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A clue to the Neocomian vertebrate fauna: initial results from the Kuwajima "Kaseki-kabe" (Tetori Group) in Shiramine, Ishikawa, central Japan

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ABSTRACT

More than 30 vertebrate species have been collected from the Kuwajima "Kaseki-kabe" (fossil-bluff), an outcrop of the Lower Cretaceous Kuwajima Formation (Tetori Group), in Shiramine Village, Ishikawa Prefecture. This means the site is one of the most fertile Early Cretaceous fossil localities in the world. The diversity includes four fishes, one frog, tritylodontids, three turtles, probably three pterosaurs, seven dinosaurs, seven lizards, one choristodere, one bird and two mammals. In this paper, the vertebrate assemblage of the "Kaseki-kabe" is documented to reaffirm its significance.

INTRODUCTION

Late Jurassic to Cretaceous was the period when modern terrestrial vertebrates such as metatherian-eutherian grade mammals, birds and lizards diversified, as Pangaea broke up (e.g. Hedges et al., 1996). The Neocomian (early Early Cretaceous) was thus the essential period for the early evolution of these animals. However, the deposits recording this important event are scarce worldwide, and so the detailed scenario for the evolution of Early Cretaceous biota has not been proposed.

The Kuwajima "Kaseki-kabe" (fossil-bluff), an outcrop of the Neocomian part of the Tetori Group in Shiramine Village, Ishikawa Prefecture, is coming to be recognized recently as a wonderful fossil locality of this period. It has been well known for more than 120 years as a botanical fossil locality. In 1997, a traffic tunnel was constructed through the mountain behind the bluff, and so the Shiramine Village Board of Education organized a party to research the debris from the tunnel construction site for fossilized plants and animals. Matsuoka (2000b), research report of the fossil assemblage from the "Kaseki-kabe", informed that the fossils of about 30 vertebrate species have been found from 1997 to 2000, including four fishes, one frog, tritylodontids, three turtles, probably three pterosaurs, seven dinosaurs, seven lizards, one choristodere, one bird and two mammals. This means that the "Kaseki-kabe" is one of the most fertile Neocomian fossil sites in the world.

We aim to research the Tetori biota successively for the purpose of revealing the history of biota changing from the Jurassic to Cretaceous, because the Early Cretaceous is "the dawn of the modern vertebrate fauna". Our paleontological study on the "Kaseki-kabe" is expected to yield crucial informations to supplement the knowledge about the early stages of evolution of the modern vertebrates. We prepare this paper, documenting the vertebrate fossil assemblage of the Kuwajima "Kaseki-kabe" (mostly cited from Matsuoka, 2000b) and emphasizing the significance, as the first step of our future course.

GEOLOGIC SETTING

The Middle Jurassic to Lower Cretaceous Tetori Group is distributed in Ishikawa, Gifu, Fukui,

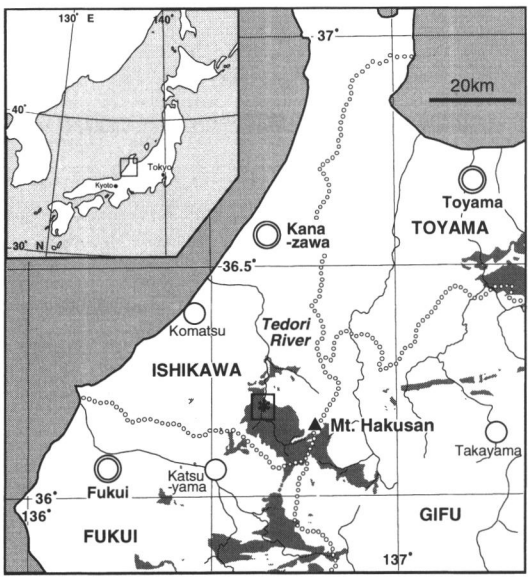

Fig. 1. Main distribution of the Tetori Group (modified after Maeda, 1961e). Asterisk showing the position of Shiramine Village, Ishikawa Prefecture.

Toyama and Nagano prefectures of the Inner Zone of central Japan (Fig. 1). It unconformably overlies the Hida Gneiss and Granite in the northern part, and the Paleozoic formations and Sangun Schists in the southern part (Maeda, 1961). The Tetori Group consists of three subgroups (Maeda, 1952, 1961): the marine deposits Kuzuryu Subgroup that yields ammonites, the non-marine Itoshiro and Akaiwa subgroups, in ascending order.

The Tetori Group is composed mainly of non-marine deposits, thus only a few strata or horizons have been dated based on index fossils. Moreover, the reliable radiometric ages of the Group have never been determined. The lowermost Kuzuryu Subgroup is the Middle to Upper Jurassic. From the upper part of the Subgroup, index fossils of ammonites that indicate Bathonian to Oxfordian have been found (Kobayashi, 1947; Maeda, 1952, 1961; Sato, 1962; Sato et al., 1963; Sato and Kanie, 1963). The succeeding Itoshiro Subgroup is the Upper Jurassic to Lower Cretaceous. The radiometric ages that indicate 140 to 120 Ma have been obtained from the upper part of the Subgroup in Shokawa Village, Gifu Prefecture (Gifu-ken Dinosaur Research Committee, 1993), though these ages were estimated based on poor foundations. The uppermost Akaiwa Subgroup is the Lower Cretaceous. The upper part of this Subgroup yields the fresh water bivalve *Nippononaia ryosekiana*, and this species indicates late Barremian to early Aptian (Isaji, 1993).

The Kuwajima Formation, from which a number of vertebrate remains have been discovered, is distributed along the Tedori River in Shiramine Village, Ishikawa Prefecture. The Tetori Group in this district is composed of the Gomijima and Kuwajima formations of the Itoshiro Subgroup and the Akaiwa and Myodani formations of the Akaiwa Subgroup in ascending order (Ishikawa Prefecture Board of Education, 1978). The Gomijima Formation contacts the Hida Gneiss with faults, and the Myodani Formation is unconformably overlain by the Upper Cretaceous Omichidani Formation (Maeda, 1958; Ishikawa Prefecture Board of Education, 1978). The Formation is thought to be deposits of fluvial dominated prograding delta system (Okazaki and Isaji, 1999; Isaji, 2000).

The index fossils for dating have seldom been collected from the non-marine Kuwajima Formation. Thus the age of the Formation should be estimated by correlations with the others of the Tetori Group. The Kuwajima Formation composes the upper most part of the Itoshiro Subgroup, and is stratigraphically much higher than the Mitarai Fromation (Kuzuryu Subgroup) that is correlated to the Callovian to ?Tithonian on the basis of ammonites and inoceramids (Hayami, 1960; Maeda, 1961; Sato, 1962; Sato and Kanie, 1963). There is a considerable vertical distance between the Kuwajima Formation and the upper Barremian to lower Aptian Myodani Formation that yields *Nippononaia ryosekiana* because the Akaiwa Formation is intercalated between them. These facts tentatively suggest that the Kuwajima Formation is the lower Neocomian.

The fossils of the Kuwajima Formation are mostly collected from the Kuwajima "Kaseki-kabe" (fossil bluff) (Fig. 2), an outcrop of the Kuwajima Formation in Shiramine, Ishikawa, which is correlated to the upper horizon of the Formation (Isaji, 2000). The Kuwajima "Kaseki-kabe" is composed of alternations of massive sandstones, fine-grained sandstones and mudstones (Isaji, 2000). The upper part of the Kuwajima Formation including the "Kaseki-kabe" appears to

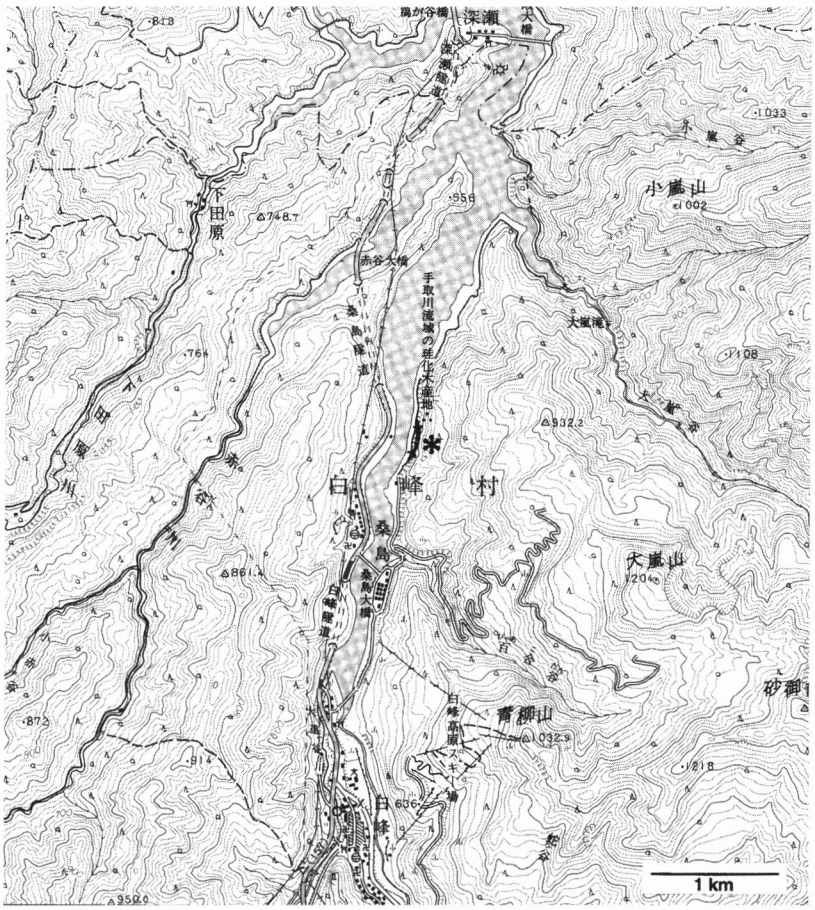

Fig. 2. Location of the Kuwajima "Kaseki-kabe" (asterisk) in Shiramine Village, Ishikawa Prefecture, based on the 1: 50,000 scale topographic map of the Geographical Survey Institute, "Shiramine".

have been deposited in the channels of braided rivers and flood plains (Okazaki and Isaji, 1999; Isaji, 2000).

The Kuwajima "Kaseki-kabe" has been well known for more than 120 years as a botanical fossil locality since a German geographer J. J. Rein collected some plant fossils from it in 1874 and his colleague H. Th. Geyler (1877) described them. Geyler proposed that they can be correlated to the Middle Jurassic flora in Siberia, and it was the first paleontological achievement determining the age of Japanese strata by fossil records, though the Kuwajima Formation including "Kaseki-kabe" is now regarded as the lower Neocomian as mentioned above. The "Kaseki-kabe" has also been recognized as a vertebrate fossil locality since several dinosaur teeth were found from it. The Kuwajima "Kaseki-kabe" was designated in 1957 to the National Natural Monument for the paleontological importance.

VERTEBRATE FOSSIL ASSEMBLAGE FROM THE KUWAJIMA FORMATION

The report of paleontological activity in 1997-1999 fiscal year (Matsuoka, 2000b), which was published by Shiramine Village Board of Education, let us know that the Kuwajima "Kaseki-kabe" have yielded totally about 80 species of plants, mollusks, insects and vertebrates. The vertebrate fossil assemblage from the "Kaseki-kabe" includes more than 30 species of the Early Cretaceous period (Fig. 3), composed of four fishes, one frog, tritylodontids, three turtles, probably three pterosaurs, seven dinosaurs, seven lizards, one choristodere, one bird and two mammals.

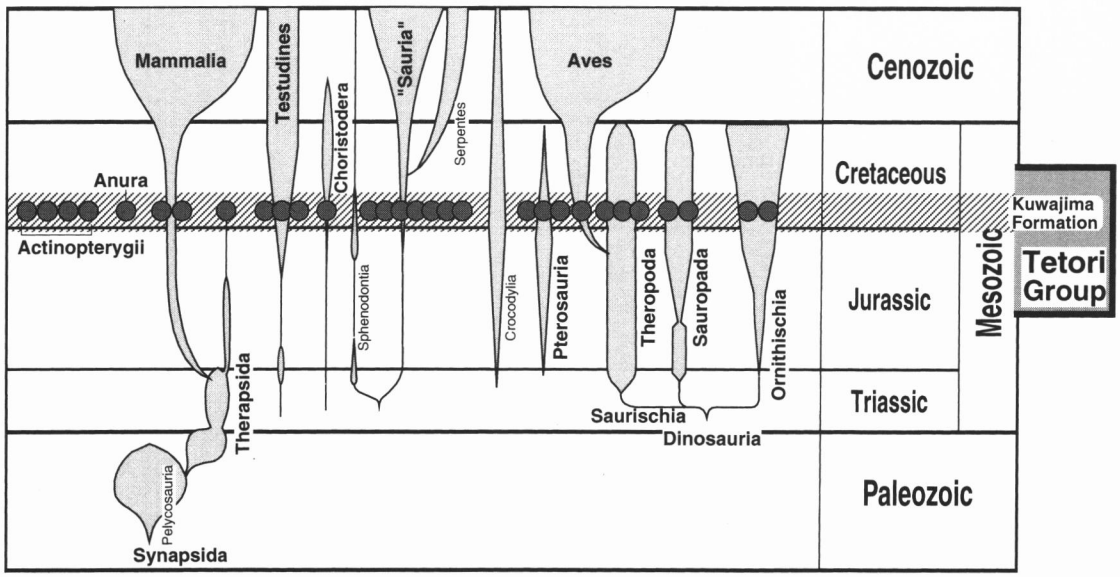

Fig. 3. Taxonomic composition of the vertebrate assemblage of the Kuwajima "Kaseki-kabe". Circles showing the collected taxa.

1. FISHES

The Kuwajima "Kaseki-kabe" yields *Lepidotes* sp., *Sinamia* sp., pachycormid, and one species of primitive Teleostei (Yabumoto, 2000). Azuma (1991) and Azuma and Hasegawa (1989) reported the specimens that are thought to be belonging Genus Sinamia (Yabumoto, 2000). The following descriptions are citation from Yabumoto (2000).

Lepidotes sp.: two scales have been found.

Sinamia sp.: premaxilla, maxilla, dentary, gular plate, frontal, hyomandibular, preopecle, supracleithrum, cleithrum, scales and centrums have been uncovered. Because all the specimens were not articulated when they were discovered, it is hard to say whether they are derived from one species or more. Forms of gular plate, hyomandibular, preopecle and supracleithrum are different from those of all species that each form is already known. Additionally, many bones, which might be of *Sinamia* sp. but difficult to recognize their positions, have been discovered.

Pachycormidae gen. et sp. indet.: dentary has been recovered. Though the shapes of this dentary and teeth are similar to those of Late Jurassic genus *Hypsocormus*, especially of *H. macrodon*, they are more or less different from those of all the known species. This specimen resembles the Late Jurassic species rather than the contemporized Cretaceous species. Family Pachycormidae had been known only from the Lower Jurassic to Lower Cretaceous marine deposits before this discovery.

A species of Teleostei: a lot of fossil cycloid scales have been unearthed. It is thought to be of a primitive Teleostei because these scales do not have groove but have ridge.

2. A FROG

The "Kaseki-kabe" has yielded a frog fossil (Matsuoka, 2000c). This is the only amphibian specimen that has been found from the Kuwajima Formation. From the Okurodani Formation that is comparable to the Kuwajima Formation in Shokawa, Gifu Prefecture, three fossil amphibians, which are one vertebra of urodele and two specimens of frogs, have been reported (Evans and Manabe, 1998). The following descriptions are quoted from Matsuoka (2000c).

The specimen from the Kuwajima Formation is the left tibiofibula that is somewhat damaged by compression. It has not yet been studied enough. However, the specimen has been compared with recent *Bombina orientalis* (Bombinatoridae), and it was found that they closely resemble each other. The frog fossils from the Okurodani Formation are

reported to be similar to bombinatorids (Evans and Manabe, 1998). The body size estimated from the Kuwajima specimen is almost the same with those from the Okurodani Formation. Thus there is a good possibility that the frogs from two formations might be quite similar to each other.

3. TRITYLODONTIDS

(Plates 1-5 to 8, 2, 3 and 4)

More than 150 isolated teeth of tritylodontids have been discovered from the "Kaseki-kabe" (Setoguchi et al., 1998; Matsuoka et al., 1999; Setoguchi et al., 1999; Matsuoka, 2000a, d; Matsuoka and Setoguchi, 2000). Family Tritylodontidae is the advanced group of mammal-like reptile and it is thought to be the closest outgroup of Mammalia because it shares a large number of synapomorphies with mammals (e.g. Benton, 1997). It appeared in the Late Triassic after most of the mammal-like reptiles had been extinct, and has been believed to be extinct in the late Middle Jurassic (e.g. Carroll, 1988). It is, however, revealed that tritylodontids survived into Cretaceous based on the reports from the Kuwajima Formation and from the Lower Cretaceous of Kemerovo, western Siberia (Tatarinov and Maschenko, 1999), which might be almost the same age as the Kuwajima Formation. Most of the following descriptions are citation from Matsuoka (2000d).

The fossil tritylodontids from the Kuwajima Formation is divided into three types based on their sizes, namely the large, middle and small types. Most of the Kuwajima materials belong to the large type, and there are some middle type specimens. Only two small type teeth are known in the fossil assemblage. Upper and lower cheek teeth and incisors of the large type, upper and lower cheek teeth of the middle type and lower cheek teeth of the small type have been found. Though cheek teeth of the large type and middle type are morphologically similar to each other, there is obvious difference in their size between two types. The teeth of small type have morphology that is different from the other two types. The studies on Kuwajima tritylodontids are mainly about the large type (Matsuoka et al., 1999; Setoguchi et al., 1999; Matsuoka, 2000a; Matsuoka and Setoguchi, 2000).

Large type

Upper cheek teeth: The cusp formula is 2−2−2. Though small accessory cusp does not exist, sometimes faint crest that is thought to be a trace of one are seen on the anterior face of the mesial cusp of middle cusp rows. The longitudinal lengths of three cusp rows are almost the same, and occlusal view of the crown is prallelogram in which buccolingual length is longer than mesiodistal. The specimen possessing roots has never been found.

Lower cheek teeth: The lingual cusp row is placed somewhat anterior to the buccal row, and the arrangement of four cusps is parallelogramatical. B-shaped single root is observed in some specimens.

Incisors: Abundant incisors of tritylodontids have been found from the Kuwajima Formation. The incisors of tritylodontids have never been morphologically described but for those of Oligokyphus (Kühne, 1956). The Kuwajima materials are divided into two types. One type is thought to be the upper incisors and another is lower. Some specimens in both types appear to be permanent teeth and not to be replaced.

Middle type: They are thought to be of the animals of the same genus with the large type. It is now being examined whether the two types are of the same species.

Small type: Two lower cheek teeth have been found. Only one of them is perfectly preserved. Anterior cusps are extremely narrow buccoligually, and the teeth of this type are morphologically different from of the other types clearly. This type of teeth is of animals that are comparatively small size among tritylodontids.

Setoguchi et al. (1999) discussed the systematics in Family Tritylodontidae based on the cusp arrangement in upper cheek teeth. They suggested that the large type of Kuwajima material is of advanced tritylodontids that have 2−2−2 cusp formula such as *Stereognatus* from the Middle Jurassic of the U. K. and *Polistodon* from the Middle Jurassic of China. Besides, *Bocatherium* from the Middle Jurassic of Mexico and *Xenocretosuchus* from the Lower Cretaceous of western Siberia have the same cusp formulae and are also thought to be advanced members, though Setoguchi et al. did not use them for the comparison. Kuwajima material appears to be a new genus that is closely related to *Stereognathus* and *Xenocre-*

tosuchus on the basis of the morphology of upper cheek teeth. Matsuoka (2000d) suggested the possibility that *Xenocretosuchus* is the synonym of *Stereognathus* based on their descriptions, but later comparison let us agree that they are classified into different genera.

4. TURTLES

The most abundant component of the vertebrate fossil assemblage of the "Kaseki-kabe" is turtle. Hirayama (1999, 2000) and Hirayama et al. (2000) reported that a lot of fossil turtles, all of them belong to Eucryptodira, have been discovered from the Kuwajima Formation exposed at the Kuwajima "Kaseki-kabe". In these specimens, three types of turtles, Trionychoidea, Testudinoidea and Sinemydidae, are distinguished, and both the trionychoids and the testudinoid represent the earliest known "modern" cryptodires (Chelomacryptodira) (Hirayama, 2000). Most of the following descriptions are citation from Hirayama (2000).

Trionychoidea fam. indet.: skulls, dentaries, cervical vertebrae, scapulae, ilium, ischium, femur and many shells, both carapaces and plastrons, have been found. The skulls lack an anterior medial process of frontals as in Trionychoidae such as *Adocus*, nanhsiungchelyids and carettochelyids (Hirayama et al., 2000). As for the dentaries, right and left dentaries are separated. This is the characteristic that is reported only in *Sinemys*. The cervical vertebrae are opistocoelous and they are similar to the fourth cervical of *Adocus*. As for the shells, plural specimens of almost all parts have been found. They appear to be of the same taxon.

Testudinoidea fam. indet.: caudal vertebrae, scapulae, humeri and many shells, both carapaces and plastrons, have been discovered. Plural specimens of many parts of the shell have been collected, and they are thought to be of the same taxon. This is obviously different from any known taxa in their carapaces and plastrons, and is considered to be the most primitive testudinoid.

Sinemydidae gen. et sp. indet.: carapaces and plastrons have been unearthed.

5. A CHORISTODERE

A vertebra of choristodere was found from the "Kaseki-kabe", although Matsuoka (2000b) missed to include in the fossil assemblage diversity. The Okurodani Formation in Shokawa, Gifu Prefecture yields a long-necked choristodere, *Shokawa ikoi* (Evans and Manabe, 1999). Since the Kuwajima material is similar to the vertebrae collected from the type locality of *Shokawa ikoi* with other additional materials, it could be referred to the close animal, though the specimen from Kuwajima Formation is larger than the vertebrae of Holotype of *Shokawa ikoi.*

6. DINOSAURS

Seven lineages of dinosaurs, two types of sauropodomorphs, three types of theropods and two types of ornithopods, have been discovered from the "Kaseki-kabe" (Manabe and Barrett, 2000; Manabe, Barrett et al., 2000). It is the characteristic of this fauna that there are not only the Early Cretaceous types of dinosaurs (Hypsilophodontidae and Iguanodontidae) but also the taxa that appeared in Late Cretaceous (unnamed clade Oviraptorosauria + Therizinosauroidea) (Manabe and Barrett, 2000). Following descriptions are mostly quoted from Manabe and Barrett (2000).

Sauropodomorpha

Type A: several teeth (Plate 6-3, 4) have been recovered. Their shapes resemble those of euhelopodids of China.

Type B: a tooth (Plate 8-8) has long been referred to Diplodocidae. Manabe and Barrett (2000) noted that it is morphologically close to that of *Phuwiangosaurus* from the Lower Cretaceous of Thailand. However, we regard this tooth as that of pterosaur.

Theropoda

Type A: some isolated teeth of large theropod (Plate 7-8) have been collected.

Type B: isolated crowns of small theropod (Plate 7-2 to 5 and 7) have been discovered. Though the outlines of the crowns are similar to those of dromaeosaurids, the specimen showing the synapomorphy of Dromaeosauridae (Velociraptorinae), that the serrations of anterior edge are less than half in size of those of posterior ridge, has never discovered.

Type C (tetanurans): a manual ungula (Plate 7-1) was found. It has a pronounced posterodorsal lip that is synapomorphy of the unnamed clade Oviraptorosauria + Therizinosauroidea (Makovicky and Sues, 1998). This specimen, therefore, is

thought to be one of the earliest records of this group (Manabe and Barrett, 2000; Manabe, Barrett et al., 2000).

Ornithopoda

Hypsilophodontidae: a slab bearing scattered skull elements (Plate 6-2) was discovered, as well as some isolated teeth. In the skull, predentary, dentary, splenial, prearticular, nasal, maxilla, prefrontal, frontal, parietal, lacrimal, palatine and pterygoid are observable. Morphologies of each element of the skull resemble well to *Hypsilophodon* of the U. K., but the crown shape in which striae are distinct is clearly different from those of *Hypsilophodon*.

Iguanodontidae: teeth and fragment of the dentary have been found. In addition to the terminally resorbed maxillary teeth (Plate 5-1 to 4), which were referred to iguanodontid first by Hasegawa et al. (1995), some wonderful specimens (Plate 5-5) and a dentary tooth (Plate 6-1) have been collected. Asia is thought to have been isolated from Euramerica by the Turgai Sea (Evans et al., 1998), but the existence of iguanodontid revealed that the isolated period was very short (Hasegawa et al., 1995).

7. PTEROSAURS AND A BIRD

Fossils of "flying vertebrates" pterosaurs and a bird have been found from the "Kaseki-kabe" (Unwin and Matsuoka, 2000). Following descriptions are quoted from Unwin and Matsuoka (2000). Pterosaurs from the Kuwajima Formation belong to three Superfamily clades, Ornithocheiroidea, Ctenochasmatidea and Dsungaripteroidea. The bird fossil is thought to be of Subclass Enantiornithes, and possibly related to the member from the Lower Cretaceous Jehol Group of northwestern China where recently various Mesozoic birds have been reported.

Order Pterosauria (Reptilia)

Family Ornithocheiridae (Superfamily Ornithocheiroidea): One almost complete tooth (Plate 8-1) was found. It can be well compared in tooth morphology with ornithocheirids from the Lower Cretaceous of Brazil (Wellnhofer, 1991) and from the lower Upper Cretaceous of Morocco and the U. K. (Wellnhofer and Buffetaut, 1999).

Subfamily Gnathosaurinae (Superfamily Ctenochasmatoidea): Several isolated teeth (Plate 8-2 to 7) have been discovered. They have very long and attenuate crowns and also long (but not longer than the crown) and slender roots. It is only ctenochasmatid pterosaurs that have such a long crown. The teeth morphology is close to those of the members of Gnathosaurinae among ctenochasmatids.

Superfamily Dsungaripteroidea?: One tooth (Plate 8-9) was unearthed. This triangular tooth might be of a member of Dsungaripteroidea, since the approximate correspondence of the Kuwajima Formation, the Amagodani Formation in Gifu Prefecture, has the osteological evidence of this type of pterosaur (Unwin et al., 1996).

Class Aves

Subclass Enantiornithes: One incomplete right humerus (Plate 7-6) has been found. Although the specimen lacks the distal end, it is clear that it is not twisted, and thus it is thought to be a humerus of a bird. The flattened profile of head of the humerus, not like the round one seen among non-enantiorns (Walker, 1981), suggests that the specimen is that of enantiorn. It morphologically resembles that of *Otogarnis genghisi* from the Lower Cretaceous Jehol Group of northeastern China.

8. LIZARDS

Seven taxa of lizards have been discovered from the "Kaseki-kabe" (Evans and Manabe, 2000). This is one of the most diverse lizard assemblages known before the Late Cretaceous, with the Lower Cretaceous beds of the Purbeck Limestone Formation, England, and the middle Cretaceous deposits of the Antlers Formation, Texas (Evens and Manabe, 2000). Following descriptions are citation from Evens and Manabe (2000).

Species 1 (herbivorous form): isolated crowns of teeth and a maxilla with teeth have been found. The morphology of the crowns is similar to that of iguanians but the basal part of the crown is short. Herbivorous form tooth possessing such a complex crown is a rare apomorphic character in lizards.

Species 2 (limbless or reduced limb form): vertebrae and ribs have been recovered. The morphology of them resembles those of the lizards that have reduced limbs such as amphisbaenians.

Species 3 (Paramacellodidae gen. et sp. indet.): a lot of isolated scales, lower jaw, pelvis and hind

limb have been collected. They are thought to belong to Paramacellodidae because of the ossified rhombic scales.

Species 4 (*Sakurasaurus* sp.): *Sakurasaurus* is a species of Scincomorpha, discovered from the Okurodani Formation in Shokawa Village, Gifu Prefecture (Evans and Manabe, 1999). Several specimens of this genus have been discovered from the Kuwajima Formation.

Species 5 (scincomorph with bicuspid teeth): a dentary fragment with bicuspid teeth was collected.

Species 6 (scincomorph with more robust dentition): a piece of dentary with teeth was collected.

Species 7 (anguimorph?): a fragment of anterior part of the lower jaw has been collected.

9. MAMMALS

Two lineages of mammalian fossils, triconodonts and multituberculates, have been collected from the "Kaseki-kabe" (Rougier et al., 1999; Manabe, Rougier et al., 2000; Takada and Matsuoka, 2001; Takada et al., 2001). From Japan, they are the first discovery in these lineages and the oldest mammalian fossil records (Manabe, Rougier et al., 2000). Following description as to triconodonts are cited from Manabe, Rougier et al. (2000) and Rougier et al. (1999), and as to multituberculates are from Takada and Matsuoka (2001) and Takada et al. (2001).

Triconodonts: several dentaries have been found (Plate 1-1 to 3). One of them is the right dentary on which P_2 to M_5 are preserved (Plate 1-1). This jaw is similar to 'amphilestid' from the Upper Jurassic of the U. K. and North America.

Multituberculates: the left dentary with P_4 and alveoli for P_2 and P_3 (Plate 1-4), and an isolated upper premolar have been recovered. Though the existence of P_2 suggests that this specimen is a member of paraphyletic suborder 'Plagiaulacida' (Kielan-Jaworowska and Hurum, 2001), it is thought to be close to Cimolodonta because of its other morphological features such as large P_4. The multituberculates from the Neocomian is one of the oldest records from Asia.

CONCLUDING REMARKS

The Kuwajima "Kaseki-kabe" is one of the most fruitful Early Cretaceous fossil localities in the world. More than 30 Neocomian vertebrate species have been collected from the "Kaseki-kabe" by the research from 1997 to 2000. The fossil assemblage consists of diverse taxa such as fishes, amphibians, reptiles, birds, and mammals (Matsuoka, 2000b).

The vertebrate fossil assemblage from the "Kaseki-kabe" gives us significant clues to understand the Jurassic to Cretaceous fauna in Asia, because the Neocomian vertebrate fossil assemblage have been collected from it. Vertebrate fossil records from the Neocomian are fewer than those of other periods in Mesozoic over the world, thus the fossil assemblage from the "Kaseki-kabe" is quite important to understand the fauna in that time. Besides, the "Kaseki-kabe" is a premium example since various vertebrate fossils have been found from only one site.

The vertebrate fossil assemblage is also quite important to understand the genetical process of the Cretaceous type fauna of East Asia in Jurassic to Cretaceous age. From the "Kaseki-kabe", Jurassic type vertebrates such as tritylodontids, Early Cretaceous type such as iguanodontids and hypsilophodontids, and Late Cretaceous types such as unnamed clade Oviraptorosauria + Therizinosauroidea and cimolodontian multituberculate have been collected (see Manabe and Barrett, 2000; Matsuoka, 2000d; Takada and Matsuoka, 2001). Although the discovery of tritylodontids from the "Kaseki-kabe" appears to support Luo's (1999) theory that East Asia was the refugium for relicts in the Early Cretaceous, a plenty of earliest records of Cretaceous type animals, at the same time, are found from it. This fact suggests that stereotyped view cannot be applied.

The Tetori Group including the "Kaseki-kabe", fortunately, is geographically and chronologically close to the famous Jehol Group, especially the Yixian Formation, northwestern China. The vertebrate remains of various taxa have also been reported from the Jehol Group (e.g. Takai, 1943; Cheng et al., 1980; Chen, 1988; Wang et al., 1989; Wang, 1990; Hou et al., 1996; Hu et al., 1997; Ji et al., 1998; Ji, Chiappe et al., 1999; Ji, Luo et al., 1999; Wang et al., 1999; Wang et al., 2000; Zhang and Zhou, 2000; Gao and Wang, 2001; Zhang et al., 2001; Zhou and Zhang, 2001). The fossil assemblage from the "Kaseki-kabe" is comparable

with that of the Jehol Group, and it provides informations about the variety and history of Asian fauna in the Mesozoic.

The Neocomian mammals have been collected from the Kuwajima "Kaseki-kabe" (Rougier et al., 1999; Manabe, Rougier et al., 2000; Takada and Matsuoka, 2001; Takada et al. 2001). The history and biogeography of mammals in Early Cretaceous are poorly understood because of the scarce fossil records in the period (Clemens et al., 1979). Further studies on the mammalian remains from the "Kaseki-kabe" will progress the knowledge about early history of the Mesozoic mammals.

The most important factor for the successful excavation of fossils is cooperation between university and museum staffs who are keen about geology and paleontology, the local people who know and love the fossil localities and students who have the pioneering spirit. The activity in the Tetori field, not only in Kuwajima but also in Shokawa, Gifu Prefecture, is one good example of successful crew, which is the clue to understanding the dawn of the modern vertebrate fauna.

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* in Japanese
** in Japanese with English abstract or summary
[ç] in French
[ü] in German
[üü] in German with English abstract or summary
[中] in Chinese
[中中] in Chinese with English abstract or summary

Note: The titles put between double quotation marks are translated in English on authors' responsibility.

APPENDIX

List of the fossil assemblage from the Kuwajima "Kaseki-kabe" (Kuwajima Formation, Tetori Group) in Shiramine Village, Ishikawa Prefecture (modified after Matsuoka, 2000b).

PLANTAE

Bryophyta
Thallites yabei (Kryshtofovich) Harris
Trachephytina
Sphenopsida
Equisetites ushimarensis (Yokoyama) Oishi
Pteropsida
Osmundopsis distans (Heer) Kimura & Sekido
Gleichenites ishikawaensis Kimura & Sekido
Gleichenites nipponensis Oishi
Gleichenites sp.
Coniopteris burejensis (Zalessky) Seward
Coniopteris sp.
Brisia onychioides (Vassilevskaia & Kara-Mursa) Sahylina
Eboracia nipponensis Kimura & Sekido
Eboracia sp.
Cladophlebis denticulate *(Brongniart)* Nathorst
Onychiopsis elongata *(Geyler)* Yokoyama
Sphenopteris sp.
Gymnospermae
Cycadopsida
Dictyozamites kawasakii Tateiwa
Dictyozamites tedoriensis Kimura & Sekido
Neozamites sp.
Nilssonia kotoi (Yokoyama) Oishi
Nilssonia nipponensis Yokoyama
Nilssonia orientalis Heer
Nilssonia sp.
Ginkgopsida
Ginkgoites digitata (Brongniart) Seward
Ginkgoites huttoni (Sternberg) Black
Ginkgoites sp.
Ginkgoidium nathorsti Yokoyama
Eretmophyllum tetoriense Kimura & Sekido
Coniferopsida
Podozamites lanceolatus (Lindley & Hutton) Braun
Podozamites anguistifolius (Eichwald) Heer
Podocarpus reinii (Geyler) Matsuo
Podocarpus yokoyamai Matsuo
Podocarpus tedoriensis Matsuo
Podocarpus sp.
Pinaceae? sp.
Sequoia? sp.
Articulatophyta
Arecaceae? sp.
Angiospermae?
Magnoliaceae? sp.

Unclassified plants
Taeniopteris emarginata Oishi
Taeniopteris sp.
Seeds
Carpolithes sp.

ANIMALIA

Mollusca
Bivalvia
Unio ogamigoensis
Sphaerium sp.
Gastropoda
Viviparus onogoensis
Micromelania? katoensis
Physidae sp. A
Physidae sp. B
Pupilloidea sp.
Arthropoda
Insecta
Nipponohagla kaga
Fulgoridium? matsuoi
Kagapsychops aranea
Coleoptera spp.
Vertebrata
Actinopterygii
Lepidotes sp.
Sinamina sp.
Pachycormidae sp.
Teleostei sp.
Amphibia
Anura sp.

Reptilia
- **Synapsida**
  - *Tritylodontidae* sp.
- **Choristodera**
  - *Choristodera* sp.
- **Testudines**
  - *Trionychoidae* sp.
  - *Testudinoidea* sp.
  - *Sinemydidae* sp.
- **Pterosauria**
  - Ornithocheiridae sp.
  - Gnathosaurinae sp.
  - Dsungaripteroidea? sp.
- **Saurischia (Dinosauria)**
  - Sauropoda sp. A
  - Sauropoda sp. B
  - Theropoda sp. A
  - Theropoda sp. B
  - Theropoda sp. C, cl. Ovira. + Therizino.
- **Ornithischia (Dinosauria)**
  - Hypsilophodontidae sp.
  - Iguanodontidae sp.
- **Squamata**
  - Sp. 1: a herbivorous species
  - Sp. 2: a limbless species
  - Sp. 3: Paramacellodidae sp.
  - Sp. 4: Sakurasaurus sp.
  - Sp. 5: Scincomorph sp. A
  - Sp. 6: Scincomorph sp. B
  - Sp. 7: Anguismorph? sp.
- **Aves**
  - Enantiornithes sp.
- **Mammalia**
  - Triconodonta sp.
  - Maltituberculata sp.

PLATES

Explanation of Plates 1 to 8

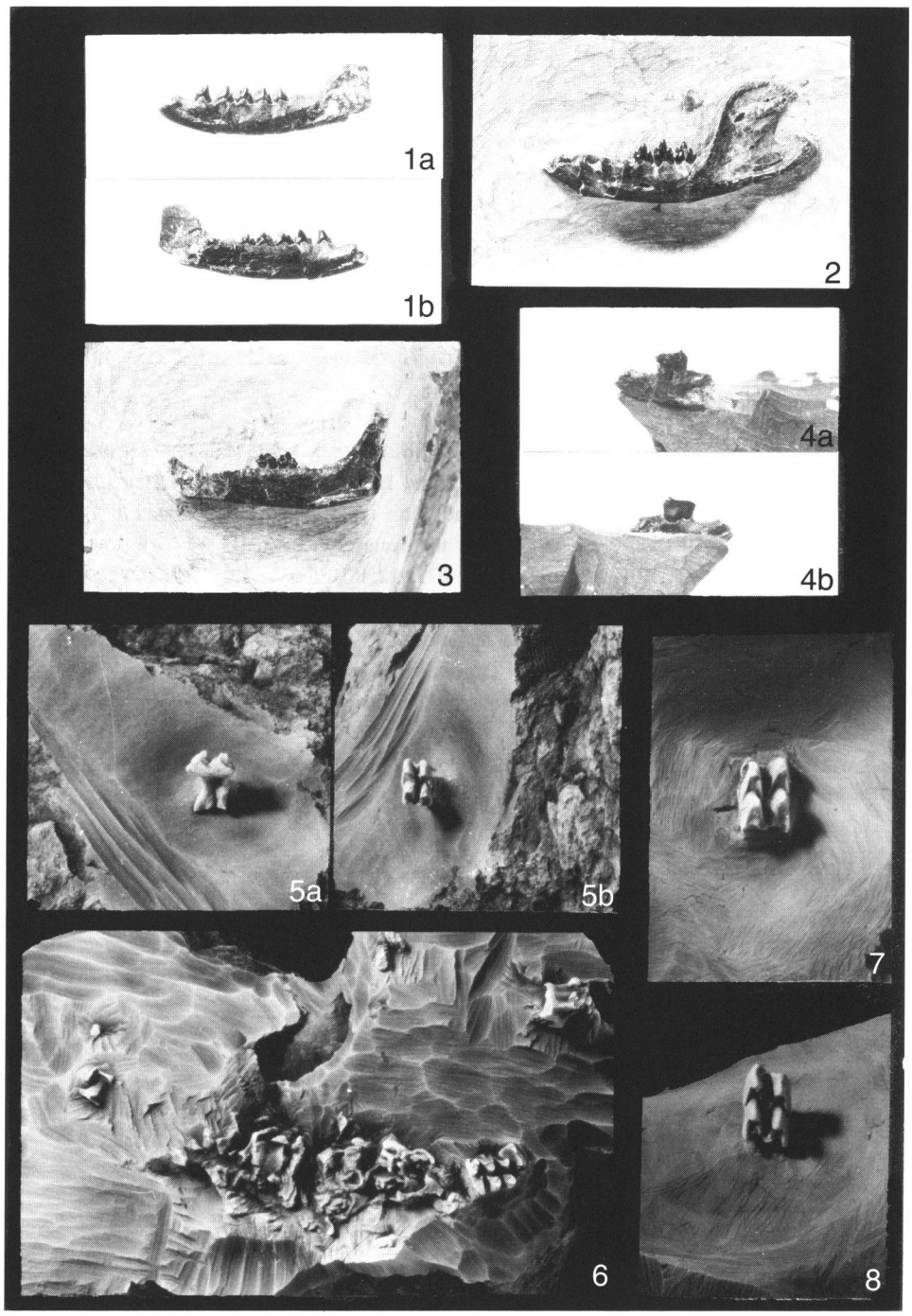
Fossils figured here are the collections from the Kuwajima "Kaseki-kabe" site, the outcrop of the Neocomian Kuwajima Formation, Tetori Group in Shiramine, Ishikawa, Japan. "SBEI" means Shiramine Board of Education, Ishikawa, the governmental organization where the specimens are housed.

Plate 1

Included taxa: Triconodonta and Multituberculata (Mammalia) and Tritylodontidae (Synapsida: Therapsida).

All x1.5

1. SBEI 006: left dentary bearing P_2-M_5 of the triconodont mammal. The buccal (**a**) and lingual (**b**) views.
2. SBEI 020: left dentary bearing three molars of the triconodont mammal, the buccal view on the matrix.
3. SBEI 015: right dentary bearing two molars of the triconodont mammal, the lingual view on the matrix.
4. SBEI 581: left dentary bearing P_4 of the multituberculate mammal. The buccal (**a**) and lingual (**b**) views.
5. SBEI 056: lower cheek tooth with partial root of the "middle type" tritylodont. The lateral (**a**) and occlusal (**b**) views.
6. SBEI 127: upper cheek teeth of the tritylodontid ("middle type") and bone fragments on a rock, probably a skull in origin. Dentary (Plate 2-21), upper and lower cheek teeth (Plate 2-18 to 20) and incisors were found together.
7. SBEI 053 and **8**, SBEI 056: lower cheek teeth of a tritylodontid ("large type"), the occlusal view on the matrix.


1a
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4a
4b
5a
5b
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Plate 2

Included taxon: Tritylodontidae (Synapsida: Therapsida).

Principal object: cheek teeth.

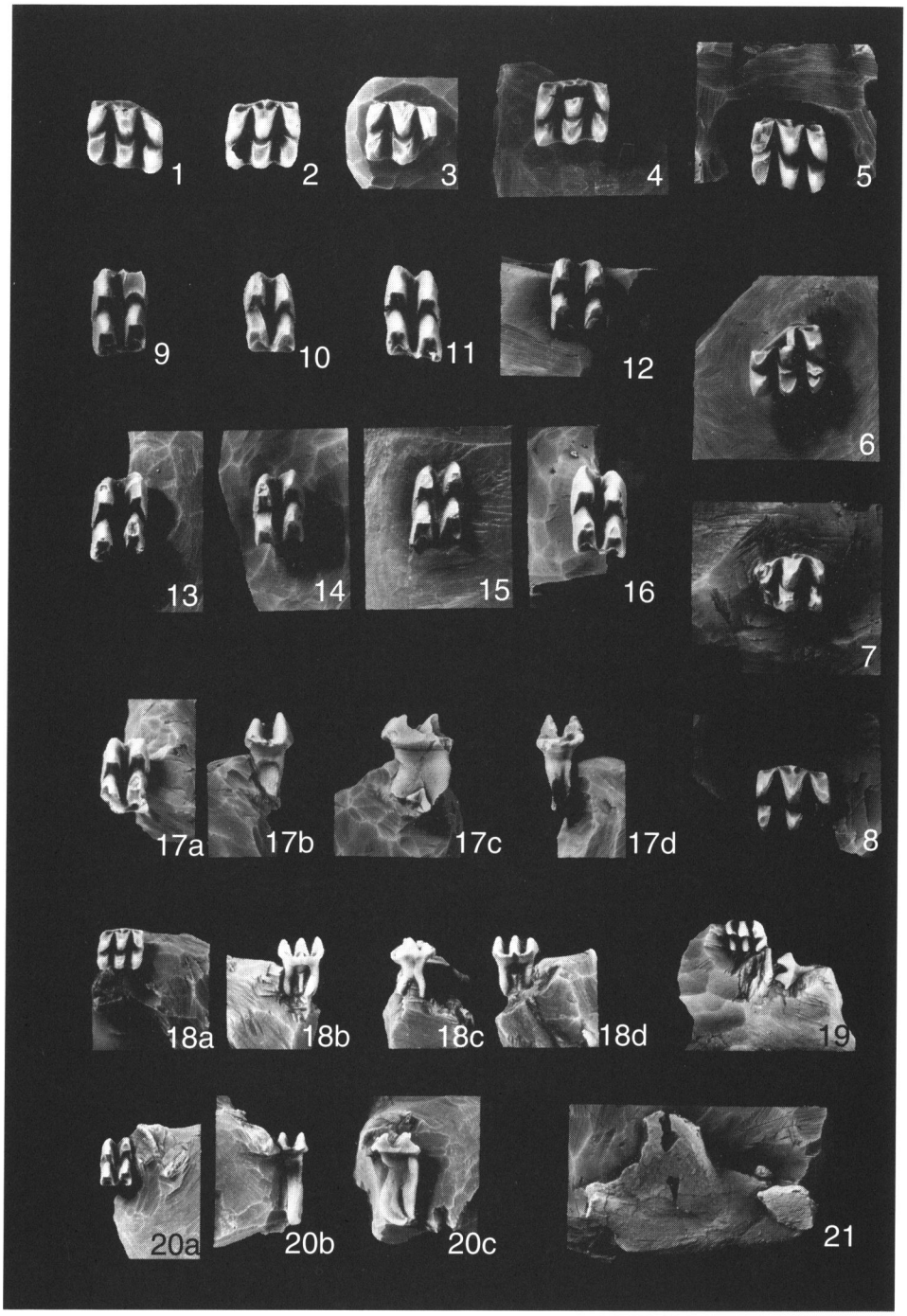
All x1.5

1, SBEI 065; **2**, SBEI 146; **3**, SBEI 043; **4**, SBEI 039; **5**, SBEI 578; **6**, SBEI 047; **7**, SBEI 044; **8**, SBEI 146; **18**, SBEI 112 and **19** including two teeth, SBEI 122: upper cheek teeth of the tritylodontids, the "large type" (1 to 8) and "middle type" (18 and 19). All figures except 18 show the occlusal views only.

9, SBEI 066; **10**, SBEI 034; **11**, SBEI 073; **12**, SBEI 051; **13**, SBEI 029; **14**, SBEI 093; **15**, SBEI 052; **16**, SBEI 062; **17**, SBEI 094 and **20**, SBEI 110: lower cheek teeth of the tritylodontids, the "large type" (9 to 17) and "middle type" (20). All figures except 17 and 20 show the occlusal views only.

For 17, 18 and 20, **a**, **b**, **c** and **d** (not in 20) show the occlusal, anterior, lateral and posterior views respectively.

21. SBEI 141: right dentary of the tritylodontid ("middle type"), the buccal view on the matrix.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18a
18b
18c
18d
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20a
20b
20c
21

Plate 3

Included taxon: Tritylodontidae (Synapsida: Therapsida).

Principal object: cheek teeth.

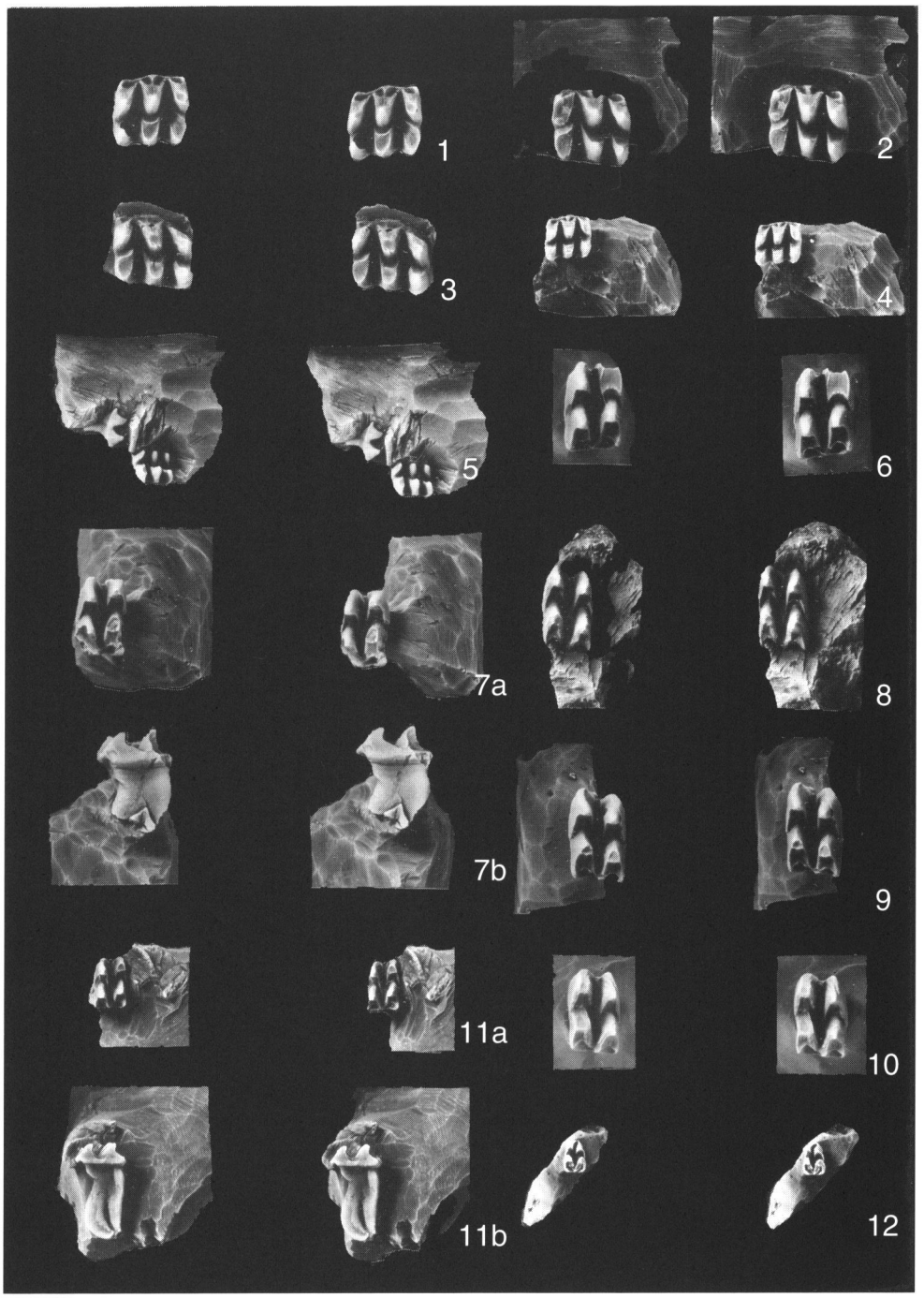
Stereophotographs

All x1.5

1, SBEI 146; **2**, SBEI 578; **3**, SBEI 065; **4**, SBEI 112 and **5**, SBEI 122: upper cheek teeth of the tritylodontids, the "large type" (1 to 3) and "middle type" (4 and 5). All figures show the occlusal views only.

6, SBEI 066; **7**, SBEI 094; **8**, SBEI 577; **9**, SBEI 062; **10**, SBEI 034; **11**, SBEI 110 and **12**, SBEI 040: lower cheek teeth of the tritylodontids, the "large type" (6 to 10), "middle type" (11) and "small type" (12). All figures except 7 and 11 show the occlusal views only.

For 7 and 11, **a** and **b** show the occlusal and lateral views respectively.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7a
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7b
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11a
10
11b
12

Plate 4

Included taxon: Tritylodontidae (Synapsida: Therapsida).

Principal object: incisors.

All x1.5

1, SBEI 049; **2**, SBEI 054; **3**, SBEI 058; **4**, SBEI 092; **5**, SBEI 125; **6**, SBEI 055: incisors of the tritylodontids. For 1, 2, 3 and 4, **a**, **b**, **c** and **d** (not in 4) show the anterior, lateral, posterior and the other side lateral views respectively. 5 and 6 show the lateral views.

7. SBEI 035: a rock in which two incisors of the tritylodontid occurred together.

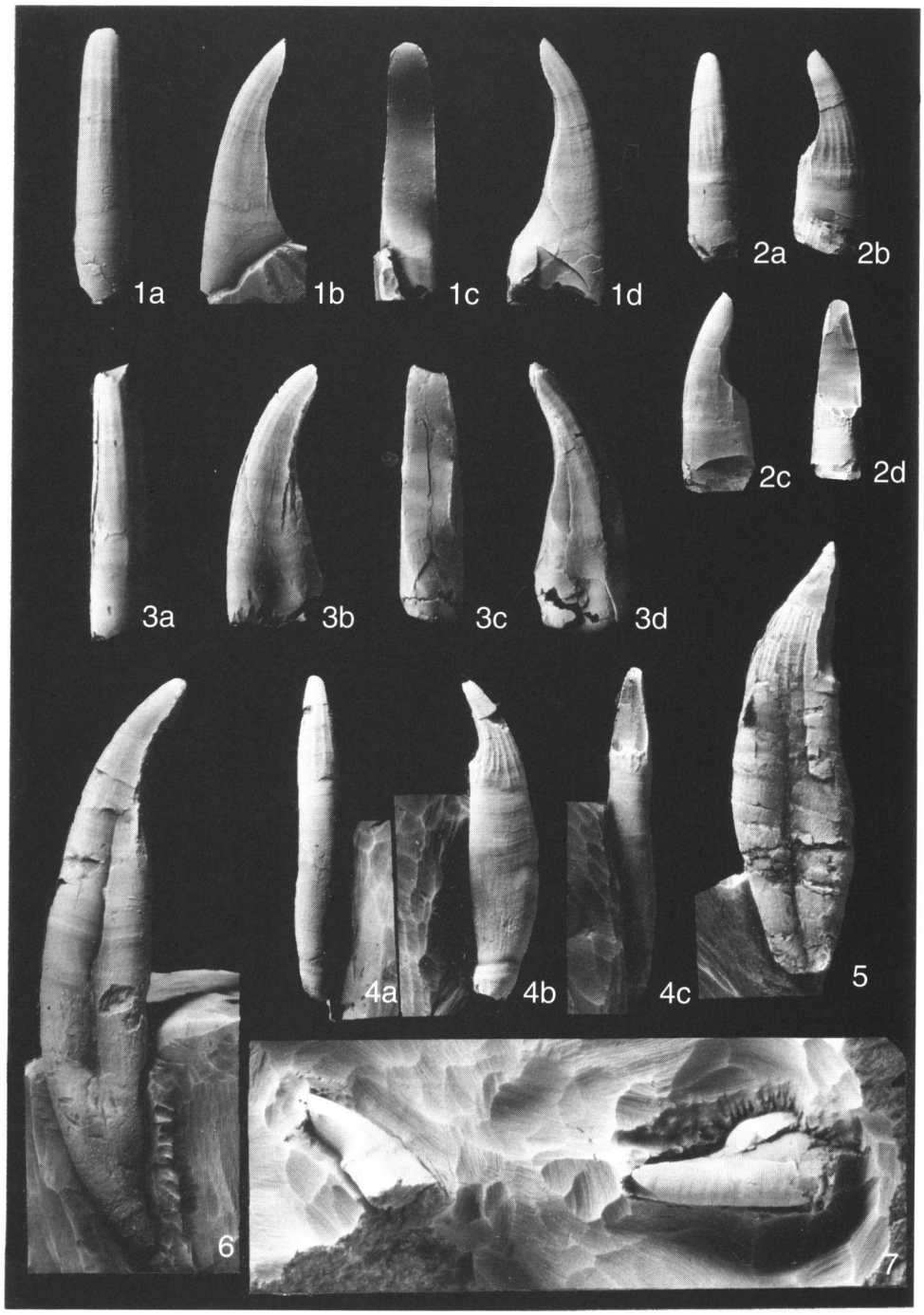
1a
1b
1c
1d
2a
2b
2c
2d
3a
3b
3c
3d
4a
4b
4c
5
6
7

Plate 5

Included taxon: Iguanodontidae (Dinosauria: Ornithopoda).

Principal object: maxillary teeth

All x1.5

1, SBEI 175; **2**, SBEI 165; **3**, SBEI 174; **4**, SBEI 164; **5**, two left teeth fossilized together, SBEI 172: maxillary teeth of the iguanodontid dinosaur.

1 to 3 show the buccal views only. For 4, **a** and **b** show the buccal and lingual views respectively. In 5: **a**, stereophotographs of the occlusal surface; **b**, buccal view; **c**, rather anterior view.

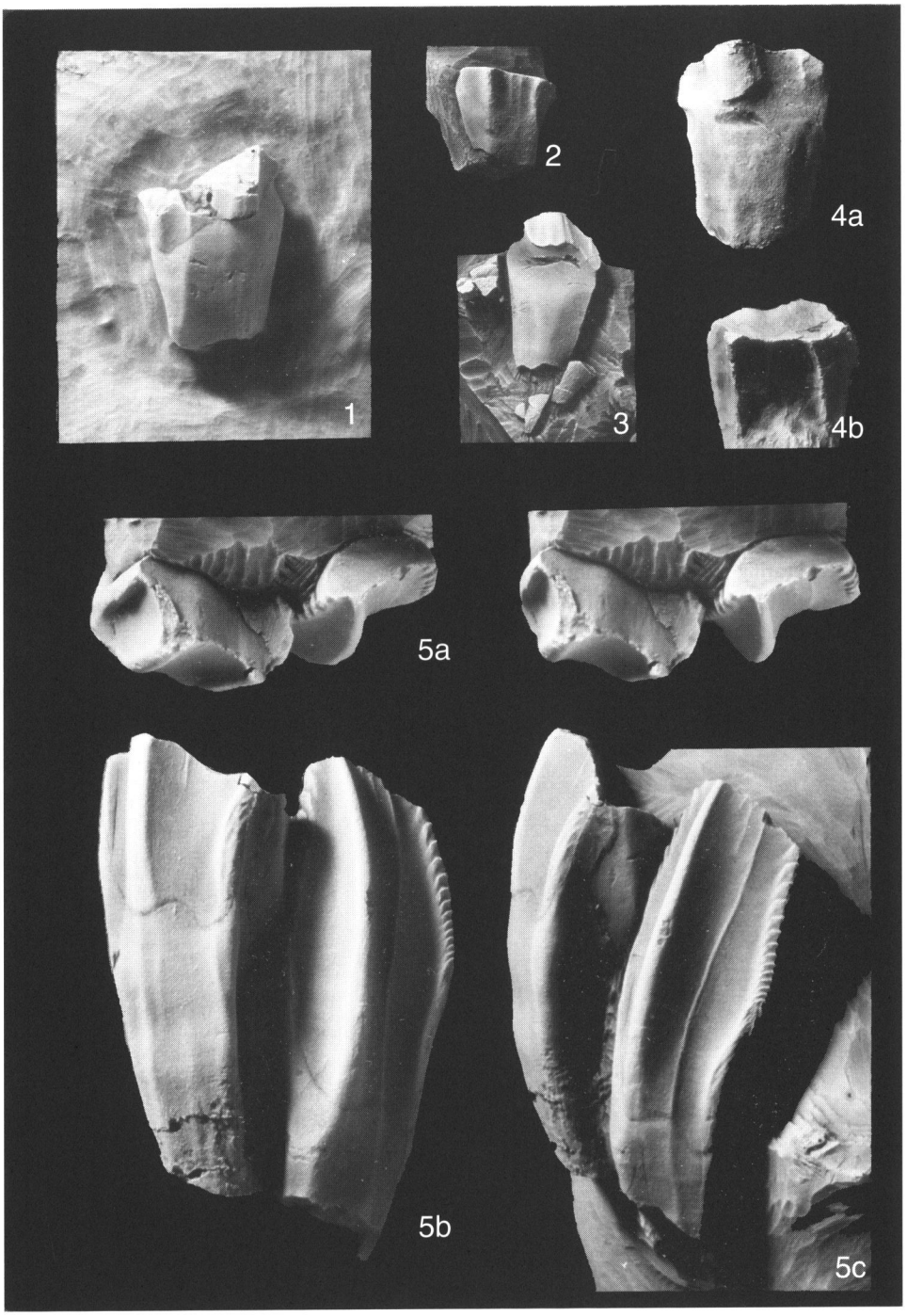
1
2
3
4a
4b
5a
5b
5c

Plate 6

Included taxa: Iguanodontidae and Hypsilophodontidae (Dinosauria: Ornithopoda) and Sauropoda (Dinosauria: Saurischia).

All except 2b: x1.5. 2b: x0.63

1. SBEI 173: left dentary tooth of the iguanodontid dinosaur. The anterior (**a**) and lingual (**b**) views.

2. SBEI 176: skull elements of the hypsilophodontid dinosaur being scattered in a slab; the close up figure of the lingual side of maxilla and dentary, both bearing teeth (**a**) and the whole aspect of the slab (**b**).

3, SBEI 183 and **4,** SBEI 160: teeth of the sauropod dinosaur. The lingual (**a**), buccal (**b**) and marginal (**c**, in 4 only) views.

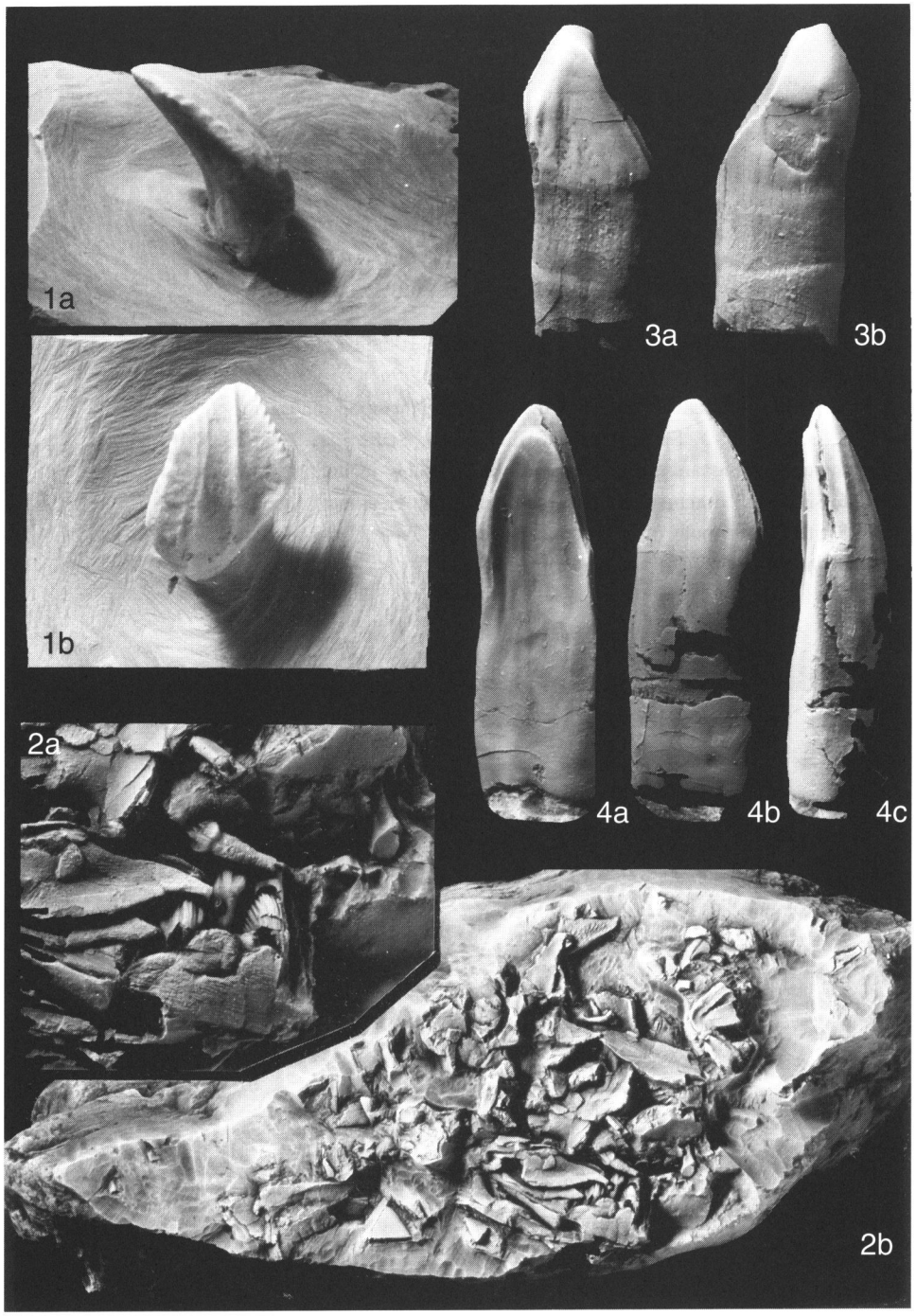
1a
1b
2a
2b
3a
3b
4a
4b
4c

Plate 7

Included taxa: Theropoda (Dinosauria: Saurischia) and a bird (Enantiornithes, Aves)
All x1.5

1. SBEI 167: manual ungual of the Tetanurae theropod dinosaur.

2, SBEI 170; **3**, SBEI 814; **4**, SBEI 156; **5**, SBEI 171; **7**, SBEI 576: teeth of theropod dinosaurs, called "Type B" but probably including plural taxa.

6. SBEI 307: fragmentally right humerus of an enantiornithine bird.

8. SBEI 008: tooth of a theropod dinosaur ("Type A"). The lateral views (**a** and **c**), anterior view (**b**) and posterior view (**d**).

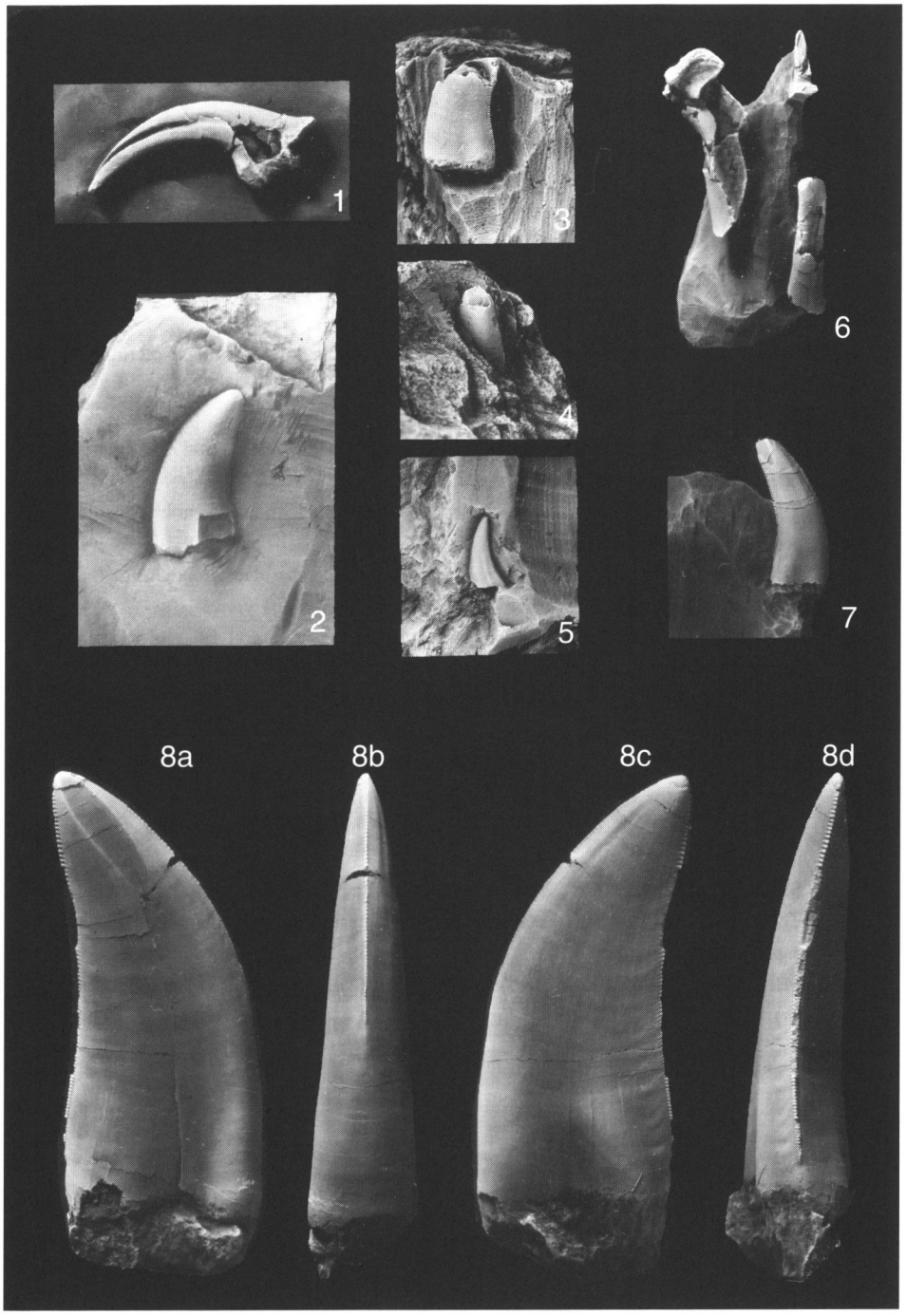
1
2
3
4
5
6
7
8a
8b
8c
8d

Plate 8

Included taxa: Ornithocheiroidea, Ctenochasmatoidea and Dsungaripteroidea? (Pterosauria).

All x1.5

1. SBEI 802: tooth of the Ornithocheiroidae ornithocheiroid pterosaur. The lingual (**a**), anterior (**b**) and buccal (**c**) views.
2. SBEI 824: tooth of the Gnathosaurinae, Ctenochasmatidae ctenochasmatoid pterosaur. The anterior/posterior (**a** and **c**) and buccal (**b**) views.
3. SBEI 804: tooth of the Gnathosaurinae, Ctenochasmatidae ctenochasmatoid pterosaur. The anterior/posterior (**a** and **c**) and lingual (**b**) views.
4. SBEI 855: tooth of a ctenochasmatoid pterosaur. The lateral (**a**) and anterior (**b**) views.
5. SBEI 309: tooth of the Gnathosaurinae, Ctenochasmatidae ctenochasmatoid pterosaur on the matrix.
6. SBEI 306: tooth of the Ctenochasmatidae ctenochasmatoid pterosaur. The anterior/posterior (**a** and **c**) and buccal (**b**) views.
7. SBEI 305: tooth of the Ctenochasmatidae ctenochasmatoid pterosaur on the matrix.
8. SBEI 012: tooth of a pterosaur (Ctenochasmatidae?), the anterior/posterior view. This tooth was identified as a sauropod dinosaur formerly, but reidentified as a pterosaur.
9. SBEI 303: tooth of a dsungaripteroid pterosaur(?). The lingual (**a**) and anterior (**b**) views.


1a
1b
1c
2a
2b
2c
3a
3b
3c
4a
4b
5
6a
6b
6c
7
8
9a
9b