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Original Article

A crocodyliform osteoderm from the Tamayama Formation (Upper Cretaceous) of Fukushima, Japan

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ABSTRACT

Crocodyliformes, such as gobiosuchids, goniopholidids, paralligatorids, and eusuchians, have widely distributed in East Asia during the Cretaceous. In Japan, the Futaba Group in Fukushima Prefecture is one of the most significant Cretaceous outcrops that have produced terrestrial vertebrate fossils, including dinosaurs. However, a definitive crocodyliform has never been reported from Futaba Group. Here we report a crocodyliform osteoderm from the Tamayama Formation (Coniacian–Santonian) of the Futaba Group. The osteoderm is rectangular, wider than long, and bears a tall keel, which can be identified as a dorsal paravertebral osteoderm. A comparison with other crocodyliforms suggests that it pertains to semi-aquatic Neosuchia, but not to Goniopholididae or Paralligatoridae. The first definitive record of a semi-aquatic, derived neosuchian (e.g., eusuchians) from the Futaba Group indicates their appearance before the Coniacian age in East Asia.

INTRODUCTION

Crocodyliformes, such as gobiosuchids, goniopholidids, paralligatorids, and eusuchians, have widely distributed in East Asia during the Cretaceous. In Asia, a variety of crocodyliform families are known from the Cretaceous; gobiosuchids, goniopholidids, paralligatorids, and eusuchians (Storrs & Efimov, 2001; Lauprasert et al., 2011; Kubo et al., 2018; Li et al., 2019). Eusuchian has been found from the lower Upper Cretaceous in Southeast Asia (Thailand, Aptian, Kubo et al., 2018) and Central Asia (Uzbekistan, Turonian, and Tadzhikistan, Santonian, Storrs & Efimov, 2001), whereas its first appearance in East Asia is during the latest Cretaceous (Maastrichtian) (a crocodyloid *Jiangxisuchus* from the of Jilin, China: Li et al., 2019).

In Japan, the Coniacian-Santonian Futaba Group in Fukushima Prefecture is one of the most significant Upper Cretaceous exposures that have produced terrestrial and marine vertebrate fossils, including dinosaurs and plesiosaurs (Hasegawa et al., 1987; Saegusa & Tomida, 2011; Ohashi et al,, 2015; Sato et al., 2005). A definitive crocodyliform has not been reported from the Futaba Group, excluding a potential crocodyliform jaw from the Ashizawa Formation (Hasegawa et al., 1987). Here we report a crocodyliform osteoderm from the Tamayama Formation (Coniacian-Santonian) of the Futaba Group.

Geological setting

The Futaba Group is composed of the lowermost Ashizawa Formation, the middle Kasamatsu Formation, and the uppermost Tamayama Formation. The Ashizawa Formation and Kasamatsu Formation have produced a mammalian dentary (Kusuhashi et al., 2016) and dinosaur materials, such as hadrosauroid teeth and vertebrae and a sauropod tooth (Hasegawa et al., 1987; Ohashi et al., 2015). The Tamayama Formation has produced a few sauropod teeth from the Kohisagawa Member (Saegusa & Tomida, 2011) and a plesiosaur *Futabasaurus* (Sato et al., 2005) from the Irimazawa Member, which overlies the Kohisagawa Member and ranges from the late

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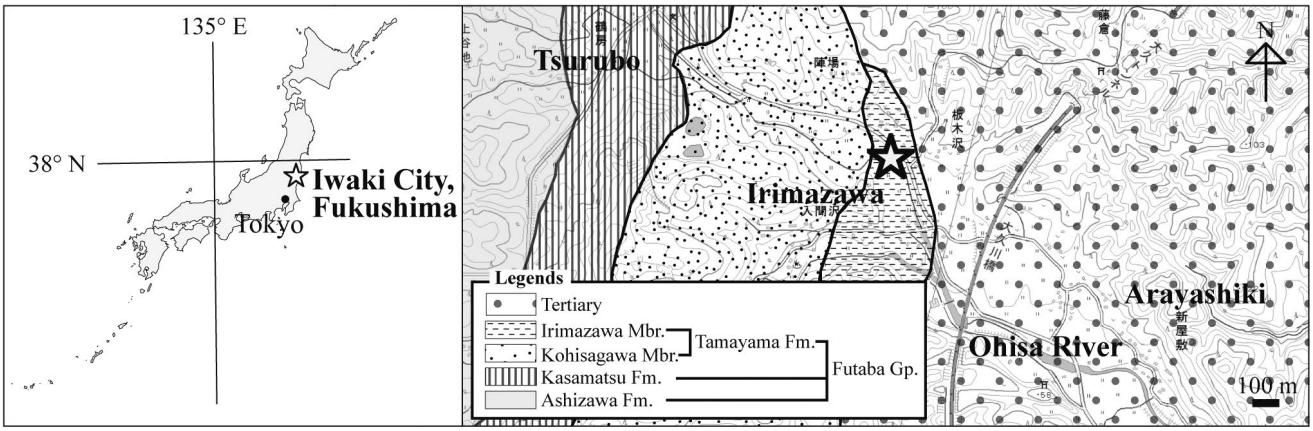

Figure 1. Discovery site of the crocodyliform osteoderm (modified from Inose 2019).

Coniacian to early Santonian based on ammonoids, inoceramids, and bivalves (Obata & Suzuki, 1969; Ando et al., 1995; Inose 2019).

MATERIAL AND METHODS

A crocodyliform osteoderm (ICFM-423360) was collected from the Irimazawa Member of the Tamayama Formation, the Futaba Group (late Coniacian-early Santonian, Late Cretaceous) at Irimazawa River in Iwaki City, Fukushima Prefecture, Japan (Fig. 1). ICFM-423360 was compared with other crocodyliform osteoderms for taxonomic identification. Also, the internal structure of ICFM-423360 was examined by a CT scanner (inspeXio SMX-225CT FPD HR, SHIMADZU) in National Science Museum, Tokyo.

Institutional abbreviation- ICFM, Iwaki City Coal and Fossil Museum.

RESULTS

Systematic Paleontology

CROCODYLIFORMES Clark 1986
NEOSUCHIA Benton & Clark 1988
Gen. et sp. indet.

Material- A dorsal paravertebral osteoderm (ICFM-423360, Fig. 2)
Locality and horizon- Iwaki City, Fukushima Prefecture, Japan. Irimazawa Member, Tamayama Formation, Futaba Group (Coniacian-Santonian, Upper Cretaceous).

Description

The osteoderm is rectangular in dorsoventral view, 53 mm wide, 44 mm long, and wider than long (Fig. 2). It bears a dorsal keel along the midline on the dorsal surface, which is 11 mm high. The keel forms an obtuse triangle in lateral view and runs slightly lateral to the midline closer to its anterior margin. In anteroposterior view, the osteoderm is dorsally curved. The medial half is nearly flat and less curved than the lateral one. The anterior margin is ambiguous in its outline due to the damage; however, three other margins are preserved. The posterior margin is concave in the midline, having a space for contacting the successive osteoderm. The medial margin is straight and would contact the neighboring osteoderm medially, while the lateral margin is dentate, indicating the absence of its neighboring osteoderm laterally. Also, the medial margin is longer than the lateral margin. Based on these morphological characters, the osteoderm can be interpreted as a left lateral-most osteoderm of the dorsal shield (Fig. 3).

On the dorsal surface, the external large pits are densely present, while the ventral surface is smooth and bearing some smaller pits which are external traces of vascular canals (Fig. 2). The pits closer to the edges are larger, elliptical, and interconnected with each other, whereas those closer to the center are smaller, more rounded, and separated from each other on the dorsal surface. The deep pits are seen in ICFM-423360 as in some neosuchians such as paralligatorids and eusuchians (Rummy et al., 2019; Kubo et al., 2018;

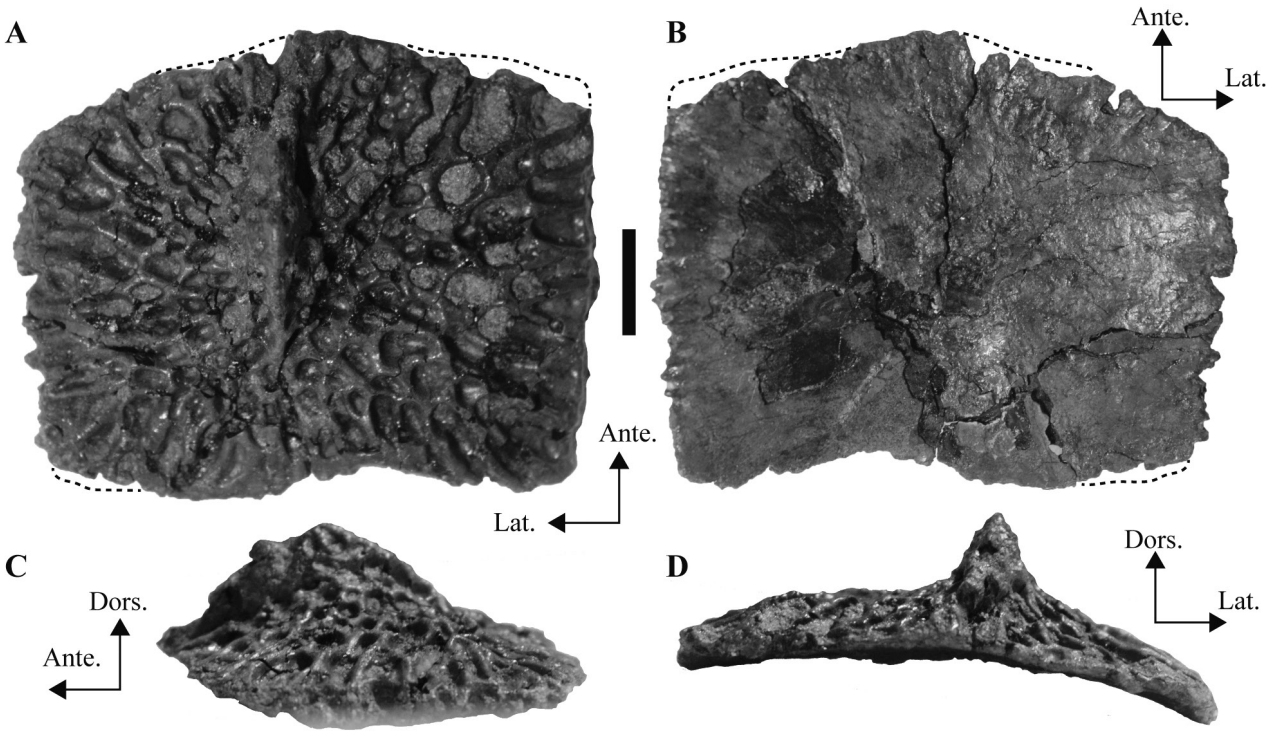

Figure 2. A neosuchian osteoderm from the Tamayama Formation. ICFM-423360 is in dorsal (A), ventral (B), left lateral (C), and anterior views (D). Scale bar = 1 cm.

Fig. 4). The internal structure revealed by the CT scanning shows that the inner cavities are concentrated on the core region of the osteoderm (Fig. 5). The porosity, the ratio of the vessels to the total cross-sectional area, is 0.19 in the sagittal midline (Fig. 5), which is as high as semi-aquatic crocodyliforms (Clarac et al., 2020).

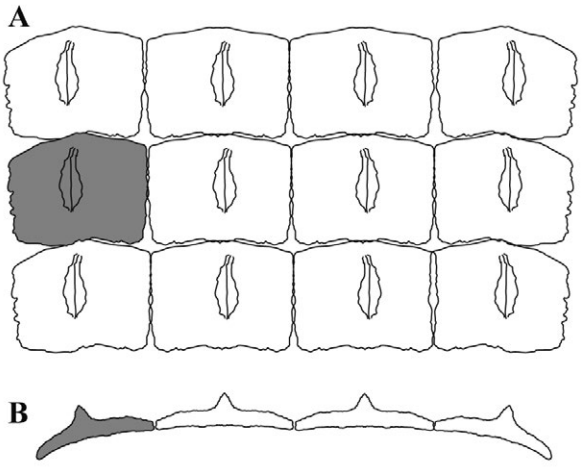

Figure 3. Inferred serial position of the osteoderm (ICFM-423360) in dorsal (A) and anteroposterior views (B).

DISCUSSION

Taxonomic assignment of the osteoderm

Preservation of a single osteoderm (ICFM-423360) makes its taxonomic identification challenging. However, as mentioned below, ICFM-423360 may belong to derived neosuchians (e.g., eusuchians), but not to goniopholidids, pholidosaurids, or paralligatorids, based on the morphological differences mentioned hereafter. Although the anterior margin of ICFM-423360 is poorly preserved, the lateral margin is smooth ventrally and not abruptly bent vertically, which differs from goniopholidids and pholidosaurids with vertically oriented lateral margin lateral to the dorsal keel. Moreover, the dorsal keel in ICFM-423360 does not reach the posterior margin of the osteoderm, unlike that in paralligatorids (Turner, 2015; Kuzmin et al., 2018; Rummy et al., 2022; Fig. 4). Furthermore, in ICFM-423360, the distinctive ornamentation, posteriorly placed keel, zigzag midline suture, and thickened posterior edge are absent, which is different from gobiosuchids from the Late Cretaceous of East Asia (Osmolska et al., 1997; Buscalioni 2017). Therefore, ICFM-423360

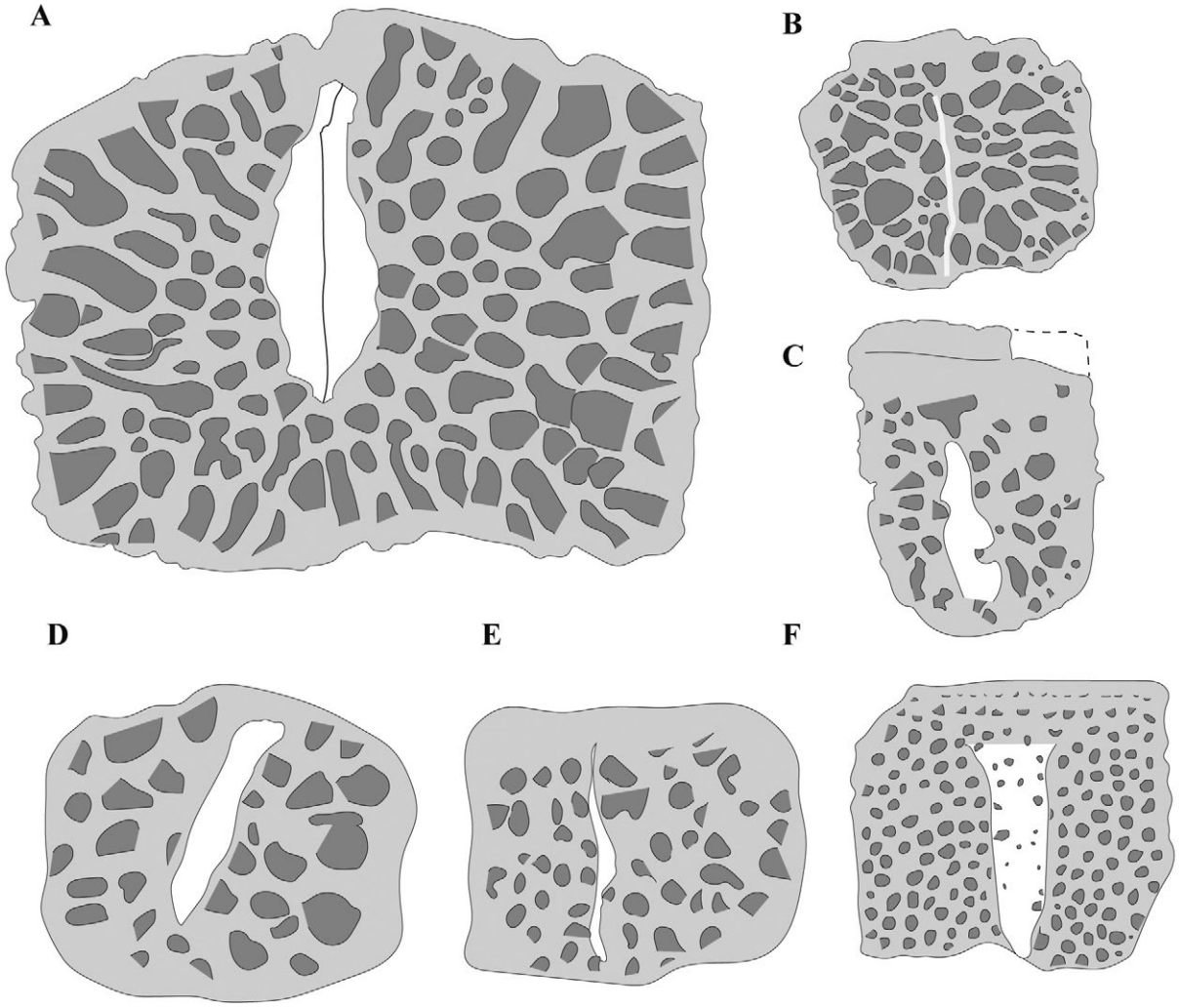

Figure 4. Comparisons of dorsal osteoderm with the Cretaceous neosuchians. (A) ICFM-423360 of Tamayama Formation, Futaba Group in Fukushima, Japan, (B) an eusuchian from Khok Kruat Formation, Thailand (redrawn from Kubo et al., 2018), (C) eusuchian *Allodaposuchus* from the Velaux-La Bastide Neuve site, France (redrawn from Martin et al., 2016), (D) crocodyloid *Albertosuchus* from Scollard Formation, Canada (redrawn from Wu & Brinkman, 2015), (E) *Susisuchus* from Crato Formation (redrawn from Figueiredo et al., 2011), and (F) paralligatorid *Rugosuchus* from Nenjiang Formation, China (redrawn from Wu et al., 2001). Not to scale.

belongs to a derived neosuchian species (e.g., hylaeochampsids and eusuchians), precluding the possibility of Gobiosuchidae, Goniopholididae, and Paralligatoridae. ICFM-423360 resembles the osteoderm of the lateral row of the tetraserial dorsal shield in derived neosuchians, which is congruent with the taxonomic assessment of this study (Fig. 3). ICFM-423360 resembles osteoderms in some eusuchians (*Allodaposuchus, Albertosuchus*, and the Khok Kruat eusuchian) in having the pronounced median ridge and the large external pits (Fig. 4), but the further taxonomic identification remains uncertain.

The paleofauna of the Tamayama Formation, Futaba Group

The Tamayama Formation was deposited in the shallow marine environment (Ando et al., 1995; Inose 2019), and has previously provided both marine and terrestrial fossils; a plesiosaur (Sato et al., 2005), inoceramids (Ando et al., 1995), ammonoids (Obata & Suzuki, 1969), bivalves (Inose 2019), a dinosaur (Saegusa & Tomida, 2011) and plants (Takahashi et al., 1999, 2007). Since most neosuchians adapted to the semi-aquatic habitat (Yoshida et al., 2021), the neosuchian osteoderm (ICFM-423360) might be washed out with plant and dinosaur materials, and

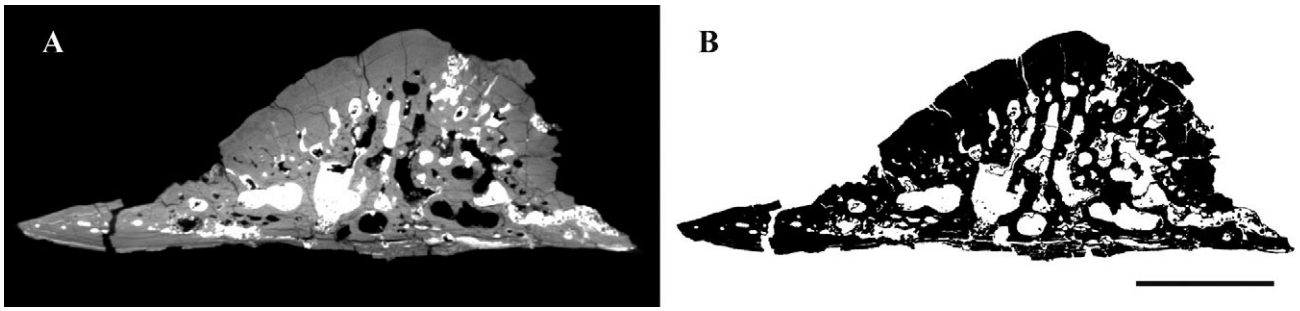

Figure 5. Cross sectional CT image of the osteoderm (ICFM-423360) along the sagittal plane (A) and its bony regions in black (B). Scale bar = 1 cm.

finally deposited in the shallow marine (brackish to inner shelf) environment (Ando et al., 1995; Inose 2019). The first semi-aquatic crocodyliform from the Futaba Group in this study increases diversity of the Coniacian Tamayama paleofauna.

Paleobiogeography of the Cretaceous neoschians in Japan and Asia

The Cretaceous deposits of Japan have produced a few crocodyliform remains [e.g., a goniopholidid from the Early Cretaceous (Aptian-Albian) Kitadani Formation of Fukui: Kobayashi 1998]. The osteoderm (ICFM-423360) from the Late Cretaceous (Coniacian-Santonian) Tamayama Formation of this study provides the first record of more derived neosuchian clade, such as eusuchians, and increase crocodyliform diversity in Japan. It also suggests that non-goniopholidid neosuchians have likely appeared no later than the early Late Cretaceous in Japan.

In East Asia, a variety of neosuchian families are known from the Cretaceous; goniopholidids, paralligatorids, and eusuchians (Storrs & Efimov, 2001; Lauprasert et al., 2011; Kubo et al., 2018; Li et al., 2019). Pre-Coniacian eusuchians have been found in Southeast Asia (Thailand, Aptian, Kubo et al., 2018) and Central Asia (Uzbekistan, Turonian, and Tadzhikistan, Santonian, Storrs & Efimov, 2001), but no definitive record of the derived neosuchians in East Asia. From post-Santonian beds, a crocodyloid eusuchian was discovered from the Maastrichtian Nanxiong Formation in Jilin, China (Li et al., 2019). The new derived-neosuchian osteoderm from the Coniacian-Santonian of the Tamayama Formation fills a spatiotemporal gap and suggests the occurrence of the derived neosuchians in East Asia before Coniacian. The detailed taxonomic identification of the osteoderm remains unclear within the derived neosuchians, but future study on neosuchian osteology and phylogeny would resolve it (Turner, 2015; Turner et al., 2015, Tennant et al., 2016). As Japan was situated in the East margin of the Asian continent and interconnected with North American through the Beringian landbridge during the Cretaceous (Russell 1993; Fiorillo 2008), Japanese fossils would provide important information for understanding paleobiogeography of Asian and pan-Pacific terrestrial faunas.

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福島県の玉山層（白亜紀後期）から産出したワニ形類の皮骨

吉田純輝*・高橋紀信**・菜花智***

要旨

白亜紀の東アジアでは、多様なワニ形類が分布し、ゴニオフォリス類、パラリゲーター類、ゴビオスクス類、正鰐類などが存在した。日本において、白亜紀の陸生脊椎動物（恐竜を含む）化石を産する重要な地層の一つが、福島県の双葉層群である。しかしながら、双葉層群ではワニ形類の確かな証拠は見つかっていなかった。本報告では、福島県いわき市の双葉層群玉山層（コニアシアン期）からワニ形類の皮骨を報告する。この皮骨は幅広い長方形で、高いキールを背側にそなえており、背側板由来と考えられる。また、既知種との形態比較から、本標本はゴニオフォリス類やパラリゲーター類ではない、半水生の派生的な新鰐類の皮骨と考えられる。本研究による、双葉層群から初めて見つかった派生的な新鰐類の確かな証拠は、彼らが東アジアにおいて白亜紀コニアシアン期には既に出現していたことを示唆した。

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