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Advanced mosasaurs from the Upper Cretaceous Nakaminato Group in Japan

Taichi Kato[1,2] | **Yasuhisa Nakajima**[3] | **Kohei Shiseki**[4] | **Hisao Ando**[5]

[1]Geological Laboratory, Ibaraki Nature Museum, Bando, Ibaraki, Japan
[2]Graduate School of Science and Engineering, Ibaraki University, Mito, Ibaraki, Japan
[3]Department of Natural Sciences, Faculty of Science and Engineering, Tokyo City University, Setagaya, Tokyo, Japan
[4]Faculty of Science, Tohoku University, Sendai, Miyagi, Japan
[5]Department of Earth Science, Graduate School of Science and Engineering, Ibaraki University, Mito, Ibaraki, Japan

Correspondence
Taichi Kato, Geological Laboratory, Ibaraki Nature Museum, 700 Osaki, Bando, Ibaraki 306-0622, Japan.
Email: taichi.kato.inm@gmail.com

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Abstract

Plotosaurus is a highly aquatically adapted mosasaur, which is supposed to inhabit the deep ocean basin. The geographic occurrence of this genus has been limited only to the west coast of North America. In this study, two *Plotosaurus*-type mosasaur caudal vertebrae derived from the Upper Cretaceous Nakaminato Group in Ibaraki Prefecture, Japan, are described with discussion on the paleobiogeographic significance of the Late Cretaceous mosasaur fauna in the Northwestern Pacific region. The two specimens are an intermediate caudal vertebra found in a beach cobble, which presumably originated from the Hiraiso Formation (upper Campanian), and a terminal caudal vertebra found in situ in the lower Isoai Formation (lower Maastrichtian). Because their relative centrum lengths (ratio of centrum length/centrum height, ~0.7) are very close to that of *Plotosaurus*, the specimens are referred to cf. *Plotosaurus* sp. The two specimens provide the first evidence that highly specialized *Plotosaurus*-type mosasaurs inhabited the Northwestern Pacific Ocean, suggesting that such forms had a wider distribution than previously recognized and might have existed since the late Campanian in the Northwestern Pacific Ocean.

KEYWORDS
Campanian–Maastrichtian, Japan, Late Cretaceous, Mosasauridae, Nakaminato Group, *Plotosaurus*

1 | INTRODUCTION

Mosasaurs (Squamata: Mosasauroidea) are extinct marine reptiles that were distributed globally during the Late Cretaceous. They swam by oscillating their bodies or tails, rather than by rowing their flippers or "flying" (Massare, 1988). Therefore, their vertebral column was the primary biomechanical structure for underwater propulsion, whereas the phalange-equipped flippers acted mainly as stabilizers and steering devices (Russell, 1967). Recent examinations of mosasaur materials with exceptionally well-preserved soft tissues revealed that the tails of some derivative mosasaurs, including *Platecarpus* and *Prognathodon*, developed bi-lobed, asymmetric, reversed-heterocercal fins, in which the caudal vertebrae extended into the main ventral lobe (Konishi et al., 2012; Lindgren et al., 2013). It has also been suggested that some derived mosasaurs swam by oscillating their tails like carcharhinid sharks, rather than by oscillating the torso like anguilliforms (Lindgren et al., 2013). Mosasaurinae had a *Varanus*-like body outline plesiomorphically and developed a spindle-shaped body and the hypocercal tail fin with a high aspect ratio through their 28 million-year-long evolutionary history (Lindgren et al., 2011; Madzia & Cau, 2020).

Plotosaurus (Figure 1a) is one of the most-derived "fishy" mosasaurs and developed a fully streamlined body and a semi-lunate tail fluke (Lindgren et al., 2007, 2011). One of the most obvious characteristics is the development of discrete structural and functional segments within the caudal skeleton by increasing the number of pygal vertebrae at the expense of intermediate caudals, enlarging the interarticular surfaces, and shortening the vertebral centra (Figure 2; Lindgren et al., 2011). The type species *Plotosaurus bennisoni* (Camp, 1942) was described under the name *Kolposaurus*, based on an ichthyosaur-like mosasaur skull and anterior body skeleton (UCMP 32778). Subsequently, this nominal taxon was renamed by Camp (1951) because it is preoccupied by a Triassic nothosaur *Kolposaurus* Skuphos, 1893. The second species, *P. tuckeri* (Camp, 1942) was described as the larger second species based on a tail (UCMP 33913), although this was later synonymized with *P. bennisoni* by

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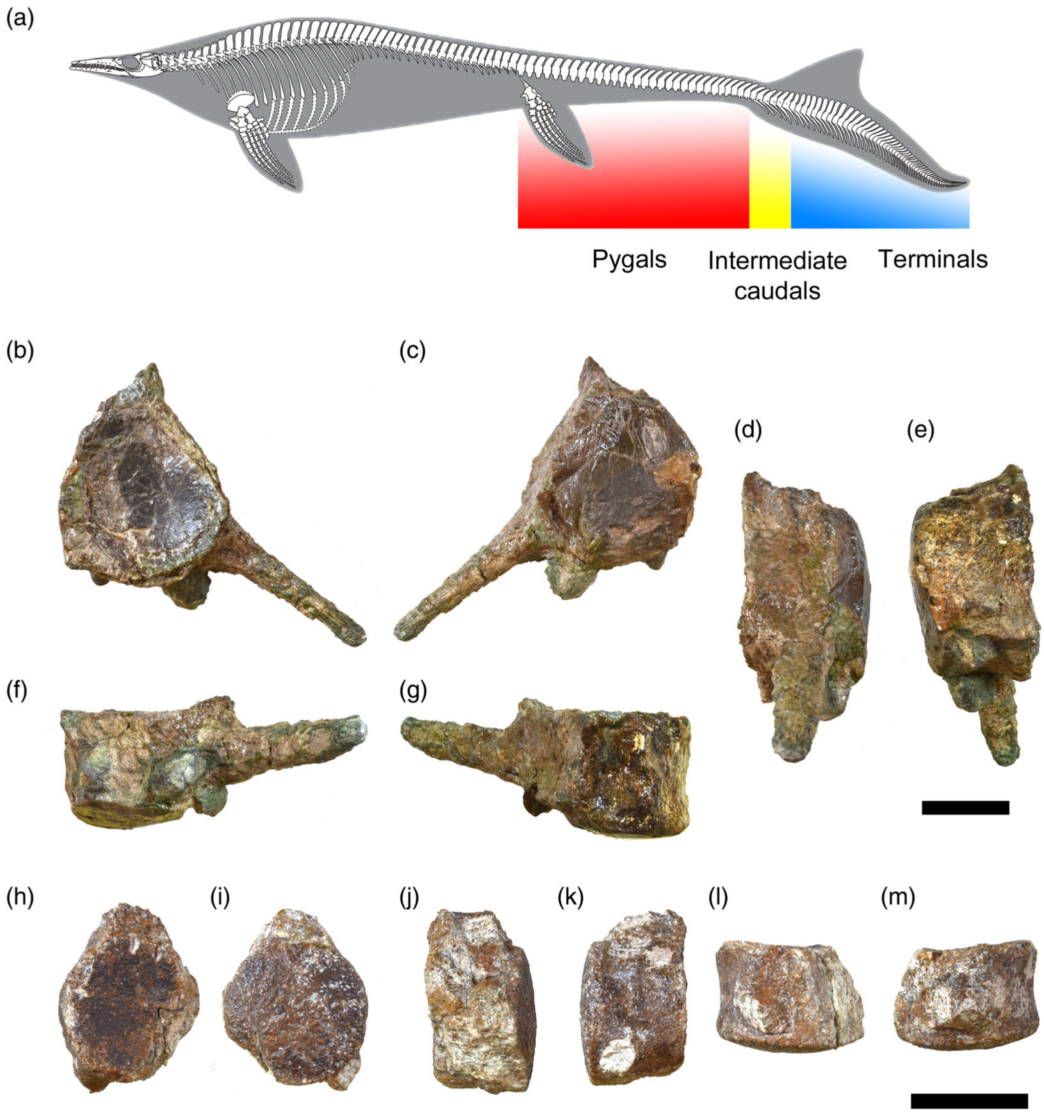

FIGURE 1 Material in this study. (a) skeletal reconstruction of *Plotosaurus* Camp, 1951. *Source*: Reproduced from Lindgren et al. (2007) with permission of John Wiley & Sons. (b–g) cf. *Plotosaurus* sp. INM-4-17907, an intermediate caudal vertebra from the Nakaminato Group in anterior (b), posterior (c), left lateral (d), right lateral (e), ventral (e), and dorsal (g) views. (h–m) cf. *Plotosaurus* sp. INM-4-15694, a terminal caudal vertebra from the Nakaminato Group in anterior (h), posterior (i), left lateral (j), right lateral (k), ventral (l), and dorsal (m) views. Scale bars: 20 mm

Lindgren et al. (2008). Hitherto, the fossil records of *Plotosaurus* are limited, ranging from the upper lower to the lower upper Maastrichtian in California (Caldwell & Konishi, 2007; Lindgren et al., 2007, 2008). The limited geographic occurrence of *Plotosaurus* suggests that this mosasaur preferred living in deep ocean basins, which is consistent with its highly aquatically adapted body plan (Lindgren et al., 2011).

In 2020, a mosasaur caudal vertebra, INM-4-17907 (Figure 1b–g), was found in a mudstone beach cobble that probably had originated from the upper Campanian Hiraiso Formation, Nakaminato Group, exposed along the Pacific coast in Ibaraki Prefecture, Japan (Figure 3). Although this specimen is not well preserved, it has a unique characteristic of *Plotosaurus*, which was previously unknown in the Northwestern Pacific region. Furthermore, when we re-examined another mosasaur vertebra, INM-4-15694 (Figure 1h–m) found previously in the lower Maastrichtian Isoai Formation, Nakaminato Group (Kato et al., 2017), we confirmed that it is also similar to caudal vertebrae of *Plotosaurus*. In this paper, we report the morphological characteristics of these mosasaur vertebrae and summarize the distribution and stratigraphic ranges of mosasaurs from the Cretaceous of Japan. Finally, we discuss the paleobiogeography of the hypocercal mosasaurs and their evolution in the Northwestern Pacific Ocean.

1.1 | Institutional abbreviations

CIT, Natural History Museum of Los Angeles County, Los Angeles, California, USA (former California Institute of Technology collection); *DMNH*, Museum of Nature and Science, Dallas, Texas, USA; *INM*, Ibaraki Nature Museum, Ibaraki, Japan; *NSM*, National Museum of Nature and Science, Tokyo, Japan; *Q*, Museo Geológico Profesor Lajós

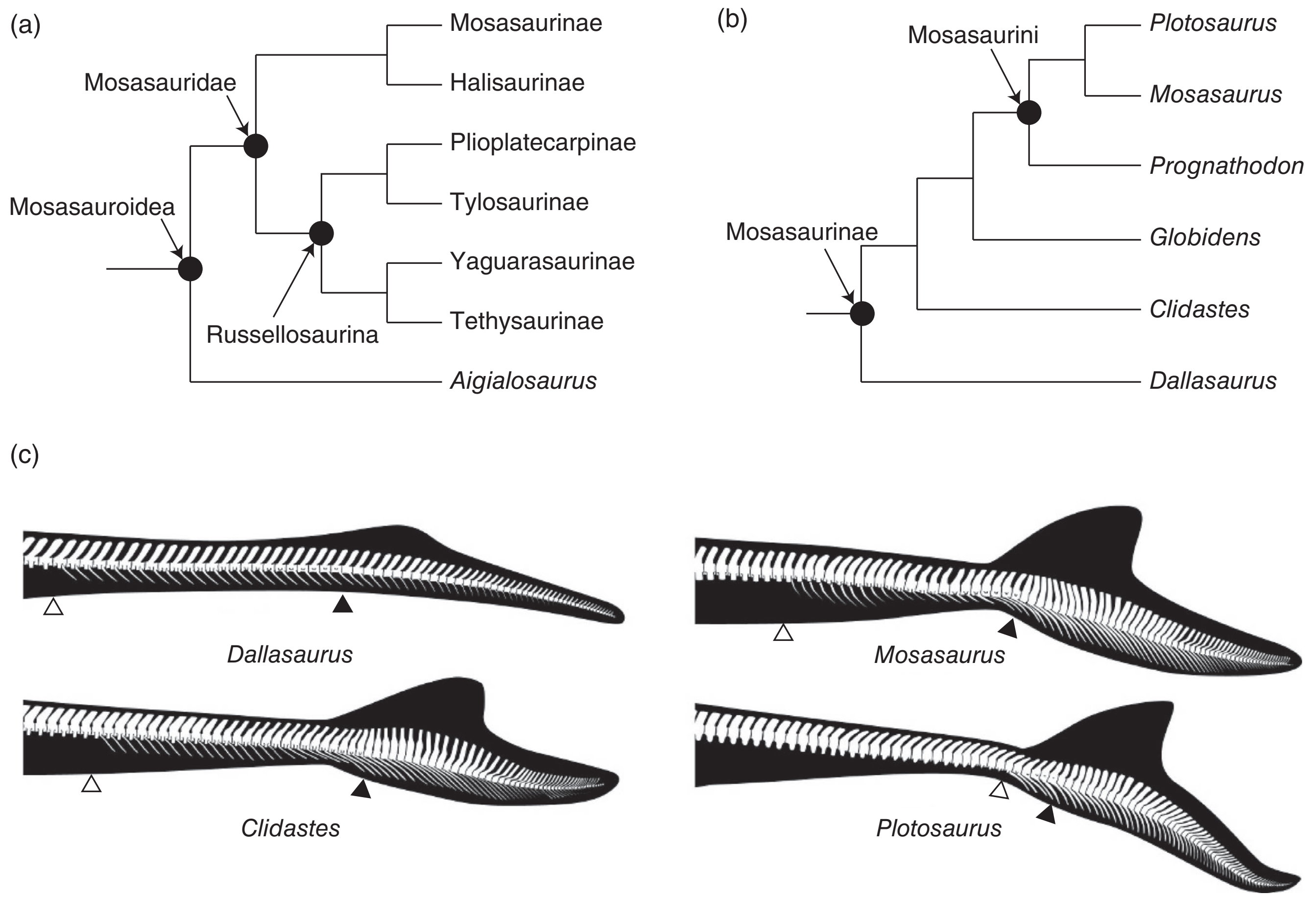

FIGURE 2 Cladograms and tail reconstructions of mosasaurs. (a) Cladogram of Mosasauroidea. (b) Cladogram of Mosasaurinae. These Cladograms are modified from Madzia and Cau (2017, 2020). (c) Tail reconstructions with hypothetical soft-tissue outlines of Mosasaurinae. *Source*: Reproduced from Lindgren et al. (2011) with permission of Cambridge University Press. White triangles indicate the boundaries of the pygal/intermediate caudals. Black triangles indicate the boundaries of the intermediate/terminal caudals

Biró, Universidad de Concepción, Concepción, Chile; *UCMP*, Museum of Paleontology, University of California, Berkeley, California, USA.

2 | MATERIAL AND METHODS

2.1 | Material

INM-4-17907 and INM-4-15694 are curated and housed at the Ibaraki Nature Museum, Bando, Ibaraki, Japan. The mudstone beach gravel containing INM-4-17907 was collected (by KS) ex situ at a wave-cut bench where the unit Hl3 of the Hiraiso Formation outcropped (Figure 3d,e) in 2020. INM-4-15694 was collected in situ from the unit Is3 of the Isoai Formation on a survey by Ibaraki University (conducted by HA) in 2008 (Figure 3c,e).

2.2 | Methods

INM-4-17907 was scanned with an XT H225ST micro-computed tomography (micro-CT) device (Nikon Solutions Co., Ltd., 1-6-3 Nishiooi, Shinagawa, Tokyo 140-0015, Japan) at the Second Metrology Office of Nikon Solutions (276-1 Naganuma, Sakae, Yokohama, Kanagawa 244-0841, Japan). INM-4-15694 was scanned with an inspeXio SMX-225CT FPD HR micro-CT device (Shimadzu Corporation, 1 Nishinokyo Kuwabara, Nakagyo, Kyoto 604-8511, Japan) at the National Museum of Nature and Science (4-1-1 Amakubo, Tsukuba, Ibaraki 305-0005, Japan). The slice image stacks generated were loaded into the software myVGL (Volume Graphics GmbH, Speyerer Straße 4-6, 69 115 Heidelberg, Germany) to visualize and examine the two-dimensional (2D) and three-dimensional (3D) images of the specimens. The color balance and contrast adjustment and labeling of the resulting 2D images were performed in Adobe Photoshop CS6 (Adobe Inc., 345 Park Avenue, San Jose, CA 95110-2704, USA).

Vertebral measurements were made using a digital caliper, CD-15CPX (Mitutoyo Corporation, 1-20-1, Sakado, Takatsu, Kawasaki, Kanagawa 213-8533, Japan). The vertebral size was measured following the scheme of Lindgren et al. (2011). The centrum height (CH) was measured on the condyle. All other measurements were compared against this standard. The centrum width (CW) was measured perpendicular to CH, whereas the centrum length (CL) was measured at right angles to both CH and CW.

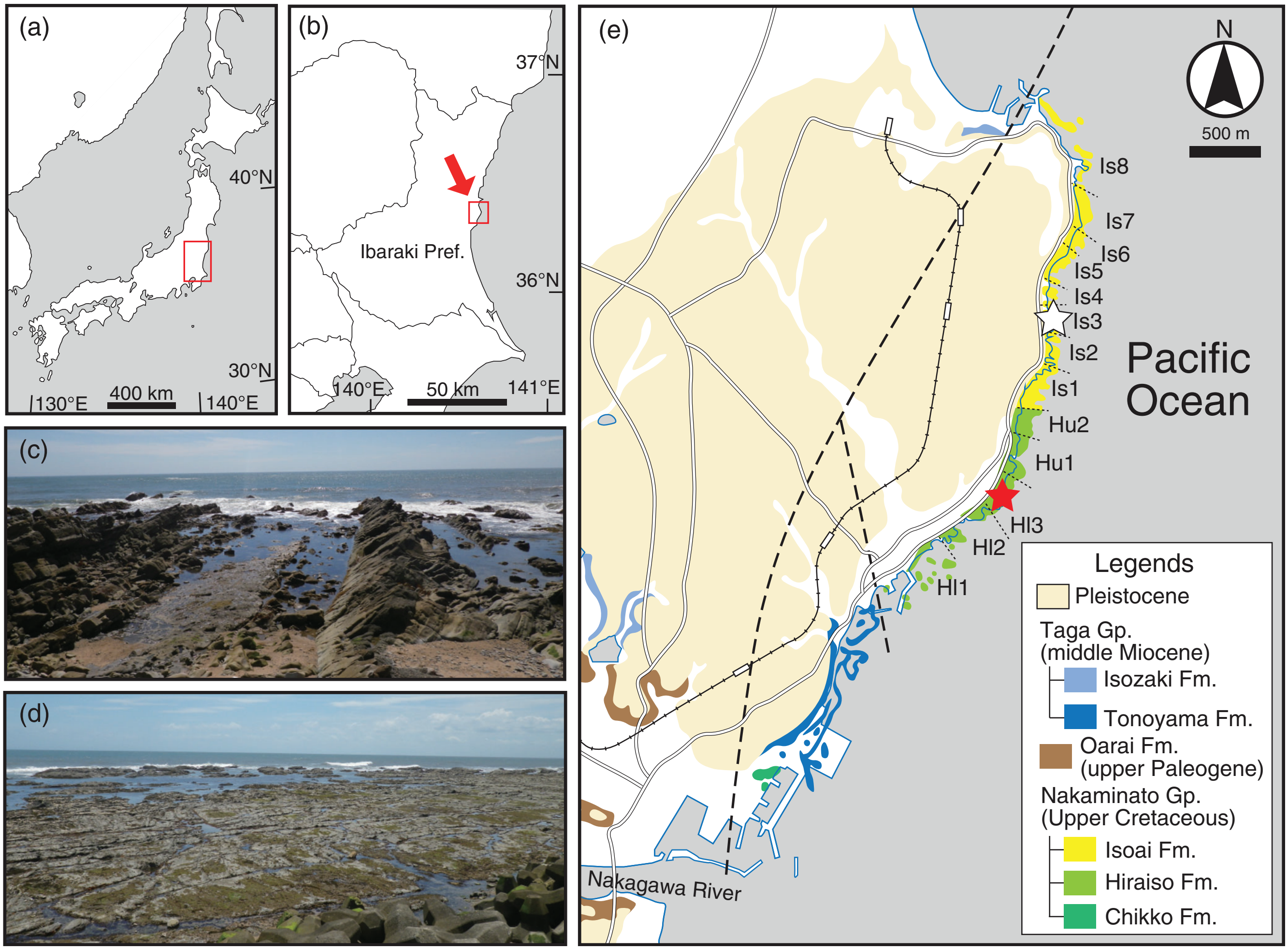

FIGURE 3 Maps of specimen localities. (a) Map of Japan. Square includes the Ibaraki Prefecture. (b) Map of Ibaraki Prefecture. Arrow pointing to the Pacific coast of Hitachinaka City. (c) Outcrop of the unit Is3 of the Isoai Formation. (d) Outcrop of the unit Hl3 of the Hiraiso Formation. (e) Pacific coast geological map around Hitachinaka City, Ibaraki Prefecture, modified from Masukawa and Ando (2018). Red and white stars indicate the localities of INM-4-17907 and INM-4-15694, respectively

2.3 | Geological setting

The Upper Cretaceous Nakaminato Group is distributed along a ~ 3.5 km north–south stretch of wave-cut benches facing the Pacific coast at Hitachinaka, Ibaraki, Japan (Figure 3; e.g., Ando, 2006; Saito, 1958, 1959, 1961, 1962). The Nakaminato Group is subdivided into the offshore mudstone of the Hiraiso Formation and the overlying sandstone and sandy turbidite of the Isoai Formation (Figure 4; Tanaka, 1970; Ando, 2006; Masukawa & Ando, 2018). The Hiraiso Formation is subdivided into five lithostratigraphic units: Hl1–Hl3 and Hu1–Hu2; the Isoai Formation is subdivided into eight units: Is1–Is8 (Masukawa & Ando, 2018; Tanaka, 1970). The Hiraiso and Isoai Formations were deposited under sedimentary environments as basin plain (Hl1) to lower submarine fan facies (Hl2–Hl3) and mid to upper submarine fan facies (Hu1–Is8) (Katsura & Masuda, 1978; Masuda & Katsura, 1978).

Heteromorph ammonoids, represented by nostoceratids and diplomoceratids, are numerically dominant among the ammonoid assemblages from the lower–middle parts of the Hiraiso Formation and from a few horizons in the Isoai Formation (Masukawa & Ando, 2018). Although several vertebrate remains, such as a mosasaur vertebra, costals and a humerus of trionychid turtles, and shark teeth, have been found in the Isoai Formation (Figure 4; Saito, 1962; Kato et al., 2017, 2019; Kato, Miyata, et al., 2020; Kato, Sonoda, et al., 2020), no vertebrate remains had been reported from the Hiraiso Formation previously.

Masukawa and Ando (2018) summarized the stratigraphic ranges of the molluscan fauna of the Nakaminato Group. The late Campanian index ammonoid *Didymoceras awajiense*, together with *Diplomoceras* sp., a few planispiral ammonoids, and several specimens of *Inoceramus (Endocostea) shikotanensis* have been found in the Hiraiso Formation, and the middle–late early Maastrichtian index species *"Inoceramus" kusiroensis* and *Baculites* spp. have been found in the Isoai Formation. Detrital zircons from a sandstone layer in the middle of unit Is8 yielded a radiometric U–Pb age of 71.1 ± 1.2 Ma (Nagata & Otoh, pers. comm., 2016, cited in Masukawa & Ando, 2018), also supporting an early Maastrichtian age for the upper Isoai Formation. The Campanian–Maastrichtian boundary is presumed to be between the uppermost Hiraiso (Hu2) and lower Isoai (Is2) Formations (Masukawa & Ando, 2018).

3 | RESULTS

SYSTEMATIC PALEONTOLOGY

Squamata Oppel, 1811.
Mosasauroidea Gervais, 1853.
Mosasauridae Gervais, 1853.
Mosasaurinae Gervais, 1853.
Mosasaurini Gervais, 1853.
Plotosaurus Camp, 1951.
cf. *Plotosaurus* sp.
Figure 1b–m

3.1 | Referred specimens

INM-4-17907 is an isolated intermediate caudal vertebra. Most parts of the neural arch and the right transverse process have been lost by weathering and abrasion. The centrum, the left transverse process, and the base of the haemal arch are partially preserved (Figure 5a–b).

INM-4-15694 is an isolated terminal caudal vertebra. Most parts of the neural and haemal arches and the left lateral surface of the centrum have been lost by weathering and abrasion. The centrum, the base of the neural arch, and the base of the haemal arch (or the haemal pedicle) are partially preserved (Figure 5c–d).

3.2 | Locality and horizon

INM-4-17907 was extracted from a dark-gray mudstone beach cobble (diameter ~ 15 cm), collected at a wave-cut bench where the unit Hl3 of the Hiraiso Formation outcrops. The dark-gray mudstone is very common in the unit Hl3 and other units of the Hiraiso Formation but rare in the Isoai Formation. Therefore, the original horizon is probably supposed to be the Hiraiso Formation. However, the possibility cannot be entirely excluded that it originated from the Isoai Formation, and thus the geological age of this specimen is supposed to be late Campanian or early Maastrichtian.

INM-4-15694 was found in situ from the lower part of the unit Is3 of the Isoai Formation. This horizon is considered to be a lower Maastrichtian deposit (Masukawa & Ando, 2018).

3.3 | Description

INM-4-17907 is identified as an intermediate caudal vertebra, located posterior to the pygal (sacral plus anterior caudal) vertebrae and anterior to the terminal caudal vertebrae, on the presence of transverse processes and a haemal arch. INM-4-15694 is identified as a terminal caudal vertebra, located in the most posterior portion of the caudal vertebrae. Kato et al. (2017) described this specimen as a pygal vertebra, but the anatomical position is revised in this study based on the presence of a haemal arch and the lack of transverse processes revealed by CT-image (Figure 5c).

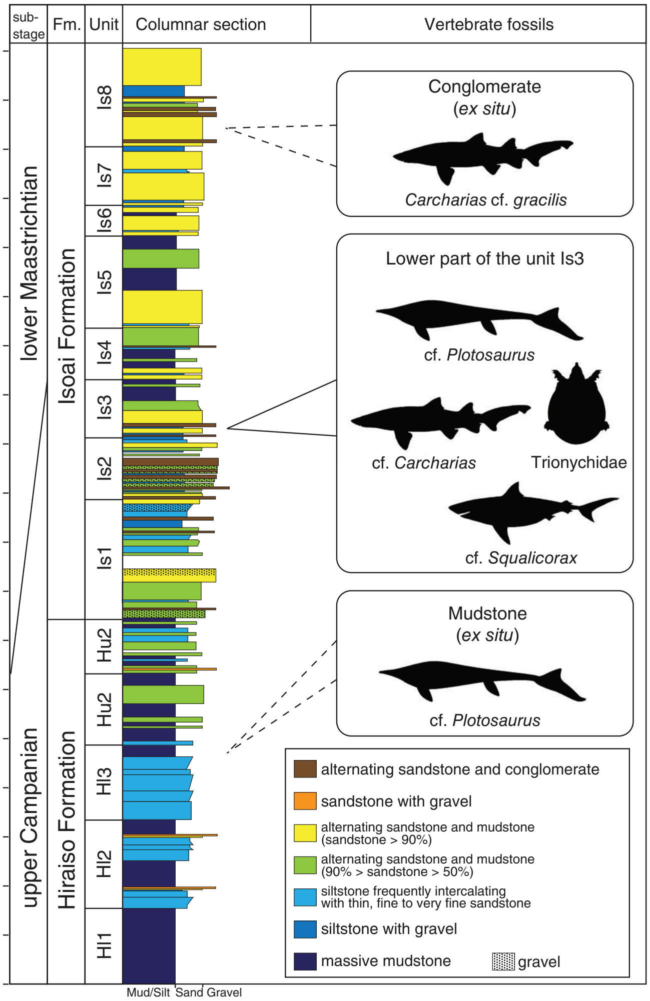

FIGURE 4 Stratigraphic column and vertebrate fossil horizons of the Nakaminato Group. *Source*: modified from Masukawa & Ando, 2018; Kato et al., 2017, 2019; Kato, Miyata, et al., 2020; Kato, Sonoda, et al., 2020. Silhouettes are drawn based on illustrations of *Apalone* (Nakajima et al., 2017), *Squalicorax* (Shimada & Cicimurri, 2006), Odontaspididae (Welton & Farish, 1993), and *Plotosaurus* (Lindgren et al., 2007)

The centra are procoelous. In the mid-sagittal virtual section, the centrum appears wedge-shaped in INM-4-17907 (Figure 5b) and rectangular in INM-4-15694 (Figure 5d). In the coronal section, it is subtriangular in INM-4-17907 (Figure 5a) and subhexagonal in INM-4-15694 (Figure 5c). The condyles and cotyles are subcircular (or slightly subtriangular in INM-4-17907). The lateral surfaces of the centra are smooth. In INM-4-17907, the centrum is 25 mm long and slightly taller (height, 37 mm) than wide (width, 35 mm), with the relative length being 0.68. In INM-4-17907, the centrum is 17 mm long

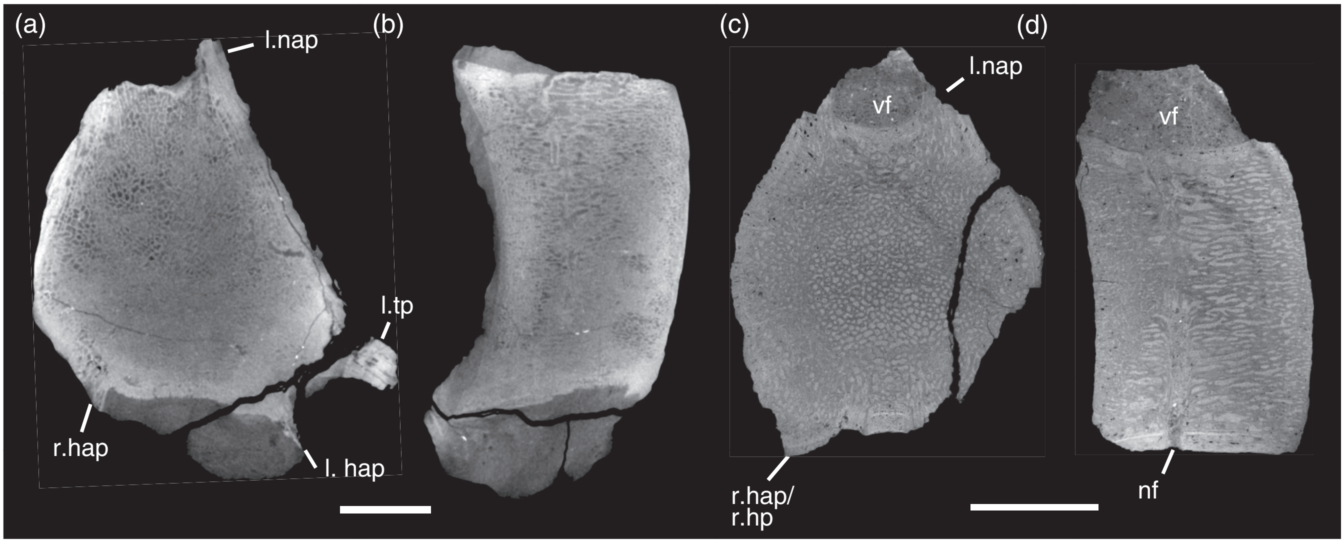

FIGURE 5 Computed-tomography-based virtual sections of INM-4-17907 (a, b) and INM-4-15694 (c, d): Transverse (a, c), and mid-sagittal (b, d) sections. Note that the cavity-filling matrix is displayed in darker gray than the bone tissue in (a and b) whereas the opposite is noted in (c) and (d). l.(r.)hap, left (right) haemal arch pedicle; r.hp, right hemapophysis; l.nap, left neural arch pedicle; l.tp, left transverse process; nf, nutrient foramen; vf, vertebral foramen. Scale bars: 10 mm

and cylindrical (height 25 mm; width 25 mm), resulting in a relative length of 0.68. The neural arches are fused to the centra (Figure 5a,c). The left transverse process occupies a ventrolateral position and is dorsoventrally compressed in INM-4-17907. The haemal arch is fused to the centrum as confirmed in the transverse sectional view (Figure 5a) and situated on the posterior portion of the ventral surface of the centrum in INM-4-17907. On the other hand, in INM-4-15694, it is unclear whether if the haemal arch was fused or articulated to the centrum (Figure 5c), and the hemapophysis (or pedicle) of the right haemal arch is located in the posterior portion of the ventral surface of the centrum.

Based on CT data, most of the cross-sectional area is occupied by cancellous bone; a thin (~3 mm thick), the surficial layer of the lateral and ventral walls consists of compact bone (Figure 5a–d). In cancellous bone, the trabeculae are homogeneously very thin and close to each other. The trabeculae are oriented longitudinally in general, except near the intervertebral surfaces where they are oriented randomly (Figure 5b,d).

3.4 | Ontogenetic assessment

Although the neurocentral sutures of these specimens are “fused” (sensu Brochu, 1996), this is not enough to determine their specific ontogenetic stage. The “open” neurocentral sutures (sensu Brochu, 1996) could be relatively good indicators of skeletal immaturity even in some vertebrae (Griffin et al., 2021), but “fused” neurocentral sutures are not so informative as indicators of skeletal or sexual maturity (Griffin et al., 2021; Waskow & Mateus, 2017; Wedel & Taylor, 2013). In this regard, it can be stated that INM-15694 and INM-4-17907 do not belong to the earliest stage of ontogeny, but their more detailed growth stage is unknown.

Although it is suggested that the trabecular network of smaller vertebrae is looser than that of larger vertebrae in *Clidastes*, the tightness depends, at least in part, on the species size and not exclusively on individual size (Houssaye & Tafforeau, 2012). Growth lines are often used to infer the age of animals (reviewed in Griffin et al., 2021), but because of intense inner bone resorption, such skeletochronological studies have little opportunity to be successful (Houssaye & Tafforeau, 2012). In addition, the number of *Plotosaurus* individuals available for histological comparison is quite limited. For these reasons, we did not perform thin sectioning of the current specimens.

3.5 | Comparison

In Russellosaurina, unfused haemal arches articulate to the vertebral centra (Polcyn & Bell Jr., 2005). Therefore, INM-4-17907 can be excluded from this taxon. In addition, the relative centrum length in the caudal vertebrae is around 1.0 in Russellosaurina (e.g., in *Tylosaurus*, *Hainosaurus*, *Platecarpus*, and *Plioplatecarpus*; Bardet et al., 2005). As an exception, the relative centrum length of the caudal vertebrae of *Platecarpus* decreases to ~0.8 at the tailbend (Lindgren et al., 2010). The caudal vertebrae at the tailbend of *Platecarpus* are wedge-shaped, whereas INM-4-15694 does not show such morphology. Therefore, INM-4-15694 can also be excluded from *Platecarpus* and other Russellosaurina.

In Halisaurinae, the caudal centrum length is greater than or equal to its height (Bardet et al., 2005). Therefore, the current specimens can also be excluded from Halisaurinae; they can be referred to as Mosasaurinae.

The microanatomical features, such as the thin and tightly packed internal trabeculae, support the Mosasaurini affinity of these specimens because these features are observed in the dorsal vertebrae of *Mosasaurus* and *Plotosaurus* but not in those of *Clidastes or Platecarpus*, although a *Tylosaurus* caudal vertebra also shows a similar vertebral microanatomy to the current specimens (Houssaye, 2008; Houssaye & Bardet, 2012; Houssaye & Tafforeau, 2012).

The length of the caudal vertebrae is shortened in derived mosasaurines, which represents one of the biomechanical transformations for aquatic life (Figure 6; Lindgren et al., 2007, 2011). In the early Maastrichtian *Mosasaurus* sp. (DMNH 21006), the relative centrum length of caudal vertebrae is 1.0–0.7 (Lindgren et al., 2011). The relative centrum length of *Plotosaurus* is shortest among all mosasaurs (Lindgren et al., 2008), ~0.7 in intermediate and terminal caudal vertebrae (Lindgren et al., 2007). This unique characteristic distinguishes this genus from the other Mosasaurinae mosasaurs, such as *Dallasaurus*, *Clidastes*, *Prognathodon*, *Eremiasaurus*, and *Mosasaurus* (Leblanc et al., 2012; Lindgren et al., 2011, 2013). The relative centrum lengths of the current specimens are 0.68, which is close to that of *Plotosaurus*. In addition, the shapes of current specimens do not contradict the referral *Plotosaurus* specimens. The shape of INM-4-17907 corresponds to those of intermediate vertebrae of UCMP 33913 (Camp, 1942: Figure 5). These centra are slightly subtriangular in the transverse section and flat on the ventral surface; the lateral surfaces are smooth. The shape of INM-4-15694 is also very similar to the centra of anteriorly situated terminal caudal vertebrae of CIT 2804 (Lindgren et al., 2008: Figure 4c–f). The condyles are subcircular; the centra are not wedge-shaped; the lateral surfaces are smooth.

The current specimens are smaller than the centra of well-preserved *Plotosaurus* caudal specimens (e.g., UCMP 33913). The centrum of an intermediate caudal vertebra of UCMP 33913 is 40 mm long, 52 mm high, and 58 mm wide; The centrum of a terminal caudal vertebra is 32 mm long, 46 mm high, and 52 mm wide (Camp, 1942). This size difference between the current specimens and the referred *Plotosaurus* specimens prevents us from confirming them as this genus simply. The allometric change in caudal vertebrae caused by the body size difference is unclear in *Plotosaurus* or other relatives because there are not enough materials for testing this matter. However, the relative centrum length of a small posteriorly situated terminal vertebra (presumably juvenile individual) is close to that of a large vertebra (presumably adult individual) in *Clidastes* (Lindgren & Siverson, 2004). In addition, the caudal vertebra of a small *Tethysaurus* individual (supposed as a "baby") is longer than high like that of a large individual (Bardet et al., 2003; Houssaye & Bardet, 2013). Based on these data available at this time, it is presumed that the shape of the caudal vertebrae of other mosasaurs would not be as short as that of *Plotosaurus*, regardless of the ontogenetic stage or individual size. Therefore, the current specimens can be referred to as cf. *Plotosaurus* sp.

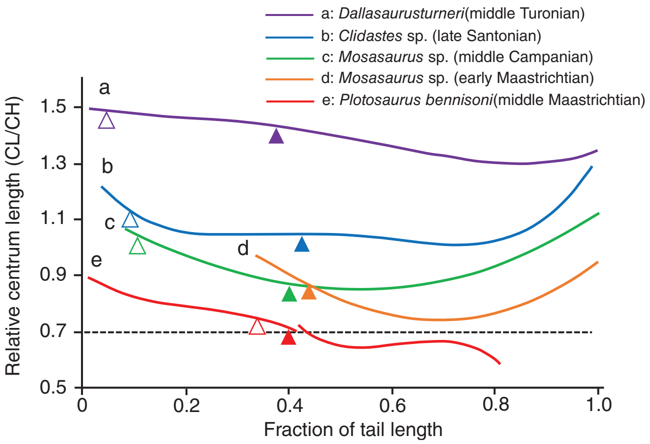

FIGURE 6 Comparative dimensional changes (relative centrum length) through the vertebral column of the mosasaurines, showing a gradual decline in relative length. *Source*: Modified from Lindgren et al., 2011. White triangles indicate the boundaries of the pygal/intermediate caudals. Colored triangles indicate the boundaries of the intermediate/terminal caudals

4 | DISCUSSION

4.1 | Body size

Although Lindgren et al. (2008) described the genus *Plotosaurus* as a large-sized (~8 m) mosasaur, the body-size variation within the only valid species *P. bennisoni* is wide, ranging from ~4.2 m (holotype UCMP 32778) to ~8 m (e.g., UCMP 33913). Although ontogenetic polymorphism seems to be the most reasonable explanation for this variation, other factors, such as sexual dimorphism, were not excluded (Lindgren et al., 2008).

INM-4-17907 is ~70% in size compared to an intermediate caudal vertebra of UCMP 33913 (Camp, 1942: Figure 5). The number of intermediate caudal vertebrae is only 3–6 in *Plotosaurus* (Lindgren et al., 2007, 2008), so that these vertebrae size variation in a single individual is limited. Therefore, INM-4-17907 is supposed to be derived from a smaller individual than UCMP 33913.

INM-4-15694 is ~53% in size compared to a terminal caudal vertebra of UCMP 33913 (Camp, 1942: Figure 5). Because the number of terminal vertebrae is more than 50 in *Plotosaurus* (Lindgren et al., 2007, 2008), these vertebrate size variation is wide in a single individual (see Lindgren et al., 2008: Figure 4c–h). Therefore, it is not clear whether the small size of INM-4-15694 is due to the body size, the anatomical position, or both.

4.2 | Paleobiogeography of *Plotosaurus*-type mosasaurs

Plotosaurus has hitherto been recorded only from the upper lower to the lower upper Maastrichtian on the west coast of North America. Accordingly, Camp (1942) and Russell (1967) suggested that this

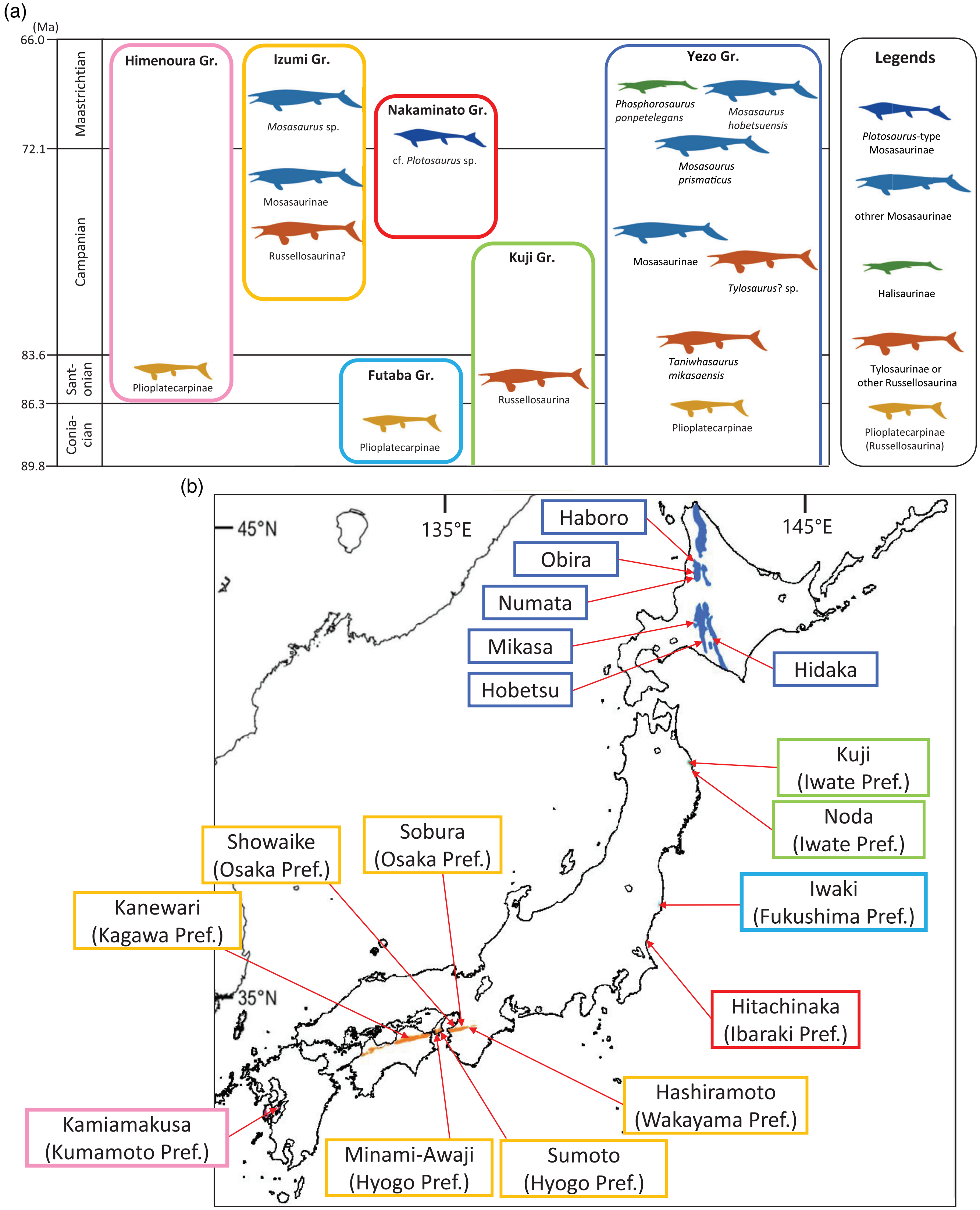

FIGURE 7 Mosasaur remains from the Late Cretaceous strata in Japan. See Table 1 for each datum. (a) Stratigraphic correlation of mosasaur remains from Japan. Mosasaur silhouettes are drawn based on skeletal reconstructions of *Tylosaurus* (Hartman, 2015), *Platecarpus* (Lindgren et al., 2010), *Phosphorosaurus* (Shinmura & Konishi, 2018), *Mosasaurus* (PWNZ3R-Dragon, 2017), and *Plotosaurus* (Lindgren et al., 2007). (b) Distribution of mosasaur fossil localities in Japan. *Source*: Map modified from Masukawa and Ando (2018)

TABLE 1 Mosasaur remains from the Upper Cretaceous in Japan

Geological unit	Stage	Identification	Specimen number	Locality
Yezo Gr.	Maastrichtian	*Phosphorosaurus ponpetelegans*	HMG 1528 (Holotype)	Hobetsu, Mukawa, Hokkaido
		Mosasaurus hobetsuensis	HMG 12 (Holotype)	Hobetsu, Mukawa, Hokkaido
		Mosasaurinae gen. et sp. indet.	HMG 10	Hobetsu, Mukawa, Hokkaido
	Campanian-Maastrichtian	*Mosasaurus prismaticus*	HMG 1065 (Holotype)	Hobetsu, Mukawa, Hokkaido
		Mosasaurinae gen. et sp. indet.	HMG 1077	Hobetsu, Mukawa, Hokkaido
		Mosasauridae gen. et sp. indet.	HMG 1076	Hobetsu, Mukawa, Hokkaido
	Campanian	*Tylosaurus*? sp.	HMG 371	Hobetsu, Mukawa, Hokkaido
		Mosasaurinae gen. et sp. indet.	NFL 33	Numata, Hokkaido
		Mosasauroidea gen. et sp. indet.	OTBE Obr-3609	Obira, Hokkaido
	Santonian-Campanian	*Taniwhasaurus mikasaensis*	MCM.M0009 (Holotype)	Mikasa, Hokkaido
		Taniwhasaurus mikasaensis	MCM.A1008 and M10	Mikasa, Hokkaido
		Taniwhasaurus mikasaensis	MCM.A600	Haboro, Hokkaido
	Santonian	Mosasauridae gen. et sp. indet.	HMG 370	Monbetsu, Hidaka, Hokkaido
	Coniacian-Santonian	Russellosaurina gen. et sp. indet.	NSM-PV15003	Hobetsu, Mukawa, Hokkaido
		Plioplatecarpinae gen. et sp. indet.	HMG 11	Hobetsu, Mukawa, Hokkaido
	Coniacian-Maastrichtian	Mosasauridae gen. et sp. indet.	HMG 1075	Hobetsu, Mukawa, Hokkaido
	(Unknown)	Mosasauridae gen. et sp. indet.	HMC uncatalogued specimen	Hidaka, Hokkaido
		Mosasauridae gen. et sp. indet.	HMC uncatalogued specimen	Hidaka, Hokkaido
Kuji Gr.	Santonian	Russellosaurina gen. et sp. indet.	IPMM 30881	Kuji, Iwate
		Mosasauridae gen. et sp. indet.	IPMM 40041	Noda, Iwate
Futaba Gr.	Santonian	Mosasauridae gen. et sp. indet.	NSM-PV22125	Iwaki, Fukushima
	Coniacian	Plioplatecarpinae gen. et sp. indet.	IMCF uncatalogued specimen	Iwaki, Fukushima
Nakaminato Gr.	Maastrichtian	cf. *Plotosaurus* sp.	INM-4-15694	Hitachinaka, Ibaraki
	Campanian-Maastrichtian	cf. *Plotosaurus* sp.	INM-4-17907	Hitachinaka, Ibaraki
Izumi Gr.	Maastrichtian	*Mosasaurus* sp.	KSNHM-F6-10 ~ 23	Sobura, Kaizuka, Osaka
		Mosasauridae gen. et sp. indet.	KSNHM-F6-5 ~ 9, 480	Sobura, Kaizuka, Osaka
		Mosasaurinae gen. et sp. indet.	KSNHM-F6-3	Showaike, Sennan, Osaka
		Mosasaurinae gen. et sp. indet.	OMNH MV-0066	Hashiramoto, Wakayama
		Mosasauridae gen. et sp. indet.	KCU uncatalogued specimen	Sumoto, Hyogo
	Campanian	Mosasaurinae gen. et sp. indet.	KSNHM-F6-2	Kanewari, Sanuki, Kagawa
		Russellosaurina?	OMNH MV-0076	Minami-awaji, Hyogo
Himenoura Gr.	Santonian	Plioplatecarpinae gen. et sp. indet.	GCM-VP 348	Kamiamakusa, Kumamoto

Note: Data compiled from Sato et al. (2012, 2018), Konishi et al. (2015), Kurosu et al. (2015), and this study. Private collections are excluded for reproducibility.

Abbreviations: GCM, Goshoura Cretaceous Museum, Amakusa City, Kumamoto Prefecture; HMC, Hidaka Mountain center, Hidaka Town, Hokkaido Prefecture; HMG, Hobetsu Museum (geology collection), Mukawa City, Hokkaido Prefecture; IMCF, Iwaki Museum of Coal and Fossils, Iwaki City, Fukushima Prefecture; INM, Ibaraki Nature Museum, Bando City, Ibaraki Prefecture; IPMM, Iwate Prefectural Museum, Morioka City, Iwate Prefecture; KCU, Kochi University, Kochi City, Kochi Prefecture; KSNHM, Natural History Museum, Kishiwada City, Osaka Prefecture; MCM, Mikasa City Museum, Mikasa City, Hokkaido Prefecture; NFL, Numata Fossils Laboratory, Numata Town, Hokkaido Prefecture; NSM, National Museum of Nature and Science, Taito ward, Tokyo Metropolis; OMNH, Osaka Museum of Natural History, Osaka City, Osaka Prefecture; OTBE, Obira Town Board of Education, Obira Town, Hokkaido Prefecture.

genus was endemic to North America. Although Obata et al. (1972) described NSM-PV15003 from the Yezo Group as *Plotosaurus* (?), Caldwell and Konishi (2007) reassigned this specimen to Russellosaurina. Frey et al. (2016) reported Q. 3105 as compare *Plotosaurus* from the upper Maastrichtian of the Quiriquina Formation in central Chile, but Jiménez-Huidobro et al. (2019) re-identified this specimen as *Halisaurus* sp. To explain this limited fossil records of *Plotosaurus*, Lindgren et al. (2007, 2011) suggested that this taxon might have preferred living in the deeper water environment off the continental coast, although most mosasaurs inhabited shallow, epicontinental seas (Bardet & Pereda Suberbiola, 1996; Harrell & Pérez-Huerta, 2015; Kiernan, 2002; Russell, 1988).

In this study, the two mosasaur specimens derived from the Nakaminato Group are described as cf. *Plotosaurus*. They are the first evidence that the highly specialized, *Plotosaurus*-type mosasaurs inhabited the Northwestern Pacific Ocean. It suggests that the *Plotosaurus*-type mosasaurs had a wider distribution than previously considered (e.g., Camp, 1942; Russell, 1967). The occurrence from the submarine fan deposits of the Nakaminato Group (Katsura & Masuda, 1978; Masuda & Katsura, 1978) is not contradictory with the hypothesis that *Plotosaurus* inhabited the off-coast environment. Furthermore, if INM-4-17907 originated from the lower part of the Hiraiso Formation, the oldest record of the *Plotosaurus*-type mosasaur could date back to the late Campanian. Further findings from the Hiraiso Formation could resolve this problem.

4.3 | Diversity of Mosasaurinae in the Northwestern Pacific Ocean

In Japan, more than 50 mosasaur remains have been reported. Most of them were found in the Yezo Group in Hokkaido and the Izumi Group in southwestern Japan (Figure 7, Table 1). Sato et al. (2012) summarized the temporal distribution pattern of mosasaurs in Japan as follows. In the Coniacian to Santonian, the record of Mosasaurinae is absent, although Russellosaurina was present. In the Campanian, whereas Russellosaurina declined, Mosasaurinae began to diversify. Finally, in the Maastrichtian, Russellosaurina disappeared, and Mosasaurinae diversified further and expanded their geographic distribution.

All identifiable Mosasaurinae remains from the Cretaceous in Japan were hitherto referred to as *Mosasaurus*. In the Yezo Group, *Mosasaurus hobetsuensis* was described from the lowermost Maastrichtian (Suzuki, 1985), and *M. prismaticus* was reported from the uppermost Campanian to lowermost Maastrichtian (Sakurai et al., 1999). In the Izumi Group, several specimens were reported as *Mosasaurus* sp. from the Maastrichtian (Tanimoto, 2005; Tanimoto et al., 1994a, 1994b, 2004).

The current specimens are the first record of non-*Mosasaurus* Mosasaurinae remains from Japan. They indicate that Mosasaurinae mosasaurs diversified and pioneered deeper water off the continental coast in the Northwestern Pacific Ocean, at least in early Maastrichtian (possibly, already in late Campanian), in addition to the Northeastern Pacific Ocean as previously known. Such diversification was presumably accelerated by their highly specialized, somewhat ichthyosaur-like body shape for cruising efficiently in the open ocean (Motani, 2002). In addition, the remarkable shortening of the centrum suppressed the flexibility of the tail contributing to its enhanced stability and a more energy-efficient swimming style (Lindgren et al., 2011). In the future, additional specimens and comprehensive reviews of known specimens will likely increase the information available on *Plotosaurus*-type mosasaurs of the Northwestern Pacific Ocean.

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CONFLICT OF INTEREST

The authors have no competing interests to declare.

ORCID

Taichi Kato https://orcid.org/0000-0003-3337-4212
Yasuhisa Nakajima https://orcid.org/0000-0001-9162-4860
Kohei Shiseki https://orcid.org/0000-0002-1230-2319
Hisao Ando https://orcid.org/0000-0002-6961-3636

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