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Authors: Ito, Ai, Aoki, Riosuke, Hirayama, Ren, Yoshida, Masataka, Kon, Hiroo, et al.

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The rediscovery and taxonomical reexamination of the longirostrine crocodylian from the Pleistocene of Taiwan

AI ITO[1,2], RIOSUKE AOKI[3], REN HIRAYAMA[4], MASATAKA YOSHIDA[1,2], HIROO KON[5] AND HIDEKI ENDO[2]

[1]*Department of Biological Sciences, Graduate School of Science, The University of Tokyo, 7-3-1 Hongo, Bunkyo, Tokyo 113-0033, Japan*
[2]*The University Museum, The University of Tokyo, 7-3-1 Hongo, Bunkyo, Tokyo 113-0033, Japan (e-mail: ai@um.u-tokyo.ac.jp)*
[3]*4-59 Uwamachi, Yokosuka, Kanagawa 238-0017, Japan*
[4]*School of International Liberal Studies, Waseda University, 1-6-1 Nishi-Waseda, Shinjuku, Tokyo 169-8050, Japan*
[5]*Archaeological Museum, Waseda University, 1136 Nishitomida, Honjo, Saitama 367-0035, Japan*

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Abstract. A partial crocodylian skull was found among the paleontological collection at the Archaeological Museum, Waseda University in Honjo-shi, Saitama Prefecture. Following a bibliographical survey, this was verified as a specimen reported by Tokunaga as the first known crocodile from Taiwan but then regarded as lost due to World War II. Molten glass debris is attached to the specimen, suggesting that it had been subject to air raids during World War II in May 1945, most likely at the Waseda University campus. Based on its largest seventh maxillary alveoli and the prominent lateral expansion towards the posterior direction, this specimen was identified as *Toyotamaphimeia* sp.; up to now a single species under this genus has been reported. The discovery demonstrates that this crocodylian genus once had a wide geographical distribution during the Pleistocene.

Key words: Crocodylidae, East Asia, Pleistocene, Taiwan, *Toyotamaphimeia machikanensis*

Introduction

The first fossil crocodile of Taiwan was reported by Tokunaga (1936) from the Neogene deposit of Tsochin (Zuozhen). Unfortunately, the Tokunaga specimen was regarded as lost during World War II (Shikama, 1972; Aoki, 1983; Shan *et al*., 2009). Since then, two species of fossil crocodylians from Taiwan have been described: *Tomistoma taiwanicus* Shikama, 1972 and *Penghusuchus pani* Shan *et al*., 2009. As for *Tomistoma taiwanicus*, Shikama (1972) pointed out its close relationship to *Toyotamaphimeia machikanensis,* a longirostrine crocodylid from the Middle Pleistocene of the Osaka Group of Japan. However, Aoki (1983) referred the fossil to *Toyotamaphimeia*.

Since October 2012, we set out to organize the paleontological collection deposited at the Archaeological Museum, Waseda University, located in Honjo-shi, Saitama Prefecture. This collection was prepared by Nobuo Naora, a former professor of the Faculty of Science and Engineering of Waseda University. According to the catalog, which Naora donated to the National Museum of Japanese History, the number of specimens is in the thousands (National Museum of Japanese History, 2008). Among these, we identified a partial crocodile snout (WU-HPAC-D007) and a caudal vertebra (WU-HPAC-D008) in August 2013. The partial snout was exfoliated with powdered sulfur emerging from exfoliated planes. Numerous black spots were found on both dorsal and ventral surfaces. A note labeled as "Tertialy (sic), Taiwan, Crocodile" was associated with the specimen, which was contained in a box.

Through a bibliographic survey, we identified WU-HPAC-D007 as the Pleistocene crocodylian snout first reported by Tokunaga (1936), and which had disappeared after World War II (Shikama, 1972; Shan *et al*., 2009). The morphological characteristics of the snout and alveoli, including the number of alveoli, locality and the geological age of WU-HPAC-D007 are largely concordant with the report by Tokunaga (1936). In addition, as the molten glass is attached anteroventrally and the specimen retains burn spots, it may have undergone damage during incendiary air raids (also known as the Yamanote Air Raid) on May 25th, 1945, most likely at the Waseda University campus in Shinjuku, Tokyo, where the Faculty of Science and Engineering was located (Tokunaga, 1985).

Tokunaga (1936) stated, "The snout is narrow and elongated, therefore this is morphologically placed within the

Table 1. Transverse snout width from M1 to M7 of the recent crocodylian species (in mm).

Species	Specimen Number	M1	M2	M3	M4	M5	M6	M7
Alligator mississippiensis	KPM-NFR 000016	77.9	84.1	91.3	98.1	100.7	102.4	104.1
Gavialis gangeticus	KPM-NFR 000017	39.1	40.0	41.0	40.0	38.6	37.7	37.7
Crocodylus siamensis	KPM-NFR 000053	41.6	48.8	54.1	60.5	66.4	68.7	69.4
Tomistoma schlegelii	KPM-NFR 000064	57.9	60.9	62.2	64.9	77.7	73.3	74.2
Tomistoma schlegelii	KPM-NFR 000065	37.4	39.0	38.5	39.4	43.8	40.8	41.0
Crocodylus porosus	KPM-NFR 000079	122.4	132.2	144.3	164.8	180.5	177.4	163.1
Caiman latirostris	KPM-NFR 000084	70.4	75.5	81.7	87.5	91.9	94.8	98.6
Gavialis gangeticus	KPM-NFR 000092	35.0	34.3	34.9	34.2	34.2	34.4	34.6
Osteolaemus tetraspis	KPM-NFR 000110	68.0	78.6	86.1	95.5	102.8	100.9	97.5
Alligator mississippiensis	KPM-NFR 000109	147.6	156.4	167.2	177.6	177.5	175.3	174.6
Alligator sinensis	UMUT 12253	39.1	43.1	48.6	52.5	53.8	54.3	54.4
Alligator sinensis	UMUT 12255	47.6	51.3	57.0	62.7	63.7	64.1	65.3
Crocodylus niloticus	UMUT 12260	56.4	66.2	72.9	80.8	89.3	90.8	90.0
Crocodylus niloticus	UMUT 12264	81.1	90.2	99.2	107.1	115.4	112.9	113.4
Crocodylus acutus × *Crocodylus rhombifer*	UMUT 12265	77.0	82.7	88.2	92.1	103.9	97.5	95.6
Paleosuchus palpebrosus	UMUT 12277	35.6	38.1	40.9	44.0	44.0	45.2	46.1
Alligator mississippiensis	UMUT 12281	124.0	133.9	144.4	151.2	150.5	148.1	146.2
Alligator mississippiensis	WU-SILS-RHb 100	49.8	87.2	94.4	102.0	104.4	104.4	104.7
Crocodylus niloticus	WU-SILS-RHb 140	32.8	36.2	39.2	40.1	47.2	46.9	46.0
Crocodylus siamensis	WU-SILS-RHb 215	49.2	53.9	59.6	67.1	72.1	71.3	71.6

Gavialidae or Tomistomidae (*sic*). However, the number of alveoli of the specimen is reduced and the teeth are enlarged, not identical with both *Tomistoma* and *Gavialis*." However, he only briefly described this specimen without presenting any figures.

Here, we describe the fossil crocodile reported by Tokunaga (1936). Recent investigations about the Neogene crocodiles of Japan and Taiwan were quite helpful to us for identification (Aoki, 1983; Kobayashi *et al*., 2006).

Geological setting

Tokunaga (1936) indicated a Plio-Pleistocene age for the fossil locality of Cailiao in Zuozhen District of Tainan, Taiwan. This locality is included within the Toukoushan Group and was dated as the lower to Middle Pleistocene by Otsuka (1984).

Material and methods

The rediscovered material (WU-HPAC-C007) was housed in the Archaeological Museum, Waseda University, located in Honjo-shi, Saitama Prefecture. Both fossil and recent species were used for comparisons. All measurements were taken using calipers. The transverse snout width from M1 to M7 of the recent species was measured and compared to determine the alveoli number for identification (Table 1). Measurement of the alveolus length of *Toyotamaphimeia machikanensis* was taken from Kobayashi *et al*. (2006).

Institutional Abbreviations.—KPM, Kanagawa Prefectural Museum of Natural History; MOU, Museum of Osaka University; UMUT, The University Museum, the University of Tokyo; WU-HPAC, Waseda University-Honjo Paleontological Archaeological Collection; WU-SILS, Waseda University, School of International Liberal Studies Ren Hirayama Collection.

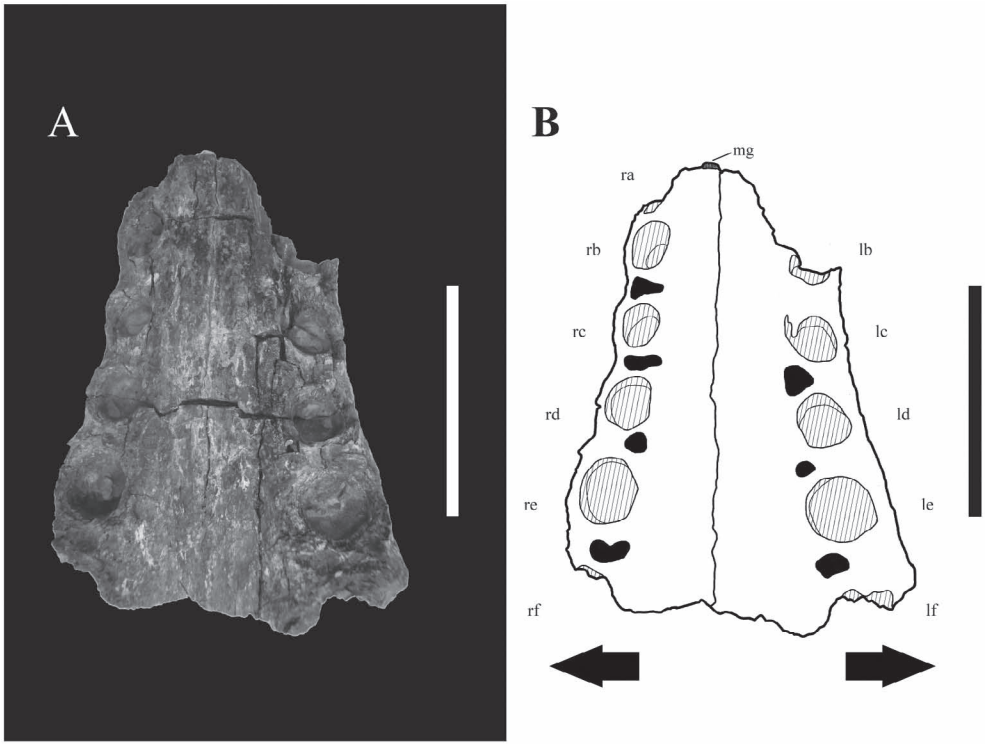

Figure 1. Fragmentary maxillae of WU-HPAC-D007 in ventral view. **A,** photograph of the maxillae in ventral view; **B,** line drawings of the maxillae in ventral view. Diagonal line indicating maxillary alveoli, black shading indicating occlusal pit, and arrows indicating lateral expansion towards the posterior direction. Scale = 100 mm.

Anatomical Abbreviations.—ra-f, right a to f maxillary alveoli; lb-f, left b to f maxillary alveoli; mg, molten glass.

Systematic paleontology

Suborder Eusuchia Huxley, 1875
Unranked Crocodylia Gmelin, 1789 (*sensu* Benton and Clark, 1988)
Family Crocodylidae Cuvier, 1807 (*sensu* Brochu, 2003)
Genus ***Toyotamaphimeia*** Aoki, 1983

Type species.—*Toyotamaphimeia machikanensis* (Kamei and Matsumoto in Kobatake *et al.*, 1965).

Toyotamaphimeia sp.

Referred specimen.—WU-HPAC-D007, partial snout.

Description.—Maxillae. The narrow maxillae markedly expand laterally, in the posterior direction. The anteroposterior length as preserved is 185 mm and maximum transverse width is 145 mm. Dorsal and lateral ornamentation is obliterated. Dorsally, maxillary contact with the nasals and the premaxillae is indistinguishable. Ventrally, the maxillae contact each other along the sagittal plane. The specimen preserves six alveoli on the right and five on the left. Among these, the two most anterior alveoli on both right and left maxillae (ra and lb) and the two most posterior alveoli (rf and lf) are incomplete (Figure 1). The alveoli are large. The largest alveoli re and le have anteroposterior lengths of 26.97 mm and 27.73 mm, respectively. Alveoli are enlarged in the posterior direction.

Depressions for occlusion of the dentary teeth are located on most of the inter-alveolus plate except between ra-rb and lb-lc. Among these, rb-rc and rc-rd bear pits, which develop mediolaterally, and the remainder, medially (Figure 1). The alveolar ridge is slightly elevated at rf and lf.

Comparison

The maximum known number of premaxillary teeth is five in crocodylians. The suture and constriction which usually develop between premaxillae and maxillae are not confirmed in this specimen. This suggests that WU-HPAC-D007 does not include premaxillae. Anteriorly, the nasal cavity is filled with sediment. The two maxillae

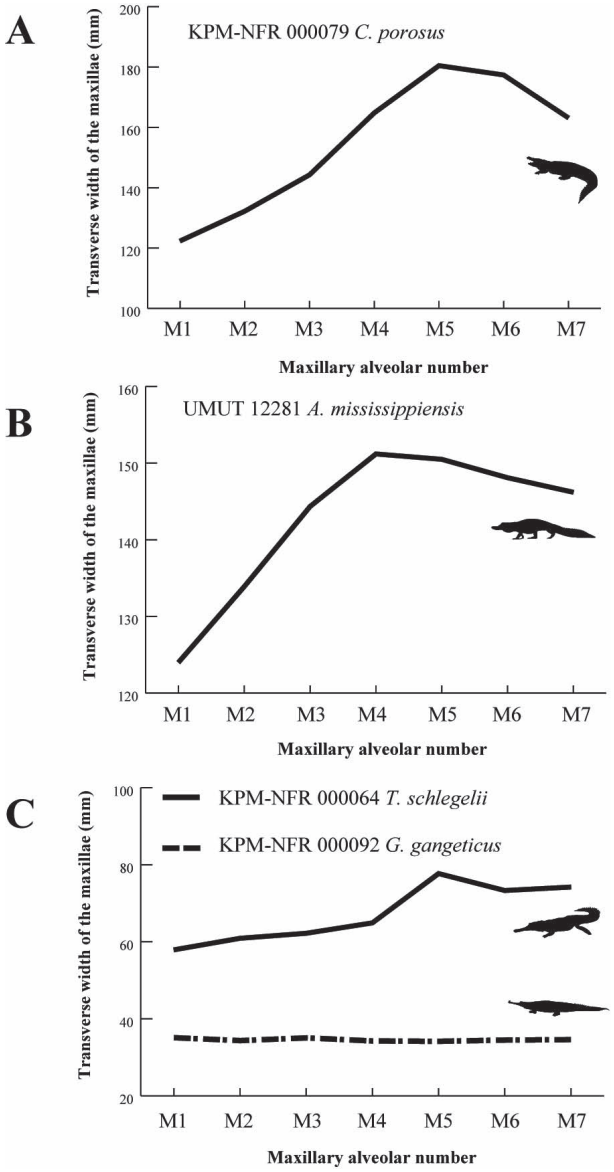

Figure 2. Transverse width of the maxillae in extant crocodylians. **A,** *Crocodylus porous* (KPM-NFR 000079) shows an extreme increase in size from fourth to fifth maxillary alveoli. **B,** *Alligator mississippiensis* (UMUT 12281) shows an extreme increase in size from third to fourth maxillary alveoli. **C,** *Tomistoma schlegelii* (KPM-NFR 000064) shows an extreme increase in size from fourth to fifth maxillary alveoli. *Gavialis gangeticus* (KPM-NFR 000092) in dashed line, shows no major increase or decrease in alveolar size. See Table 2 for alveolar size measurement of 20 specimens.

contact medially. Thus, WU-HPAC-D007 is the anterior region of the maxilla.

Alveolar size positively correlates with the transverse width of the snout (Cong *et al*., 1988) (Figure 2; Table 1). Typically, the largest maxillary alveolus is the fourth in alligatorids and fifth in crocodylids. Snout width increases most prominently towards the largest alveoli in all crocodylians except for lepto-longirostrine crocodylians such as *Gavialis* and lati-longirostrine crocodylians such as *Mourasuchus*, in which the sizes of alveoli are equal with no caniniform development. The snout distinctly expands laterally in the posterior direction from rf and lf in WU-HPAC-D007, suggesting that these are not the largest alveoli, and that the largest alveoli are positioned more posteriorly.

WU-HPAC-D007 preserves six consecutive anterior maxillary alveoli. This excludes the possibility that WU-HPAC-D007 belongs to an ordinary species of Alligatoridae or Crocodylidae by not possessing the largest fourth and fifth maxillary alveoli.

Among the few exceptions, seventh maxillary teeth are uniquely the largest among anterior maxillary teeth in the longirostrine crocodylid *Toyotamaphimeia machikanensis* from the Middle Pleistocene of the Osaka Group. The 12th and 13th maxillary teeth are the largest in this species (Aoki, 1983; Kobayashi *et al*., 2006). Also, seventh maxillary teeth are the largest in the longirostrine crocodylid *Penghusuchus pani* from the Miocene of the Yuwentao Formation near Neian of Shiyu, Penghu Island (Shan *et al*., 2009). WU-HPAC-D007, *T. machikanensis* and *P. pani* all possess distinctively large alveoli observed among longirostrine crocodylids. However, the lateral expansion of the snout width towards the posterior direction is clearly more gradual in *P. pani* compared to both *T. machikanensis* and WU-HPAC-D007.

Kobayashi *et al*. (2006) discussed the position of the fragmentary dentary of the holotype of *Toyotamaphimeia machikanensis* in relation to the thickness of the maxillary interalveolar plate. Interalveolar plate length in WU-HPAC-D007 increases substantially from a-b to b-c, and then decreases from b-c to c-d (Table 2). This pattern exhibited by WU-HPAC-D007 is similar to that observed in the second to third, third to fourth, and fourth to fifth maxillary teeth for *T. machikanensis* (Kobayashi *et al*., 2006). The succeeding interalveolar plate length drops sharply from c–d to d–e, converse to the gradual decline seen in the fifth to sixth maxillary teeth of *T. machikanensis*. However, the configuration of the occlusal pits of WU-HPAC-D007 is dissimilar to that of *T. machikanensis*, which bears depressions that are located medially from the eighth to thirteenth maxillary teeth (Kobayashi *et al*., 2006).

Nevertheless, the matching pattern of the interalveolar plate between WU-HPAC-D007 and *Toyotamaphimeia machikanensis* indicates that the preserved alveoli of WU-HPAC-D007 correspond to the second to seventh maxillary alveoli. Consequently, the seventh maxillary alveoli are the largest in WU-HPAC-D007. In addition,

Table 2. Interalveolar plate length of WU-HPAC-D007 (in mm.).

Position of interalveolar plate	Right	Left	Average
a–b	11.36	–	11.36
b–c	14.29	–	14.29
c–d	10.53	10.19	10.36
d–e	5.98	5.16	5.57
e–f	11.64	6.76	9.23

the increasing pattern of the diameters of the alveoli from b to e in WU-HPAC-D007 is similar to that of the third to sixth maxillary alveoli in *T. machikanensis* (Figure 3).

While the configuration of the occlusal pits of WU-HPAC-D007 does not coincide with that of *Toyotamaphimeia machikanensis*, the seventh maxillary teeth are the largest in the referred specimen. Seventh maxillary teeth are also the largest anterior maxillary teeth in *Penghusuchus pani.* Yet, the lateral expansion of its snout width towards the posterior direction is more gradual. Thus, we identify this specimen as *Toyotamaphimeia* sp.

Discussion

Since the disappearance of the Tokunaga specimen, there have been two major reports on crocodylians from Taiwan, including *Tomistoma taiwanicus* (*Toyotamaphimeia*) and *Penghusuchus pani* (Shikama, 1972; Aoki, 1983; Shan *et al*., 2009). Based on the fragmentary skull and isolated teeth, Shikama (1972) reported a new crocodylian, *Tomistoma taiwanicus* (*Toyotamaphimeia*) from the Upper Pliocene of Tsochin, east of Tainan. These specimens show exceptional similarities to Japanese specimens (Aoki, 1983), and additional comparison among crocodylids of Taiwan is required.

Additional material

A caudal vertebra (WU-HPAC-D008) with anteroposterior length of 85 mm was also discovered in the Naora collection, but there was no information regarding this material. It is comparable to *Toyotamaphimeia machikanensis* due to its large size, yet, it can only be identified as Eusuchia indet. in terms of its morphology.

Conclusion

A partial crocodile snout reported by Tokunaga (1936) was rediscovered in the Naora Collection housed at the Archaeological Museum, Waseda University in Saitama Prefecture. Molten glass attached on WU-HPAC-D007 suggested that it had been subject to the Yamanote air raids on May 25th, 1945.

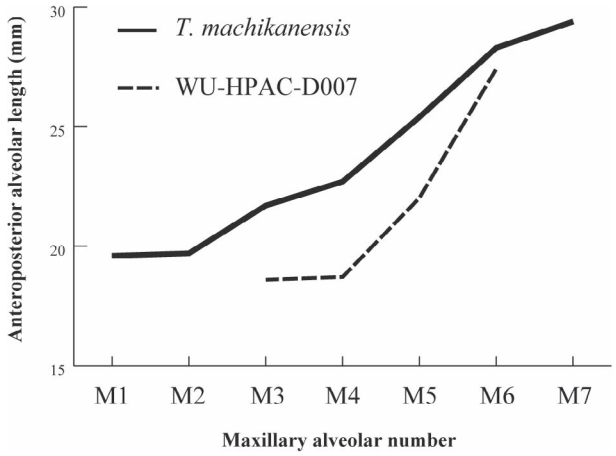

Figure 3. Anteroposterior maxillary alveolar length of WU-HPAC-D007 and *Toyotamaphimeia machikanensis* (Kobayashi *et al*., 2006). The average of right and left anteroposterior diameters of *T. machikanensis* (solid line) and WU-HPAC-D007 (dashed line) are plotted.

Alveoli and maxillae significantly expand laterally towards the largest seventh maxillary alveoli in the specimen, comparably to the holotype of *Toyotamaphimeia machikanensis*. Thus, we identify this specimen as *Toyotamaphimeia* sp.

Toyotamaphimeia has been reported from several Pliocene and Pleistocene localities of Japan (Taruno, 1999; Aoki, 2001; Iijima *et al*., 2015), suggesting a wide distribution, including both Taiwan and Japan.

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Author contributions

A. I. initiated the research and is mainly responsible for the taxonomic analysis. R. A. is also responsible for the taxonomic reexamination. R. H. contributed on the geological setting. M. Y pursued the bibliographical survey. H. K. initiated the organization of the collection, including WU-HPAC-D007, and lastly, H. E. contributed to the comparison with the modern species. All authors contributed to the writing of the paper.