Crocodylian princess in Taiwan: Revising the taxonomic status of *Tomistoma taiwanicus* from the Pleistocene of Taiwan and its paleobiogeographic implications

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Abstract.—*Toyotamaphimeia* is an extinct crocodylian lineage whose name is derived from a mythological Japanese princess. Here, we re-examine the type specimens of a long-forgotten species: *Tomistoma taiwanicus* from the Pleistocene of Tainan (Taiwan) and revise its taxonomic status to *Toyotamaphimeia taiwanicus* n. comb., leading to the first recognized species of *Toyotamaphimeia* outside Japan. Our phylogenetic analyses also support this taxonomic assignment and, more interestingly, further suggest an East Asian lineage. In addition, *Toyotamaphimeia taiwanicus* n. comb. represents a tropical species, resolving a long-standing puzzle of why *Toyotamaphimeia* only inhabited a much higher latitudinal area (Japan). Given the large body size of *Toyotamaphimeia taiwanicus* n. comb. (∼7 m) and the fact that it is geologically older than *Toyotamaphimeia machikanensis* from Japan, we propose a novel evolutionary scenario: the genus *Toyotamaphimeia* originated in Taiwan and evolved to a large body size with gigantothermic physiology, which resulted in migration out of Taiwan and dispersal farther north to Japan. Our taxonomic identification shows the presence of an extinct endemic crocodylian species from the Pleistocene of Taiwan with large-scale paleogeographic implications. This study, with our recent progress in vertebrate paleontology in Taiwan, should provoke more in-depth paleontological research on the Pleistocene extinction.

Introduction

Toyotamaphimeia is an extinct crocodylian lineage, the name of which derives from a Japanese myth, depicting the transformation of a princess into a crocodile. After the original discovery and subsequent taxonomic revision of the type species, *Toyotamaphimeia machikanensis* (Kamei and Matsumoto in Kobatake et al., 1965), and its holotype (Kobatake et al., 1965; Aoki, 1983), *Toyotamaphimeia* remained only known to Japan. Interestingly, a recent paper reported the first possible occurrence of *Toyotamaphimeia* outside of Japan (Ito et al., 2018) based on a historic specimen (WU-HPAC-D 007) originally collected in Tainan, Taiwan (Tokunaga, 1936). That specimen (a partial rostrum) was long considered to have been lost during World War II, and its rediscovery in the Waseda University collection (Tokyo, Japan) offers the first evidence of *Toyotamaphimeia* in Taiwan. As in the Japanese material, the largest maxillary tooth of the Waseda specimen likely occupies the 7th alveolus, but given the limited material, the presence and evolutionary

implications of the *Toyotamaphimeia* lineage in Taiwan remain elusive.

In addition to the Waseda specimen (also from the Pleistocene of Tainan), the second formally published report of crocodylian fossils from Taiwan, corresponding to *Tomistoma taiwanicus*, which was described as a new species by Shikama (1972). WU-HPAC-D 007 and the NSMT materials of *Tomistoma taiwanicus* likely come from the Chiting Formation in Tainan, broadly dated from 0.8–0.4 Ma (Middle Pleistocene). The syntype of *Tomistoma taiwanicus* includes six specimens: an isolated tooth and five skull/mandible fragments. Owing to the incomplete nature of the type specimens, Shikama (1972, p. 126) used a question mark in *Tomistoma* (?) *taiwanicus*, indicating the uncertain generic attribution of the species. Shikama (1972) also noticed the morphological similarity between *Tomistoma taiwanica* and *Tomistoma machikanense*, later assigned to *Toyotamaphimeia* by Aoki (1983).

An obvious pending question then arises: does *Tomistoma taiwanicus* also belong to *Toyotamaphimeia*? To clarify this taxonomic issue, we re-examined the type specimens of *Tomistoma taiwanicus* and conducted phylogenetic analyses to test this hypothesis. Further relevant to this taxonomic question

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are the underlying paleogeographic interpretations. Taiwan is geographically between the Pleistocene occurrence of *Toyotamaphimeia* (Japan) and the extant distribution of *Tomistoma* (Southeast Asia); thus, whether those crocodylian fossils belong to either *Tomistoma* or *Toyotamaphimeia* leads to entirely disparate evolutionary scenarios. In addition, if *Tomistoma taiwanicus* indeed pieces together with the *Toyotamaphimeia* lineage, this resolves the paleogeographic puzzle of a crocodylian lineage, *Toyotamaphimeia*, solely inhabiting relatively high latitudes (Japan).This is because *Tomistoma taiwanicus*, from the Pleistocene of Tainan, is geographically farther south and geologically older, which offers a novel perspective to understand the origin and evolutionary history of *Toyotamaphimeia*.

Geological setting

The exact locality of *Tomistoma taiwanicus* remains uncertain because the late and famous local collector, C. M. Chen, collected the specimen in Tainan without properly documenting specific information and sent it to Japan for study. After the description of *Tomistoma taiwanicus*, principal paleontologists in Taiwan at that time (e.g., T. Shikama or H. Otsuka) likely acquired more collecting information from C. M. Chen, pinpointing three localities along the Tsailiao River (Fig. 1; Otsuka and Shikama, 1978; Otsuka, 1984). Based on our recent field experience around the Tainan area, those three identified localities likely do not represent the actual fossil-bearing sites, but pick-up spots that accumulated fossils washed away along the river. A field-digging program teamed up with local government agencies and led by CHT aims to collect more complete materials and reveal the fossil-bearing horizon to further discuss the paleoecological settings. Given the discovery of abundant vertebrate fossils from the Chiting Formation in Tainan since the early twentieth century (Hayasaka, 1932; Shikama, 1937; Otsuka and Lin, 1984; Chang et al., 2012; Tsai et al., 2013; Lin et al., 2019; Tsai and Mayr, 2021; Tsai and Tseng, 2022), the age of *Tomistoma taiwanicus* can be broadly established as 0.8–0.4 Ma (late Early to early Middle Pleistocene; Fig. 1). Of note, Shan et al. (2009) suggested a Late Pliocene/Early Pleistocene age, but this should be corrected to Middle Pleistocene, as we discussed here.

Materials and methods

We follow Kobayashi et al. (2006), Shan et al. (2009), and Iijima et al. (2018) for the anatomical terms. To further explore the phylogenetic position of the Tainan tomistomine, we combined *Tomistoma taiwanicus* and WU-HPAC-D 007 as a single operational taxonomic unit (OTU) in order to achieve a higher percentage of coding in the cladistic analysis (see Systematic Paleontology section). We adopted the matrix of Iijima and Kobayashi (2019), which is mainly based on Brochu (1999) and Jouve et al. (2015). In addition, we expanded the dataset by adding newly discovered fossils, including *Hanyusuchus sinensis* Iijima et al., 2022, *Gunggamarandu maunala* Ristevski et al., 2021, *Toyotamaphimeia* cf. *T. machikanensis* (reported by Iijima et al., 2018), *Melitosaurus champsoides* Owen, 1849, *Tomistoma calaritanum* Capellini, 1890, *Tomistoma gaudense*

(Hulke, 1871) (reported by Nicholl et al., 2020), and NTUM-VP 200702 (a partial skull from another locality in Taiwan). We also modified Character 145 to a multistate character with (three states) based on Nicholl et al. (2020) and updated the scorings of *Toyotamaphimeia machikanensis* and *Penghusuchus pani* Shan et al., 2009. Our dataset then includes 254 characters and 77 OTUs (see Supplementary material for the updated dataset). We performed the maximum parsimony analysis in TNT v 1.5 (Goloboff et al., 2008; Goloboff and Catalano, 2016) under Traditional Search. Detailed settings include 1000 Wagner tree replicates; saving ten trees per replicate under tree bisection reconnection branch swapping; equal-weighted and unordered for all characters. Additionally, we performed a second round of skull-only cladistic analysis (193 characters) to test the phylogenetic position of *Tomistoma taiwanicus* due to the preservation of the type specimens.

Repositories and institutional abbreviations.—KSNHM, Natural History Museum, Kishiwada City, Osaka, Japan; MOU, Museum of Osaka University, Osaka, Japan; NMNS, National Museum of Natural Science, Taichung, Taiwan; NSMT, National Museum of Nature and Science (previously known as National Science Museum, Tokyo), Tsukuba, Japan; NTUM-VP, Vertebrate Paleontology (Laboratory of Evolution and Diversity of Fossil Vertebrates), Museum of Zoology, National Taiwan University, Taipei, Taiwan; WU-HPAC, Waseda University-Honjo Paleontological Archaeological Collection, Tokyo, Japan.

Systematic paleontology

Crocodylia Gmelin, 1789 (sensu Benton and Clark, 1988)
Tomistominae Kälin, 1955 (sensu Brochu, 2003)
Toyotamaphimeia Aoki, 1983

Type species.—*Toyotamaphimeia machikanensis* (Kamei and Matsumoto in Kobatake et al., 1965) from the Kasuri Tuff of the Osaka Group, Osaka, Japan. The holotype is MOUF00001.

Toyotamaphimeia taiwanicus (Shikama, 1972) new combination
Figures 2–4, 5.1–5.5

1972 *Tomistoma* (?) *taiwanicus* Shikama, p. 126, pl. 2, figs. 1–14, pl. 3, figs. 1–7, text-fig. 1.

Type materials.—The original type specimens include six specimens: NSMT-P-9121, an isolated tooth (Fig. 2.4); NSMT-P-9122, a partial frontal/prefrontal complex (Fig. 3); NSMT-P-9123, originally identified as a partial parietal by Shikama (1972), but here revised to be a partial frontal (see our discussion; Fig. 3); NSMT-P-9124, a partial rostrum, including the anterior portion of the maxilla and the dorsal posterior process of the premaxilla (Fig. 4); NSMT-P-9125, a middle section of the left lower jaw (Fig. 5.1–5.5) identified as the anterior segment of the lower jaw by Shikama (1972); and NSMT-P-9126, a middle section of the lower jaw (Fig. 2.1–2.3). Our detailed re-examination confirms the existence of at
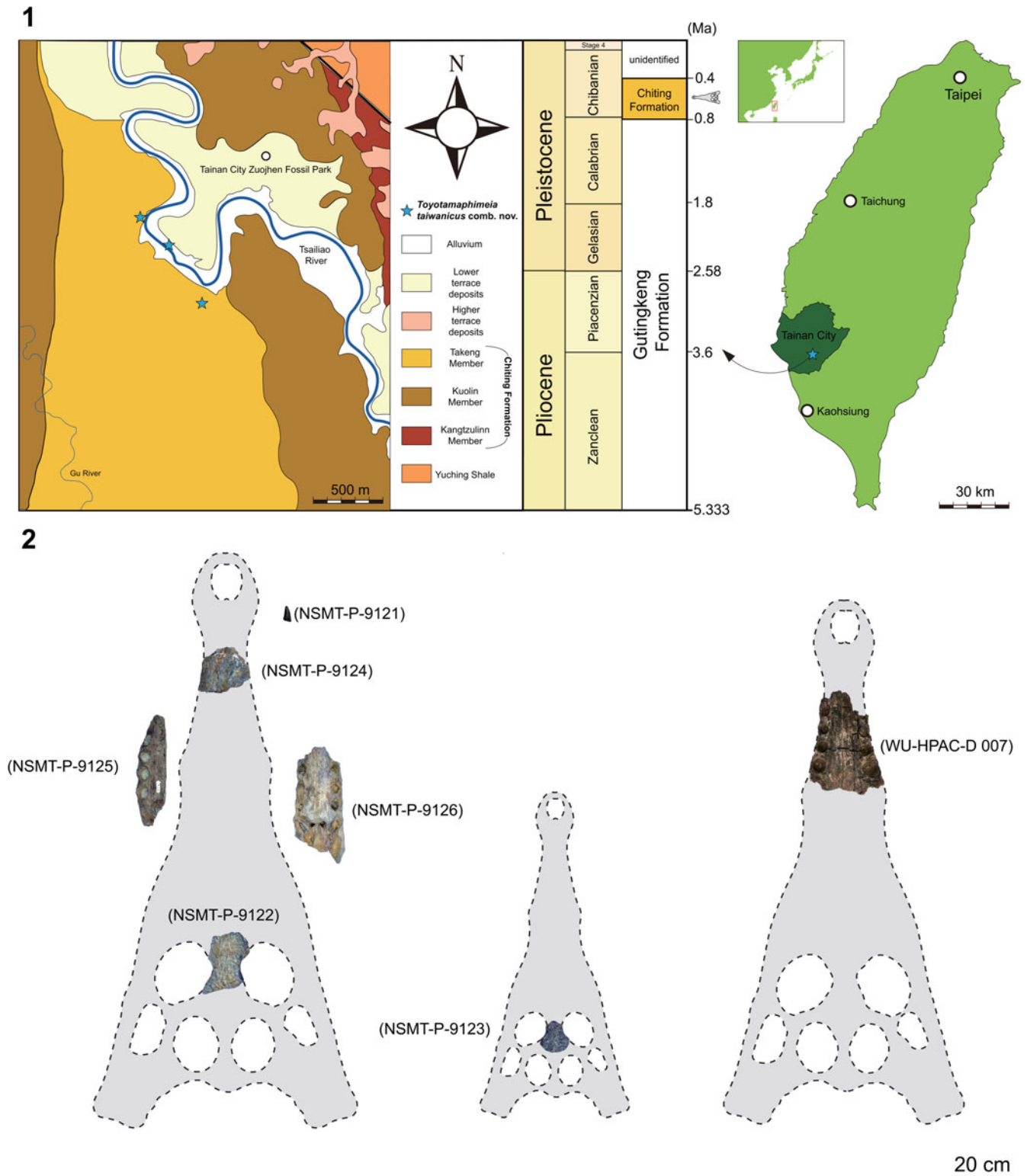
Figure 1. The occurrence of *Toyotamaphimeia taiwanicus* n. comb. (**1**) Location and geological map and generalized stratigraphic column with collecting information (modified from Otsuka, 1984). (**2**) Fossil materials of *Toyotamaphimeia taiwanicus* n. comb. and the possible positions.

least two individuals in the type specimens—two frontals, likely indicating the size disparity between a large adult (NSMT-P-9122) and a young juvenile (NSMT-P-9123). All six specimens are syntypes, and we refrain from designating a lectotype, for now, owing to the incomplete nature of the type specimens. The high-resolut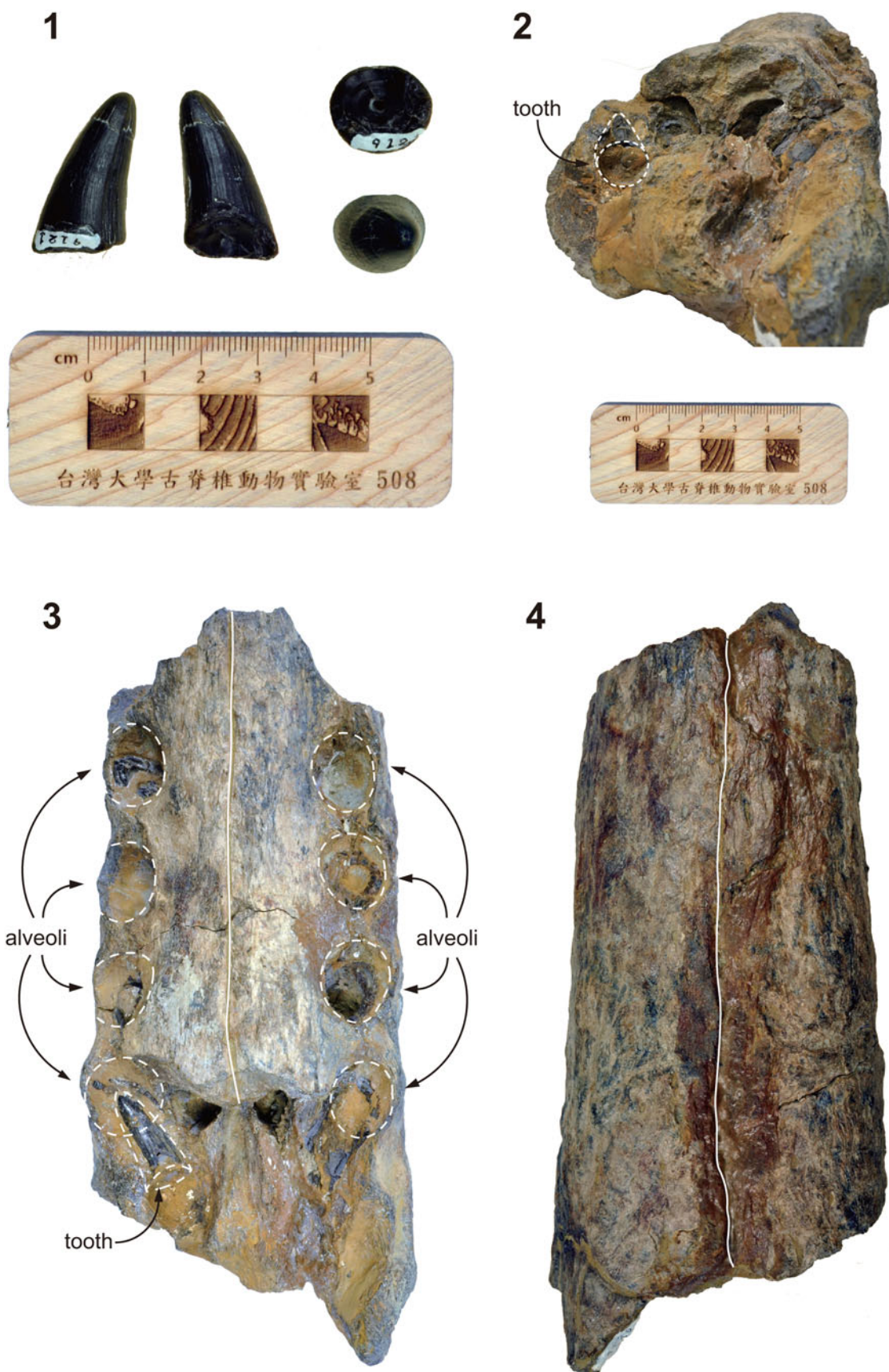ion 3D data of the NSMT materials are freely available at: https://doi.org/10.5281/zenodo.7340097 or https://scholars.lib.ntu.edu.tw/handle/123456789/625770.

Figure 2. *Toyotamaphimeia taiwanicus* n. comb. (**1**) NSMT-P-9121, an isolated tooth; (**2–4**) NSMT-P-9126, a middle section of the lower jaw: (**2**) posterior view; (**3**) dorsal view; (**4**) ventral view. White lines indicate the suture; dashed lines represent the proposed border. Left scale (**1**); right scale (**2–4**).
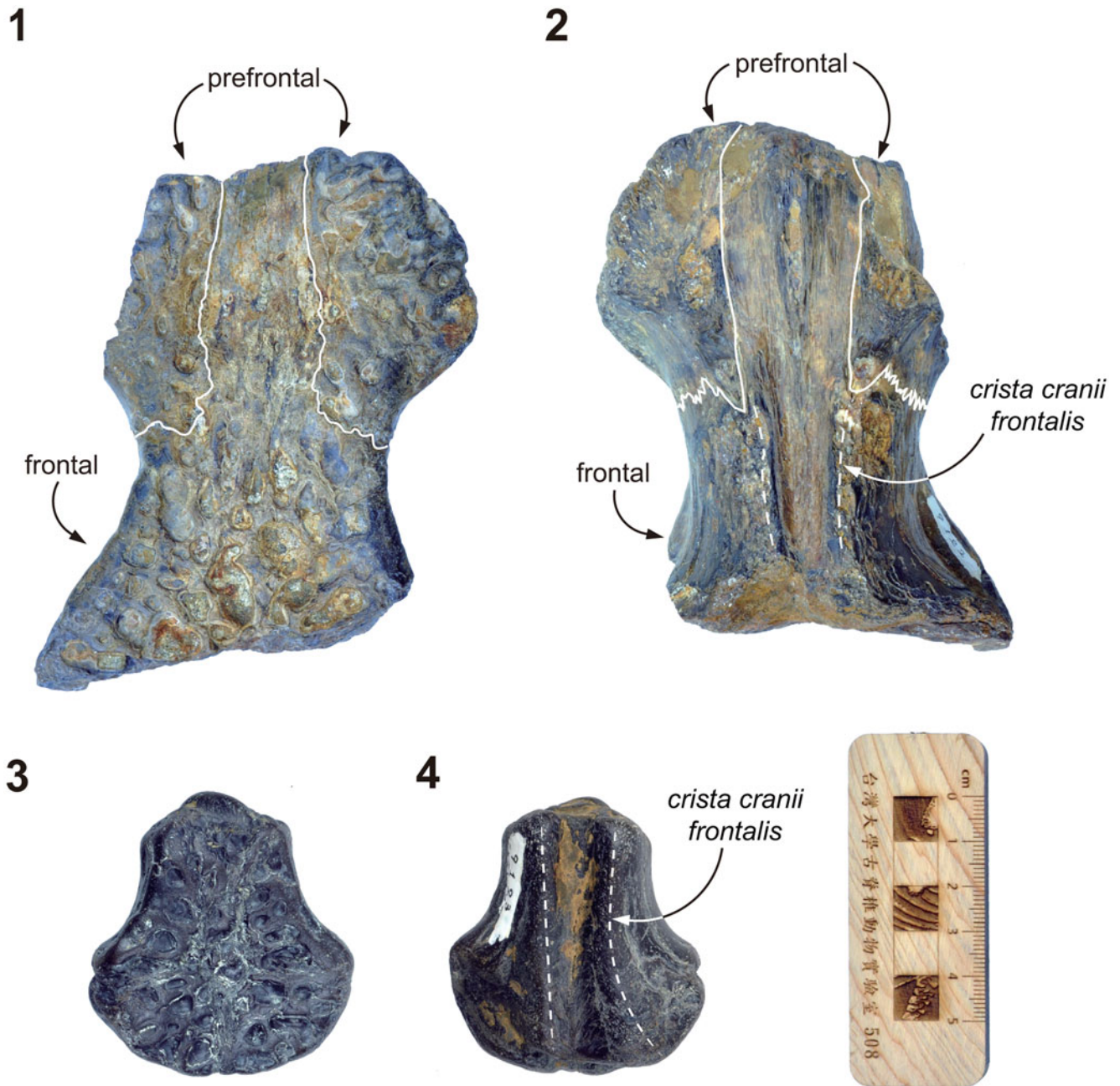
Figure 3. *Toyotamaphimeia taiwanicus* n. comb. (**1, 2**) NSMT-P-9122, a partial frontal/prefrontal complex: (**1**) dorsal view, (**2**) ventral view; (**3, 4**) NSMT-P-9123, a partial frontal (misidentified by Shikama, 1972, as the parietal): (**3**) dorsal view, (**4**) ventral view. White lines indicate sutures; dashed lines represent proposed borders.

Diagnosis.—Our examination shows that the morphological combination seen in NSMT-P-9122 (frontal/prefrontal complex) corresponds to that of all known *Toyotamaphimeia* specimens (Figs. 6, 7), which differ from *Tomistoma schlegelii* (Muller, 1838) (NSMT-H-5870) by having medially curving posterolateral margin of the prefrontal (Fig. 6) and a slightly, but not prominent, upturned orbital margin (Fig. 7). More importantly, there is a difference between the Tainan material and *Toyotamaphimeia machikanensis* in the position of the medial maxillary occlusal pits. The Tainan materials

(both NSMT and the Waseda specimens) exhibit those pits near the anterior (2nd–7th) maxillary teeth (Fig. 8.1, 8.2), whereas in *Toyotamaphimeia machikanensis* these are positioned farther posteriorly, near the 8th–13th teeth (Fig. 8.3).

Our morphological comparisons allow a reliable assignment of *Tomistoma taiwanicus* to *Toyotamaphimeia*, creating *Toyotamaphimeia taiwanicus* n. comb. Of note, based on the morphological similarity between the Waseda specimen (WU-HPAC-D 007) and the NSMT materials, we assign WU-HPAC-D 007 to *Toyotamaphimeia* cf. *T. taiwanicus*
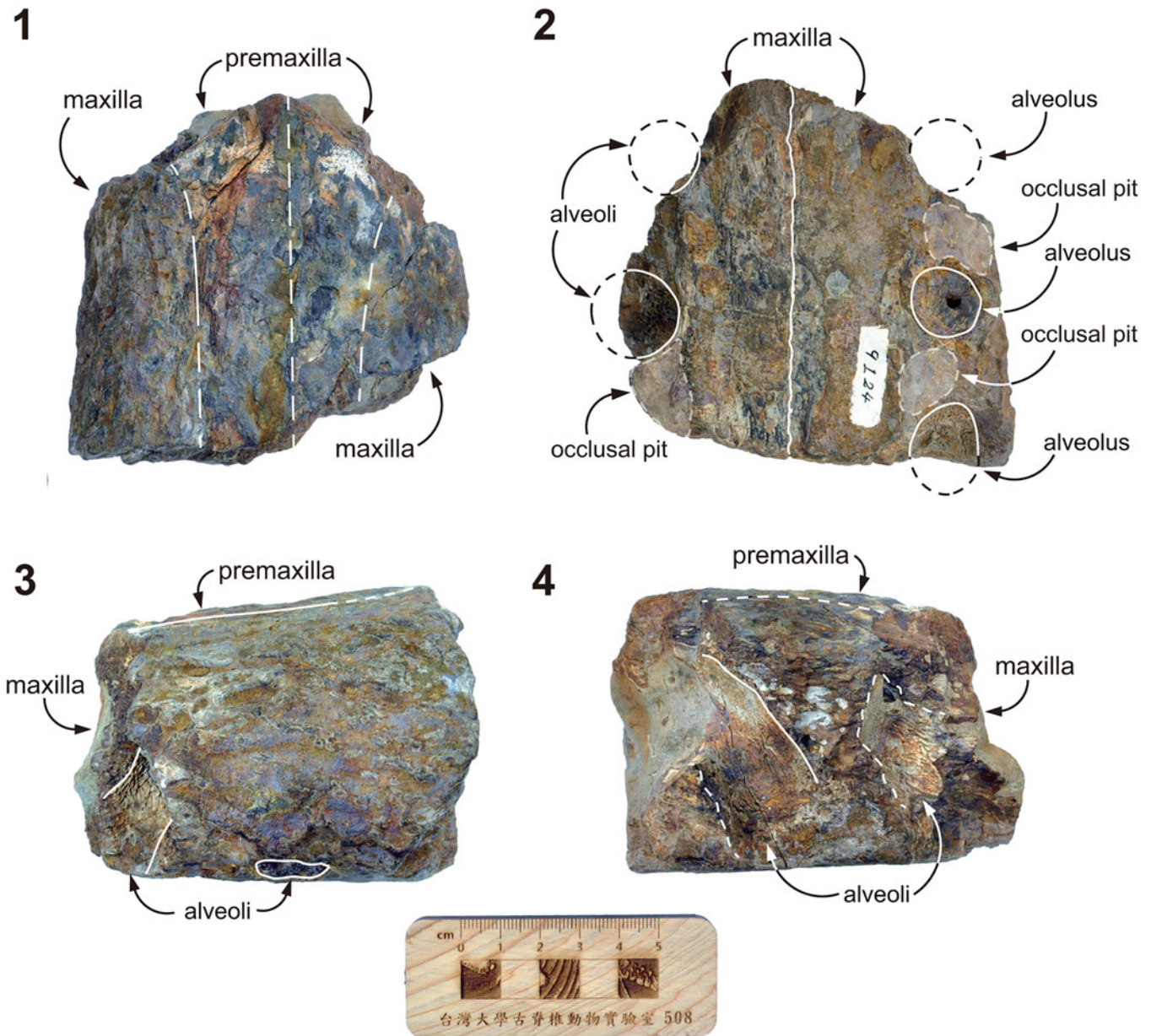
Figure 4. *Toyotamaphimeia taiwanicus* n. comb. (**1–4**) NSMT-P-9124, a partial rostrum including the anterior portion of the maxilla and the dorsal posterior process of the premaxilla: (**1**) dorsal view, (**2**) ventral view, (**3**) left lateral view, and (**4**) right lateral view. White lines indicate sutures; dashed lines represent proposed borders.

n. comb., because no definite morphological differences exist between WU-HPAC-D 007 and NSMT-P-9126, and both specimens likely come from the same geological horizon. In addition, both the rostral outlines of *Toyotamaphimeia taiwanicus* n. comb. represented by WU-HPAC-D 007 and *Toyotamaphimeia machikanensis* show a curved and prominent expansion at the level of 7th alveolus (Fig. 8), in contrast to the more gradual and moderate expansion of the rostral outlines of *Hanyusuchus sinensis* and *Penghusuchus pani* (Fig. 8). All the fossil materials described here (except NSMT-P-9123) likely belong to physically and sexually mature individuals (>4 m and up to 7 m long; Iijima and Kubo, 2020; Iijima et al., 2022), eliminating the likelihood of ontogenetic differences (Iijima, 2017).

Description of the type specimens.—Both the NSMT and Waseda materials have been described in detail by Shikama (1972) and Ito et al. (2018), respectively. We aim to describe new morphological observations and conduct further comparisons with other relevant and newly discovered fossils. One of the most critical re-identifications is that NSMT-P-9123, originally recognized as the parietal by Shikama (1972), is in fact a frontal, because of the presence of a narrow crista cranii frontalis in ventral view (Fig. 3.4). The posterolateral margin of the orbit in NSMT-P-9123 is circular, and its dorsal orbital margin is nearly smooth (Fig. 3.3), similar to that of NSMT-P-9122. The size disparity between NSMT-P-9122 and NSMT-P-9123 suggests that they represent a large individual and a young juvenile.
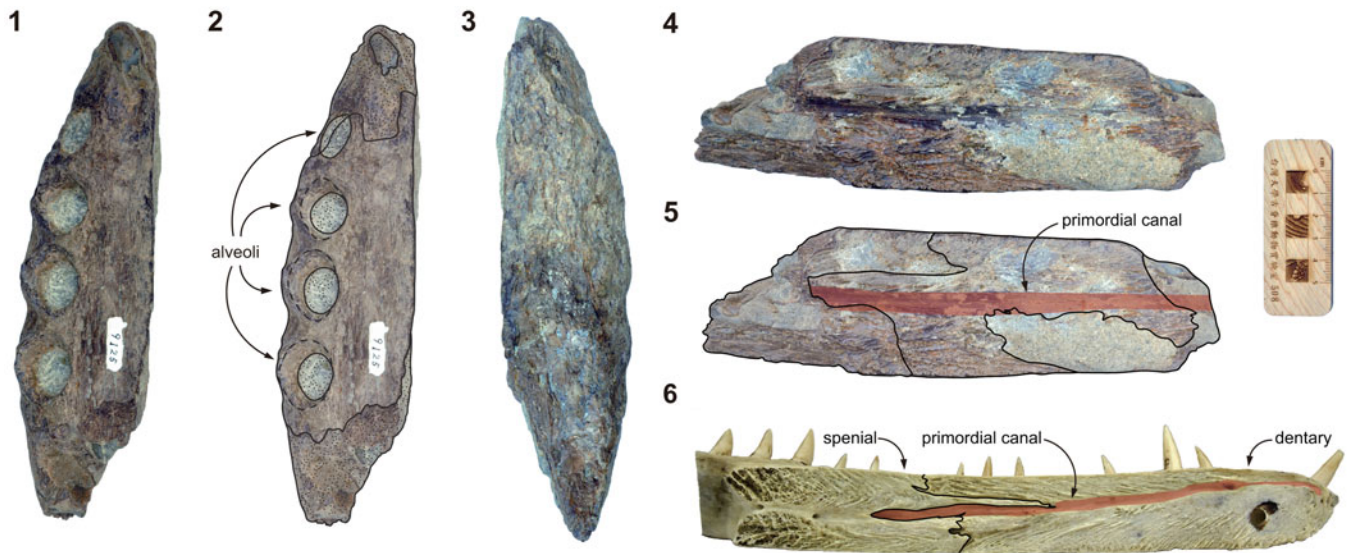
Figure 5. *Toyotamaphimeia taiwanicus* n. comb. (**1–5**) NSMT-P-9125, a middle section of the lower jaw: (**1, 2**) dorsal view, (**3**) ventral view, (**4, 5**) medial view. (**6**) NSMT-H-5870, a left lower jaw of *Tomistoma schlegelii* in medial view. The red areas show the primordial canal in the lower jaw. Dotted areas indicate eroded regions. Black lines indicate sutures; dashed lines represent proposed borders.

NSMT-P-9121 is an isolated tooth (Fig. 2.4). NSMT-P-9126, a middle section of the lower jaw, accommodates another partial tooth (Fig. 2.1, 2.3). Both teeth are large and robust, slightly curved, and with a blunt apex. Two carinae are seen on the tooth surface, forming an angle of almost 90° to its curving axis (Fig. 2.2). The tooth crown exhibits a series of minor striations. The overall morphology of the tooth is similar to the teeth of *Toyotamaphimeia machikanensis* and different from the elongated and strongly curving teeth with a sharp apex of the extant *Tomistoma schlegelii*.

The NSMT-P-9122 partial frontal/prefrontal complex (Fig. 3.1, 3.2) is large and comparable to that of the holotype of *Toyotamaphimeia machikanensis*. Shikama (1972) oriented NSMT-P-9122 in a reverse anteroposterior direction and missed the existence of the prefrontal. Our re-examination confirms a brief notice by Shan et al. (2009) that NSMT-P-9122 includes both the frontal and prefrontal. The inner orbital margin of NSMT-P-9122 is linear, whereas both the extant *Tomistoma schlegelii* and the Miocene *Penghusuchus pani* show an apparent "inflection point" at the level of the narrowest part of the interorbital (Fig. 6). The posterolateral margin of the prefrontal in NSMT-P-9122 is medially curved and forms the anteromedial margin of the orbit, making a circular margin along the inner orbit (Figs. 2.1, 6.1). This condition also occurs in *Toyotamaphimeia machikanensis*, *Hanyusuchus sinensis*, and *Penghusuchus pani*, but the inner orbital margin of *Penghusuchus pani* is more angular (Fig. 6). The posterolateral margin of the prefrontal is straight instead of medially curving, as in the extant *Tomistoma schlegelii* in which the general orbital shape is like a capital D (Fig. 6). In addition, the dorsal margin of the orbit is fairly smooth, similar to that of *Toyotamaphimeia machikanensis*, *Hanyusuchus sinensis*, and *Penghusuchus pani*, but different from the prominent upturned ridge of *Tomistoma schlegelii* (Fig. 7).

The dorsal surface of a partial rostrum (NSMT-P-9124; Fig. 4) is covered by a thin sediment layer, hampering identification of the premaxilla–maxilla. The suture is likely anteroposteriorly linear, gradually curving anterolaterally. The rostrum is lateromedially narrow, with the lateral margins of the anterior portion parallel in dorsal view with a gentle posterior expansion. Ventrally, no trace of premaxilla or palatine is preserved. The left maxilla preserves one intact alveolus in NSMT-P-9124, and the alveoli increase slightly in size posteriorly, along with a gradual lateral expansion of the maxilla. Prominent concavities along the lateral margin of the maxilla between consecutive alveoli represent occlusal pits for the lower dentition. The equal size of the alveoli and the parallel margins of the preserved maxilla suggest that NSMT-P-9124 is more likely an anterior-most portion of the maxilla preserving the 1st–3rd alveoli.

NSMT-P-9125, recognized as the anterior portion of the lower jaw by Shikama (1972), seems to belong to the middle segment of the lower jaw, given the presence of a primordial canal extending horizontally along its dorsoventral center instead of being displaced dorsally or on the dorsal half (Fig. 5). The position of the primordial canal remains unknown in the *Toyotamaphimeia* lineage, but future finds and CT data should help to test if it is like the extant *Tomistoma schlegelii* (Fig. 5.6). Based on our close examination, the narrow anterior tip of NSMT-P-9125 likely results from post-mortem erosion and damage, making the overall morphology like the anterior part of the dentary. In addition, the size of the alveoli in both NSMT-P-9125 and NSMT-P-9126 is similar and shows no enlargement along the lower jaws. We also found no remains of the splenial in both specimens, suggesting that NSMT-P-9125 and NSMT-P-9126 belong to lower jaw sections anterior to the splenial symphysis and posterior to the enlarged 4th alveoli.

Referred specimen.—WU-HPAC-D 007, a partial rostrum, including the anterior portion of the maxilla and an uncertain
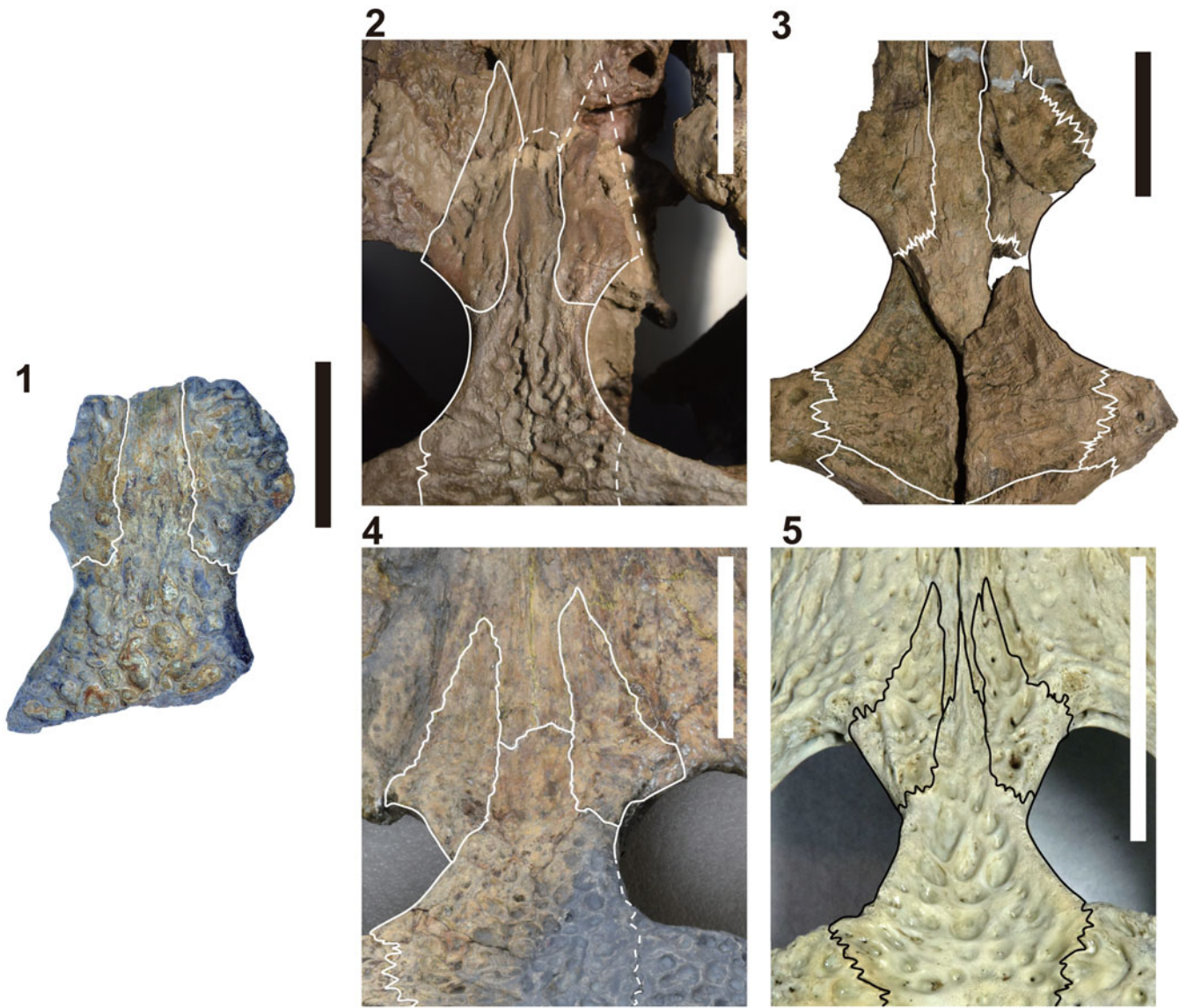
Figure 6. Comparison of the interorbital regions of studied specimens in dorsal view. (**1**) *Toyotamaphimeia taiwanicus* n. comb. (NSMT-P-9122). (**2**) *Toyotamaphimeia machikanensis* (NSMT-P-20510). (**3**) *Toyotamaphimeia* cf. *T. machikanensis* from Kishiwada (KSNHM-F7-6). (**4**) *Penghusuchus pani* (NMNS-005645). (**5**) *Tomistoma schlegelii* (NSMT-H-5870). Solid lines indicate sutures; dashed lines represent proposed borders. All scale bars = 5 cm.

piece of the premaxilla. This historic specimen has long been considered to have been lost during World War II after a brief report (Tokunaga, 1936), but fortunately was rediscovered in the Waseda collection (Ito et al., 2018).

Body size.—Based on the size estimation of *Toyotamaphimeia machikanensis* (Iijima and Kubo, 2020), the body size of *Toyotamaphimeia taiwanicus* n. comb. is comparable (i.e., >6 m and up to 7 m long). The sizes of given anatomical parts of NSMT-P-9122, 9124, 9125, and 9126 are almost identical to those of the holotype of *Toyotamaphimeia machikanensis*. For example, the interorbital width is 49 mm in NMST-P-9122 and 49.6 mm in *Toyotamaphimeia machikanensis*. In addition, the much smaller size of NSMT-P-9123, re-identified here as a frontal, compared to NSMT-P-9122, plus our comparison with extant crocodylians, suggests that NSMT-P-9123 belongs to a juvenile individual likely ranging from 2–3 m long.

Remarks.—The original diagnosis of "*Tomistoma* (?) *taiwanicus*" of Shikama (1972, p. 126) is ambiguous and unfounded for the following reasons: (1) because preservation of the anterior-most maxilla NSMT-P-9124 is incomplete, we cannot be sure that its snout is "more elongate" than that of *Toyotamaphimeia machikanensis*; (2) NSMT-P-9124 represents the anterior portion of the upper jaw, showing the suture between the maxilla and premaxilla instead of occurring more posteriorly between the maxilla and nasal, hence we cannot confirm the presence of an "obsolete suture between the maxilla and nasal"; (3) the isolated tooth (NSMT-P-9121) and preserved alveoli of the rostrum fall within the size range of *Toyotamaphimeia machikanensis* teeth, and are not "relatively large"; (4) the diastema between consecutive teeth also are similar to those in *Toyotamaphimeia machikanensis*; (5) we found the crista cranii frontalis on the ventral side of NSMT-P-9123,
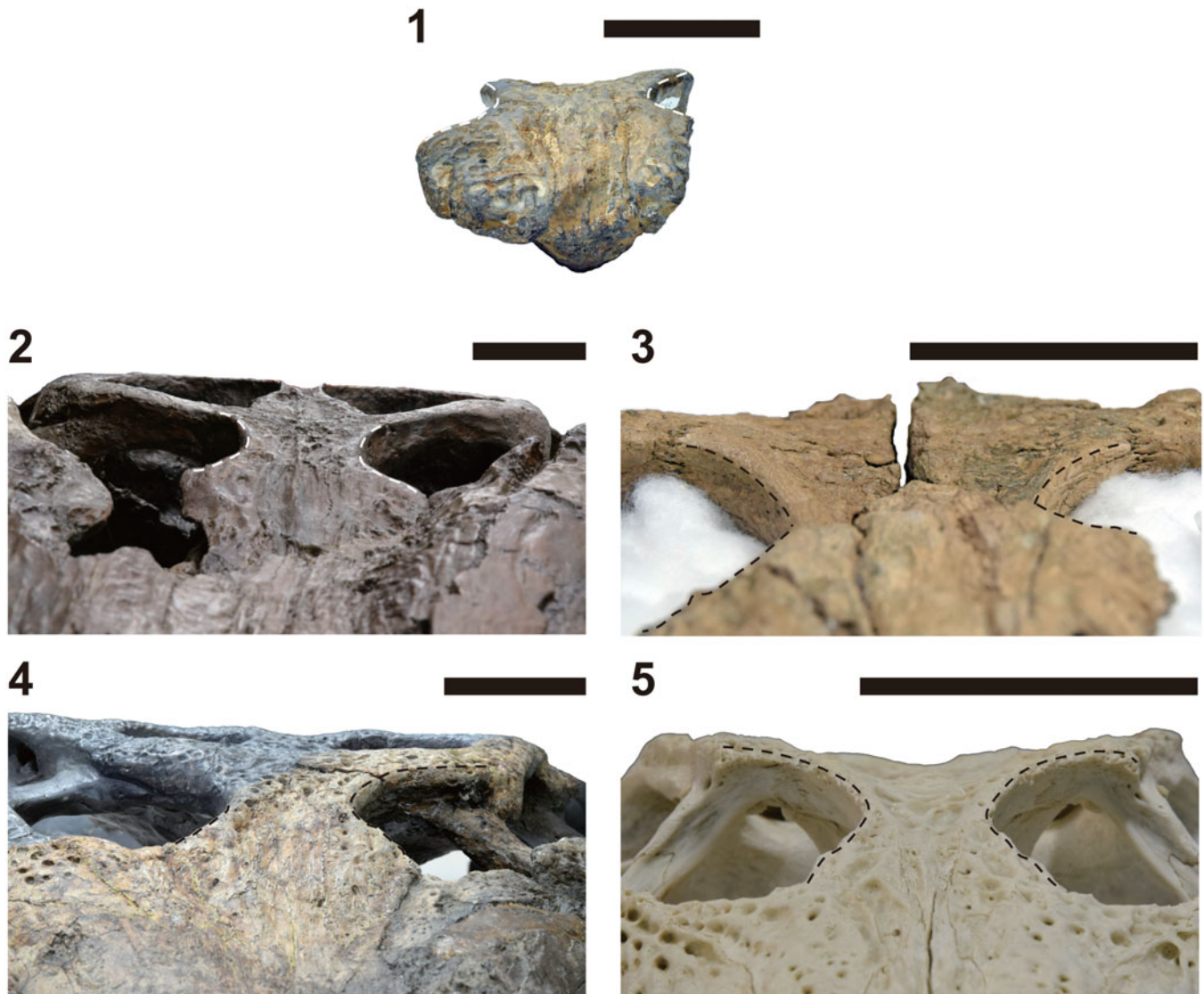
Figure 7. Comparison of the orbital regions of studied specimens in anterior view. (**1**) *Toyotamaphimeia taiwanicus* n. comb. (NSMT-P-9122). (**2**) *Toyotamaphimeia machikanensis* (NSMT-P-20510). (**3**) *Toyotamaphimeia* cf. *T. machikanensis* from Kishiwada (KSNHM-F7-6). (**4**) *Penghusuchus pani* (NMNS-005645). (**5**) *Tomistoma schlegelii* (NSMT-H-5870). Dashed lines indicate the dorsal orbital margins. All scale bars = 5 cm.

indicating it is a frontal instead of a parietal, so that the "very narrow parietal" is an illegitimate diagnostic trait; (6) the distinctly angulated "inner margin of orbital foramen" seems a more probable diagnostic feature, but comparison with other tomistomines (Fig. 6) shows that the orbit of NSMT-P-9123 has a circular and smooth inner margin. In the end, our comprehensive re-examination clearly demonstrates that the previous diagnosis of "*Tomistoma* (?) *taiwanicus*" is rather problematic.

Phylogenetic results

In the first round of our cladistic analysis (including all characters), we recovered 710 most parsimonious trees (MPTs) with 974 steps (see details in the Supplementary material). The 50% majority-rule consensus of those trees (time-calibrated, after Nicholl et al., 2020, and Iijima et al., 2022; Fig. 9) shows *Toyotamaphimeia taiwanicus* n. comb. (NSMT materials

+ WU-HPAC-D 007) in a polytomy with two clades, one formed by *Hanyusuchus sinensis* plus an undescribed tomistomine (NTUM-VP 200702, currently under study by YYC and CHT), and one formed by the three *Toyotamaphimeia* specimens from Japan. The sister taxon of this polytomy is the Miocene *Penghusuchus pani* from Taiwan. The next more externally branching lineage includes two species of *Thecachampsa* from the Miocene of North America.

We conducted an additional skull-only analysis (inactivating the post-cranial characters) and recovered 2760 MPTs of 814 steps (see details in the Supplementary material). Their 50% majority-rule consensus tree shows polytomy with five lineages (*Toyotamaphimeia taiwanicus* n. comb., *Hanyusuchus sinensis*, *Penghusuchus pani*, NTUM-VP 200702, and a clade including the three *Toyotamaphimeia* from Japan). Surprisingly, this skull-only analysis generated a topology in which tomistomines are included within Gavialoidea, as reported in a more recent morphology-based phylogeny (Rio and Mannion, 2021).
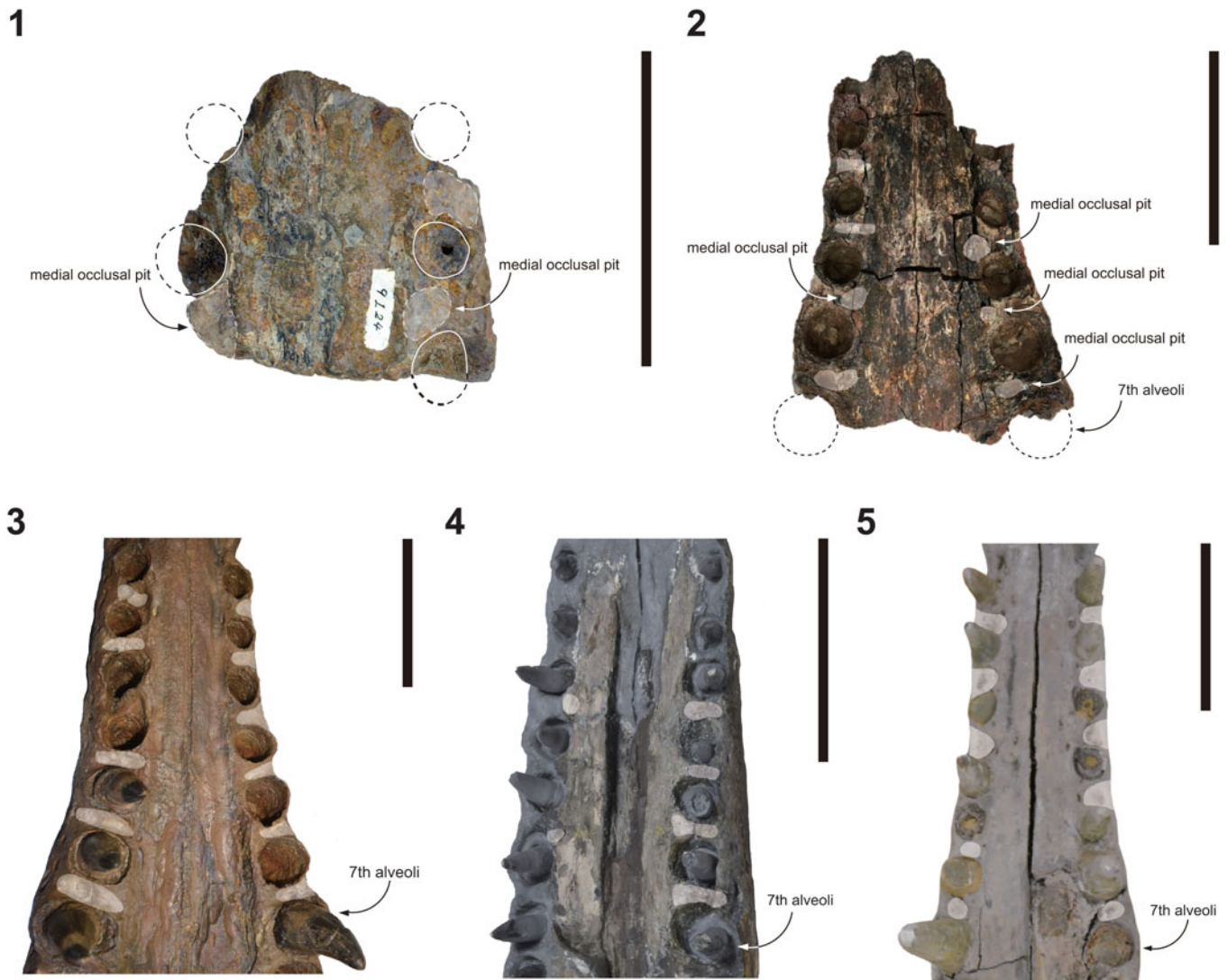
Figure 8. Comparison of the occlusal pit positions and anterior rostral shapes (the portion of 1st–7th alveoli). (**1**) *Toyotamaphimeia taiwanicus* n. comb. (NSMT-P-9124). (**2**) *Toyotamaphimeia taiwanicus* n. comb. (WU-HPAC-D 007). (**3**) *Toyotamaphimeia machikanensis* (NSMT-P-20510). (**4**) *Penghusuchus pani* (NMNS-005645) (**5**) *Hanyusuchus sinensis* (SM S01812; from the supplementary material of Iijima et al., 2022, under the license of CC-BY 4.0). White translucent areas indicate occlusal pit positions; dashed lines represent proposed borders. All scale bars = 10 cm.

Interestingly, both the all-character and skull-only analyses suggest the existence of an East Asian lineage, including the Miocene *Penghusuchus pani* (Taiwan), the Pleistocene *Toyotamaphimeia taiwanicus* n. comb. (Taiwan) and *Toyotamaphimeia machikanensis* (Japan), and the Holocene *Hanyusuchus sinensis* (southeastern China). Seven unambiguous synapomorphies support this lineage: (1) the largest maxillary alveolus in the "first wave" is the 7th (Cha. 89-7); (2) the dorsal premaxillary processes are long and extend beyond the 5th maxillary alveolus (Cha. 145-2); (3) the opening of the lateral eustachian canals is lateral to the medial eustachian canal (Cha. 147-1); (4) the surangular-articular suture is oriented anteroposteriorly (Cha. 162-0); (5) the ventral processes of the exoccipital are oriented lateroventrally in occipital view (Cha. 189-1); (6) the largest maxillary tooth in the second "wave" posterior to the 9th tooth is the 12th or a more posterior tooth (Cha. 227-1); and (7) the maxillary teeth are not widely spaced, with the 7th and 8th teeth not more spaced than other diastemas (Cha. 235-0).

Discussion

Our detailed morphological re-examination of the type specimens and phylogenetic analyses allow a confident reassignment of *Tomistoma taiwanicus* to *Toyotamaphimeia taiwanicus* n. comb., suggesting an East Asian, instead of Southeast Asian, influence for evolution of the Pleistocene crocodylians from Tainan, Taiwan. Similarly, our study also allowed assignment of the Waseda specimen to *Toyotamaphimeia* cf. *T. taiwanicus* n. comb. because it shares medial maxillary occlusal pits on the anterior part of the maxillary dentition (2nd–7th teeth) with the NSMT materials, rather than more posteriorly (8th–13th teeth), as in *Toyotamaphimeia machikanensis*. The Waseda specimen (WU-HPAC-D 007) and the NSMT materials (NSMT-P-9121, 9123, 9124, 9125, and 9126) firmly confirm the existence of *Toyotamaphimeia* in Taiwan.

Toyotamaphimeia taiwanicus n. comb. from the Pleistocene of Taiwan represents a tropical species of
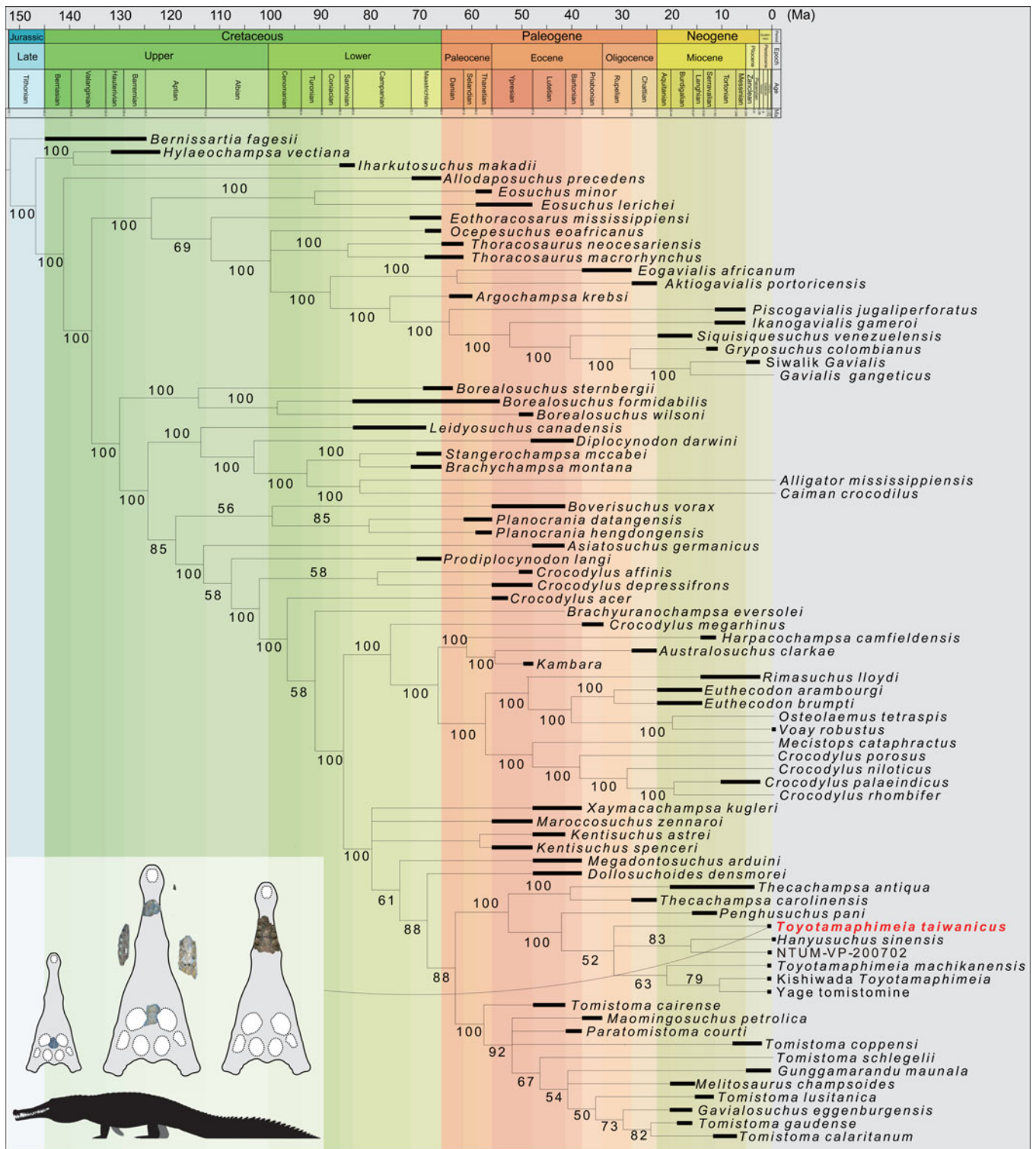
Figure 9. Phylogenetic assessment of *Toyotamaphimeia taiwanicus* n. comb. 50% majority tree under the all-character analysis (254 characters and 77 OTUs) with time-calibrated information after Nicholl et al. (2020) and Iijima et al. (2022). *Toyotamaphimeia* silhouette downloaded from phylopic.org and illustrated by Armin Reindl under the license CC BY-NC 3.0.

Toyotamaphimeia and provides new insights into a long-standing puzzle as to why and how *Toyotamaphimeia machikanensis* solely inhabited a relatively high-latitudinal region (Japan), given that crocodylian physiology generally conforms to low-latitudinal warmer areas. A mid-latitude occurrence is more likely, within the northern boundaries of the extant crocodylian distribution range (Iijima et al., 2018; de Celis et al., 2020), but not beyond 35° (Nicolaï and Matzke, 2019). For instance, the fossil record of *Gavialis gangeticus* Gmelin, 1789, indicates a farther northern distribution than today

(Nanda et al., 2016; Martin, 2019). Similarly, the past distribution of *Alligator sinensis* Fauvel, 1879, also ranges from Thailand to farther north in Japan (Iijima et al., 2016). *Crocodylus niloticus* Laurenti, 1768, is widely distributed across the entirety of Africa, including colder areas (Fergusson, 2010), and the extant largest *Crocodylus porosus* Schneider, 1801, also shows a wide distribution range (Webb et al., 2010). This suggests a past distribution expansion to mid-latitude regions for Crocodylia (including the extant Alligatoridae, Crocodylidae, and Gavialidae). We then should expect to find a low-latitude member of the *Toyotamaphimeia* lineage, and our *Toyotamaphimeia taiwanicus* n. comb. from the tropical Pleistocene of Tainan resolves this paleogeographic conundrum.

Temperature is one of the most critical abiotic factors restricting crocodylian range and the distribution of crown-Crocodylia has been restricted to tropical or subtropical areas between 35°N and 35°S latitude after a global cooling event in the Late Miocene (Markwick, 1998a, b; Mannion et al., 2015). The repeated glacial–interglacial cycles during the Pleistocene resulted in constant environmental change and forced large-scale dispersal events. Macro-plant fossils coeval with *Toyotamaphimeia machikanensis* suggest an environmental temperature close to the lowest boundary for crocodylian survival during the interglacial period in Japan, and the lineage may have dispersed farther south during the Pleistocene glaciations (Iijima et al., 2018). However, our recognition of *Toyotamaphimeia*, which is larger and geologically older than *Toyotamaphimeia machikanensis* (*T. taiwanicus* n. comb.: 0.8–0.4 Ma; *T. machikanensis*: 0.6–0.5 Ma), in a Pleistocene tropical site (Tainan, Taiwan), provides a novel interpretation. We propose that *Toyotamaphimeia* originated in Taiwan and evolved to a large body size (i.e., reaching 7 m long), with a thermoregulation likely similar to that of the "saltwater crocodile" *Crocodylus porosus*. This is the largest extant crocodylian (>6 m long) with a gigantothermic physiology that allows maintaining its body temperature under cold conditions (Grigg et al., 1998; Seebacher et al., 1999). The gigantic *Toyotamaphimeia taiwanicus* n. comb. also may have been equipped with a gigantothermic physiology, allowing an out-of-Taiwan migration, dispersing to higher latitudinal regions, such as Japan.

Surprisingly, both our all-character and skull-only phylogenetic analyses generated a consistent "East Asian tomistomine clade," including *Penghusuchus pani* (Taiwan), *Toyotamaphimeia machikanensis* (Japan), *Toyotamaphimeia taiwanicus* n. comb. (Taiwan), *Hanyusuchus sinensis* (southeastern China), and an undescribed specimen (NTUM-VP 200702, Taiwan), but under disparate large-scale phylogenetic scenarios—tomistomines nested either in the crocodyloid or in the gavialoid clade (Fig. 9; see Supplementary material for all topologies). This emphasizes the phylogenetic instability with different taxa and character data, highlighting the gharial problem. A recent extensive morphology-based phylogeny (Rio and Mannion, 2021) recovered a tomistomine lineage nested within gavialoids, as in our skull-only analysis. Nevertheless, *Penghusuchus pani* and *Toyotamaphimeia* form a ladder topology towards the extant *Gavialis* (Rio and Mannion, 2021) rather than an "East Asian tomistomine clade," as both of our analyses suggest. More fossil crocodylians with well-preserved materials and critical assessment of character descriptions should be key

to resolving such phylogenetic inconsistencies. In addition, detailed description and phylogenetic assessment of the undescribed NTMU-VP 200702 (or more-complete specimens of *Toyotamaphimeia taiwanicus* n. comb. and *Penghusuchus pani*) from Taiwan should help illuminate hidden diversity, perhaps revealing a more robust phylogenetic structure.

Interestingly, our re-examination of *Toyotamaphimeia taiwanicus* n. comb. resulted in the discovery of size disparity between individuals present among the type specimens. NSMT-P-9122 represents a large adult reaching ∼7 m long, similar in size to the holotype of *Toyotamaphimeia machikanensis*, whereas NSMT-P-9123 is a younger juvenile, likely 2–3 m long. Prior to our present study, two crocodylian lineages were reported from the same locality and horizon (Chiting Formation of Tainan): *Tomistoma taiwanicus* Shikama, 1972, and *Toyotamaphimeia* sp. (Ito et al., 2018). After examining all relevant specimens (NSMT and Waseda materials), we conclude that they all belong to *Toyotamaphimeia taiwanicus* n. comb. However, given that the oldest crocodylian (the tomistomine *Penghusuchus pani*) from Taiwan can be traced back to the Middle Miocene, a much higher crocodylian or tomistomine diversity may be anticipated for the Pleistocene of Tainan, because coexistence and niche partitioning among crocodylians are fairly common (Young et al., 2011; Salas-Gismondi et al., 2015; Staniewicz et al., 2018).

Causes for the complete extinction of crocodylians in Taiwan have never been discussed or explored. Our discussion here, based on the updated crocodylian taxonomy from Taiwan, lays a foundation for future endeavors. Environmental changes have been linked to the crocodylian extinction (e.g., Cosette et al., 2020; Hocknull et al., 2020; Solórzano et al., 2020), but the paleoecological aspects associated with crocodylian fossils in Taiwan remain virtually unknown, and this again highlights the long-ignored vertebrate paleontology of the country. For example, here we revised the taxonomy of historic crocodylian specimens—the first and the second fossil crocodylians in the history of Taiwan—which are properly curated in the NSMT and Waseda collections in Japan, making our study possible. On the contrary, some historic specimens from Taiwan should have been curated for future research, but the original fossils are lost, likely owing to the indifference to paleontological research (e.g., Liaw and Tsai, 2022; Tsai and Tseng, 2022). Our current efforts into the development of vertebrate paleontology in Taiwan aims to better understand the Pleistocene paleo-ecosystems and to further elucidate the driving factors of extinctions in the island. For instance, the coexistence of the huge *Toyotamaphimeia* and the carnivorous, machairodontine felid *Homotherium* (Tsai and Tseng, 2022) in Tainan, should draw far-ranging attention and lead to more in-depth paleontological research in Taiwan.

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Author contributions

CHT conceived and designed this study; YYC and CHT collected the data, and YYC analyzed the dataset; both authors wrote and discussed the content of the manuscript; both authors approved the final submission for publication.

Declaration of competing interests

The authors declare no competing interests.

Data availability statement

Data available from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.7340097 and http://doi.org/10.5281/zenodo.7937137.

References

Aoki, R., 1983, A new generic allocation of *Tomistoma machikanense*, a fossil crocodilian from the Pleistocene of Japan: Copeia, v. 1983, p. 89–95.

Benton, M.J., and Clark, J.M., 1988, Archosaur phylogeny and the relationships of the Crocodylia, *in* Benton, M.J., ed., The Phylogeny and Classification of the Tetrapods Volume 1, Amphibians, Birds, and Reptiles: Oxford, UK, Clarendon Press, p. 295–338.

Brochu, C.A., 1999, Phylogenetics, taxonomy, and historical biogeography of Alligatoroidea: Journal of Vertebrate Paleontology, v. 19, p. 9–100.

Brochu, C.A., 2003, Phylogenetic approaches toward crocodylian history: Annual Review of Earth and Planetary Sciences, v. 31, p. 357–397.

Capellini, G., 1890, Sul coccodrilliano garialoide (*Tomistoma calaritanus*) scoperto nella collina di Cagliari nel 1868: Rendiconti della Reale Accademia dei Lincei, ser. 4, v. 6, p. 149–151.

Chang, C.-H., Takai, M., and Ogino, S., 2012, First discovery of colobine fossils from the Early to Middle Pleistocene of southern Taiwan: Journal of Human Evolution, v. 63, p. 439–451.

Cossette, A.P., Adams, A.J., Drumheller, S.K., Nestler, J.H., Benefit, B.R., McCrossin, M.L., Manthi, F.K., Juma, R.N., and Brochu, C.A., 2020, A new crocodylid from the Middle Miocene of Kenya and the timing of crocodylian faunal change in the late Cenozoic of Africa: Journal of Paleontology, v. 94, p. 1165–1179.

de Celis, A., Narváez, I., and Ortega, F., 2020, Spatiotemporal palaeodiversity patterns of modern crocodiles (Crocodyliformes: Eusuchia): Zoological Journal of the Linnean Society, v. 189, p. 635–656.

Fauvel, A.A., 1879, Alligators in China: Journal of the North China Branch of the Royal Asiatic Society, v. 13, p. 1–36.

Fergusson, R.A., 2010, Nile crocodile *Crocodylus niloticus*, *in* Manolis, S.C., and Stevenson, C., eds., Crocodiles. Status Survey and Conservation Action Plan, 3rd ed.: Darwin, Australia, Crocodile Specialist Group, p. 84–89, http://www.iucncsg.org/365_docs/attachments/protarea/15_C-cf25967f.pdf.

Gmelin, J.F., 1789, Regnum animal, *in* Caroli a Linné Systema naturae, 13th ed., Tom 1, Pars 3: Lipsiae, G.E. Beer, v. 1, p. 1033–1516.

Grigg, G.C., Seebacherd, F., Beard, L.A., and Morris, D., 1998, Thermal relations of large crocodiles, *Crocodylus porosus*, free ranging in a naturalistic situation: Proceedings of the Royal Society of London, Series B: Biological Sciences, v. 265, p. 1793–1799.

Goloboff, P.A., and Catalano, S.A., 2016, TNT version 1.5, including a full implementation of phylogenetic morphometrics: Cladistics, v. 32, p. 221–238.

Goloboff, P.A., Farris, J.S., and Nixon, K.C., 2008, TNT, a free program for phylogenetic analysis: Cladistics, v. 24, p. 774–786.

Hayasaka, I., 1932, [On a new occurrence of fossil elephant tooth in Taiwan]: Taiwan Tigaku Kizi, v. 3, p. 78. [in Japanese, with English abstract]

Hocknull, S.A., Lewis, R., Arnold, L.J., Pietsch, T., Joannes-Boyau, R., et al., 2020, Extinction of eastern Sahul megafauna coincides with sustained environmental deterioration: Nature Communications, v. 11, n. 2250, https://doi.org/10.1038/s41467-020-15785-w.

Hulke, J.W., 1871, Note on some reptilian fossils from Gozo: Quarterly Journal of the Geological Society of London, v. 27, p. 29–33.

Iijima, M., 2017, Assessment of trophic ecomorphology in non-alligatoroid crocodylians and its adaptive and taxonomic implications: Journal of Anatomy, v. 231, p. 192–211.

Iijima, M., and Kobayashi, Y., 2019, Mosaic nature in the skeleton of East Asian crocodylians fills the morphological gap between "Tomistominae" and Gavialinae: Cladistics, v. 35, p. 623–632.

Iijima, M., and Kubo, T., 2020, Vertebrae-based body length estimation in crocodylians and its implication for sexual maturity and the maximum sizes: Integrative Organismal Biology, v. 2, n. obaa042, https://doi.org/10.1093/iob/obaa042.

Iijima, M., Takahashi, K., and Kobayashi, Y., 2016, The oldest record of *Alligator sinensis* from the Late Pliocene of western Japan, and its biogeographic implication: Journal of Asian Earth Sciences, v. 124, p. 94–101.

Iijima, M., Momohara, A., Kobayashi, Y., Hayashi, S., Ikeda, T., Taruno, H., Watanabe, K., Tanimoto, M., and Furui, S., 2018, *Toyotamaphimeia* cf. *machikanensis* (Crocodylia, Tomistominae) from the Middle Pleistocene of Osaka, Japan, and crocodylian survivorship through the Pliocene–Pleistocene climatic oscillations: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 496, p. 346–360.

Iijima, M., Qiao, Y., Lin, W., Peng, Y., Yoneda, M., and Liu, J., 2022, An intermediate crocodylian linking two extant gharials from the Bronze Age of China and its human-induced extinction: Proceedings of the Royal Society B, v. 289, n. 20220085, https://doi.org/10.1098/rspb.2022.0085.

Ito, A., Aoki, R., Hirayama, R., Yoshida, M., Kon, H., and Endo, H., 2018, The rediscovery and taxonomical reexamination of the longirostrine crocodylian from the Pleistocene of Taiwan: Paleontological Research, v. 22, p. 150–155.

Jouve, S., Bouya, B., Amaghzaz, M., and Meslouh, S., 2015, *Maroccosuchus zennaroi* (Crocodylia: Tomistominae) from the Eocene of Morocco: phylogenetic and palaeobiogeographical implications of the basalmost tomistomine: Journal of Systematic Palaeontology, v. 13, p. 421–445.

Kälin, J.A., 1955, Zur stammesgeschichte der Crocodilia: Revue Suisse de Zoologie, v. 62, p. 347–356.

Kobatake, N., Chiji, M., Ikebe, N., Ishida, S., Kamei, T., Nakaseko, K., and Matsumoto, E., 1965, [Discovery of crocodile fossil from the Osaka Group]: The Quaternary Research [Daiyonki Kenkyu], v. 4, p. 49–58. [in Japanese]

Kobayashi, Y., Tomida, Y., Kamei, T., and Eguchi, T., 2006, Anatomy of a Japanese tomistomine crocodylian, *Toyotamaphimeia machikanensis* (Kamei et Matsumoto, 1965), from the Middle Pleistocene of Osaka Prefecture: the reassessment of its phylogenetic status within Crocodylia: National Science Museum Monographs, v. 5, p. 1–121.

Laurenti, J.N., 1768, Specimen Medicum, Exhibens Synopsin Reptilium Emendatum cum Experimentatis Circa Venena et Antiodota Reptilium Austriacorum: Vienna, J. T. de Trattnern, 214 p.

Liaw, Y.-L., and Tsai, C.-H., 2022, Taxonomic revision of *Chinemys pani* (Testudines: Geoemydidae) from the Pleistocene of Taiwan and its implications of conservation paleobiology: The Anatomical Record, v. 306, p. 1501–1507, https://doi.org/10.1002/ar.25082.

Lin, C.H., Chien, C.W., Lee, S.W., and Chang, C.W., 2019, Fish fossils of Taiwan: a review and prospection: Historical Biology, v. 33, p. 1362–1372.

Mannion, P.D., Benson, R.B., Carrano, M.T., Tennant, J.P., Judd, J., and Butler, R.J., 2015, Climate constrains the evolutionary history and biodiversity of crocodylians: Nature Communications, v. 6, n. 8438, https://doi.org/10.1038/ncomms9438.

Markwick, P.J., 1998a, Crocodilian diversity in space and time: the role of climate in paleoecology and its implication for understanding K/T extinctions: Paleobiology, v. 24, p. 470–497.

Markwick, P.J., 1998b, Fossil crocodilians as indicators of Late Cretaceous and Cenozoic climates: implications for using palaeontological data in reconstructing palaeoclimate: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 137, p. 205–271.

Martin, J.E., 2019, The taxonomic content of the genus *Gavialis* from the Siwalik Hills of India and Pakistan: Papers in Palaeontology, v. 5, p. 483–497.

Müller, L., 1838, Waarnemingen over de Indische krokodillen en Beschrijving van eene nieuwe sort: Tydschrift voor Natuurlijke Geschiedenis en Physiologie, v. 5, p. 61–87.

Nanda, A.C., Schleich, H.H., and Kotlia, B.S., 2016, New fossil reptile records from the Siwalik of North India: Open Journal of Geology, v. 6, p. 673–691, https://doi.org/10.4236/ojg.2016.68052.

Nicholl, C.S.C., Rio, J.P., Mannion, P.D., and Delfino M., 2020, A re-examination of the anatomy and systematics of the tomistomine crocodylians from the Miocene of Italy and Malta: Journal of Systematic Palaeontology, v. 18, p. 1853–1889.

Nicolaï, M.P., and Matzke, N.J., 2019, Trait-based range expansion aided in the global radiation of Crocodylidae: Global Ecology and Biogeography, v. 28, p. 1244–1258.

Otsuka, H., 1984, Stratigraphic position of the Chochen vertebrate fauna of the T'ouk'oushan Group in the environs of the Chochen District, southwest Taiwan, with special reference to its geologic age: Journal of Taiwan Museum, v. 37, p. 37–55.

Otsuka, H., and Lin, C.C., 1984, Fossil rhinoceros from the T'ouk'oushan Group in Taiwan: Journal of Taiwan Museum, v. 37, p. 1–35.

Otsuka, H., and Shikama, T., 1978, Fossil Cervidae from the Toukoushan Group in Taiwan: Reports of the Faculty of Science, Kagoshima University (Earth Sciences and Biology), v. 11, p. 27–59.

Owen, R., 1849, A History of British Fossil Reptiles, vol. 1: London, Cassell, 657 p.

Rio, J.P., and Mannion, P.D., 2021, Phylogenetic analysis of a new morphological dataset elucidates the evolutionary history of Crocodylia and resolves the long-standing gharial problem: PeerJ, v. 9, n. e12094, https://doi.org/10.7717/peerj.12094.

Ristevski, J., Price, G.J., Weisbecker, V., and Salisbury, S.W., 2021, First record of a tomistomine crocodylian from Australia: Scientific Reports, v. 11, n. 12158, https://doi.org/10.1038/s41598-021-91717-y.

Salas-Gismondi, R., Flynn, J.J., Baby, P., Tejada-Lara, J.V., Wesselingh, F.P., and Antoine, P.O., 2015, A Miocene hyperdiverse crocodylian community reveals peculiar trophic dynamics in proto-Amazonian mega-wetlands: Proceedings of the Royal Society B: Biological Sciences, v. 282, n. 20142490, https://doi.org/10.1098/rspb.2014.2490.

Schneider, J.G., 1801, Historiae Amphibiorum Naturalis et Literariae. Fasciculus Secundus Continens Crocodilos, Scincos, Chamaesauras, Boas. Pseudoboas, Elapes, Angues. Amphisbaenas et Caecilias: Jena, Frommanni, 374 p.

Seebacher, F., Grigg, G.C., Beard, L.A., 1999, Crocodiles as dinosaurs: behavioural thermoregulation in very large ectotherms leads to high and stable body temperatures: Journal of Experimental Biology, v. 202, p. 77–86.

Shan, H.-Y., Wu, X.-C., Cheng, Y.-N., and Sato, T., 2009, A new tomistomine (Crocodylia) from the Miocene of Taiwan: Canadian Journal of Earth Sciences, v. 46, p. 529–555.

Shikama, T., 1937, Fossil cervifauna of Syatin near Tainan, southwestern Taiwan (Formosa): Science Reports of the Tohoku Imperial University: Geology, v. 19, p. 75–85.

Shikama, T., 1972, Fossil Crocodilia from Tsochin, southwestern Taiwan: Science Report of Yokohama National University: Biological and Geological Sciences, v. 19, p. 125–131.

Solórzano, A., Núñez-Flores, M., Inostroza-Michael, O., and Hernández, C.E., 2020, Biotic and abiotic factors driving the diversification dynamics of Crocodylia: Palaeontology, v. 63, p. 415–429.

Staniewicz, A., Behler, N., Dharmasyah, S., and Jones, G., 2018, Niche partitioning between juvenile sympatric crocodilians in Mesangat Lake, East Kalimantan, Indonesia: Raffles Bulletin of Zoology, v. 66, p. 528–537.

Tokunaga, S., 1936, [Discovery of fossil crocodile in Japan]: Journal of the Geological Society of Japan, v. 43, p. 432. [in Japanese]

Tsai, C.-H., and Mayr, G., 2021, A phasianid bird from the Pleistocene of Tainan: the very first avian fossil from Taiwan: Journal of Ornithology, v. 162, p. 919–923.

Tsai, C.-H., and Tseng, Z.J., 2022, Eurasian wanderer: an island sabre-toothed cat (Felidae, Machairodontinae) in the Far East: Papers in Palaeontology, v. 8, n. e1469, https://doi.org/10.1002/spp2.1469.

Tsai, C.-H., Fordyce, R.E., Chang, C.-H., and Lin, L.-K., 2013, A review and status of fossil cetacean research in Taiwan: Taiwan Journal of Biodiversity, v. 15, p. 113–124.

Webb, G.J., Manolis, S.C., and Brien, M.L., 2010, Saltwater crocodile *Crocodylus porosus*, *in* Manolis, S.C., and Stevenson, C., eds., Crocodiles. Status Survey and Conservation Action Plan, 3rd ed.: Darwin, Australia, Crocodile Specialist Group, p. 99–113, https://www.iucncsg.org/365_docs/attachments/protarea/18%20–8088e67a.pdf.

Young, M.T., Bell, M.A., de Andrade, M.B., and Brusatte, S.L., 2011, Body size estimation and evolution in metriorhynchid crocodylomorphs: implications for species diversification and niche partitioning: Zoological Journal of the Linnean Society, v. 163, p. 1199–1216.