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# Titanosauriform teeth from the Cretaceous of Japan

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**ABSTRACT**

Sauropod teeth from six localities in Japan were reexamined. Basal titanosauriforms were present in Japan during t
Early Cretaceous before Aptian, and there is the possibility that the Brachiosauridae may have been included. Bas
titanosauriforms with peg-like teeth were present during the "mid" Cretaceous, while the Titanosauria with peg-li
teeth was present during the middle of Late Cretaceous. Recent excavations of Cretaceous sauropods in Asia show
that multiple lineages of sauropods lived throughout the Cretaceous in Asia. Japanese fossil records of sauropods a
conformable with this hypothesis.

**Key words:** Sauropod, Titanosauriforms, tooth, Cretaceous, Japan.

## INTRODUCTION

Although more than twenty four dinosaur fossil localities have been known in Japan (Azuma and Tomida 1998, Kobayashi et al. 2006, Saegusa et al. 2008, Ohara 2008. Hirayama et al. 2010), most of them have provided isolated teeth and/or fragmentary bones, except for the Tetori Group in Katsuyama City of Fukui Pref. and Sasayama Group in Tamba City of Hyogo Pref. However, the dinosaur fossil bearing beds in Japan has contacts with tuff beds and/or index fossils bearing marine beds in many cases (Matsumoto et al. 1982). Thus, it is advantageous to know the detailed geologic ages. Therefore, even fragmentary fossils can very likely contribute to solve the evolutionary history of dinosaurs, if they are correctly identified.

Sauropod fossils have so far been reported from 8 localities in Japan (Hasegawa et al. 1991, Tanimoto and Suzuki 1997, Azuma and Tomida 1998, Tomida et al. 2001, Barrett et al. 2002, Saegusa et al. 2008, Azuma and Shibata 2010). Except for a badly preserved humerus from the Upper Cretaceous Miyako G
Moshi, Iwaizumi Town, Iwate Pref. (Hasegawa
1991), all other localities provided fossil teeth (
et al. 2001, Tomida and Tsumura 2006, Saegus
2008, Azuma and Shibata 2010). In this paper, the
pod teeth fossils from the Matsuo Group, Futaba
and Sasayama Group, which were directly exa
and those from three other localities, which w
scribed in other publications, were reexamined
geologic age and morphology. Based on this ex
tion, the kind of sauropods that lived in Japan dur
Cretaceous, and whether they are conformable w
fossil records of the titanosauriforms from other a
East Asia were discussed. In addition, an issue o
wear facet characters to identify isolated teeth w
discussed.

## MATERIALS AND METHODS

### TERMINOLOGY

The following terms are used as defined here.

broad ridge running parallel to the long axis (apicobasal axis) of the crown on its lingual surface (Barrett et al. 2002); Slenderness index (SI): the ratio of crown height to maximum mesiodistal crown width (Upchurch 1998, Barrett et al. 2002).

### Dental Orientation Terminology

Among the sauropod teeth with low SI value, the orientation of isolated teeth is being identified based on the asymmetry of mesiodistal and labiolingual directions of tooth morphology including skewness of apex and D-form cross section (e.g. Barrett et al. 2002, Takakuwa et al. 2008). On the other hand, among the sauropod teeth with high SI value, such asymmetry is often lost, and it is difficult to identify the tooth orientation. However, it is extremely difficult to describe the tooth morphology without using some kind of orientation terms. Therefore, among the isolated teeth without asymmetry in mesiodistal and/or labiolingual direction, we use expediently the terms "labial" and "lingual" for the directions in which the whole tooth crown curvature in mesiodistal view is convex and concave, respectively, "distal" for the side with better developed wear facet, and "mesial" with less developed or without wear facet. Using quotation marks indicates that the orientation terms may not be the same as true orientation. Except for these orientation terms for isolated tooth proposed above, the orientation terminology follows Smith and Dodson (2003).

### Wear Facet Types

The wear facet formed by tooth to tooth contact is characteristic in some of the basal Sauropoda and most of Eusauropoda, and is thought to be acquired in the early stage of the sauropod phylogeny (Carballido and Pol 2010). In this paper, we classified the wear facets into four types and used them to describe the tooth wear (Fig. 1). In the wear facet type 1, in which the upper and lower dentitions occlude each other, the facet is formed by both mesial and distal margins, and both facets meet at the apex forming a V-shaped facet. Either one of the mesial or distal facet is larger than the other in the major-gin is further enlarged, and the other one is extremely small. The enlarged facet more strongly faces lingually or labially, and crosses the long axis of the tooth by a low angle, the labiolingual axis by a high angle, and the mesiodistal axis by an angle of about 45 degrees. In type 3, only one of either mesial or distal facet is present (Fig. 2E). Because there still is a gap between the long axes of upper and lower teeth, the retained facet further skews mesially or distally. The facet crosses the labiolingual axis by a high angle, while it crosses the long, and mesiodistal axes by a low angle. This type corresponds to the oblique facet of Buffetaut and Suteethorn (2004, p. 156). The type 3 is typical on titanosauriforms, but the facet of the basal sauropod *Amygdalodon patagonicus* (Carballido and Pol 2010) is also type 3. In type 4, the facet is present at the center of the tooth and crosses the labiolingual axis by a high angle and the long axis by a low angle, but does not cross the mesiodistal axis of the tooth. Type 4 is seen on the titanosauriforms (e.g. Upchurch 1999, Fig. 4; Curry Rogers and Forster 2004, Fig. 32). It is supposed that the long axes of upper and lower teeth match each other. Two or three of these four types often co-exist on the dentition of a single individual or on a single tooth.

## SAUROPOD TEETH FROM THE CRETACEOUS IN JAPAN

### 1) An Isolated Sauropod Tooth from Sebayashi Formation of Gunma Prefecture (Table I)

An isolated sauropod tooth (NDC-Use 0001) was found in the lower member of the Sebayashi Formation at Kamigahara, Kan-na Town, Gunma Pref. by the joint project of Gunma Pref. Museum of Natural History and Kan-na Town Dinosaur Center (Takakuwa et al. 2008). The specimen NDC-Use 0001 is called the Sebayashi sauropod tooth hereafter. The sauropod-bearing lower member of the Sebayashi Formation can be correlated to the Barremian (see Appendix).

Takakuwa et al. (2008) reported the occurrence of a sauropod tooth fossil from the Sebayashi Formation and discussed its stratigraphic horizon and the significance of the fossil occurrence, but did not describe its morphology. Fortunately, because Takakuwa et al.

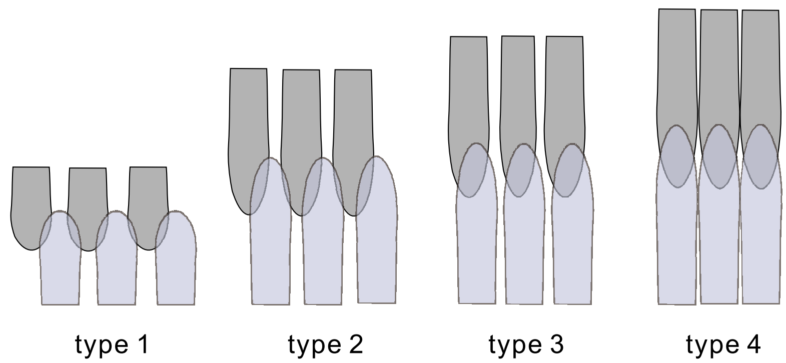


Fig. 1 – Model of wear facet types of the sauropod teeth. Upper and lower teeth are indicated by dark and light colors, respectively.
differences, among the wear facet types, in presence/absence, positions, and size of the facets that would be made at the area where the u
lower teeth overlap.

**TABLE I**
**Measurements (in mm) and SI values of sauropod teeth from Japan.**

| specimen | specimen number | maximum height of crown | maximum mesiodistal width of crown | SI | Reference |
|---|---|---|---|---|---|
| Toba sauropod tooth | | 19.5 | 9.6 | 2.03 | pers. obs. |
| Sebayashi sauropod tooth | NDV-USe0001 | 20.5 | 10.2 | 2.01 | Takakuwa et al. 2008 |
| Tamba sauropod | 090227IS02 | 44.6 | 9.2 | 4.85 | pers. obs. |
| Tamba sauropod | 090221IS13 | 32.5 | 8.5 | 3.82 | pers. obs. |
| Tamba sauropod | 070225-43 | 21.6 | 6.5 | 3.32 | pers. obs. |
| Kohisa | IMCF No. 959 | 31.1< | 7.5 | 4.2< | pers. obs. |

diameter does not change from the cervix to the middle height of the crown. The apical half of the crown is spatulate and asymmetrical mesiodistally, and the apex is located more mesially and curves lingually. There is a weak mesial protuberance right below the apex in labiolingual view, but a clear increase of width in the mesiodistal direction is also not seen in the apical half. The wear facet type 1 is developed on the mesiodistal margins, and the facet on the distal margin is more developed than the mesial one. Whether the lingual ridge and the labial groove are present can not be judged only by photos.

2) An Isolated Sauropod Tooth from Matsuo Group of Toba City, Mie Pref. (Fig. 2A; Table I)

sauropod hereafter). The geologic age of the
Group is the Valanginian to Barremian (see App
The partial skeleton of the Toba sauropod was
vated by the Dinosaur Research Group of Mie
ture organized by the Mie Pref. Museum in 19
Tomida et al. (2001) and Tomida and Tsumura
described it as a member of Titanosauria. A gr
amateur fossil collectors visited the same loc
1998 and collected a sauropod caudal vertebra
(Fig. 2A), and some fragmentary bones (Tanim
Mizutani 1999a, b, Tanimoto and Kishimoto 199
sauropod tooth (it is called the Toba sauropo
hereafter) was collected by Mr. Takao Mizutani
currently in his private collection. A cast of the
stored at the Museum of Nature and Human Ac

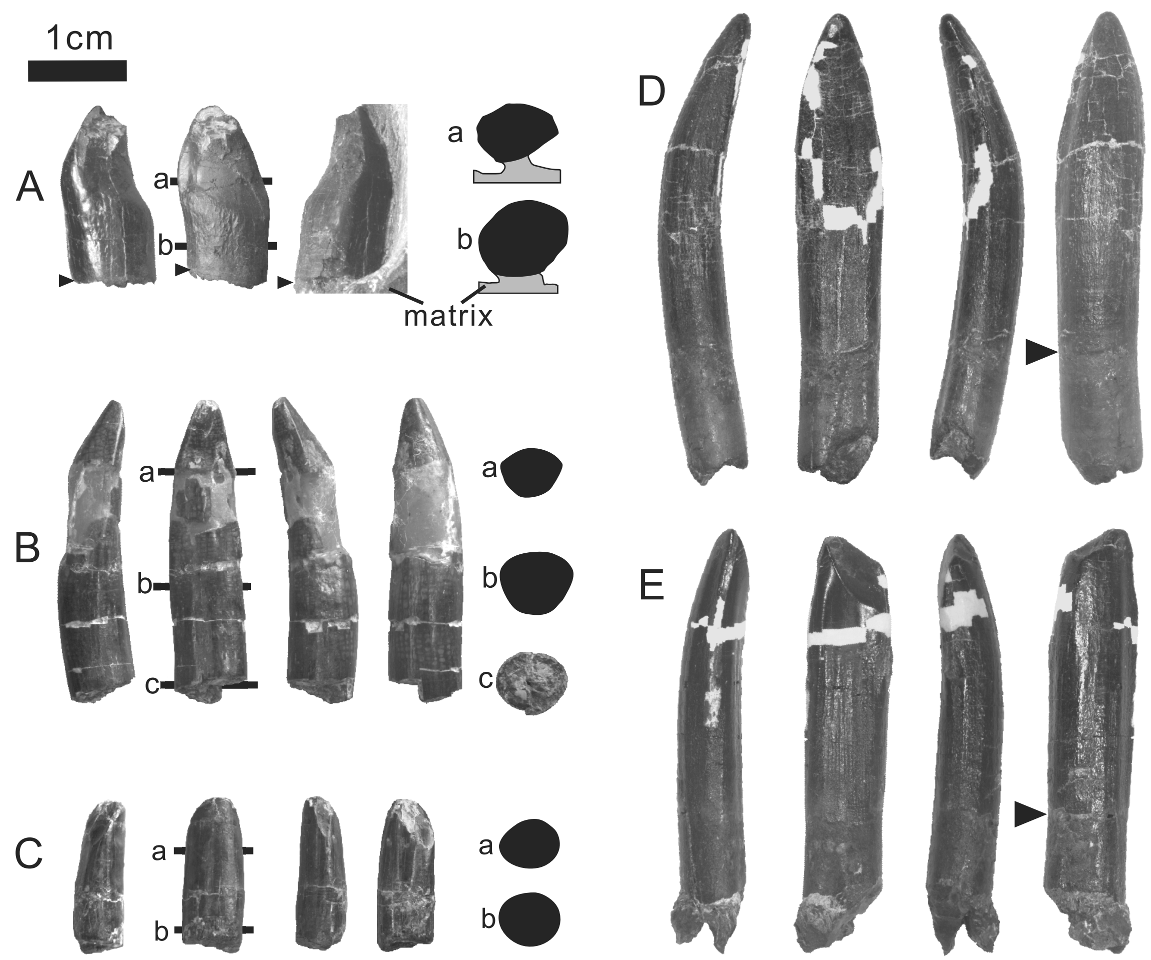


Fig. 2 – Sauropod teeth from Japan. A: Sauropod tooth from the Matsuo Group (the Toba sauropod tooth); B and C: Sauropod teeth from the Futaba Group (the Kohisa specimens), IMCF no. 959 and 1122, respectively; D and E: Sauropod teeth from the Sasayama Group (the Tamba sauropod). In A, the three photos from left to right are in mesial, lingual, and distal views, respectively. In B through E, the four photos from left to right are “mesial”, “lingual”, “distal”, and “buccal” views, respectively. In A, D, and E, a solid triangle indicates the position of the cervix. In A to C, silhouettes and photos arranged from top to bottom on the right side are horizontal cross sections of the tooth, and their positions are indicated by horizontal lines with small letters a, b, and c. In horizontal cross sections of A to C, lingual is to the top, and distal is to the right of the page.

sauropod) of Titanosauria excavated by the Mie Pref. Museum. The partial skeleton of the Toba sauropod was found in a narrow area within a single horizon, and no duplication of skeletal elements was observed. Based on these conditions and the fact that the fossil bearing bed is shallow marine sediment that is supposed to be deposited by a storm event, the partial skeleton of the Toba found in a float nearby the exposure where Toba sauropod was excavated, and there is no other exposure that includes bone fossils.

The Toba sauropod tooth preserves the crown nearly complete except for the tip, but the root is missing at right below the cervix. The crown is asymmetric mesiodistally. The basal one-third of the crown has lingual surface, the apical two-thirds of the crown is smooth, concave apicobasally and convex mesiodistally. The specimen is divided into two parts by the lingual ridge that is located more mesially than the mid line. Because of this, the surface distal to the lingual ridge is mesiodistally wider and extends more basally than the mesial side. The crown apex is located on the extended line of the lingual ridge and more mesially than the midline, but is somewhat broken. Although the central part of the labial surface is in the matrix, it is convex mesiodistally and apicobasally, and is wrinkled, based on the exposed part. The point where the labial surface projects most labially is located more mesially than the midline as in the lingual ridge. Although the labial surface is mostly free from the matrix, the labial groove is not seen. The wear facet type 1 is developed on the mesial and distal margins, and the facet on the distal margin is more developed than the mesial one.

The Toba sauropod tooth was first identified as Titanosauroidea fam. gen. et sp. indet. by Tanimoto and Mizutani (1999a), then as Nemegtosauridae gen. et sp. indet. later (Tanimoto and Mizutani 1999b). However, Barrett et al. (2002) denied both identifications and identified it as a member of the Titanosauriforms.

#### 3) Sauropod Teeth from the Kuwajima Formation, Tetori Group of Shiramine, Ishikawa Prefecture

Multiple sauropod teeth, together with other vertebrate fossils, were collected from the Kuwajima Formation at Kuwajima, Hakusan City, Ishikawa Pref., when a tunnel was built (Matsuoka 2000). The geologic age of the Kuwajima Formation is the late Hauterivian – early Barremian (see Appendix). These teeth from the Kuwajima Formation are called the Kuwajima sauropod teeth hereafter. These teeth consist of 9 teeth, which were described in detail by Barrett et al. (2002), but some notes on the facet and SI are given below. The wear facet of the Kuwajima sauropod teeth is all type 1, except for one specimen (SBEI 583), which shows type 4. In terms of SI, Barrett et al. (2002) mentioned that they would be between 2 and 3, and SI and measurements of individual tooth were not given. Electronic supplementary material (ESM hereafter) of Chure et

(2002). The SI value between 2 and 3 by Barre
(2002) is used in this paper.

#### 4) Sauropod Teeth from the Kitadani Forma
Katsuyama City, Fukui Prefecture

Kitadani Formation of the Tetori Group that is e
along the Sugiyama River in Katsuyama City,
Pref, has provided many dinosaur fossils, includ
theropod *Fukuiraptor kitadaniensis* and the orni
*Fukuisaurus tetoriensis*, as well as some sauropo
through several excavations (Azuma 2003). Th
logic age of the Kitadani Formation is estimated
Barremian (see Appendix). Recently, a new ger
new species of titanosauriform, *Fukuititan nippo*
was described based on a partial skeleton and
ated teeth (Azuma and Shibata 2010). It is clear
*nipponensis* is a basal titanosauriform, but becau
sil material is limited to isolated teeth, incomple
bones, fragmentary vertebrae, and some other fra
tary postcranial bones, its phylogenetic relationsh
other titanosauriforms is unknown. In terms of th
isolated teeth associated with the partial skeleto
a short and simple description was given in Azu
Shibata (2010). Based on this description and
we can presume they are extremely asymmetric
distally, their labial surface is convex, and a weal
groove is either present or absent. The lingual su
weakly concave and is subdivided into two parts,
and distal, by the lingual ridge. The measureme
not given, but based on the photos, SI is between
2.5. The wear facet is not described.

#### 5) Sauropod Teeth from Sasayama Group of Tamba City, Hyogo Prefecture (Fig. 2D, E; Table I)

Part of a sauropod skeleton (called the Tamba
pod hereafter) was found in the “lower formatio
Appendix) of the Sasayama Group that is expo
a riverbank at Kamitaki, Tamba City, Hyogo P
amateur paleontologists in 2006. The geological
the “lower formation” of the Sasayama Group
Aptian-Cenomanian (see Appendix).

Through the excavations of four winter s pod, as well as teeth of other dinosaurs and small vertebrate fossils such as squamates and anurans, have been collected (Saegusa et al. 2008, Saegusa et al. 2010a). Although the preparation of the Tamba sauropod has not been completed, it is certain that the Tamba sauropod is one of the basal titanosauriforms (Saegusa et al. 2008). Twenty six sauropod teeth have been found in the Tamba sauropod locality, and at least six are considered to belong to a single individual based on the occurrence and preservation condition (Saegusa et al. 2010a). The crown somewhat widens mesiodistally at the level of the middle height of the crown, and from this point, the distinct (but without serrations) mesial and distal carinae extend toward the apex, narrowing the distance to each other, and end at the apex. The horizontal cross section of the apical half of the crown is D-shaped, with the labial surface strongly convex and the lingual surface slightly convex. On the other hand, the mesial and distal carinae run nearly parallel from the middle height of the crown toward the cervix and disappear near the cervix. The horizontal cross section of the crown near the cervix and that of the root are oval to circular in outline, and the diameter of the tooth does not change from this point to the root apex. The crown height of the Tamba sauropod teeth is relatively high and is similar to that of the Titanosauria. Although the teeth show comparatively derived morphology among the titanosauriforms, following two characters are relatively primitive: the horizontal cross section of the crown at middle height is D-shaped, and the mesial and distal carinae are distinct. In the Tamba sauropod, thirteen teeth have the wear facet type 3 (Fig. 2E), while only two teeth show type 2 wear facet.

### 6) Two Teeth from Futaba Group of Iwaki City, Fukushima Prefecture (Fig. 2B, C; Table I)

Two damaged sauropod teeth (IMCF No. 959 IMCF No. 1122) were found at Minamizawa, Kohisa, Iwaki City, Fukushima Prefecture, by amateur paleontologists in 1986 and 1987, and they are now housed at the Iwaki Museum of Coal and Fossils. They are called Kohisa specimens together hereafter. Kohisa specimens were

Kohisa specimens are supposed to be found from the Tamayama Formation of Futaba Group. The geologic age of the middle or lower member of the Tamayama Formation that produced Kohisa specimens is the late Coniacian (Appendix).

The specimen represented by the collection number IMCF no. 959 (Fig. 2B) is a peg-like tooth. It is broken into three pieces: apical, basal, and lingual fragments of the middle part, and all three pieces are connected and repaired by wax. This fixed part by wax is between 8 and 19 mm from the apex, but none of these three pieces have any direct contact, and the accuracy of these joints is unknown. It seems that the curvature at the fixed part in mesiodistal view is somewhat too strong, but a weak curvature is present on the basal fragment in mesiodistal view, and the direction of this curvature matches with the curvature of the whole tooth made by repair. The basal end of the basal piece is broken surface, and no dental pulp cavity nor cervix can be seen. This breakage surface is oval (7.9 × 6.8 mm) in outline, but the horizontal cross section of the tooth 15 mm above the bottom is rounded trapezoid, and weak carinae appear at mesial and distal edges. The carinae continue to the apical piece, become more distinct toward the apex, and continue to the apex. The labiolingual diameter begins to reduce at a point where carinae appear on the basal piece, and continues to reduce the diameter until the apex. The apical piece is divided into labial and lingual surfaces by carinae, and both surfaces are convex, but the labial one is more strongly. A few millimeters of the crown apex are missing. Contacting with this broken surface, the wear facet type 3 (apicobasal length is ca 3 mm) in the apex is present on the lingual surface, and it contacts the "distal" carina. The surface of the basal part of the basal piece is wrinkled, but the surface of other parts of the tooth is smooth and unwrinkled because the enamel surface is polished.

The specimen IMCF no. 1122 (Fig. 2C) is a fragment of the apex area of a worn tooth, and the apex surface is unnatural because of breakages. The surface of the most preserved part is polished, smooth and unwrinkled. No carina is seen. The apicobasal length of apical direction is very limited. IMCF no. 1122 shows the wear facet type 2 and has a pair of large and small wear facets. Because the horizontal cross section of the apex is oval, the labiolingual asymmetry of the cross section cannot be used for orientation identification. However, a slight curvature in the labiolingual direction is seen on the remained crown part in mesiodistal view, and because of this, it is interpreted that a large wear facet is present on the "labial" and a small wear facet on the mesial edge. The large wear facet crosses the labiolingual and mesiodistal axes by higher angles, and the long axis by a lower angle.

## COMPARISONS

All the sauropod teeth from six localities in Japan show the well-developed wrinkled enamel, except for the area where the enamel is worn. This character is shared by the Eusauropoda (Wilson and Sereno 1998) and following basal Sauropoda: *Tazoudasaurus*, *Gongxianosaurus*, *Chinshakiangosaurus*, and *Amygdalodon* (Allain and Aquesbi 2008, Upchurch et al. 2007a, b, Carballido and Pol 2010). Therefore, these teeth from six localities in Japan, which are mentioned in the above section, are all identified as sauropods teeth.

The Sauropod teeth from these six localities in Japan can be divided into two groups: the first group with SI value 3 or less, and the second group with SI value over 3 (Table I). The first group consists of the Early Cretaceous sauropod teeth from four localities in Japan of Barremian or earlier in age (Fig. 3; Table I). The crown does not strongly widen mesiodistally right above the cervix, the tooth is mesiodistally asymmetrically spatulate, and SI is between 1.7 and 3. The Toba sauropod tooth (Fig. 2A) and one tooth of *Fukuititan nipponensis* show somewhat a stronger mesiodistal widening compared to the Kuwajima sauropod teeth and the Sebayashi sauropod tooth. However, the differences of this kind and amount can be observed on the same dentition of a single individual, such as *Brachiosaurus* (Janensch 1935-1936) and *Euhelopus* (Wiman 1929), and cannot be used as taxonomic indices.

Because the teeth of *Fukuititan nipponensis* and

group, the Kuwajima sauropod teeth and the Seb
sauropod tooth are somewhat problematic. The
between 2 and 3. Because the lower limit of t
served range of SI is larger than 3 in Diplodo
and derived Titanosauria (Electronic supplemen
rial of Chure et al. 2010), the possibility of any
docoidea and derived Titanosauria being included
first group is almost zero. However, in non-Neo
poda from the Jurassic of China, such as *Shuno*
*Mamenchisaurus*, *Omeisaurus*, and several taxa
basal Titanosauriformes, the upper limit of the ob
range of SI is 3 or close to it (Barrett and Wang
Electronic supplement material of Chure et al.
Thus, based on the SI value alone, the possib
the Kuwajima sauropod teeth and the Sebayashi
pod tooth being one of these taxa cannot be re
Fortunately, the Kuwajima sauropod teeth and t
bayashi sauropod tooth can possibly be separate
the Jurassic non-Neosauropoda from China. By c
isons with photos of published papers, the teeth
separated based on the following aspects: in the
jima sauropod teeth and the Sebayashi sauropod
the mesiodistal diameter of the crown shows alm
change from the cervix to the middle height
crown, expands slightly mesially at the middle
and then reduces toward the apex. In other wor
mesiodistal diameter at any height within the crow
not exceed that of cervix. On the other hand, in
*saurus lii*, *Omeisaurus junghsiensis*, and *Euhelop*
tooth crown is ovate to lanceolate with a rounde
in labiolingual view, and the mesiodistal diam
the crown increases from the cervix toward the
becomes maximum at the point between 1/3 a
height from the base, and reduces from this po
ward the apex (Zhang 1988, plate 5; Chatterj
Zheng 2002, Fig. 4; Dong et al. 1983, plate 8;
1929, plate 2). In *Omeisaurus tianfuensis* and *O*
*ianus*, the mesiodistal diameter of the crown in
from the cervix toward the apex, becomes ma
at a height between 1/2 and 2/3 from the bas
reduces very quickly toward the apex (He et al
Figs. 16-17; Tang et al. 2001, Fig. 15). This

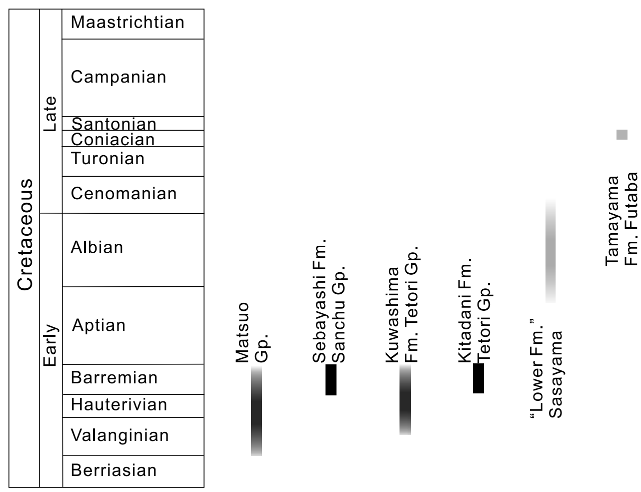


Fig. 3 – Geologic age of the sauropod bearing formations in Japan. The formations indicated by black bars (left four bars) provided the sauropod teeth, with the SI value less than 3, while those indicated by gray bars (right two bars) provided those with the SI value over 3.

distal to these are obovate to oblanceolate (Russell and Zheng 1993, pl. 2; Ouyang and Ye 2002, Figs. 8-10). In addition to the crown outline in labiolingual view, *Shunosaurus*, *Mamenchisaurus*, and *Omeisaurus* differ from the Kuwajima sauropod teeth and the Sebayashi sauropod tooth in having prominent ridges that surround the lingual concavity (Barrett and Wang 2007). Considering the geologic age, *Shunosaurus*, *Mamenchisaurus*, and *Omeisaurus* are from Jurassic of Asia, and the possibility of these genera or non-neosauropods similar to them being included in the first group is very low.

On the other hand, some teeth of *Brachiosaurus* and similar basal titanosauriforms share characters with the Kuwajima sauropod teeth and Sebayashi sauropod tooth. In *Brachiosaurus* dentition, the dental morphology varies widely, and the distal teeth are obovate to oblanceolate, while the mesial teeth are cylindrical in type. So, the mesiodistal diameter does not change much from the cervix to the middle height of the crown (Janensch 1935-1936, pls. 11-12). The teeth of following dinosaurs can probably be included in this category of cylindrical type tooth: *Paluxysaurus jonesi* (Rose 2007), *Astrodon johnsoni* (Carpenter and Tidwell 2005), and *Pleurocoelus*-like tooth (Ostrom 1970, plate 14) from the Early Cretaceous of North America, tooth

Khao Formation of Thailand (Buffetaut and Suteethorn 2004), and *Asiatosaurus mongoliensis* from the Early Cretaceous of Mongolia (Osborn 1924).

Thus, the character that the mesiodistal diameter at any height of the crown clearly exceed the mesiodistal diameter at the cervix has been widely observed in presumable brachiosaurid taxa, but it does not necessarily mean that this character is shared with all members of the Brachiosauridae. Further comparisons with the tooth morphology of the taxa that are classified in the Brachiosauridae follow. As a result of cladistic analysis, or based on the reason that derived characters shared only with *Brachiosaurus* are present, the following taxa are classified as sister taxon of *Brachiosaurus*: *Cedarosaurus weiskopfae* (Tidwell et al. 1999), *Sauroposeidon proteles* (Wedel et al. 2000a, b), *Paluxysaurus jonesi* (Rose 2007), *Qiaowanlong kangxii* (You and Li 2009), and *Abydosaurus mcintoshi* (Chure et al. 2010). Although *Cedarosaurus* was originally classified in the Brachiosauridae based on the ratio of limb bone length (Tidwell et al. 1999), recent cladistic analyses indicate it either as a sister taxon of *Brachiosaurus* (Wilson and Upchurch 2009), or a non-sister taxon (Rose 2007, Canudo et al. 2008, Hocknull et al. 2009). Therefore, it may be possible that *Cedarosaurus* is not Brachiosauhas cylindrical teeth, and a V-shaped facet is present (Rose 2007). On the other hand, the wear facet of the tooth in *Abydosaurus* is only elliptical on the mesial edge, and no V-shaped facet is present (Chure et al. 2010). The upper teeth are twisted 45 degrees along the longitudinal axis, while the lower teeth are not twisted (Chure et al. 2010). Thus, *Abydosaurus* teeth show a different morphology from *Brachiosaurus*. So, the tooth and wear facet morphology is diverse among the Brachiosauridae, and the cylindrical teeth may be a character that is shared by only part of that family, such as *Brachiosaurus*. Therefore, the first group of teeth with SI value 3 or less from four Japanese localities and whose age is the Barremian or older, may include *Brachiosaurus* or similar taxa within the Brachiosauridae, and further detailed comparative study may be capable of identifying it.

On the other hand, sub-circular swelling or boss developed on the unworn part of the lingual crown surface (Barrett and Wang 2007, Wilson and Upchurch 2009, Amiot et al. 2010), which is characteristic in *Euhelopus*, is not seen on any teeth of the first group. Therefore, the possibility that *Euhelopus* and basal titanosauriforms similar to it are included in the first group is extremely low. Thus, the possibility that the first group includes basal titanosauriforms other than *Euhelopus*, especially *Brachiosaurus* and other similar taxa is quite high.

The wear facet of Japanese sauropod teeth from the Barremian or older, which is classified as the first group mentioned above, is all type 1, except for one of the Kuwajima specimens (SBEI 583) that shows a wear facet type 4. A condition that few teeth of type 4 are mixed in the majority of type 1 teeth within a same dentition is possible among the basal titanosauriforms. In *Brachiosaurus*, in addition to the V-shaped wear facets (that are type 1 or 2), a wear facet developed on the crown apex (that is type 4 or 3) is present on a same dentition (Janensch 1935-1936, Upchurch and Barrett 2000).

Among the Japanese sauropods, teeth of the second group from the mid-Cretaceous or younger age of

accompanying the decline and extinction of the
do-coidea in the mid-Cretaceous and later, it is t
that they have evolved in the Titanosauriforme
(Upchurch 1995, 1998, Wilson and Sereno 199
rett et al. 2002, Barrett and Upchurch 2005, C
al. 2010). Therefore, the SI value alone cannot s
the Diplodocoidea from derived Titanosauriform

Except for the horizontal cross section be
shaped, the Tamba sauropod teeth (Fig. 2D,
superficially quite similar to those of the diplo
*Dicraeosaurus* in SI value (electronic suppleme
terial of Chure et al. 2010), the presence of
at the middle height of the crown (Upchurch an
rett 2000; Janensch 1935-1936), and the outline
crown (compare Fig. 2 of this paper and pl. 12
nensch 1935-1936). However, because the Tamba
pod teeth were unearthed with a partial skeleton
ing the characters of the Titanosauriformes, the
similarity is a result of convergence. The Tamba
pod teeth are also very similar to those of *Ph*
*gosaurus* in that the horizontal cross section
tooth is labiolingually flattened and D-shaped,
value (electronic supplement material of Churc
2010), and in that the wear facet type 3 is domin
Saegusa's personal observation). However, the
sauropod is totally different from *Phuwiangosa*
the morphology of caudal vertebrae, ribs, and iliu
is clearly a different genus (Saegusa et al. 2010b)
the similarity of teeth in both taxa is likely a conve

The Kohisa specimens from the Futaba Gro
isolated teeth only (Fig. 2B, C). Because of the
age, the SI of Kohisa specimens is only known
4.2 (Table I). However, because the ratio of the
lingual diameter of the crown over mesiodistal di
is larger in the Kohisa specimens than the Tamba
pod, it can be said that the Kohisa specimens ar
derived than the Tamba sauropod and *Phuwiango*
Carinae are less developed in the Kohisa spe
than the Tamba sauropod. High SI value and the
ical to cylindrical horizontal cross-section are
ters seen in both the Titanosauria and Diplodo
Recently, the first Asian diplodocoid was found

But the possibility that the diplodocoids continued up to the Coniacian is fairly low. According to the fossil records of South America, the youngest age of the specimen surely be diplodocoid is the Coniacian in Argentina (Gallina and Apesteguía 2005, Apesteguía 2007). Considering the gaps in geography and the geologic age, the possibility that the Kohisa specimens are diplodocoids is extremely low, and it is more reasonable to consider the Kohisa specimens as being Titanosauria.

The Kohisa specimens were described as cf. *Nemegtosaurus* sp. by Tanimoto and Suzuki (1997), then identified as *Nemegtosaurus* sp. by Tanimoto et al. (2006). Their bases to identify so are their peg-like morphology and the V-shaped facet (which corresponds to the wear facet type 2) seen on IMCF no. 1122. Tanimoto and Suzuki (1998), Tanimoto and Mizutani (1999b), and Tanimoto et al. (2006) thought that the V-shaped facet was diagnostic for the Nemegtosauridae, and included *Huabeisaurus* (Pang and Cheng 2000), the Toba sauropod tooth, and *Borealosaurus* (You et al. 2004), all of which with facets of this type, in the Nemegtosauridae.

However, the V-shaped facet and the peg-like crown morphology alone cannot decide for Nemegtosauridae or *Nemegtosaurus*. The Peg-like crown is a form that has evolved in multiple lineages by convergence. V-shaped facet itself, which is another character that Tanimoto and his colleagues emphasized, is considered to be rather plesiomorphic within the Titanosauriformes and cannot be the diagnosis of a monophyletic group.

The V-shaped facet (wear facet types 1 and 2) is a character that basal sauropods acquired (Allain and Aquesbi 2008, Carballido and Pol 2010). Except for the most distal teeth of some taxa, the V-shaped wear is developed on the teeth of basal Eusauropoda and basal Macronaria such as *Camarasaurus* (Calvo 1994, Salgado and Calvo 1997, Wilson and Sereno 1998, Upchurch and Barrett 2000, Chatterjee and Zheng 2002). Although the V-shaped wear is supposed to be formed by the occlusion of the upper and lower teeth (Fig. 1), the occlusion style had changed in Diplodocoidea and Titanosauriformes, and another facet, which differs from the V-shaped wear facet, appeared (Calvo 1994, Wilson and Barrett 2000, Wilson and Upchurch 2009), the wear facet that crosses the longitudinal axis by a low angle (wear facet type 4 of this paper) is developed in *Brachiosaurus* and Titanosauria (Calvo 1994, Salgado and Calvo 1997, Wilson and Sereno 1998, Upchurch and Barrett 2000, Curry Rogers and Forster 2004, Novas 2009). The V-shaped wear facet is a primitive character in the Titanosauria, and the idea that the V-shaped facet is diagnostic for the Nemegtosauridae by Tanimoto and Suzuki (1998), Tanimoto and Mizutani (1999b), and Tanimoto et al. (2006), is not acceptable. However, there were some taxa with V-shaped facet among the Titanosauria (including *Nemegtosaurus*) in East Asia, as Tanimoto and his colleagues mentioned, and if the Titanosauria in South America actually possesses teeth only with wear facet type 4, on the other hand, this character can possibly be autapomorphic for South American Titanosauria and would be useful in the identification of isolated teeth.

Tanimoto and his colleagues (Tanimoto and Suzuki 1998, Tanimoto and Mizutani 1999b, Tanimoto et al. 2006) interpreted that the co-presence of V-shaped facet (types 1 and 2) and low angle wear facet (type 4 of this paper) on the same single dentition is a unique character restricted to *Nemegtosaurus* and closely related taxa of Asia, and thought that it would be diagnostic for the Nemegtosauridae. In fact, *Huabeisaurus* (Pang and Cheng 2000) and *Borealosaurus* (You et al. 2004) are the only taxa whose teeth are peg-like among the Asian Titanosauria other than *Nemegtosaurus*, and they both have V-shaped facets. Thus, they seem to support the interpretation of Tanimoto and others. However, this fact does not support the idea that Titanosauria with a V-shaped facet is unique to Asia. Although *Nemegtosaurus* is the only narrow crowned titanosaurs whose full dentition has been described (Wilson 2005), diverse types of facets are seen on the teeth from areas other than Asia when descriptions of isolated teeth of other Titanosauria are examined. Isolated teeth of *Karongasaurus* from the lower Cretaceous of Malawi were found together with the skeleton, and show the wear facet type 4 and type 1 or 2 (Gomani 2005). Nuserved: type 4 only, facets developed on both lingual and labial surfaces, which is similar to those of *Nigersaurus* (Sereno and Wilson 2005), and facets developed on labial and mesial or distal surfaces (Kellner 1996). Because the skeletal fossils from the Bauru Group is represented by Titanosauridae within sauropods, these isolated teeth are identified as Titanosauria (Kellner 1996).

In *Alamosaurus* (Kues et al. 1980) and *Rapetosaurus* (Curry Rogers and Forster 2004), isolated teeth are found with the skeleton, and teeth with the facet type 4 are illustrated. These reports seemingly support the view that some titanosaur species have the wear facet type 4 dominant or type 4 only. However, in order to confirm the dominance of the wear facet type 4 over other facet types in these species, some statistical tests, for instance G-test (Sokal and Rohlf 1995), should be conducted. Unfortunately, the above two reports do not fulfill this requirement. In case of *Rapetosaurus*, the number of teeth showing type 4 facet is not reported (Curry Rogers and Forster 2004) and, thus, a statistical test for this species is currently impossible. As for *Alamosaurus*, the tooth described as having type 4 facet is the only tooth of *Alamosaurus* whose wear facet has been described (Kues et al. 1980).

Isolated peg-like teeth with the facet type 4 are reported from the Kem Kem Group in Morocco, but without the skeleton, and the reason for identifying them as Titanosauria is the low angle wear facet (type 4) (Sereno et al. 1996, Kellner and Mader 1997). These Moroccan sauropod teeth cannot be the evidence that there were Titanosauria with the facet type 4 dominant or type 4 only, because the presence of type 4 facet itself was the criterion used for the taxonomic identification of Moroccan sauropod teeth.

There is no definitive evidence that there were Titanosauria with the facet type 4 dominant or type 4 only. Rather, wear facets are diverse among the Titanosauria from areas other than Asia, and it may not be strange to find some taxa with V-shaped facets (types 1 and 2) and low angle wear facet (type 4). It is obvious that reliable examples of descriptions on wear facets are too

**DISCUSSION**

Although fossil material in Japan is poor, such
information of foreign material to compare wit
the following statements can be made. During th
Cretaceous, Barremian or older there were basal
sauriforms existed in Japan, and it may be possi
the brachiosaurids were included in this group.
the mid Cretaceous, the titanosauriforms with p
teeth were present in Japan, and Titanosauria wi
like teeth were present during the Coniacian (Fig

These fossil records of sauropods in Jap
conformable with the results in China, Mongol
far eastern Russia where even during the Late
ceous the multiple lineages of sauropods were p
From the Late Cretaceous of these areas, the
ing sauropods are known: *Huanghetitan ruya*
(Lü et al. 2007), *Dongyangosaurus sinensis* (L
2008), *Ruyangosaurus giganteus* (Lü et al. 2009
*tianmansaurus henanensis* (Zhang et al. 2009),
*xiusaurus youjiangensis* (Mo et al. 2008), *Sonid*
*saihangaobiensis* (Xu et al. 2006), *Huabeisaur*
*cotus* (Pang and Cheng 2000), *Borealosaurus*
(You et al. 2004), *Nemegtosaurus mongoliens*
winski 1971), *Opisthocoelicaudia skarzynskii* (
Bialynicka 1977), *Quaesitosaurus orientalis* (Ku
and Bannikov 1983), and *Arkharavia heterocoeli*
ifanov and Bolotsky 2010). The following multip
of the sauropods are reported from the Late Cret
in Europe: *Atsinganosaurus velauciensis* (Garc
2010), *Lirainosaurus astibiae* (Sanz et al. 1999),
*losaurus atacis* (Le Loeuff 1995), and *Magyaro*
*dacus* (Nopcsa 1915). Therefore, it is possible
sider that the diversity of sauropods was mainta
Eurasia during the Cretaceous. On the other h
is known in North America that the sauropod
became extinct at the Albian/Cenomanian bo
(Lucas and Hunt 1989, Maxwell and Cifelli 200
liamson and Weil 2008), then suddenly migrate
another continent in the Maastrichtian (D'Emi
2010). Thus, the diversity of sauropods had be
until the Late Cretaceous in most areas in the N
Hemisphere, except for North America, and the e

fossils from the Late Cretaceous in Eurasia have detailed information at stage level on the geologic age. Undescribed sauropod teeth from the Turonian Dzharakuduk Formation in Uzbekistan (Sues and Averianov 2004) and the Kohisa specimens from the Coniacian Futaba Group in Japan are the only exceptions. Therefore, the latter are the fossils with highly reliable geologic age and have a certain value, although they are isolated poorly preserved sauropod teeth. Thus, although Japanese dinosaur fossils are mostly poorly preserved, the fossil bearing beds often interfinger with tuff beds that make age measurements possible and marine beds that contain index fossils, and it is expected that they will contribute at a certain level to discussions on the sauropod distributional change and evolutionary history, if they are identified correctly.

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**RESUMO**

Dentes de saurópodes de seis localidades no Japão foram reexaminados. Titanosauriformes basais estiveram presentes no Japão durante o Cretáceo Inferior antes do Aptiano, e existe a possibilidade de que os Brachiosauridae integrassem este grupo. Titanosauriformes basais com dentes similares a pregos estiveram presentes durante o Cretáceo Médio, enquanto Titanosauria com dentes similares a pregos estava presente durante meados do Cretáceo Superior. Escavações recentes de saurópodes do Cretáceo na Ásia mostraram que múltiplas linhagens de saurópodes viveram ao longo do Cretáceo na Ásia. Registros fósseis japoneses de saurópodes são concordantes

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## APPENDIX

The geological age of the sauropod bearing forn of Japan

### 1) SEBAYASHI FORMATION

The lower member of the Sebayashi Formatio non-marine sediments (Matsukawa 1983) and d contain any marine invertebrates as index fossils ever, the uppermost part of the underlying Ishi mation is interpreted as Barremian based on th tained ammonoid fossils (Matsukawa 1983), and per member of the Sebayashi Formation is inte as Barremian to Aptian based also on ammon sils (Matsukawa and Obata 1988, Terabe and Ma 2009). Therefore, the sauropod-bearing lower n of the Sebayashi Formation can be correlated Barremian.

### 2) MATSUO GROUP

the upper Berriasian to Hauterivian (Honda 2001), Valanginian to Barremian (Kawabata 2001), and $138 \pm 7$ Ma (Saka 2001), respectively, which are somewhat different from each other. The basis of the molluscan age is an occurrence of Shirai type non-marine molluscs of Matsukawa (1979) from the dinosaur bearing bed. However, the reliability of the biostratigraphical value of the non-marine Mesozoic molluscan fossils has been questioned by Matsukawa himself and his colleague (Matsukawa and Ito 1995, Matsukawa and Tomishima 2009). On the other hand, the radiolarian fossil biostratigraphy since Jurassic is established based on continuous core samples from the deep see, and its reliability has been accepted worldwide. Thus, the radiolarian fossil age is accepted as the geologic age of the Matsuo Group in this paper. Based on the fission-track age, the Berriasian is also included within the range of error, but the majority of the radiolarian assemblages is restricted to the Valanginian and/or later age. Thus, the possibility that the geologic age of the Matsuo Group extends down to the Berriasian is almost none (Kawabata 2001).

#### 3) Kuwajima Formation

The geologic age of the Kuwajima Formation is rather controversial because this formation is barren of reliable index fossils. Isaji et al. (2005) tentatively assigned it to the Valanginian stage on the basis of the stratigraphic relationship of the Mitarai, Kitadani, and Akaiwa formations. Fujita (2003) assigned it to the Hauterivian on the basis of the occurrence of the Tatsukawa type bivalve fauna from the Kuwajima Formation. Matsumoto et al. (2006) reported zircon U-Pb age of $130.7 \pm 0.8$ Ma for tuff bed of the Kuwajima Formation. However, because this tuff bed contains many reworked clasts and its stratigraphic relationship with the fossil-bearing horizon of the Kuwajima Formation is unclear (N. Kusuhashi, pers. comm.), Matsumoto et al. (2006) did not accept the U-Pb age, but accepted the age estimate of the Okurodani Formation at Shokawa area in Gifu Pref. (Kusuhashi et al. 2006), which has been traditionally correlated with the Kuwajima Formation, and concluded that the geologic age of the Kuwajima Formation is the

monite *Neocosmoceras* from the Mitarai Formation (Sato et al. 2008). The zircon U-Pb age at Shokawa area needs to be revised.

The Kuwajima Formation has traditionally been correlated lithostratigraphically with Izuki Formation (Maeda 1961), and Goto (2007) correlated the Izuki Formation to the late Hauterivian – early Barremian age on the basis of the occurrence of the ammonoid *Pseudothrumannia*.

In this paper, we consider that the lithostratigraphy by Maeda (1961) and the ammonoid biostratigraphy are more reliable than other age estimates, and accept the late Hauterivian – early Barremian age of Izuki Formation as the geologic age of Kuwajima Formation.

#### 4) Kitadani Formation

The geologic age of the Kitadani Formation is estimated as the Barremian based on the occurrence of the non-marine mollusc *Nippononaia ryosekiana* (Kozai et al. 2002) and charophyte gyrogonites (Kubota 2005).

#### 5) Sasayama Group

The Sasayama Group is composed of unnamed lower and upper formations (Yoshikawa 1993). A fission track age of $138 \pm 9$ Ma has been obtained from rhyolitic tuff within the "lower formation" of the Sasayama Group (Matsuura and Yoshikawa 1992). However, the Tamba sauropod was found together with basal neoceratopsians, a basal hadrosauroid, and a basal tyrannosauroid (Saegusa et al. 2009, 2010a), and this fauna from the "lower formation" of the Sasayama Group is rather similar to that of the Xinminpu Group of Gongpoquan Basin, Gansu Province, China (You and Luo 2008). Recently, Hayashi et al. (2010) re-measured the fission track age and reexamined ostracode and conchostracan fossils from the "lower formation", and estimated the geologic age of the "lower formation" of the Sasayama Group as Aptian-Cenomanian. We accept the geologic age of Hayashi et al. (2010), which is conformable with the age suggested by the faunal composition in this paper.

a detailed stratigraphic horizon has not been published. However, because the upper member of the Tamayama Formation is exposed only at a small area where the Ohisa River and the Irimazawa River meet (Ando et al. 1995), The Kohisa specimens are supposed to be found either in the lower or middle member of the Tamayama Formation. The lower and middle members of the formation are fluvial deposits, while the upper member is a shallow marine deposit and produces marine invertebrate and vertebrate fossils (sharks and the elasmosaur *Futabasaurus suzukii*) (Obata et al. 1970, Ando et al. 1995, Sato et al. 2006). The upper member of the Tamayama Formation has yielded *Inoceramus mihoensis*

and *I. amakusensis*, indicating the late Coniacian t
Santonian (Obata and Suzuki 1969). Underlying
and lower members of this formation and the Kas
Formation are of terrestrial sediments and do n
tain marine index fossils. Further underlying As
Formation is considered to be the early to middle
cian based on the included inoceramids and amm
(Obata and Suzuki 1969, Matsumoto et al. 1982,
Therefore, it is reasonable to consider that the g
age of the middle or lower member of the Tam
Formation that provided the Kohisa specimens
Coniacian.