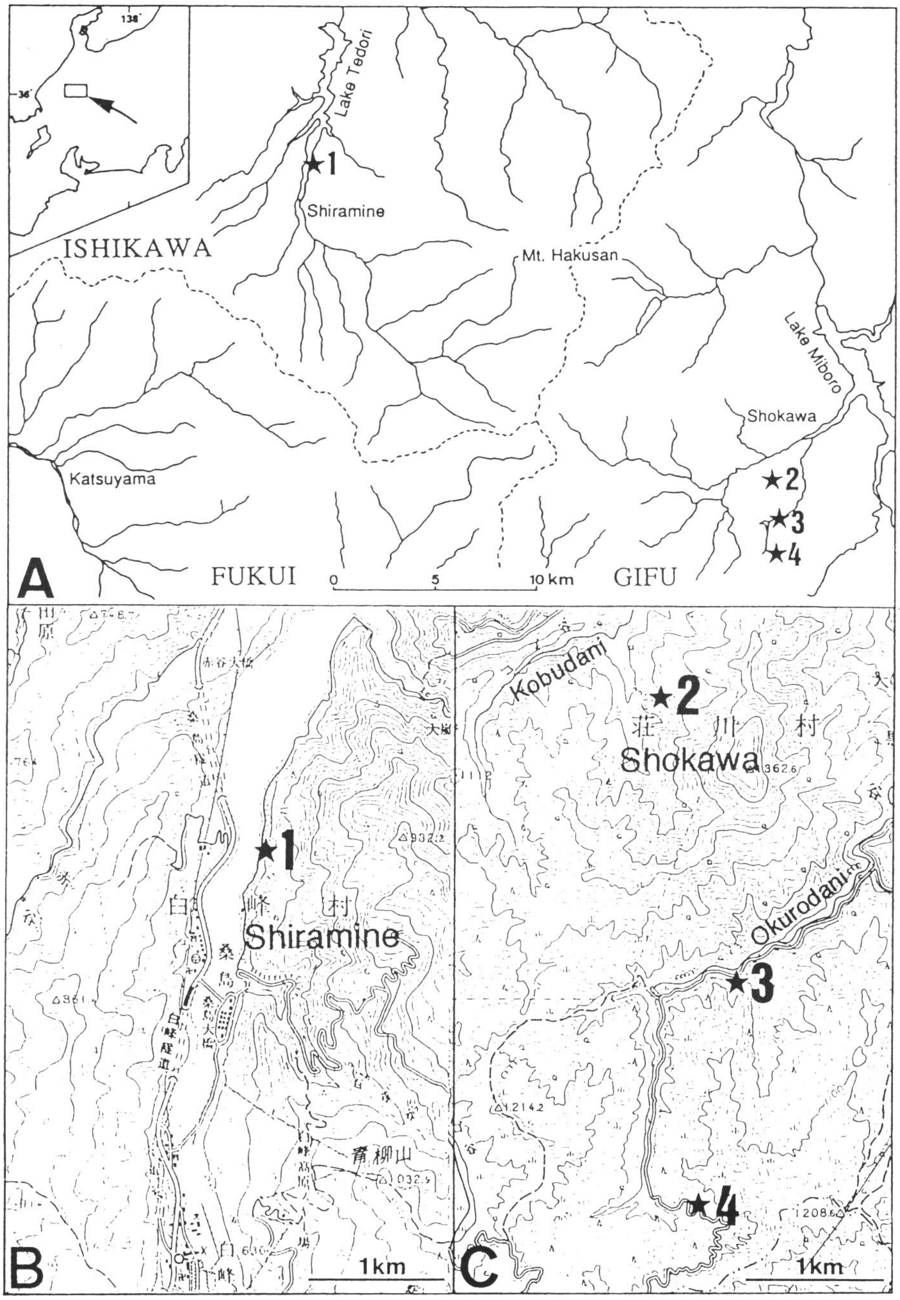

Fig. 1. A; Map showing the localities of the described specimens. B; Loc. no. 1, plotted on 1 : 50000-scale topographic map of Japan, Quadrangles "Shiramine", Geographical Survey Institute. C; Loc. nos. 2, 3, 4, plotted on 1 : 50000-scale topographic map of Japan, Quadrangles "Hakusan", Geographical Survey Institute.

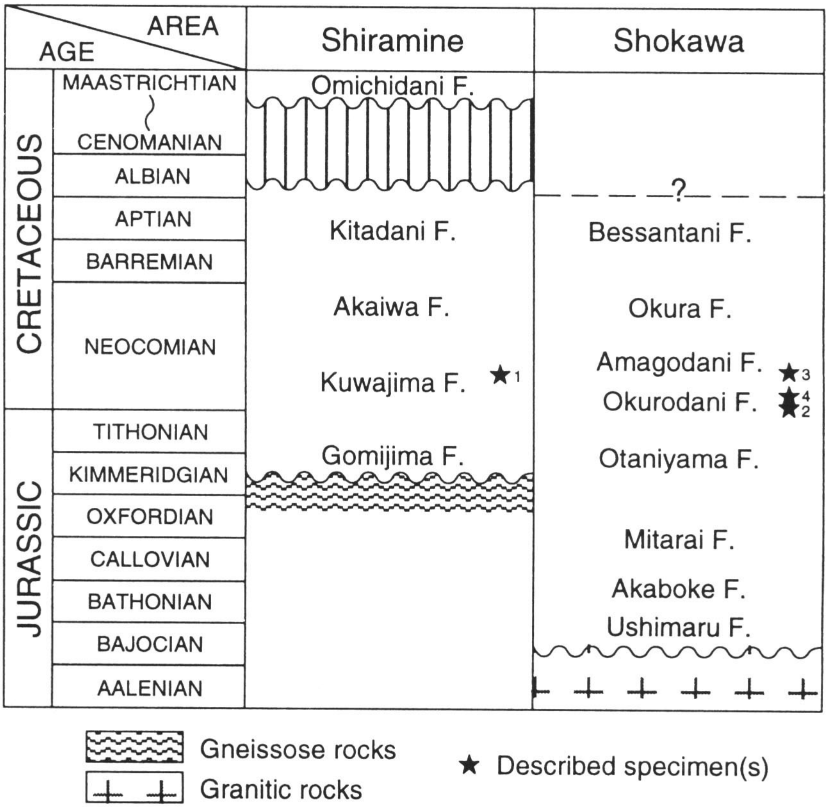

Fig. 2. Stratigraphic chart of the Tetori Group correlating between the Shiramine and Shokawa areas (Modified from MAEDA, 1952, 1961). Star marks with number indicate the stratigraphic positions and localities shown in Fig. 1 of iguanodontid teeth described in this paper.

Locality 2

Specimens: IS-KO-1, 2, 3 and 4.

Location: At the road cut along the branch system of the Kobudani Valley, Shokawa Village, Gifu Prefecture (Locality 2 in Fig. 1A, 1C, 36°03′N, 136°53′E).

Stratigraphic position: The lowermost of the Okurodani Formation (GIFU-KEN DINOSAUR RESEARCH COMMITTEE, 1993).

Lithofacies: Alternating beds of fine-grained sandstone, mudstone and coarse-grained sandstone with a tuff bed. The dinosaur teeth were obtained from a muddy fine-grained sandstone bed.

Locality 3

Specimen: MO-09/Cr/90/03.

Location : At the road cut along the Okurodani Valley, Shokawa Village, Gifu Prefecture (Locality 3 in Fig. 1A, 1C, 36°02′N, 136°53′E).

Stratigraphic position : The lowermost of the Amagodani Formation (GIFU-KEN DINOSAUR RESEARCH COMMITTEE, 1993).

Lithofacies : Alternating beds of mudstone and fine-grained sandstone with a channel-shaped sandstone bed which underlies a dinosaur bearing fine-grained sandstone bed.

Locality 4

Specimen : NSM PV 20034

Location : At the road cut along the Okurodani Valley, Shokawa Village, Gifu Prefecture (Locality 4 in Fig. 1A, 1C, 36°01′N, 136°53′E).

Stratigraphic position : The lower part of the Okurodani Formation (GIFU-KEN DINOSAUR RESEARCH COMMITTEE, 1993).

Lithofacies : Alternating beds of muddy fine-grained sandstone, mudstone and coarse-grained sandstone. The dinosaur tooth was collected from a muddy fine-grained sandstone bed.

Sedimentary environments

All the outcrops are made up of alternating beds of fine-grained sandstone, mudstone and thick coarse-grained sandstone. Thick coarse-grained sandstone beds are regarded as in-channel sandstone, and alternating beds of fine-grained sandstone and mudstone as inter-channel deposits on fluvial, braided-delta plains (MASUDA *et al.*, 1991). Therefore, fossiliferous argillaceous beds bearing the dinosaur teeth are regarded as flood plain deposits of inter-channel facies on fluvial plains.

Geologic Age

All the specimens described herein were obtained from the upper part of the Itoshiro Subgroup. As suggested by MATSUMOTO *et al.* (1982) and TAMURA (1981, 1990), the age of the formations of the Itoshiro Subgroup is not known in detail, because these non-marine formations are quite barren of reliable index fossils and are not in contact with marine strara containing ammonites and other index fossils. The Mitarai Formation of the underlying Kuzuryu Subgroup, however, yields characteristic marine bivalves, ammonites and belemnites, indicative of Late Jurassic Callovian to Oxfordian age (HAYAMI, 1959a, 1959b, MAEDA, 1952, 1961, SATO, 1962). The Kitadani Formation of the overlying Akaiwa Subgroup is assigned to the late Late Barremian to Aptian in age, based upon the occurrence of *Nippononaia ryosekiana* (ISAJI, 1993). Therefore, the upper part of the Itoshiro Subgroup is estimated to be Early Neocomian age.

Systematic Palaeontology

Class Reptilia LINNAEUS, 1758
Subclass Diapsida OSBORN, 1903
Superorder Dinosauria OWEN, 1842
Order Ornithischia SEELEY, 1888
Suborder Ornithopoda MARSH, 1871
Infraorder Iguanodontia DOLLO, 1881
Family Iguanodontidae COPE, 1869
Iguanodontidae gen. et sp. indet.

Diagnosis: As far as the teeth are concerned, dentary teeth are approximately diamond-shaped in lingual view and asymmetrical, with primary and secondary ridges separated by a median groove, and distal denticulate margin rolled mesially to produce a slight cingulum; maxillary teeth narrow, lozenge-shaped asymmetrical in labial view with very prominent primary ridge which is offset posteriorly (e.g. MANTELL, 1848: 186–188; NORMAN, 1980: 28–29).

Comments: The familial diagnosis here is also applicable for the genus *Iguanodon* (e.g. NORMAN, 1986: 294–295), but this diagnosis is merely an extract of the dental characters from the set of numerous characters in the skull and postcranium. Are the teeth alone characteristic enough? The justification of the identification is discussed later.

Materials: Isolated maxillary teeth (IS-KO-1, 2, 3, and 4; MO-09/Cr/90/03; NSM PV 20034 and 20036; and SBEI 001, 002, 003, 004, and 005, see Fig. 5, 1–16). Terminally resorbed shed teeth without root.

Description: The specimens are identifiable as maxillary teeth because the iguanodontid maxillary crowns are much narrower than those of the dentary and the arrangement of enamel ridges is clearly distinctive. The enamelled face is divided unequally by a primary ridge instead of two ridges in the dentary teeth. The primary ridge divides the broader anterior from the posterior face of the crown. The anterior is divided further by the several small secondary ridges (e.g. NORMAN, 1980: 28). The mesial side is represented by heavily grooved resorption facets. The enamelled surface of the crown is lateral, on the contrary to dentary teeth where the enamelled surface is mesial. In iguanodontid's maxillary teeth replacement, a root of a functional tooth is resorbed completely from beneath by odontoclastic activity on the epithelium of a replacing tooth. These specimens are examples of naturally shed teeth. There is never more than one replacement tooth per tooth position, although a rudimentary second replacement tooth is reported for *Probactrosaurus alashanicus* (NORMAN and WEISHAMPEL, 1990: 518). It is therefore likely that these terminally resorbed teeth came from the first generation of the functional teeth.

SBEI 001 (Fig. 5-1) is used here to describe the general morphology of a terminally resorbed right maxillary tooth. As preserved, it is 23 mm in dorso-ventral length, 16 mm in anteroposterior length, and 18 mm in lateromesial length. When laterally viewed, the distal margin of the crown shows the primary ridge offset slightly posteriorly (r, Fig. 3A) and two secondary ridges anteriorly (s, Fig. 3A). Anterior and posterior edges (a and p respectively, Fig. 3A) are here reminiscent of what used to form curled shelves leading up to denticulate crown

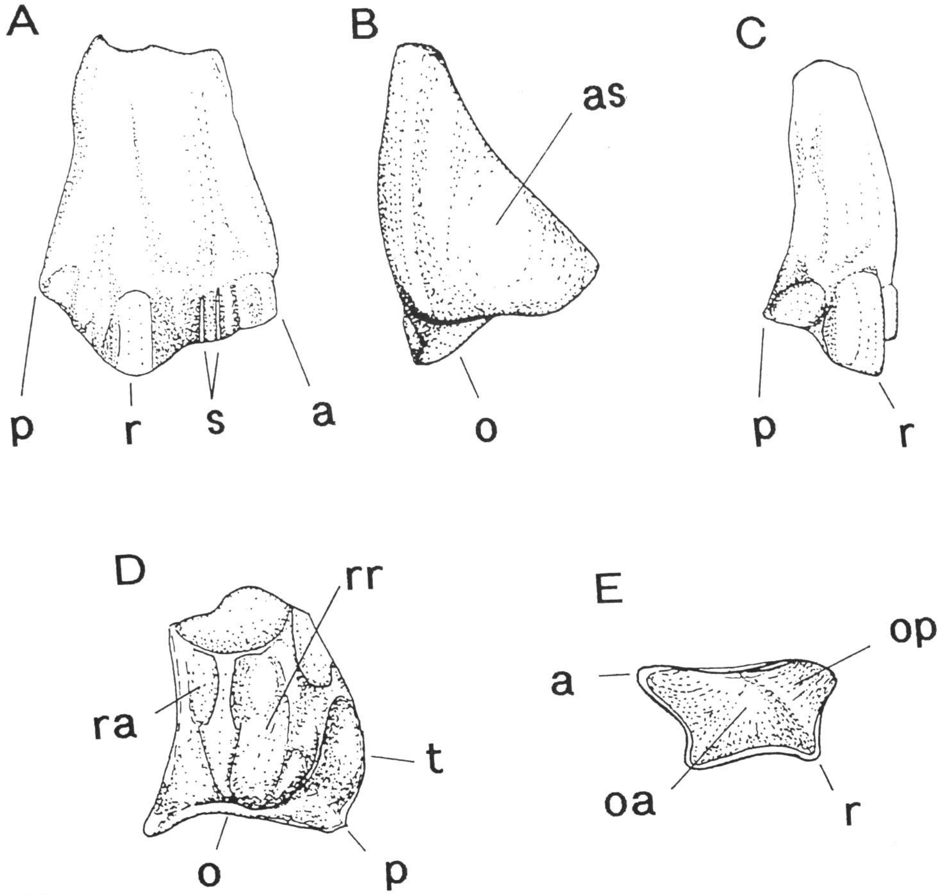

Fig. 3. A, lateral view of a right maxillary tooth (SBEI 001); B, anterior view of SBEI 001; C, posterior view of SBEI 001; D, mesial view of another right maxillary tooth (SBEI 003); and E, occlusal view of SBEI 003. a, anterior edge of the crown; as, anterior shelf for the adjacent tooth; o, occlusal surface; oa, occlusal surface for the dentary tooth; op, occlusal surface for another dentary tooth; p, posterior edge of the crown; r, primary ridge; ra, resorption facet for the anterior edge of the replacing tooth; rr, resorption facet for the primary ridge of the replacing tooth; and t, tongue-shaped mesial extension of the occlusal surface that was not in function.

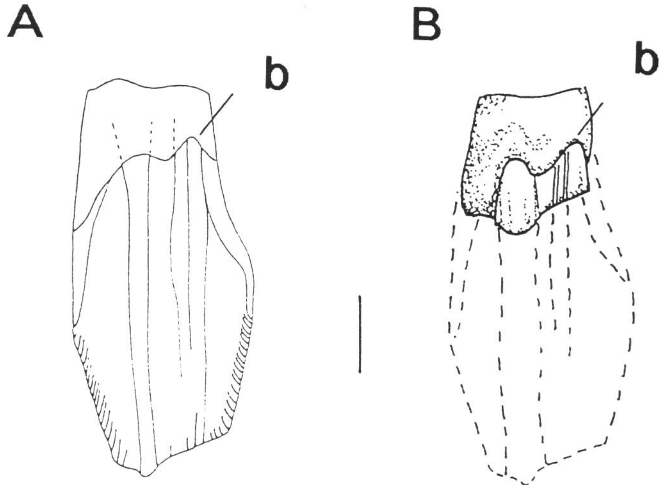

Fig. 4. Reconstruction of a terminally resorbed tooth (IS-KO-2). Lateral view of a right maxillary tooth (IS-KO-2) with reconstructed crown (B) based on NSM PV 20035 in the mirror image (A); b, the boundary between the enamelled face and dentine; and Scale bar is 10 mm.

margins distally. The level where ridges and margins terminate indicates the proximal margin of the enamel surface. The boundary in IS-KO-2, Fig. 4B and 5-8, matches perfectly well with that of *Iguanodon* sp. from the Isle of Wight (cast: NSM PV 20035; Fig. 4A). The left maxillary tooth, NSM PV 20035, is shown in Fig. 4A in the mirror image in order to show the exact match with the right maxillary tooth (IS-KO-2).

In the teeth yet to be resorbed, the primary ridge turns into seven or so low striations just like secondary ridges, at the base of enamel surface. The margin where the enamel layer terminates is well marked by the disappearance of shiny enamel layer, but the secondary ridges and striations continue to dentine and

Fig. 5. 1, Iguanodontid right maxillary tooth in lateral view from Kuwajima Formation in Kasekiheki, Shiramine, Ishikawa Prefecture (SBEI 001); 2, *ditto*, (SBEI 002); 3, *ditto*, (SBEI 003); 4, left maxillary tooth, *ditto*, (SBEI 004); 5, right maxillary tooth, *ditto*, (SBEI 005); 6, right maxillary tooth from Amagodani Formation in Okurodani Valley, Shokawa, Gifu Prefecture, (MO-09/Cr/90/03); 7, left maxillary tooth from Okurodani Formation in Kobudani Valley, Shokawa, Gifu Prefecture (IS-KO-3); 8, right maxillary tooth, *ditto*, (IS-KO-2); 9, *ditto*, (IS-KO-1); 10, *ditto*, (IS-KO-4); 11, left maxillary tooth from Okurodani Formation in Okurodani Valley, Shokawa, Gifu Prefecture (NSM PV 20034); 12, left maxillary tooth in occlusal view from Kuwajima Formation in Kasekiheki, Shiramine, Ishikawa Prefecture (NSM PV 20036); 13, IS-KO-1, *ditto*; 14, IS-KO-2, *ditto*; 15, NSM PV 20034 in occlusal view; and 16, SBEI 003 in occlusal view. Scale bar is 10 mm.

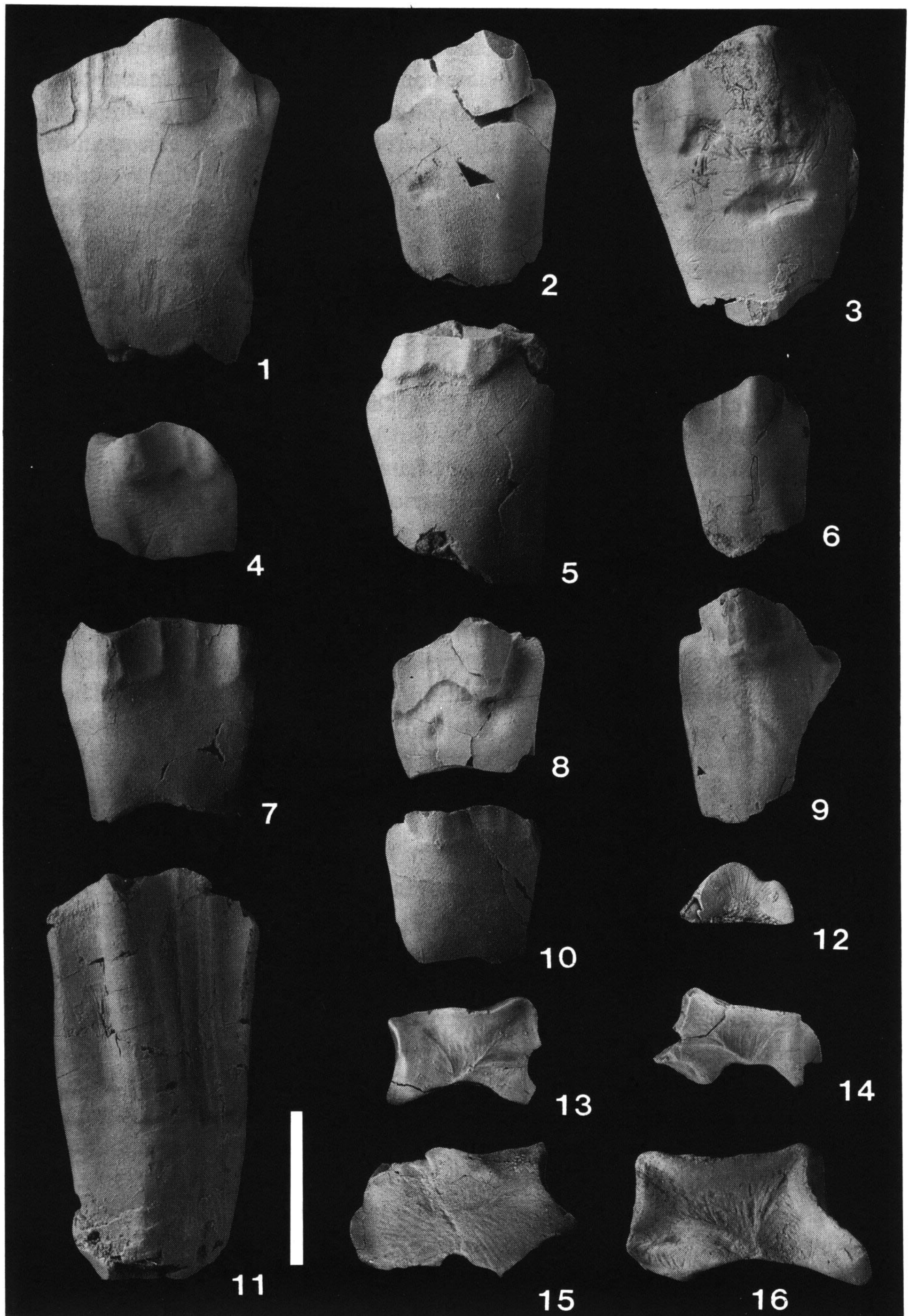

Fig. 5.

there is no marked ridge at the boundary. In the terminally resorbed teeth like SBEI 001 and SBEI 003 (Fig. 5-3), the boundary is far more pronounced, as proximal ends of the primary ridges are elevated by 1 to 2 mm. This oblique shelf is also seen almost always in terminally resorbed teeth of European specimens, such as *Iguanodon* sp. teeth from the Tilgate Forest area of the Wealden of Sussex, England (BMNH 36503). The shelf matches perfectly well with the boundary of enamel and dentine in the yet-to-be-resorbed teeth. It is rather difficult to identify if the shelf developed as the tooth grows older, or as the bearer of the tooth gets older, or as the tooth advances in fossilisation.

When anteriorly viewed, the anterior edge continues to form a concave shelf which used to accommodate an adjacent tooth (as, Fig. 3B). The shelf is only partially preserved due to the resorption from the tooth directly underneath that is to replace the tooth being described.

In the posterior view, the posterior edge (p, Fig. 3C) is seen here as less pronounced ridge in comparison to the anterior one. The posterior shelf should have formed larger depression which accommodated a posterior adjacent tooth, but it is completely resorbed mesially. The shelf was inclined more towards the enamelled surface in comparison to the anterior shelf.

The mesial side is better preserved in another specimen (SBEI 003, Fig. 5-3). SBEI 003 is also a right maxillary tooth, slightly smaller in size than SBEI 001. This side clearly shows resorption from the replacement tooth beneath. The two distinctive grooves should have accommodated primary ridge, anterior and posterior margins of the replacement tooth (rr and ra, respectively, Fig. 3D). The occlusal surface (o, Fig. 3D) seems to curve posteromesially up to the mesial side and it sometimes forms a tongue-shaped smooth surface (t, Fig. 3D) along the posterior margin.

In SBEI 003, the occlusal surface is rimmed laterally and forms a basin mesially. There is a radiated structure from the bottom of the basin. The surface is subdivided into two unevenly divided faces: the larger face is anterior from the primary ridge (oa, Fig. 3E) and the smaller face is posterior to it (op, Fig. 3E). The anterior face occluded against a dentary tooth and the posterior face against the adjacent posterior dentary tooth. The degree of the depression of the occlusal surface varies from one tooth to another. In SBEI 001, the lateral rim is far less distinctive and there is no radiated structure. Since the root was completely resorbed in all the specimens, the proximal side is reduced to merely a thin wall dividing the lateral and mesial sides.

The least resorbed tooth is a right maxillary tooth (NSM PV 20034, Fig. 5-11) from Okurodani Formation. It seems to have been a proximal half of the crown. It is 27 mm in dorsoventral length, 15 mm in anteroposterior length, and 9 mm in lateromesial length.

The most resorbed tooth is a left maxillary tooth (NSM PV 20036, Fig. 5-12) from Kuwajima Formation. It is reduced to only 4 mm in dorsoventral length, 7 mm in anteroposterior length, and 5 mm in lateromesial length. As far as this specimen is concerned, the last area to be resorbed seems to be the primary ridge and the posterior ridge.

Discussion

The described teeth are almost identical to the teeth of *Iguanodon* sp. (BMNH 36503). They are also similar to *I. atherfieldnesis* (NORMAN, 1986, fig. 22 FGH), *I.* sp. (NORMAN, 1980, fig. 20), *I.* sp. (MANTELL, 1848, pl. XVIII, fig. 2), and generalised iguanodontids (BMNH 1895).

The largest specimen is a right maxillary tooth (SBEI 001) from the Kasekiheki in Shiramine. It is 16 mm in anteroposterior length at the base of the enamel ridge. The tooth is comparable in size to that of *Iguanodon bernissartensis* (IRSNB 1536) whose jaw is approximately 650 mm in length (NORMAN, 1980, pl. 3). The skull size suggests that it might have been an individual of 3.5 m in height based upon the posture reconstructed in NORMAN (1980, fig. 75).

Earlier we raised the question: are the teeth alone characteristic enough? Although the described specimens are isolated and not even complete teeth, we believe that the teeth have enough characteristics to be identified as iguanodontid teeth, and even probably as those of *Iguanodon.* To confirm our claim, we made comparisons in the dentition beyond iguanodontids.

Iguanodontidae is a family of Iguanodontia which is a paraphyletic array of closely related forms (e.g. NORMAN & WEISHAMPEL, 1990: 528–531). NORMAN & WEISHAMPEL (1990: table 25.1) listed two families (Camptosauridae and Iguanodontidae) and four genera (three genera as Iguanodontia incertae sedis and *Probactrosaurus* as an unnamed taxon) as Iguanodontia.

Having very large primary ridge, in the maxillary tooth, arising from the base of the crown, the described teeth certainly fall into Iguanodontia. The maxillary teeth diagnosis quoted earlier precludes the possibility of the teeth falling into the three genera currently classified as Iguanodontia incertae sedis. They are *Rhabdodon*, *Muttaburrasaurus*, and *Craspedodon* (NORMAN & WEISHAMPEL, 1990: 519). *Probactrosaurus* is also excluded from the possibility as having ridges symmetrical on either side of the median primary ridge in maxillary teeth (NORMAN & WEISHAMPEL, 1990: 529). *Camptosaurus* seems to have a less pronounced primary ridge and it is far too small: 8 mm in anteroposterior length at the base of enamel shelf (from fig. 8 in GALTON, 1980) whereas it is 16 mm in SBEI 001 and 15 mm in SBEI 003, for example. The remaining candidate is Iguanodontidae which includes *Iguanodon* and *Ouranosaurus.* The dental morphology of the two genera is very similar (NORMAN, 1986: 328), but *Ouranosaurus* is much smaller: 9 mm in anteroposterior length at the base of enamel shelf (from fig. 67 in NORMAN, 1986). Therefore the specimens in question are likely to be *Iguanodon.*

The genus *Iguanodon* was founded by Gideon Mantell in 1825 on the basis of seven teeth which had been collected from the Tilgate Forest area of the Wealden of Sussex, England. It had been a tooth genus (not species!; see NORMAN, 1986: 283–285). Following some confusion, there are currently seven valid species of *Iguanodon* (NORMAN & WEISHAMPEL, 1990: table 25.1). It seems that inter-specific variations in the dentition are very little and the main differences are those of size (e.g. NORMAN, 1986: 294). "*Iguanodon*" *orientalis* is the only species reported so far from Asia. Although its skull has some distinctive characters especially in the premaxilla and nasal, the dentition does not seem to be distinguishable from the European *Iguanodon* such as *I. bernissartensis* and *I. atherfieldensis.* A maxillary tooth measures 12 mm in anteroposterior length at the base of enamel shelf (YNUGI 11002) and it is smaller than the typical English *Iguanodon* (20 mm in NSM PV 20035; 19 mm in YNUGI 11004). It is in accordance with the skull size differences; skull length is approximately 400 mm in "*I*" *orientalis*, where it is 850 mm in *I. bernissartensis* (NORMAN, 1980: 13). As far as the maxillary tooth size is concerned, the specimens from the Tetori Group are more like European *Iguanodon.*

Needless to say, our knowledge of variations in the dentition is very limited and, at this moment, we have not had the privilege of studying all the type specimens of the species currently classified as Iguanodontia. It is also not advisable to discuss systematics solely on the dentition. We therefore refrain from identifying the specimens herein beyond the level of the family.

Species of *Iguanodon* are best known from the Wealden of England, Belgium, Spain, France, and Germany, a unit that has been dated as Valanginian to Barremian. The Wealden is thought to represent extensive lagoonal or lacustrine mudflat habitats that are repeatedly invaded by progradational braided stream environment (WEISHAMPEL & BJORK, 1989: 64–65). The Tetori Group also represents a similar environ: the localities are interpreted as inter-channel deposits in fluvial and braided-delta plains (see Geological Setting in the text).

The iguanodontid teeth are some of the first vertebrate taxa, identifiable at the level of family, represented on both sides of the Hakusan divide: in Kuwajima Formation (Ishikawa Prefecture) and Amagodani/Okurodani Formation (Gifu Prefecture).

Iguanodontians had a Euramerican distribution in the Jurassic, and in the Early Cretaceous, they extended their distribution as far as Asia, Africa, and Australia. In the Late Cretaceous, they were greatly restricted and found only in Europe (NORMAN & WEISHAMPEL, 1990: 531). It is confirmed that the iguanodonts dispersed as far as the eastern edge of the Asian continent by Neocomian times which predates the appearance of "*I.*" *orientalis* and *Probactro-*

saurus in Mongolia in Aptian-Albian. There are more materials of the iguanodontids from the geologically younger Kitadani Formation of the Tetori Group (DONG *et al.*, 1990), and the iguanodonts from the Group are the first reported from East Asian Cratons, such as the Sino-Korean and Yangtze Cratons. This suggests that the group migrated to East Asia from Western Europe, the suggested centre of origin (WEISHAMPEL & WEISHAMPEL, 1983), before the Neocomian times. It also suggests the presence of a land connection in the Turgai Sea at that time, and the end of endemism in the dinosaur fauna in Asia.

The claim is also supported by the presence of a hypsilophodontid tooth which is believed to be from Amagodani Formation in Shokawa (HASEGAWA *et al.*, 1991). The occurrences of iguanodontids and hypsilophodontid suggest the existence of a "Wealden" type fauna in East Asia and its association in Japan not with the Indo-Europe palaeoflora, but with the Siberian palaeoflora (KIMURA, 1988).

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