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[Original report]

Scincomorphan Lizards from the Lower Cretaceous Sasayama Group, Hyogo, Japan

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Abstract

A terrestrial vertebrate fossil assemblage of dinosaurs, small mammals, anurans, and lizards was discovered in the Lower Cretaceous Sasayama Group, Hyogo Prefecture, Japan. Here, some fragmentary lizard fossils are described briefly, and taxonomic allocations are tentatively identified. The combination of some osteological characters on each fragmentary remain indicates that these fossil lizards are assigned to the infraorder Scincomorpha, and the general morphological differences between each fossil suggest that the lizard fauna of the Lower Cretaceous Sasayama Group contains at least four taxa of Scincomorphan lizards.

Key words: Lizard, Lower Cretaceous, Sasayama Group, Hyogo, Scincomorpha.

Introduction

Lizards belong to the Squamata, along with snakes and amphisbaenas. Lizards currently include more than 5600 species and are distributed extensively over every continent except Antarctica (Uetz, 2013). The origin, phylogenetic relationships, and evolutionary processes of the Squamata based on neontological (morphological and molecular), and paleontological studies have been discussed by many authors over the past several decades (e.g., Camp, 1923; Estes, 1983, 1988; Lee, 1998; Evans *et al*., 2005; Conrad, 2008; Vidal and Hedge, 2009; Gauthier *et al*., 2012). Fossil lizards, which substantiate the existence of each species at each geological time, play an important role in the discussion, and new discoveries of fossil lizards provide an increased understanding of the lizard's evolutionary history.

The earliest fossil lizard, *Bharatagama rebbanensis*, was reported from the Early-Middle Jurassic Kota Formation of India (Evans *et al*., 2002), and the origin of the Squamata was estimated at around the Middle Triassic based on paleontological and molecular data (e.g., Evans, 2003; Vidal and Hedge, 2005). Early diversification in lizards as well as other reptiles has been hypothesized to originate during the Mesozoic era. However, the fossil record of the era to substantiate the evolutionary event is patchy and limited (e.g., Evans, 2003). Among the lizard fossils from the Mesozoic era, Early Cretaceous remains are significant for investigating the faunal transition from the archaic lizards of the Jurassic (e.g., paramacellodids and *Ardeosaurus*) to the modern lizards of the Late Cretaceous (e.g., varanoids and teiids) (Alifanov, 1993; Evans, 1993; Gao and Hou, 1995). Lizard fossils of the Early Cretaceous are relatively rare compared with those of the Late Cretaceous, but some fossil lizard assemblages of the Early Cretaceous are currently known from Europe;

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North, Central, and South America; Africa; and Asia (e.g., Hoffstetter, 1967 ; Gao and Nessov, 1998 ; Nydam, 1999 ; Evans and Searle, 2002). More recently, new fossil representatives of the Early Cretaceous such as *Pachygenys* (Gao and Cheng, 1999), *Xianglong* (Li *et al*., 2007), *Kuwajimalla* (Evans and Manabe, 2008), and *Liushusaurus* (Evans and Wang, 2010) have been successively reported from China, Inner Mongolia, and Japan.

In addition to the fossil records mentioned above, the present study reports on the Early Cretaceous fossil lizard assemblage in a new locality. Moreover, taxonomic allocations of fragmentary lizard remains from the 'Lower Formation' of the Sasayama Group are described based on taxonomic accounts of lizards by previous authors (e.g., Estes, 1988).

Institutional Abbreviations: MNHAH, Museum of Nature and Human Activities, Hyogo, Japan

Geological background

The fragmental fossils of the lizards described here were found from the 'Lower Formation' of the Sasayama Group, in the eastern part of Hyogo Prefecture, Japan (Fig. 1). The group is divided into the 'Lower Formation' and the 'Upper Formation'

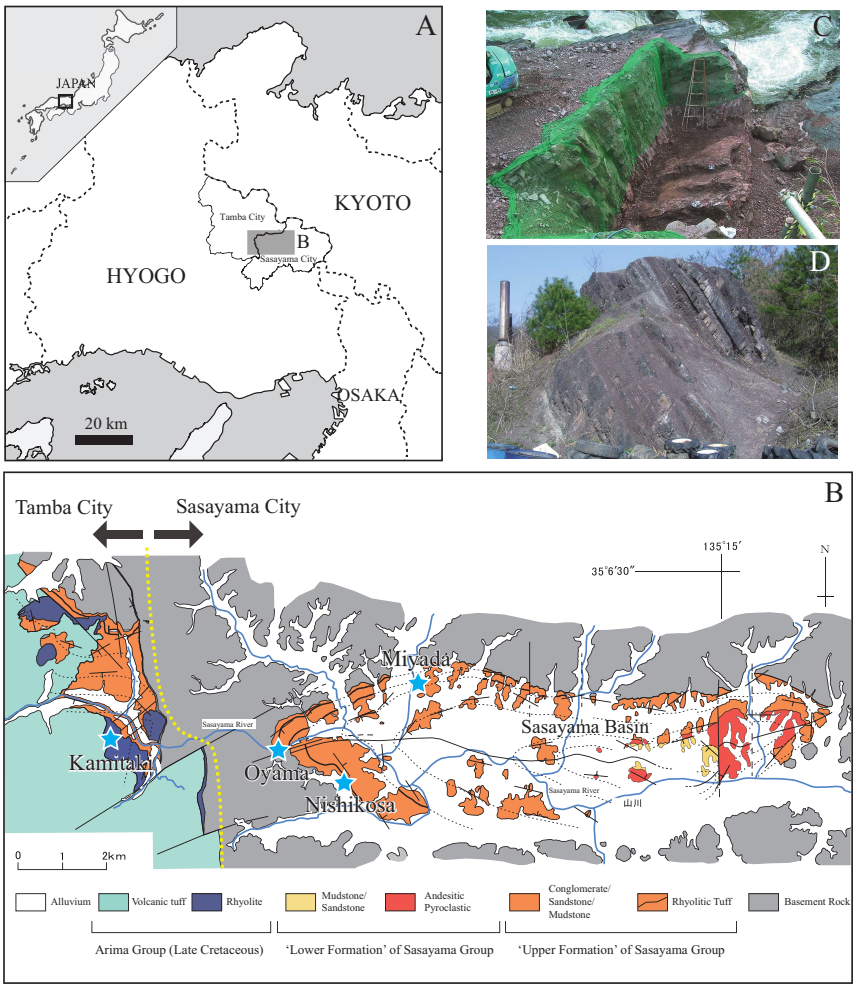

Fig. 1. A, Map showing the geograhical location Tamba and Sasayama City, Hyogo, Japan. The gray area denotes the distributional area of the Sasayama Group. B, Geological Map of Tamba-Sasayama Area ; modified after Yoshikawa (1993). Blue stars represents the fossil localities of the Sasayama Group. C, a view of "Kamitaki" fossil locality. D, a view of "Miyada" fossil locality.

based on lithological characters (Yoshikawa, 1993; Kusuhashi *et al*., 2013). The 'Lower Formation' is composed mainly of conglomerate, sandstone, and mudstone intercalating several tuff beds, and the 'Upper Formation' is represented by hornblende andesite pyroclastic rocks, tuffaceous sandstone, and mudstone (Yoshikawa, 1993). In the past several years, abundant vertebrate remains of dinosaurs, small mammals, anurans, and lizards have been found from the 'Lower Formation' of the Sasayama Group in some localities, i.e., at Kamitaki in Tamba City and at Oyama, Miyada, and Nishikosa in Sasayama City (Fig. 1) (Saegusa *et al*., 2008 a, b; Ikeda and Saegusa, 2009; Saegusa *et al*., 2009; Ikeda *et al*., 2010; Saegusa *et al*., 2010 a, b; Saegusa and Tomida, 2011).

The geological age of the 'Lower Formation' of the Sasayama Group remains still controversial. A zircon fission track age of 138 ± 9 Ma was obtained from rhyolite tuff beds in the 'Lower Formation' of the group (Matsuura and Yoshikawa, 1992). Recently, Hayashi *et al*. (2010) reexamined ostracode and conchostracan biostratigraphies and zircon fission track dating of the Sasayama Group and estimated the geological age of the 'Lower Formation' of the group as Aptian-Cenomanian. Recently Kusuhashi *et al*. (2013) obtained a high-precision U-Pb age of zircons from a tuff bed in the lower part of the 'Lower Formation' using a sensitive high-resolution ion microscope (SHRIMP II), and estimated the date of the stratum, from which fossils of *Sasayamamylos kawaii* were excavated with the lizard mandibles examined here, to be 112.1 ± 0.4 Ma. In the present study, we adopt this last estimation as the date of our materials.

Material and Methods

Five fragmental dentaries of fossil lizards, described here, were collected from two localities. One of the five dentaries was found in red mudstone of the 'Lower Formation of the Sasayama Group exposed on riverbank of the Sasayama River at Kamitaki in Tamba City together with a partial skeleton of a titanosauriform sauropod, shed teeth of theropods and ornithopods, and many anurans (e.g., Ikeda *et al*., 2010; Saegusa *et al*., 2008 a, b) (Fig. 1). The other dentaries were reported from red mudstone in the Lower Formation of the Sasayama Group at Miyada in Sasayama City (Fig. 1). The fossil assemblages at Miyada are characterized by microvertebrate remains that contain many fragmentary cranial and postcranial elements of lizards, some mammalian lower jaws which were described as *S. kawaii*, and a few cranial remains of dinosaurs (e.g., Ikeda and Saegusa, 2009; Kusuhashi *et al*., 2013; Saegusa *et al*., 2009).

In the present study, the terminology used for cranial osteological features mainly follows Gao and Fox (1996), and Evans (2008). The terminology used to describe tooth morphology follows Kosma (2004), who prescribed terms for tooth forms based on extant and extinct Scincomorphan lizards. Orientation terminology also follows Gao and Fox (1996). Researchers have discussed the taxonomic definitions and systematics of lizards since the end of the 19th century (see Historical Analysis of Conrad [2008]), and controversies continue. Here, the classification follows Estes *et al*. (1988), who defined the diagnosis of each higher taxon based on the osteological features of extant lizards in systematic paleontology because it is widely accepted by many authors and is used as a standard for investigating squamate relationships (e.g., Conrad, 2008).

Systematic paleontology

SQUAMATA Oppel, 1811
SCINCOGEKKONOMORPHA Sukhanov, 1961
SCLEROGLOSSA Estes *et al*., 1988
SCINCOMORPHA Camp, 1923

Scincomorpha gen. et sp. indet.

Material: Three fragmental right dentaries (MNHAH D1-032077, D1-032152, and D1-032440), and two fragmental left dentaries (MNHAH D1-032154 and D1-032159).

Locality and horizon: Four specimens (D1-032077, D1-032152, D1-032154, and D1-032159) and one specimen (D1-032440) were discovered from the lower part of the 'Lower Formation' of the Sasayama Group at Miyada in Sasayama City (35° 05′ 34″ N, 135° 10′ 40″ E) and at Kamitaki in Tamba City (35° 08′ 21″N, 135° 10′ 53″E), respectively, in Hyogo Prefecture, Japan. The approximate geological age of the formation is considered as early Albian (Early

Cretaceous).

Indeterminate Type A

Description of D1-032077 (Fig. 2)

D1-032077 is an incomplete right dentary missing its anterior end and posterior portions, and preserves 16 tooth positions, two complete teeth (d, e), and eleven incomplete teeth (a, b, c, g, h, j, k, l, m, o, p). The total length of the specimen is 13.9 mm.

The lateral surface of D1-032077 is smooth and convex, and has six mental foramina (inferior alveolar foramina of Gao and Fox [1996]). The dorsal margin of the dentary is nearly straight, whereas the ventral margin is convex. The subdental shelf is tall and robust anteriorly (approximately one-third of the tooth height) but gradually narrows posteriorly. The subdental gutter is narrow and shallow. Posteriorly, the Meckelian canal is wide, opens medially, and narrows anteriorly. The articular facet for the splenial is preserved on the ventral surface of the subdental shelf and extends anteriorly to the (i) tooth position. The lateral border of the Meckelian canal also bears the facet on the medial side. Both articular facets of the specimen indicate that the splenial originally extended to the (h) tooth position. The inferior alveolar canal is situated ventral to the (m) tooth position, on the roof of the Meckelian canal. The posterior projection of the intramandibular septum is not developed. The teeth are pleurodont and are attached to the medial wall of the dentary. Each tooth is narrowly spaced along the tooth row. The anterior teeth are posteriorly inclined, but the teeth in the middle and posterior positions are straight. The tooth shafts are cylindrical. The tooth crowns of the anterior teeth (d, e) are unicuspid and moderately pointed, with weak mesial and distal ridges. Due to the poor preservation of the specimen, other features of the tooth crown such as striae and the cuspis lingualis are not clearly observed in the anterior teeth (d, e) with a stereomicroscope. Because the tooth crowns of the middle and posterior teeth are not preserved, detailed structures of these tooth crowns cannot be evaluated. Small replacement pits are observed at the bases of some tooth positions (h, m, o, p).

Remarks for D1-032077

The combination of characters, such as pleurodont teeth, a developed subdental shelf, and no apparent posterior projection of the intramandibular septum

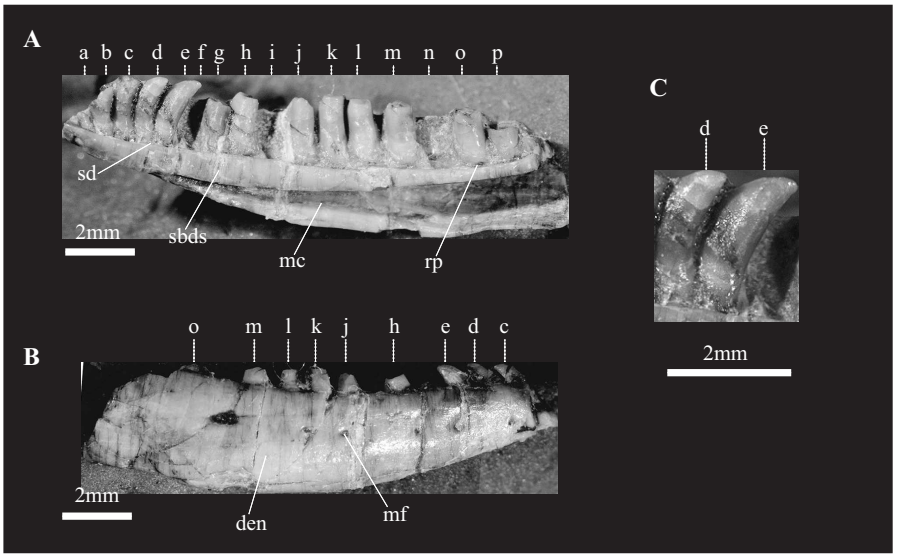

Fig. 2. Scincomorpha gen. et sp. indet. (D1-032077 : Type A) from the 'Lower Formation' of the Sasayama Group at Miyada in Sasayama city (Hyogo Pref., Japan). A, a photograph in medial view. B, a photograph in lateral view. C, close up of "d, e" teeth in medial view. Addriviations : den, dentary ; mc, Meckelian canal ; mf, mental foramen ; rp, replacement pit ; sbds, subdental shelf ; sd, sulcus dentalis.

indicates that the D1-032077 is assigned to the infraorder Scincomorpha (see Discussion). Moreover, some character states of the specimen (e.g., shapes of the dorsal and ventral margins of the dentary and slightly recurved anterior teeth) are shared with *Sakurasaurus shokawensis*, which was reported from the Early Cretaceous Okurodani Formation of Gifu Prefecture, Japan (Evans and Manabe, 1999, 2009). However, further investigations of other Mesozoic lizards such as the Chinese lizard *Yabeinosaurus* (Endo and Shikama, 1942), which is believed to be closely related to *Sakurasaurus* (Evans and Manabe, 2009), and additional remains are required to determine the taxonomic allocation of D1-032077 in detail.

Indeterminate Type B

Description of D1-032152 (Fig. 3)

D1-032152 is a partial right dentary with 14 tooth positions, two nearly complete teeth (b, l), and eight incomplete teeth (d, f, g, i, j, k, l, n). The specimen is missing the anterior part of the bone and the posteroventral and coronoid processes from the posterior end of the bone. The length of this specimen is 11.9 mm.

The lateral surface of D1-032152 is smooth and moderately convex and bears three mental foramina. The dorsal and ventral margins of the dentary are nearly straight. The subdental shelf is well developed and tall anteriorly (approximately one-half of the tooth height) but narrows posteriorly. The subdental gutter is narrow and shallow. The Meckelian canal is wide posteriorly and opens medially. The canal gradually narrows anteriorly. The vertebral surface of the subdental shelf bears a shallow groove for the articulation of the splenial that extends anteriorly to beneath the (d) tooth position. The facet for the splenial cannot be recognized on the medial side of the lateral border of the Meckelian canal due to the poor preservation of the specimen. The shallow groove for the articulation of the splenial, however, indicates the presence of the splenial reaching to at least beneath the (d) tooth position. The inferior alveolar canal is located ventral to the (h) tooth position, on the roof of the Meckelian canal. There is no apparent posterior projection of the intramandibular septum. The specimen has pleurodont teeth, which are attached to the medial wall of the dentary. Each tooth is narrowly spaced along the tooth row, and is straight. The tooth shafts

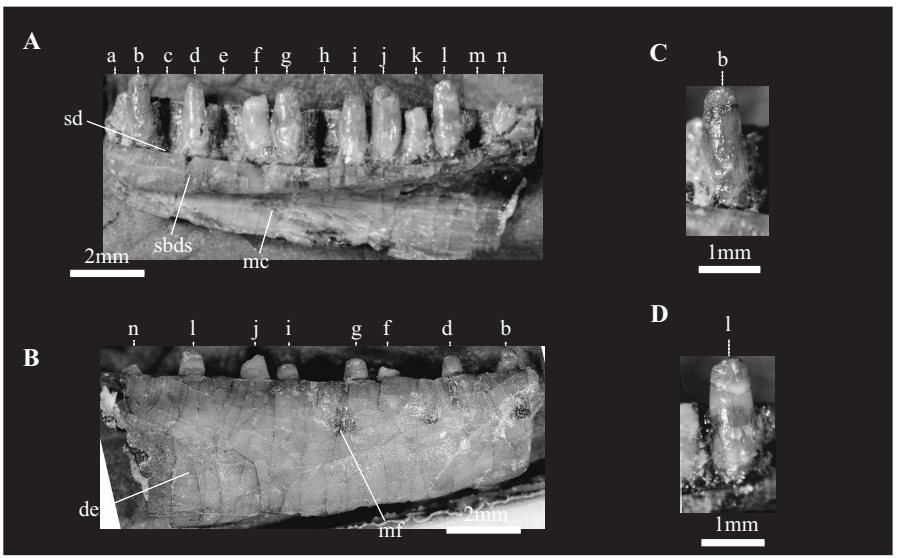

Fig. 3. Scincomorpha gen. et sp. indet. (D1-032152 : Type B) from the 'Lower Formation' of the Sasayama Group at Miyada in Sasayama city (Hyogo Pref., Japan). A, a photograph in medial view. B, a photograph in lateral view. C, close up of "b" tooth in medial view. D, close up of "l" tooth in medial view. Addriviations : den, dentary ; mc, Meckelian canal ; mf, mental foramen ; sbds, subdental shelf ; sd, sulcus dentalis.

are cylindrical, whereas the medial surfaces of the tooth crowns (b, l) are slightly curved lingually and flattened. The tooth crowns (b, l) of the tooth are almost blunt. The crista mesialis of each tooth crown (b, l) is longer than the crista distalis (approximately twice as long). Other features of the tooth crowns such as the striae, cuspis lingualis, and culmen lateris cannot be identified because the specimen is covered with Paraloid, an acrylic polymer used to protect fossil specimens. The replacement pits at the tooth base cannot be evaluated due to the poor preservation of the specimen and the protective flux.

Description of D1-032154 (Fig. 4)

D1-032154 is a fragmental left mandible preserving the middle and posterior portion of the dentary, the anterior portions of the splenial and suranglar, and the anterior tip of the anteromedial process of the coronoid. The dentary of the specimen has at least 12 tooth positions, six complete teeth (f, g, h, i, k, l) and five incomplete teeth (a, b, c, d, e). The total length of the mandible is 12.4 mm.

The lateral surface of the dentary is slightly convex and smooth. Three mental foramina open on the lateral surface. In lateral view, the posterior portion of the dentary has a single large notch (surangular notch), and the posterodorsal and posteroventral processes of the dentary are well developed. The degree of development of these processes, however, is not obvious due to the poor state of preservation of the specimen. The dentary presents relatively straight dorsal and ventral margins. The subdental shelf is tall and robust anteriorly (approximately one-half of the tooth height) but narrows posteriorly. The subdental gutter is narrow and shallow. The splenial covers the Meckelian canal of the specimen medially and preserves two well-developed foramina : the large anterior inferior alveolar foramen opens close to the splenodentary suture, and the small anterior mylohyoid foramen is situated posteroventrally to the former foramen, beneath the (j) tooth position. Although most of the coronoid is broken off, the anteromedial process of the coronoid extends anteriorly and reaches under the (j) tooth position. The dentary has straight teeth that are narrowly spaced along the tooth row, and the mode of tooth attachment is pleurodont. The shape of each tooth shaft is cylindrical. The tooth crowns are blunt, and the medial surfaces of these crowns are slightly

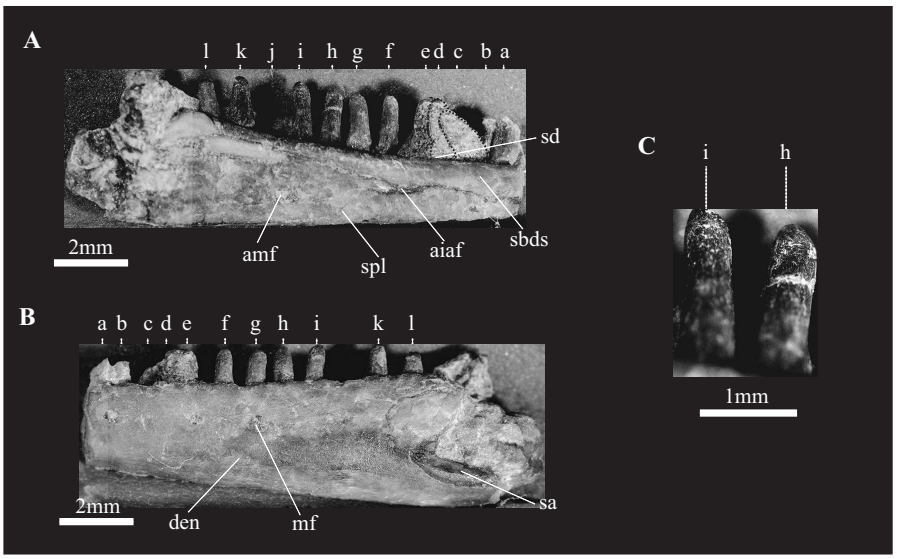

Fig. 4. Scincomorpha gen. et sp. indet. (D1-032154 : Type B) from the 'Lower Formation' of the Sasayama Group at Miyada in Sasayama city (Hyogo Pref., Japan). A, a photograph in medial view. B, a photograph in lateral view. C, close up of "i, h" teeth in medial view. Addriviations : aiaf, anterior inferior alveolar foramen ; amf, anterior mylohyoid foramen ; den, dentary ; mf, mental foramen ; sa, surangular ; sbds, subdental shelf ; sd, sulcus dentalis ; sp, splenial.

curved lingually and flattened. The anterior tooth (a) and posterior teeth (k, l) are relatively robust compared to the middle teeth. The crista mesialis and the crista distalis are recognized on each tooth crown (f, g, h, i, k, l), and the crista mesialis is approximately twice as long as the crista distalis. The states of preservation of these tooth crowns are too poor to determine other crown features in detail. No tooth base bears an obvious replacement pit.

Remarks for D1-032152 and D1-032154

D1-032152 and D1-032154 are classified in the infraorder Scincomorpha based on the combination of characters, such as pleurodont teeth, a developed subdental shelf, and no apparent posterior projection of the intramandibular septum (see Discussion). Moreover, D1-032152 and D1-0032154 are briefly assigned to indeterminate type B of the scincomorphan lizard, because these specimes exhibit same characters such as the shapes of the dentary and tooth crown, and number and position of the mental foramen. Furthermore, the tooth structure of these specimens resembles that of the Paramacellodidae, a widespread extinct group reported from the Middle Jurassic to the Lower Cretaceous in Europe, North America, Africa, and Asia (Evans, 2003). However, the significant characters for evaluating taxonomic position, such as the cuspis lingualis and stria dominans, cannot be observed in these specimens due to the poor state of preservation. Further observations of the tooth crowns of D1-032152 and D 1-032154 using an electron microscope, careful comparisons within the Mesozoic lizards, and more complete materials are required for more reliable taxonomic determinations of these specimens.

Indeterminate Type C

Description of D1-032159 (Fig. 5)

D1-032159 is a partial left mandible missing the posteriormost portion of the element. The mandible preserves the dentary, the anterior portion of splenial and suranglar, and the anteromedial process of the coronoid. The dentary of the specimen has at least 22 tooth positions, three complete teeth (l, n, o), and 14 incomplete teeth (c, d, e, f, h, i, j, m, q, r, s, t, u, v). The total length of the mandible is 9.7 mm.

The specimen has a smooth lateral surface that is moderately convex. The dentary carries six mental foramina on the surface. A surangular notch

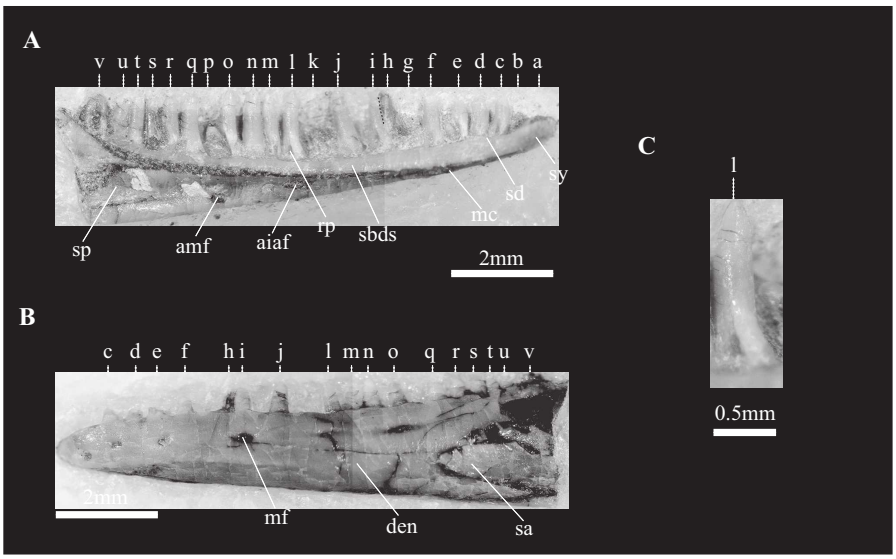

Fig. 5. Scincomorpha gen. et sp. indet. (D1-032159 : Type C) from the 'Lower Formation' of the Sasayama Group at Miyada in Sasayama city (Hyogo Pref., Japan). A, a photograph in medial view. B, a photograph in lateral view. C, close up of "l" teeth in medial view. Addriviations : aiaf, anterior inferior alveolar foramen ; amf, anterior mylohyoid foramen ; den, dentary ; mc, Meckelian canal ; mf, mental foramen ; rp, replacement pit ; sa, surangular ; sbds, subdental shelf ; sd, sulcus dentalis ; sp, splenial ; sy, symphysis.

is well developed on the posterior portion of the dentary in lateral view, and the posterodorsal process of the dentary is relatively robust and extends posteriorly compared to the posteroventral process based on the scar of the surangular notch. The dorsal and ventral margins of the dentary are straight in the lateral view. The subdentral shelf is tall anteriorly (nearly one-third of the tooth height) and narrows posteriorly. The symphysis forms a flat surface ventrally, extending under the anteriormost three tooth positions (a, b, c). The subdental gutter is narrow and shallow. The Meckelian canal of the specimen is largely covered with the splenial and opens ventrally under the anterior tooth positions (c, d, e, f). A large inferior alveolar foramen of the mandible opens close to the splenodentary suture on the splenial, and a small anterior mylohyoid foramen is positioned posteriorally to the former foramen, beneath the (p) tooth position. The anteromedial process of the coronoid extends anteriorly and reaches under the (t) tooth position. The teeth are pleurodont, with narrow, cylindrical tooth shafts, and are closely spaced along the tooth row. Tooth crowns are conical and unicuspid (l, n, o). The medial surfaces of these crowns are slightly concave. The distinct cutting edges of the tooth crown are not clearly observed with a stereomicroscope. The replacement pits open at the bases of the (e, n, o) tooth positions and are slightly posterior to the centers of their teeth. The position of the replacement pits indicates lingual tooth replacement, and the replacement teeth are recognized on the (e, p) tooth positions.

Remarks for D1-032159

On the basis of the combination of characters such as pleurodont teeth, a developed subdental shelf, and base positions of tooth replacement pits, D 1-032159 is assigned to the infraorder Scincomorpha (See Discussion). D1-032159 presents a slender dentary, and the morphology of the specimen is clearly distinct from any of the other lizards recovered from the lower formation of the Sasayama Group. Moreover, some characters of the specimen, such as the slender dentary and shapes of the tooth shaft and crown, are similar to these of *Saurillus robustidens* (Paramacellodidae), which was reported from the Early Cretaceous Lulworth Formation in England (Hoffstetter, 1967 ; Evans and Searle, 2002). A more confident taxonomic identification of D1-032159 requires detailed observations of the tooth crown of the specimen with an electron microscope as well as careful comparisons within the Mesozoic lizards.

Indeterminate Type D

Description of D1-032440 (Fig. 6)

D1-032440 is an incomplete right dentary with 11 tooth positions, four complete teeth (c, e, f, g), and six incomplete teeth (a, b, d, i, j, k). The specimen is missing the anterior tip and posterior part of the bone, and the total length of the dentary is 3.9 mm.

The lateral surface of D1-032440 is smooth and convex. The mental foramen on the lateral

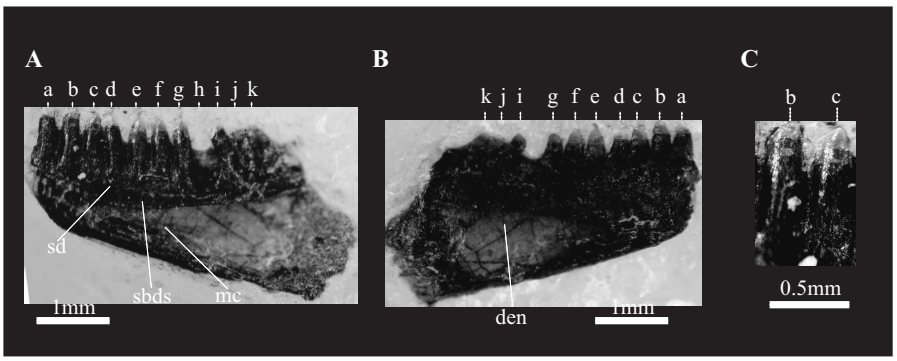

Fig. 6. Scincomorpha gen. et sp. indet. (D1-032440 : Type D) from the 'Lower Formation' of the Sasayama Group at kamitaki in Tamba city (Hyogo Pref., Japan). A, a photograph in medial view. B, a photograph in lateral view. C, close up of "b, c" teeth in medial view. Addriviations : den, dentary ; mc, Meckelian canal ; sbds, subdental shelf ; sd, sulcus dentalis.

surface is not clearly visible. The dorsal margin of the specimen is weakly convex. The shape of the preserved ventral margin of the specimen indicates that the dentary originally had a convex ventral margin. The specimen shows a moderately developed subdental shelf that is thicker anteriorly, and the subdental gutter is narrow and shallow. The Meckelian canal is widely open medially in the posterior part of the specimen and narrows anteriorly. There are no obvious articulation facets for the splenial on the ventral margin of the subdental shelf and on the medial side of the lateral border of the Meckelian canal. The inferior alveolar canal and intramandibular septum are not recognized on the dentary. The teeth of the specimen, which are attached to the medial surface of the mandible, are pleurodont and quite robust. Each tooth is straight and closely spaced along the tooth row. The tooth shafts are cylindrical, and the shape of the tooth crowns is slightly pointed. Tooth crowns (c, e, f, g) are slightly concave medially and present the crista mesialis and the crista distalis. The former is approximately twice as long as the latter. Observation with a stereomicroscope reveals no other features of the tooth crown due to the protective flux and small size of the specimen. The replacement pits of the tooth base cannot be clearly identified.

Remarks for D1-032440

D1-032440 is assigned to the infraorder Scincomorpha based on the combination of characters such as pleurodont teeth, a developed subdental shelf, and no apparent posterior projection of the intramandibular septum (see Discussion). The size of the specimen is remarkably small compared with other described lizards from the Sasayama Group, and the incomplete right dentary is relatively tall in a dorsoventral direction. Here, the taxonomic allocation of the specimen is not identified in detail, but morphological differences between D1-032440 and the other specimens reported here suggest that the specimen belongs to a different taxon.

Discussion

Conrad (2008) and Gauthier *et al*. (2012) performed comprehensive cladistic analyses using numerous phenotypic characters of extant and extinct lizards and revised the definitions and diagnoses for each clade suggested in previous studies. The diagnostic features for each clade that were redefined in these studies were composed of a mixture of character states derived from several skeletal elements. However, not all of the clades had the diagnostic features that were derived from the fragmentary parts (e.g., dentary, maxilla, and vertebra) commonly found as fossils (Conrad, 2008).

The teeth of the fossil specimens described here are pleurodont, which is a general character in lizards except Agamidae and Chamaeleontidae, which have acrodont teeth (Estes *et al*., 1988; Conrad, 2008). Fossil specimens also present a well-developed subdental shelf, described as a synapomorophy of the Scleroglossa by Estes *et al*. (1988). Moreover, Estes *et al.* (1988) mentioned that a subdental shelf is absent in helodermatids, *Lanthanotus*, *Varanus*, some agamids, iguanids, chamaeleontids, and amphisbaenians. Conrad (2008) suggests an absence of the subdental shelf in Acrodonta, Amphisbaenia, and Serpentes. The replacement pits of the tooth row are not clearly observed in the fossil specimens except in D1-032077 and D1-032159, which have replacement pits at the tooth base or slightly posterior to the center of the tooth, respectively. The replacement mode of the fossil specimens, however, is assumed to be "iguanid replacement" or "intermediate condition" rather than "varanid replacement" based on closely spaced tooth row and well-developed subdental shelf of the fossils (Edmund, 1960, 1969). The tooth replacement type also implies that these fossil specimens have more affinity with the Scincomorpha than with the Anguimorpha (Estes, *et al*., 1988; Conrad, 2008). The well-developed intramandibular septum, which is common in Anguimorpha (Estes *et al*., 1988; Evans, 2008), is not observed in some fossil specimens. The closed Meckelian canal and fused dentary tube are described as synapomorphic characters of Gekkota by Estes *et al.* (1988), and these characters also occur in Xantusiidae and in some species of other families (Estes *et al*., 1988; Conrad, 2008; Evans, 2008). The Meckelian canal of fossil specimens is medially open and restricted anteriorly, which is quite different from the closed condition of these taxa. Considering the characters mentioned above, the fossil specimens examined here are selectively assigned to the infraorder Scincomorpha. Moreover, the morphological

differences within these specimens indicate that these fossils are divided into four indeterminate types of Scincomorpha lizards and that the lizard fauna of the Lower Cretaceous Sasayama Group consist of at least four different taxa. Other fragmental remains of lizards, such as vertebrae, maxillae, and braincases, were also discovered in the 'Lower Formation' of the Sasayam Group (Ikeda and Saegusa, 2009). Further investigations including these unexamined specimens and additional materials might increase the richness of the faunal composition.

Although fragmental fossil specimens of lizards occur frequently around the world, identification is often difficult even at the family level based on only a few characteristic features (e.g., Rieppel, 1994 ; Rees, 2000 ; Brizuela and Albino, 2011). Unambiguous diagnostic characters of fragmental remains such as dentaries have not been clearly determined at each taxonomic level ; nevertheless, these remains have often been reported as a new species by previous authors (e.g., Seiffert, 1973 ; Allifanov, 1993 ; Gao and Fox, 1996; Kosma, 2004). In the present study, taxonomic allocations of fossil specimens were not determined in detail. We tentatively compared these fossils with some Mesozoic lizards found in Japan, China, and Europe. Results of the preliminary comparison showed that D1-032077 (a fragment right dentary) shares some characters, such as shape of the dentary and slightly recurved anterior tooth with weak crown ridges, with *Sakurasaurus shokawensis*, which occurred from the Early Cretaceous Okurodani Formation of Gifu Prefecture, Japan (Evans and Manabe, 1999, 2009). Moreover, other specimens (D1-032152, 032154, 032159, and 032440) exhibit a crista mesialis and crista distalis on each tooth crown ; the tooth structures of these fossils are somewhat similar to those of paramacellodid lizards, which is a group ranging from the Middle Jurassic to the Early Cretaceous in Europe, North America, Africa and Asia (Evans, 2003 ; Kosma, 2004). Furthermore, D1-032159, which has a slender dentary and narrow, cylindrical tooth shafts, is roughly similar to *Saurillus robustidens* (Paramacellodidae) from the Early Cretaceous Lulworth Formation in England (Hoffstetter, 1967 ; Evans and Searle, 2002). However, the fossil specimens described here are too fragmented to perform a detailed comparison with other Mesozoic lizards, and further materials and advanced investigations, such as the use of an electron microscope and CT scaning, are needed to determine the accurate taxonomic allocations of these specimens. In particular, comprehensive studies of fragmental elements, such as the dentaries of extant and extinct lizards, are essential for accurate identifications of these fragmental fossil lizards and for resolving the taxonomic problem of Mesozoic lizards such as the Paramacellodidae (Nydam and Cifelli, 2002b).

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References

Alifanov, V. (1993) Some peculiarities of the Cretaceous and Palaeogene lizard faunas of the Mongolian People's Republic. *Kaupia* **3**, 9-13.

Brizuela, S. and Albino, A. (2011) A Scincomorpha lizard from the Campanian of Patagonia. *Cret. Res.* **32**, 781-785.

Camp, C. L. (1923) Classification of the lizards. *Bull. Amer. Mus. Nat. Hist*. **48**, 289-480.

Cifelli, R. L., Gardner, J. D., Nydam, R. L. and Brinkman, D. L. (1997) Additions to the vertebrate fauna of the Antlers Formation (Lower Cretaceous), Southeastern Oklahoma. *Oklahoma Geol.* **57**, 124-131.

Conrad, J. L. (2008) Phylogeny and systematics of Squamata (Reptilia) based on morphology. *Bull. Amer. Mus. Nat. Hist*. **310**, 1-183.

Edmund, A. G. (1960) Tooth replacement phenomena

in the lower vertebrates. *R. Ont. Mus., Life Sci. Div., Contr*. **52**, 1-190.

Edmund, A. G. (1969) Dentition. In : Gans, C., Bellairs, A. and Parson, T. (eds) *Biology of the Reptilia 1*, pp. 117-200, Academic Press, New York.

Endo, R. and Shikama, T. (1942) Mesozoic reptilian fauna in the Jehol mountainland, Manchoukuo. *Bulletin of the Central National Museum of Manchoukuo* **3**, 1-19.

Estes, R. (1983) *Sauria terrestria, Amphisbaenia*. Gustav Fischer Verlag, New York, 249 pp.

Estes, R., de Queiroz, K. and Gauthier, J. (1988) Phylogenetic relationships within Squamata. In : Estes, R. and Pregill, G. (eds) *Phylogenetic relationships of the lizard families*, pp. 119-281, Stanford University Press, Palo Alto.

Evans, S. E. (1993) Jurassic lizard assemblages. *Revue de Paleobiologie (Suisse)* **7**, 55-65.

Evans, S. E. (2003) At the feet of the dinosaurs : the origin, evolution and early diversification of squamate reptiles (Lepidosauria : Diapsida). *Biol. Rev.* **78**, 513-551.

Evans, S. E. (2008) The skull of lizards and tuatara. In : Gans, C. Gaunt, A. S., and Adler, K. *Biology of the Reptilia 20*, pp. 1-344, Ithica, New York.

Evans, S. E. and Barbadillo, L. J. (1997) Early Cretaceous lizards from Las Hoyas, Spain. *Zool. Jour. Linn. Soc. Lond*. **119**, 23-49.

Evans, S. E. and Barbadillo, L. J. (1998) An unusual lizard (Reptilia, Squamata) from the Early Cretaceous of Las Hoyas, Spain. *Zool. Jour. Linn. Soc. Lond*. **124**, 235-266.

Evans, S. E. and Barbadillo, L. J. (1999) A short-limbed lizard from the Early Cretaceous of Spain. *Spec. Pap. Palaeontol*. **60**, 73-85.

Evans, S. E. and Manabe, M. (1999) Early Cretaceous lizards from the Okurodani Formation of Japan. *Geobios* **32**, 889-899.

Evans, S. E. and Manabe, M. (2008) An early herbivorous lizard from the Lower Cretaceous of Japan. *Palaeontol.* **51**, 487-498.

Evans, S. E. and Manabe, M. (2009) The Early Cretaceous lizards of eastern Asia : new material of Sakurasaurus from Japan. *Spec. Pap. Palaeontol*. **81**, 43-59.

Evans, S. E. and Searle, B. (2002) The lepidosaurian assemblage of the Purbeck Limestone Group. *Spec. Pap. Palaeontol*. **68**, 145-159.

Evans, S. E. and Wang, Y. (2005) Early Cretaceous lizard Dalinghosaurus from China. *Acta Palaeont. Pol*. **50**, 725-742.

Evans, S. E. and Wang, Y. (2010) A new lizard (Reptilia : Squamata) with exquisite preservation of soft tissue from the Lower Cretaceous of Inner Mongolia, China. *Jour. Syst. Palaeontol*. **8,** 81-95.

Evans, S. E. and Yabumoto, Y. (1998) A lizard from the Early Cretaceous Crato Formation, Araripe Basin, Brazil. *N. Jb. Geol. Palaont. Mh*. **1998**, 349-364.

Evans, S. E., Prasad, G. V. R. and Manhas, B. K. (2002) An acrodont iguanian from the Mesozoic Kota Formation of India. *Jour. Vertebr. Paleontol.* **22**, 299-312.

Evans, S. E., Wang, Y. and Jones, M. E. H. (2007) An aggregation of lizard skeletons from the Lower Cretaceous of China. *Senkenbergiana Lethaea* **87**, 147-156.

Evans, S. E., Wang, Y. and Li, C. (2005) The Early Cretaceous lizard genus Yabeinosaurus from China : resolving an enigma. *Jour. Syst. Palaeontol*. **3**, 319-335.

Evans, S. E, Manabe, M., Noro, M., Isaji, S. and Yamaguchi, M. (2006) A long-bodied lizard from the Lower Cretaceous of Japan. *Palaeontol*. **49**, 1143-1165.

Gauthier, J. A., Kearney, M., Maisano, J. A., Rieppel, O. and Behlke, A. D. B. (2012) Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. *Bull. Pea. Mus. Nat. His.* **53**, 3-308.

Gao, K. Q. and Cheng, Z. (1999). A new lizard from the Lower Cretaceous of Shandong, China. *Jour. Vertebr. Paleontol*. **19**, 456-465.

Gao, K. Q. and Fox, R. C. (1996) Taxonomy and evolution of Late Cretaceous lizards (Reptilia: Squamata) from western Canada. *Bull. Carnegie Mus. Nat. Hist.* **33**, 1-107.

Gao, K. Q. and Hou, L. H. (1995) Iguanians from the Upper Cretaceous Djadochta Formation, Gobi Desert, China. *Jour. Vertebr. Paleontol*. **15**, 57-78.

Gao, K. Q. and Nessov, L. A. (1998). Early Cretaceous squamates from the Kyzylkum Desert, Uzbekistan. *Neues Jahrb. Geol. P–A.* **207**, 289-309.

Hayashi, K., Matuskawa, M., Ohira, H., Chen, P., Zhen, J., Ito, M., Koarai, K. and Obata, I. (2010) Revised age of the Sasayama Group, southwest Japan, based on ostracoda and conchostracan

biostratigraphy and zircon fission-track dating. *Jour. Geol. Soc. Japan* **116**, 283-286. (in Japanese with English abstract).

Hoffstetter, R. (1967) Coup d'oeil sur les sauriens des couches de Purbeck (Jurassique superieur d'Angleterre). *Coll. Intern. du Centre nat. de la Rech. Sci.* **163**, 349-371.

Ikeda, T. and Saegusa, H. (2009) Preliminary report on fossil lizards from the Lower Cretaceous Sasayama Group of Hyogo Prefecture, SW Japan. *Jour. Vertebr. Paleontol.* **29** (3, supplement), 119A.

Ikeda, T., Saegusa, H. and Handa, K. (2010) A fossil anuran from the Lower Cretaceous Sasayama Group of Hyogo Prefecture, SW Japan. *Jour. Vertebr. Paleontol.* **30** (4, supplement), 109A.

Ji, S. A., Lu, L.W. and Bo, H. C. (2001) New material of *Yabeinosaurus tenuis* (Lacertilia). *Land and Resources* 2001, 41-43. (In Chinese)

Kusuhashi, N., Tsutsumi, Y., Saegusa, H., Horie, K., Ikeda, T., Yokoyama, K., and Shiraishi, K. (2013) A new Early Cretaceous eutherian mammal from the Sasayama Group, Hyogo, Japan. *Proceedings of the Royal Society B* 280, 20130142.

Kosma, R. (2004) The Dentition of Recent and Fossil Scincomorphan Lizards (Lacertilia,Squamata)-Systematics, Functional Morphology, Palecology. 188 pp. Unpublished Ph. D. dissertation, Dem FachbereichGeowissenschaften der Universitat Hannover, Hannovre.

Lee, M. S. Y. (1998) Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. *Biol. J. Linnean Soc*. **65**, 369-453.

Li, J. L. (1985) A new lizard from the Late Jurassic of Subei, Gansu. *Vertebrat. PalAsiatic.* **23**, 13-18.

Li, J., Wu, X. and Zhang, F. (2008). *The Chinese fossil reptiles and their kin, second edition*. Science Press, Beijing, 473 pp.

Li, P. P., Gao, K. Q., Hou, L. H. and Xu, X. (2007). A gliding lizard from the Early Cretaceous of China. *Proc. Natl. Acad. Sci. USA* **104**, 5507-5509.

Matsuura, H. and Yoshikawa, T. (1992) Radiometric ages of the Early Cretaceous Sasayama Group, Hyogo Prefecture, Southwest Japan. *Jour. Geol. Soc. Japan* **98**, 635-643.

Nydam, R. L. (1999) Polyglyphanodontinae (Squamata : Teiidae) from the medial and Late Cretaceous : new records from Utah, USA, and Baja California del norte, Mexico. In : Gillette, D. D. (ed) *Vertebrate Paleontology in Utah*, pp. 303-317, Utah Geological Survey Miscellaneous Publication 99-1, Salt Lake City.

Nydam, R. L. and Cifelli, R. L. (2002a) A new teiid lizard from the Cedar. Mountain Formation (Albian-Cenomanian boundary) of Utah. *Jour. Vertebr. Paleontol*. **22**, 276-285

Nydam, R. L. and Cifelli, R. L. (2002b) Lizards from the Lower Cretaceous (Aptian-Albian) Antlers and Cloverly Formations. *Jour. Vertebr. Paleontol*. **22**, 286-298.

Nydam, R. L. and Fitzpatrick, B. M. (2009) The occurrence of Contogenys-like lizards in the Late Cretaceous and Early Tertiary of the western interior of the U.S.A. *Jour. Vertebr. Paleontol.* **28**, 677-701.

Rees, J. (2000) An Early Cretaceous scincomorph lizard dentary from Bornholm, Denmark. *Bull. Geol. Soc. Denmark* **48**, 105-109.

Reynoso, V. H. (1995) Lepidosaurian reptiles from the Cantera Tlayua (Albian), Tepexi de Rodriguex, Pubela, Mexico. In : Lleida-Cuenca (ed) II International Symposium on Lithographic Limestones, *Extended Abstracts*, pp. 131-132, Spain.

Reynoso, V. H. (1998) *Huehuecuetzpalli mixtecus* gen. et sp. nov: a basal squamate (Reptilia) from the Early Cretaceous of Tepexi de Rodrí guez, Central Me´xico. *Philos. T. Roy. Soc. B*. **353**, 477-500.

Reynoso, V. H. and Callison, G. (2000) A new scincomorph lizard from the Early Cretaceous of Puebla, Me´xico. *Zool. Jour. Linn. Soc.* Lond. **130**, 183-212.

Rieppel, O. (1994) The Lepidosauromorpha: an overview with special emphasis on the Squamata. In: Fraser, N. C. and Sues, H. D. (eds) *In the Shadow of the Dinosaurs*, pp. 23-37, Cambridge University Press, New York.

Saegusa, H. and Tomida, Y. (2011) Titanosauriform teeth from the Cretaceous of Japan. *An. Acad. Bras. Cienc.* **83**, 247-265

Saegusa, H., Ikeda, T. and Handa, K. (2010a) Specific and generic status of a sauropod from the Sasayama Group of Tamba City, Hyogo Prefecture, SW Japan. *Abstracts with Programs the 75th Anniversary of the Founding and the 2010 Annual Meeting of the Palaeontological Society of Japan* 6. (in Japanese)

Saegusa, H., Tanaka, S. and Ikeda, T. (2010b) Preliminary observations on the dinosaur teeth

from the Lower Cretaceous Sasayama Group in Tamba City, Hyogo Prefecture and additional notes on the pneumaticity of the postcranial skeleton of Tamba sauropod. *Jour. Fossil Res*. **42**, 56-65. (in Japanese with English abstract)

Saegusa, H., Ikeda, T., Kusuhashi, N., Tanaka, S., and Matsubara, T. (2008a) A titanoform sauropod (Dinosauria: Saurischia) and microvertebrates from the lower Cretaceous of Hyogo Prefecture, SW Japan. *Jour. Vertebr. Paleontol.* **28** (3, supplement), 135A.

Saegusa, H., Ikeda, T., Tanaka, S., Matsubara, T., Furutani, H., and Handa, K. (2009) Preliminary observations on vertebrate fossils from the Lower Cretaceous Sasayama Group in Hyogo Prefecture SW Japan. In : Organizing and Scientific Committee of The IGCP 507 Symposium (ed) *Abstracts and Post-symposium Field Excursion Guidebook 4th International Symposium of the IGCP 507*, pp. 60-61, Kumamoto, Japan.

Saegusa, H., Tanaka, S., Ikeda, T., Matsubara, T., Furutani, H. and Handa, K. (2008b) On the occurrence of sauropod and some associated vertebrate fossils from the Lower Cretaceous Sasayama Group of Hyogo Prefecture, SW Japan. *Jour. Fossil Res.* **41**, 2-12. (in Japanese with English abstract)

Seiffert, J. (1973) Upper Jurassic lizards from central Portugal. *Memorias Serviços Geológicos de Portugal* **22**, 1-85.

Vidal, N. and Hedges, S. B. (2005) The phylogenyof squamate reptiles (lizards, snakes, and amphisbaenians) inferred from nine nuclearprotein-coding genes. *C. R. Biol.* **328**, 1000-1008.

Vidal, N. and Hedges, S. B. (2009) The molecular evolutionary tree of lizards, snakes, and amphisbaenians. *C. R. Biol.* **332**, 129-139.

Winkler, D. A., Murry, P. A. and Jacobs, L. L. (1990) Early Cretaceous (Comanchean) Vertebrates of Central Texas. *Jour. Vertebr. Paleontol.* **10**, 95-116.

Yoshikawa, T. (1993) Stratigraphy and structure of the Lower Cretaceous Sasayama Group in Sasayama area, Hyogo Prefecture, Southwest Japan. *Jour. Geol. Soc. Japan* **99**, 29-38.

Uetz, P. (2013) The Reptile Database. http : //www. reptile-database.com. Research Center Karlsruhe, Accessed 2013.