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Tomistominae gen. et sp. indet. (Crocodylia: Crocodylidae) from the Lower Yage Formation (Middle Pleistocene) in Hamamatsu City, Shizuoka Prefecture, Japan

Koji Nojima* and Junji Itoigawa**

*864-2 Nakano-cho, Higashi-ku, Hamamatsu City, Shizuoka 435-0004, Japan
< nojima-k1130@qc.commufa.jp>
**5125-4 Hiyoshi-cho, Mizunami City, Gifu 509-6251, Japan

Abstract

A total of approximately 1200 well-preserved fossil crocodylian bones was recovered from the freshwater fish-bone bed of the Lower Yage Formation (Middle Pleistocene, MIS 9, 367–347 ka) in Yage, Inasa-cho, Hamamatsu City, Shizuoka Prefecture, Japan. These specimens are identical with Tomistominae gen. et sp. indet. Skulls, mandibles, ribs, vertebrae, humeri, femora, and osteoderms are described.

Key words: Crocodylia, Tomistominae, Middle Pleistocene, Lower Yage Formation, Japan

Introduction

Pleistocene crocodylian in Japan were previously studied by Kobatake *et al.* (1965), Kobatake and Kamei (1966), Aoki (1983), Taruno (1999), Aoki (2001), Kobayashi *et al.* (2006), and Kobayashi and Eguchi (2010).

Members of the Geology Club of the Hamamatsu Kita High School (Hamamatsu City) first discovered fossil crocodylians from the Middle Pleistocene Lower Yage Formation in Yage, Hamamatsu City, Central Japan (Fig. 1), in 1968. During the survey of these members until 1980, more than 1200 specimens of various anatomical parts of the skeletons were collected from the locality (Fig. 1). Tomida (1978), Nakashima and Hasegawa (1982), Nojima (2002), Nojima *et al.* (2007), and Nojima *et al.* (2014) provisionally reported these occurrences. However, these

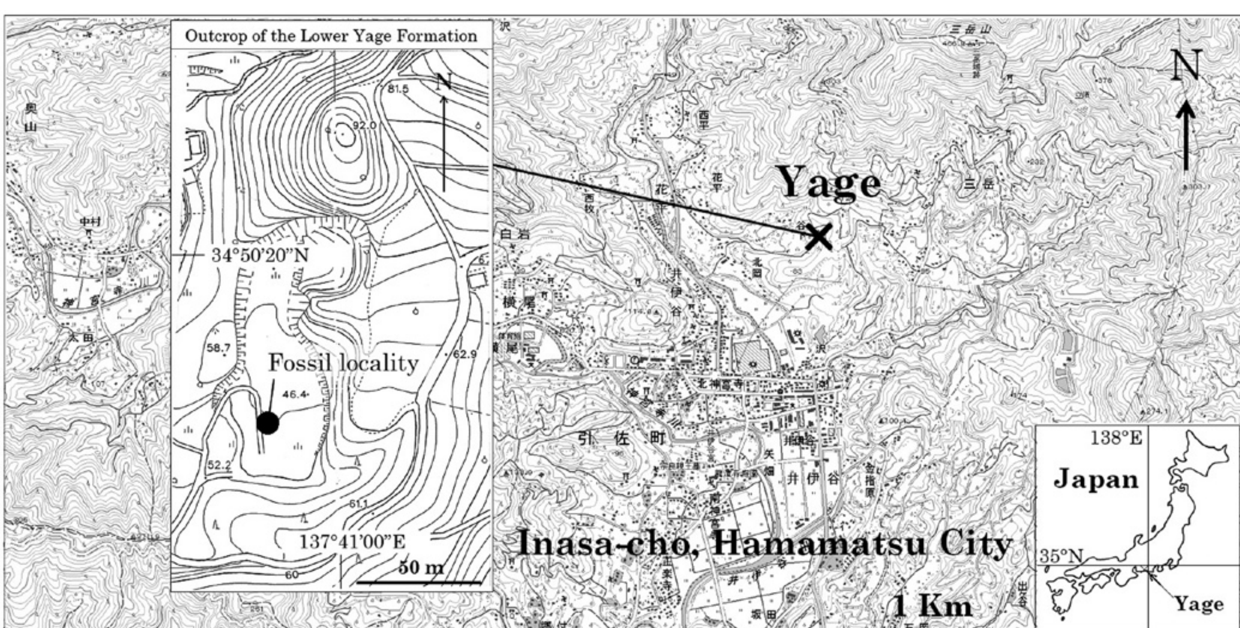

Fig 1. Map showing the fossil locality. 1:25,000 scale topographic map "Kiga" and "Idaira" published by GSI and 1:2,500 scale topographic map published by Inasa-cho are used.

crocody lian specimens have not yet been described and deposited in the Academic institution.

The purpose of the present paper is to briefly describe the Yage specimens and identified with Tomistominae gen. et sp. indet.

Geology

The Middle Pleistocene Lower Yage Formation (*e.g.* Tomida, 1978) is distributed in Yage, a northen part of the Hamanako Lake. It covers the Paleozoic-Mesozoic basement rocks. The stratigraphy is shown in Fig. 2. The crocodilian fossils were found in the F3 bed in the lower part of the Lower Yage Formation (star mark of Fig. 2). The F3 bed consists of sandy clay and contains many fossil fish bones associated with the remains of a turtle and otter (Nojima *et al*. 2007). The fishes consist of *Carassius* sp. (approximately 86%), *Cyprinus* sp. (10%), and *Distoechodon* sp. (approximately 4%) (Nojima, 2002).

To determine the geologic age of the fossils, mineralogical analysis was conducted on pumices included in the Yage Tephra of the Lower Yage Formation. Compared with the results of the analyses of pumices in the tephra beds in the Middle Pleistocene formation of nearby areas, the Yage Tephra correlates with the Ha-1 Tephra at Mikatagahara and the At-5 Tephra at Tempakubara (Nojima *et al*., 2014). These tephra beds dated to Marine Isotope Stage (MIS) 9 (367–347 ka) of the oxygen isotope chronology of the Late Pleistocene (Nojima *et al*., 2014).

Specimens

The specimens are listed in Table 1. They are recognized as various parts of crocodylians ranging from immature to adult stages, based on comparison with extant and fossil crocodylians. A total of 302 specimens were excluded from this study. The present specimens are deposited in the Hamamatsu City History Museum. 2013-021-HH is the register number of the Hamamatsu City History Museum. The head part (2013-021-) is omitted in Figs. 5, 6, and 8.

The described specimens are:

Cranial table (parietal, postorbitals, and squamosals): 2013-021-HH709 (Figs. 3-1a, b), 2013-021-HH711 (Figs.

Table 1. Number of partial bones. Deposition: Hamamatsu City History Museum.

Element	number	Element	number
Cranial table	4	Caudal vertebrae	20
Premaxilla	1	Scapula	6
Maxilla	42	Humerus	7
Nasal	5	Coracoid	3
Dentary of rostrum	4	Ulna	2
Dentary	14	Radius	5
Teeth	17	Ilium	8
Mandible	6	Ischium	3
Jugal	14	Pubis	5
Interclavicle	5	Fibula	5
Proatlas	1	Femur	13
Cervical vertebrae	11	Tibia	4
Cervical rib	10	Tarsal or Carpal	7
Dorsal vertebrae	135	Metacarpal or Metatarsal	38
Dorsal rib	134	Phalange	27
Sacral vertebrae	3	Osteoderm	148
			707

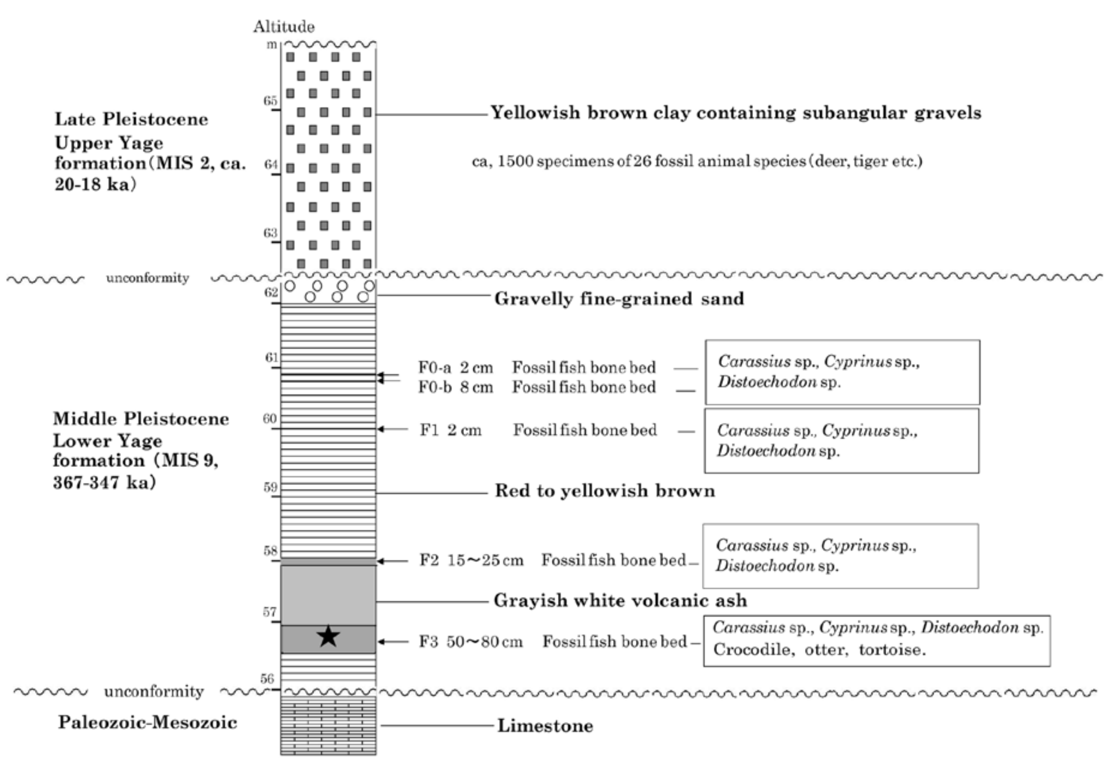

Fig. 2. Geologic column of the locality. Star is horizon of fossil crocodile.

Fig. 3. Tomistominae gen. et sp. indet. Cranial table. 1a, b 2013-021-HH709, 2a, b 2013-021-HH711, 3a, b 2013-021-HH712.

3-2a, b), and 2013-021-HH712 (Figs. 3-3a, b).

Premaxilla: 2013-021-HH253 (Figs. 5-1a, b).

Maxilla: 2013-021-HH126 (Figs. 5-2a, b), 2013-021-HH241 (Figs. 5-3a, b), and 2013-021-HH586 (Fig. 5-4a, b).

Nasal: 2013-021-HH440 (Fig. 5-5) and 2013-021-HH439 (Fig. 5-6).

Dentary of the rostrum: 2013-021-HH708-1 (Fig. 5-7a–d), 2013-021-HH708-2 (Figs. 5-8a–c), 2013-021-HH589-1 (Fig. 5-9a, b), and 2013-021-HH589-2 (Figs. 5-10a, b).

Dentary: 2013-021-HH584 (Figs. 6-1a, b) and 2013-021-HH583 (Figs. 6-2a, b).

Mandible: 2013-021-HH596 (Figs. 6-3a, b).

Teeth: 2013-021-HH597, 2013-021-HH606, 2013-021-HH605, 2013-021-HH644, 2013-021-HH641, 2013-021-HH609, 2013-021-HH600, and 2013-021-HH652 (Figs. 5-11–8).

Proatlas: 2013-021-HH137 (Figs. 6-6a, b).

First sacral vertebra: 2013-021-HH414 (Fig. 6-11a, b).

Description of specimens

General

The morphological features defining this taxon are as follows: the trapezoidal cranial table has two sub-rounded fenestrae that are longitudinally sub-round. The outer bone surface of the cranial table is ornamented with small and irregular oval shaped dints. The nasal is long and cylinder-like shaped, not reaching the external narial opening of the premaxilla. The mandible with the angular, articular, and surangular has irregular fusiform and branched anteriorly. The articular has a sharply pointed anterior end, and its posterior end roundly protrudes. The tooth number in the upper or lower jaw is approximately 19. The teeth are variable in shape and size and lacks sharp edges. The long, narrow teeth of the frontal snout are strongly curved on the posterior sides. The form of the proatlas is trapezoidal, thin, and plate-like with a median ridge on its dorsal side. The sacral rib of the first sacral vertebra is posteriorly tilted to 14° in the dorsal view.

Skull and mandible

Cranial table: 2013-021-HH709, 2013-021-HH711, and 2013-021-HH712 (Figs. 3-1a, b; 2a, b; 3a, b)

The form is trapezoid and composed of a parietal, two postorbitals, and two squamosals. Two prongs of the squamosal are developed at both ends of its base. The rhombic frontal attaches the parietal. Each part of the cranial table is thick and irregular in form. On the other hand, the parts of the table (frontal, postorbital, parietal, and squamosal) are defined by clear suture lines among them. The outer surface has many small, irregular oval dints (4–6 mm in length and 4–15 mm in width). The inner surface is rough and uneven. The fenestra is large and antero-posteriorly oval. Its upper margin is pointed and the lower one is arched on the posterior side. Although the orbit part is severely damaged, the remaining part shows that its shape is sub-oval. The size of the bone is shown in Table 2-1, and the outline of the cranial tables are shown in Fig. 4.

Table 2. Dimensions of the specimens.

2-1. cranial table.

	Length	Height	Thickness (in cm)
HH709	15.7	19.2	ca. 2.1
HH711	15.6	15.6	-
HH712	15.9	17.5	-

2-2. maxilla.

	Length	Height (maximum)(in cm)
HH126(left)	9.6	3.1
HH241(left)	16.8	3.0
HH586(right)	14.2	4.2

2-3. nasal.

	Length	Height (in cm)
HH440 (left)	8.0	0.4–0.9
HH439 (right)	16.6	0.4–1.1

2-4. dentary (rostrum part).

	Length	Height	Thickness (in cm)
HH708-1(left)	9.8	2.8	3.7
HH708-2(right)	6.1	2.8	3.7
HH589-1(left)	8.6	2.2	-
HH589-2(right)	7.7	2.2	-

2-5. dentary.

	Length	Height	Thickness (in cm)
HH584(left)	18.7	2.8	4.2
HH583(right)	16.2	2.7	4.2

2-6. teeth.

	Height	Height (crown)	Diameter (in cm)
HH597	5.7	2.1	1.1
HH606	4.7	2.2	1.1
HH605	4.5	2.1	0.9
HH644	3.6	2.2	1.0
HH641	4.0	2.2	0.9
HH609	2.5	1.2	0.9
HH600	2.9	1.0	1.3
HH652	3.4	1.0	1.2

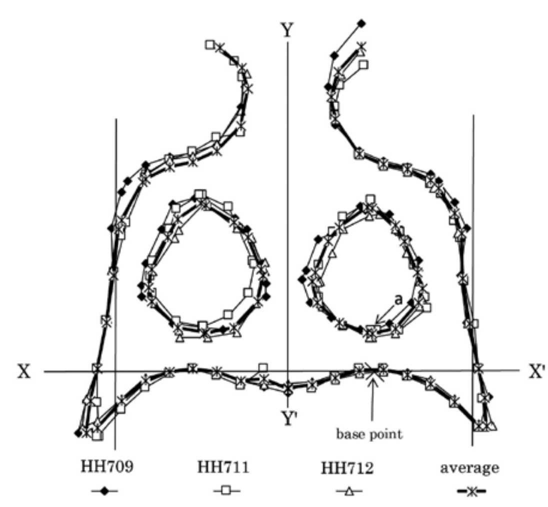

Fig. 4. Outline of the cranial tables.

Premaxilla: 2013-021-HH253 (right) (Figs. 5-1a, b)

The premaxilla has an irregular, long rhombic form. The outer surface has many small pits and the inner surface is rather smooth. The left edge shows a finely jagged suture line. The bone has two tooth sockets that are almost round and shallow with their curvature to the central direction of the posterior side of the sockets. The finely jagged suture line indicates that the nasal does not reach the terminal narial opening. The largest size of the bone is 7.6 cm in length and 3.0 cm in width.

Maxilla: 2013-021-HH126, 2013-021-HH241, and 2013-021-HH586 (Figs. 5-2a, b; 3a, b; 4a, b)

Two left and one right fragmentary specimens are examined. The left maxillae are slightly tapered in front, the outer surface is wrinkled with small pits, and the inner one is slightly rough with the pleural number of shallow tooth sockets (approximately 2.4–2.6 cm in diameter). A narrow groove runs along the inner side of the alveolus. The right maxilla has a small blade form that is narrow anteriorly and expands posteriorly. Six tooth sockets are clearly recognized, which are deep and directed anteriorly without groove. The measurements of the bone are shown in Table 2-2.

Nasal: 2013-021-HH440 and 2013-021-HH439 (Figs. 5-5, 6)

The specimens include one broken left (Fig. 5-5) and right (Fig. 5-6) nasals. The long nasal tapering anteriorly cylindrical with a sub-round section. The surface has faint striations. The nasal does not reach the external narial opening. Measurements are shown in Table 2-3.

Dentary (rostrum part): 2013-021-HH708-1, 2013-021-708-2, 2013-021-HH589-1, and 2013-021-HH589-2 (Figs. 5-7a–d; 8a–c; 9a, b; 10a, b)

Two presumably pair (right and left) fragmentary bones were examined. Each bone is cylinder-like with a small, rugged margin. The outer surface has small, irregular-shaped pits randomly arranged. The inner surface is slightly wrinkled with 2 or 3 tooth sockets that are deep and directed to the pointed front end. Measurements are shown in Table 2-4.

Dentary (main part): 2013-021-HH584 and 2013-021-HH583 (Figs. 6-1a, b; 2a, b)

A pair of the left and right fragmentary bones (right: Fig. 6-1a, b and left: Fig. 6-2a, b) were examined. They are both cylinder-like. The left bone is slightly arched with a quadrangular section. The outer side is smooth with small, irregular, randomly distributed dints, similar to the condition in the dentary of the rostrum. The inner side is almost smooth with weak wrinkles. There are four or sometimes six tooth sockets on the inner side. They are sub-round, deep, and regularly oriented anteriorly in a line. Table 2-5 shows their measurements.

Mandible (posterior portion: angular, articular. and surangular): 2013-021-HH596 (Figs. 6-3a, b)

The specimen comprises the angular, articular, and surangular (left side) with partial missing. It shows irregular fusiform, being branched anteriorly (angular and surangular), but protruding posteriorly, and forms a cylinder-like, elongated articular and angular. The posterior end of the articular is roundly protruded and the anterior end is sharply pointed. The articular protrudes dorsally with the posterior part with triangular outline. The anterior end of the surangular is square-shaped in lateral view. The external surface is slightly rough and the internal is smooth with weak undulation. The maximum size of the bone is 26.6 cm in length and 6.8 cm in width.

Teeth: 2013-021-HH597, 2013-021-HH606, 2013-021-HH605, 2013-021-HH644, 2013-021-HH641, 2013-021-HH609,

Table 3. Comparison of the skull of Tomistominae gen. et. sp. indet. with ones of other 6 living and 2 fossil species of crocodile. ○: concordance, ×: discordance.

species	form	nasal-nares opening connection	right—left maxillary connection	fenestra	orbit	no. of tooth	family subfamily
Tomistominae gen. et sp. indet. (restored specimen)	rod-like rostrum	break	break	big	oval	ca.19	
living							
Alligator mississippiensis	ellipsoid ×	connect ×	break ○	small ×	triangle ×	19-20 ○	Alligatoridae Alligatorinae
Alligetor sinensis	ellipsoid ×	connect ×	break ○	small ×	triangle ×	18-20 ○	
Gavialis gangeticus	rod-like rostrum ○	break ○	connect ×	big ○	oval (○)	25-29 ×	Gavialidae
Crocodylus porosus	triangle ×	connect ×	break ○	small ×	triangle ×	14-16 ×	Crocodylidae Crododylinae
Osteolaemus tetraspis	triangle ×	connect ×	break ○	small ×	triangle ×	-	
Tomistoma schlegelii	long rod-like rostrum (○)	break ○	break ○	big ○	triangle-oval (○)	19-20 ○	Crocodylidae Tomistominae
fossil							
Tomistominae (Kishiwada-wani) (restored specimen)	long rod-like rostrum ○	break ○	break ○	big ○	oval ○	-	
Toyotamaphimeia machikanensis	triangle ×	break ○	break ○	big ○	oval ○	~18 (○)	

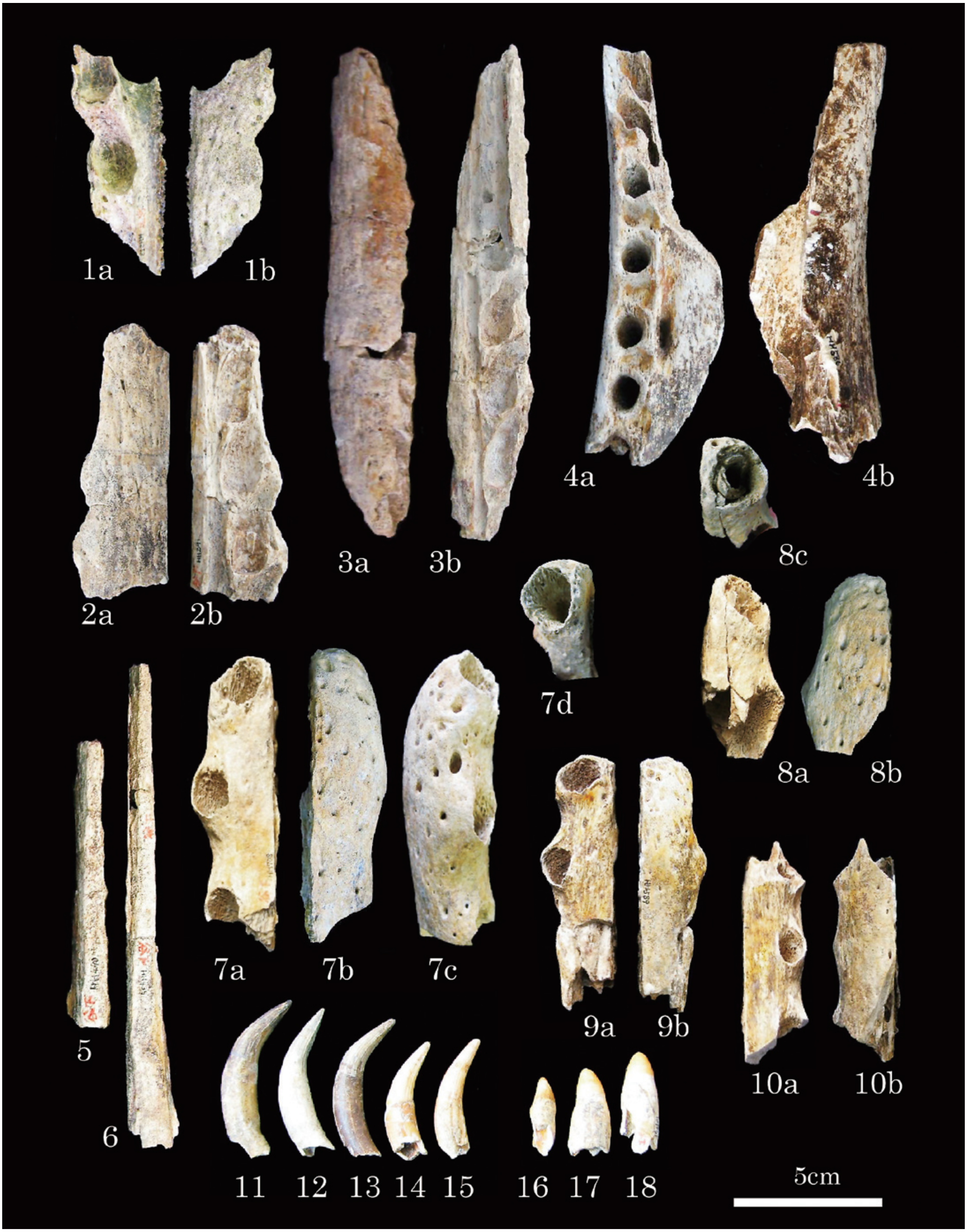

Fig. 5. Tomistominae gen. et sp. indet.

1a, b. 2013-021-HH253, Premaxilla. 2a, b. 2013-021-HH241, Maxilla. 3a, b. 2013-021-HH126, Maxilla. 4a, b. 2013-021-HH586, Maxilla. 5. 2013-021-HH440, Nasal. 6. 2013-021-HH439, Nasal. 7a, b, c, d. 2013-021-HH708-1, Dentary of rostrum. 8a, b, c. 2013-021-HH708-2, Dentary of rostrum. 9a, 9b. 2013-021-HH589-1, Dentary of rostrum. 10a, b. 2013-021-HH589-2. Dentary of rostrum. 11. 2013-021-HH597, Teeth. 12. 2013-021-HH606, Teeth. 13. 2013-021-HH605, Teeth. 14. 2013-021-HH644, Teeth. 15. 2013-021-HH641, Teeth. 16. 2013-021-HH609, Teeth. 17. 2013-021-HH600, Teeth. 18. 2013-021-HH652. Teeth.

Fig 6. Tomistominae gen. et sp. indet.
1a, b. 2013-021-HH584, Dentary. 2a, b. 2013-021-HH583, Dentary. 3a, b. 2013-021-HH596, Mandible. 4, 5. Jugal. 6a, b. 2013-021-HH137, Proatlas. 7. Interclavicle. 8. Cervical rib. 9. Dorsal rib. 10. Cervical vertebrae. 11a, b. 2013-021-HH414, First sacral vertebrae. 12. Caudal vertebrae.

Fig 7. Tomistominae gen. et sp. indet.
1. Coracoid. 2. Scapula. 3. Humerus. 4. Ulna. 5. Radius. 6, 7. Metacarpal or Metatarsal. 8. Tarsal or Carpal. 9, 10, 11. Phalange. 12. Ilium. 13. Ischium. 14. Pubis. 15, 16. Femur. 17. Tibia. 18. Fibula. 19a, b. 20, 21. Osteoderm.

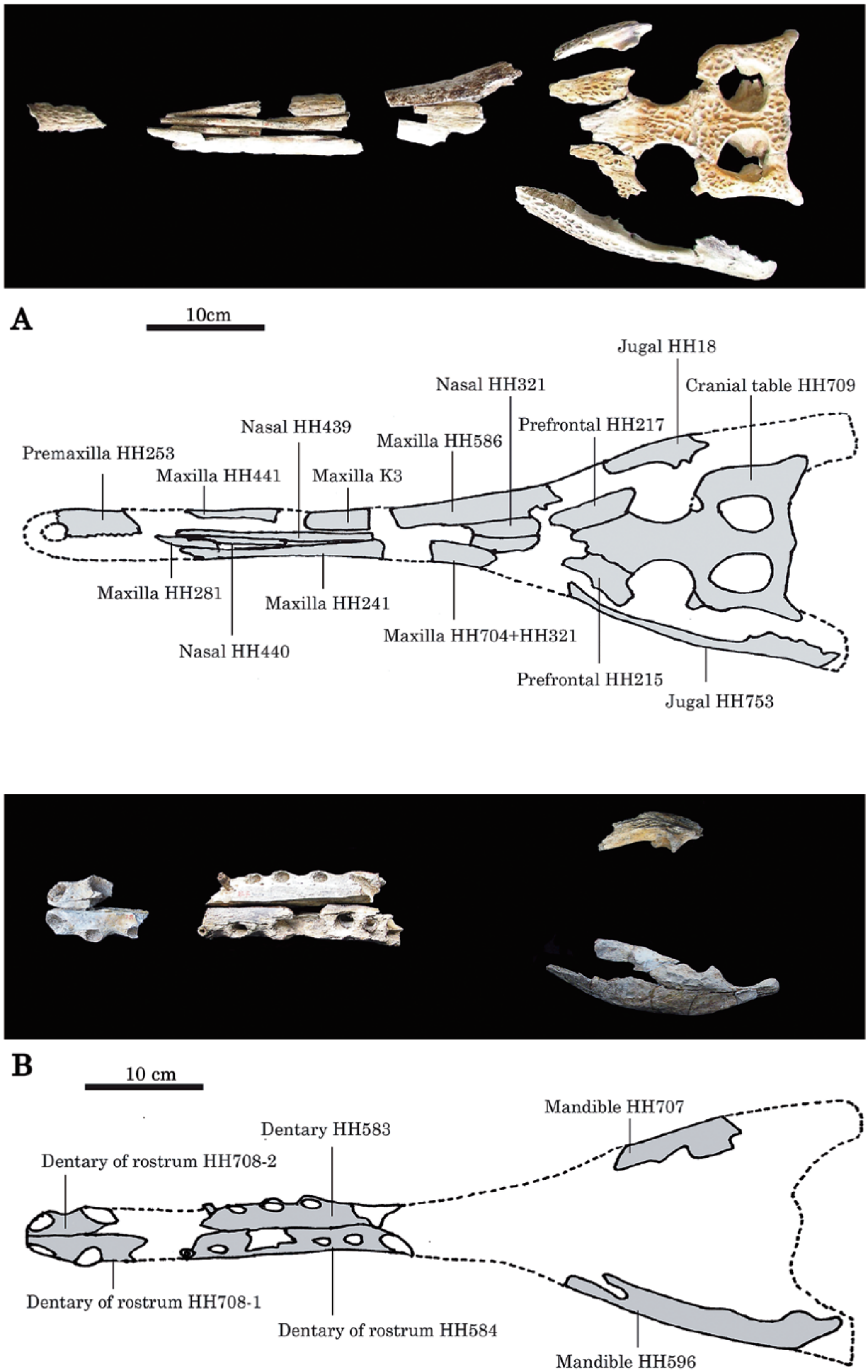

Fig 8. Restored skull and mandible, and their illustrations. A. Skull, B. Mandible and Dentary.

2013-021-HH600, and 2013-021-HH652 (Figs. 5-11–18)

We choose eight well-preserved teeth for description. Among them, five teeth (Figs. 5-11–15) are slender with acute points and curved slightly posteriorly. In those specimens, the root bears 2/3 to 1/2 in dorso-ventral length, and the entire tooth showing a smooth surface, or sometimes with vertical striation. The other three specimens (Figs. 5-16–18) are short, buccolingually thick, and vertically straight with dull points. Each of those five specimens has two parts, namely the root and crown. Although the root is rather smooth, the crown is weakly striated. Measurements on the teeth are shown in Table 2-6. It is possible to identify the location of the teeth on the jaw based on comparison with a modern crocodylian, as the longer teeth are situated at the snout (anterior part of the jaw) and the shorter ones at the posterior part of the jaws.

Proatlas: 2013-021-HH137 (Figs. 6-6a, b)

The present specimen has a trapezoidal shape in the dorsal and ventral view, with a wide basis and thin top plate. The dorsal side of the bone has a median ridge. Its width is 3.7 cm at the base and approximately 1.9 cm at the top with a height of 2.1 cm.

First sacral vertebra: 2013-021-HH414 (Figs. 6-11a, b)

A vertebral centrum has left and right sacral ribs. The neural spine is broken and missing. The clearly defined vertebral foramen has a weak sulcus on the ventral side of the body. The sacral ribs are posteriorly tilted to 14° (Fig. 6-11b) in the dorsal view. The distal end of the sacral ribs is posteriorly expanded. The bone surface is smooth with proximodistally developed fine striation. The anterior articular surface of the centrum is concave and its width is double in height. The concave posterior articular surface is smaller than the anterior one and wider than height. The anteroposterior length of the centrum is 5.1 cm and the transverse width is 18.1 cm.

The other bones in various portions are illustrated in Figs. 6 and 7.

Discussion

The restoration of the skull specimens was first treated. The fragmentary bones described above were compared with their counterparts in extant and other fossil crocodylians for identification of their anatomical positions. A skull of the taxon is restored based on comparison (Fig. 8). The present specimens were described a species, *Yagesius yagesius* ("Yage-wani") by Nojima *et al.* (2007). However the generic and specific names of *Yagesius yagesius* is a nomendubium under ICZN Code13 and 16 (I.C.Z.N., 1999).

Our observation and reconstructed form of the skeleton indicate that the specimens of Tomistominae gen. et sp. indet. have the following characteristics: 1) a stem-based, long, narrow, and rod-like rostrum, 2) well-developed fenestrae of the cranial table, 3) a separate nasal-naris opening, 4) a detached right-left maxillary, 5) an oval orbit, and 6) approximately 19 teeth.

Table 4. Character's concordance (○) and discordance (×) of Tomistominae gen. et sp. indet. with other 3 species, *Toyotamaphimeia machikanensis*, Tomistominae (Kishiwadawani) and *Tomistoma schlegelii*.

Species / *Item*	Tomistominae gen. et sp. indet.	1. *Toyotamaphmeia machikanensis*		2. Tomistominae (Kishiwada-wani)		3. *Tomistoma schlegelii**	
1) width of cranial table (cm)	14.5	27.1	×	23.9	×	20.5	×
2) holes on outer surface	over all		×		×	over all	○
3) ratio of area of supratemporal fenestra to cranial table	0.27	0.37	×	0.24	×	0.17~0.28	○
4) heiglt and width ratio of supratemporal fenestra	H > W		○		×	H > W	○
5) outline of cranial table			×		×		×
6) principal component analysis of cranial table			×		×		×(○)
7) dentary of rostrum	stick		×		—	stick	○
8-1) direction of teeth on dentary of rostrum	front	back, vertical	×		—	front	○
8-2) form of teeth	thin, long, with small tip angle	thick, short, with large tip angle	×		—	thin, long , with small tip angle	○
9-1) curve of back and front side of teeth	large	nearly straight	×		—	small	×
9-2) curve of left and right side of teeth	nothing	nothing	○		—	small	×
9-3) edge of teeth	no edged	no edged	○		—	edged	×
10) articular of mandible	fluent U-shaped		×		—	fluent U-shaped	○
11) shape of proatlas	trapezoid	boomelang-like	×		—		—
12) rib of the first sacral vertebrae	14° inclined to below	nearly horizontal	×		—		—

*Specimens of *Tomistoma schlegelii*
(Atagawa tropical and alligator garden, Zoological science center of Kobe municipal Oji zoo)

Fig 9. Tentatively restored skeleton of Tomistominae gen. et sp. indet.

The combination of these characteristics indicates that this taxon belongs to the subfamily Tomistominae Kälin, 1955 (family Crocodylidae).

Gavialid crocodylians (*e.g.*, *Gavialis gangeticus* (Gmelin, 1789)) have a similar, long and narrow rod-like rostrum; however, the rostrum is in contact with the right and left maxillae, a small premaxilla, being longer and more slender than those of the Yage specimen. The gavialids have finer and a large number of teeth in the upper and lower jaws, up to 29, 25 in minimum. Their body length reaches 6 m.

A comparison of skull characteristics of the specimens in some extant and fossil species of crocodylian families is shown in Table 3. A comparison revealed that the Yage specimens are a member of the subfamily Tomistominae.

For further investigation of the specimens (Tomistominae gen. et sp. indet.), we compared with three species, namely *Toyotamaphmeia machikanensis* (Kamei et Matsumoto, 1965), and an unamed tomistomine (Taruno, 1999), (Kishiwada-wani) from the Pleistocene Osaka Group and *Tomistoma schlegelii* (Müller, 1838), an extant species in Southeast Asia. The results are shown in Table 4.

The composition and size of the bones allows us to assume that the crocodilian assemblage from the studied area is composed of approximately 10 individuals that measured 3.0–3.5 m in length as adults with a slender, long rostrum. These individuals may belong to a single species.

The specimens of Tomistominae gen. et sp. indet. consist of partial bones at various stages of ontogeny that range from immature to adult through increase of their size.

A skeleton of Tomistominae gen. et sp. indet. is restored by the members of the 'Yage-wani' Skeleton Research Group of Hamamatsu City History Museum as an exhibition of these specimens at the museum in 2011 (Fig. 9).

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