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Mandibular morphology of *Stegolophodon pseudolatidens* (Proboscidea, Stegodontidae) from the lower Miocene of Japan

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Abstract. We describe two well-preserved mandibles of *Stegolophodon pseudolatidens* (Mammalia, Proboscidea, Stegodontidae) discovered from the lower Miocene (*ca.* 16.9–16.6 Ma) in Northeast Japan. The mandible of *Sl. pseudolatidens* is primitive within the Stegodontidae in having a short symphysis with lower tusks, tetralophodont lower molars, and a mandibular canal with the large dorsoventral diameter in the anterior segment. It is characterized by a perpendicular mandibular ramus (forming an almost right angle between the anterior margin of the mandibular ramus and the dorsal horizontal surface of the corpus), and many scratches in mesial direction on the occlusal surface of m3, implying that *Sl. pseudolatidens* appears to have acquired a proal jaw movement during mastication. While the mandibular morphology of *Sl. pseudolatidens* is comparable to that of other species of the genus that of *Stegolophodon* cf. *stegodontoides* from the upper Miocene of Myanmar differs from that of these species in having a shorter symphysis, which is a derived condition.

Keywords: early Miocene, mandible, Natori Group, Shirado Group, Stegodontidae, *Stegolophodon*

Introduction

A stegodontid proboscidean genus *Stegolophodon* Schlesinger, 1917 was widely distributed in Asia and Africa during the Neogene. Its type species, *Stegolophodon latidens* Schlesinger, 1917, is recorded from the lower Pliocene at the upper-stream area of the Irrawaddy River in Myanmar. More than 10 species of *Stegolophodon* have been described from the lower Miocene to Pliocene in various areas of Asia: Thailand, Myanmar, India, Pakistan, China, Indonesia, and Japan (Saegusa *et al*., 2005). In Japan, three species of *Stegolophodon* have been known from the lower to middle Miocene (Koda, 2003; Saegusa, 2008): *Stegolophodon pseudolatidens* (Yabe, 1950), *Stegolophodon tsudai* Shikama and Kirii, 1956, and *Stegolophodon miyokoae* Hatai, 1959. *Sl. pseudolatidens* was initially described as *Eostegodon pseudolatidens* by Yabe (1950) based on molars, a partial cranium, and a mandible. However, because there are minor variations in the cusp position on M3/m3, Saegusa *et al*. (2005) and Saegusa (2008) attributed these three Japanese species of *Stegolophodon* to *Sl. pseudolatidens*. Monophyly of the Stegodontidae has been stated by Tassy (1990, 1996a), Saegusa (1996b), Shoshani (1996), and Shoshani *et al*. (1998). By contrast, Kalb and Mebrate (1993) and Kalb *et al*. (1996) allocated the genera *Stegolophodon* and *Stegodon* to the basal parts of the Elephantidae and stated that these genera do not constitute a monophyletic group. Although the tooth morphology of *Stegolophodon* has been relatively well studied (e.g. Saegusa, 1996b, 2008; Saegusa *et al*., 2005), its skull (cranium + mandible), which often bears important phyletic and paleoecological information, has been poorly understood.

In this study, we precisely describe the mandibular morphology of two well-preserved specimens of *Sl. pseudolatidens* from the lower Miocene in Northeast Japan. We examined their internal mandibular structures such as the mandibular canal and tooth roots with X-ray computed tomography (CT) scanner images. Based on the

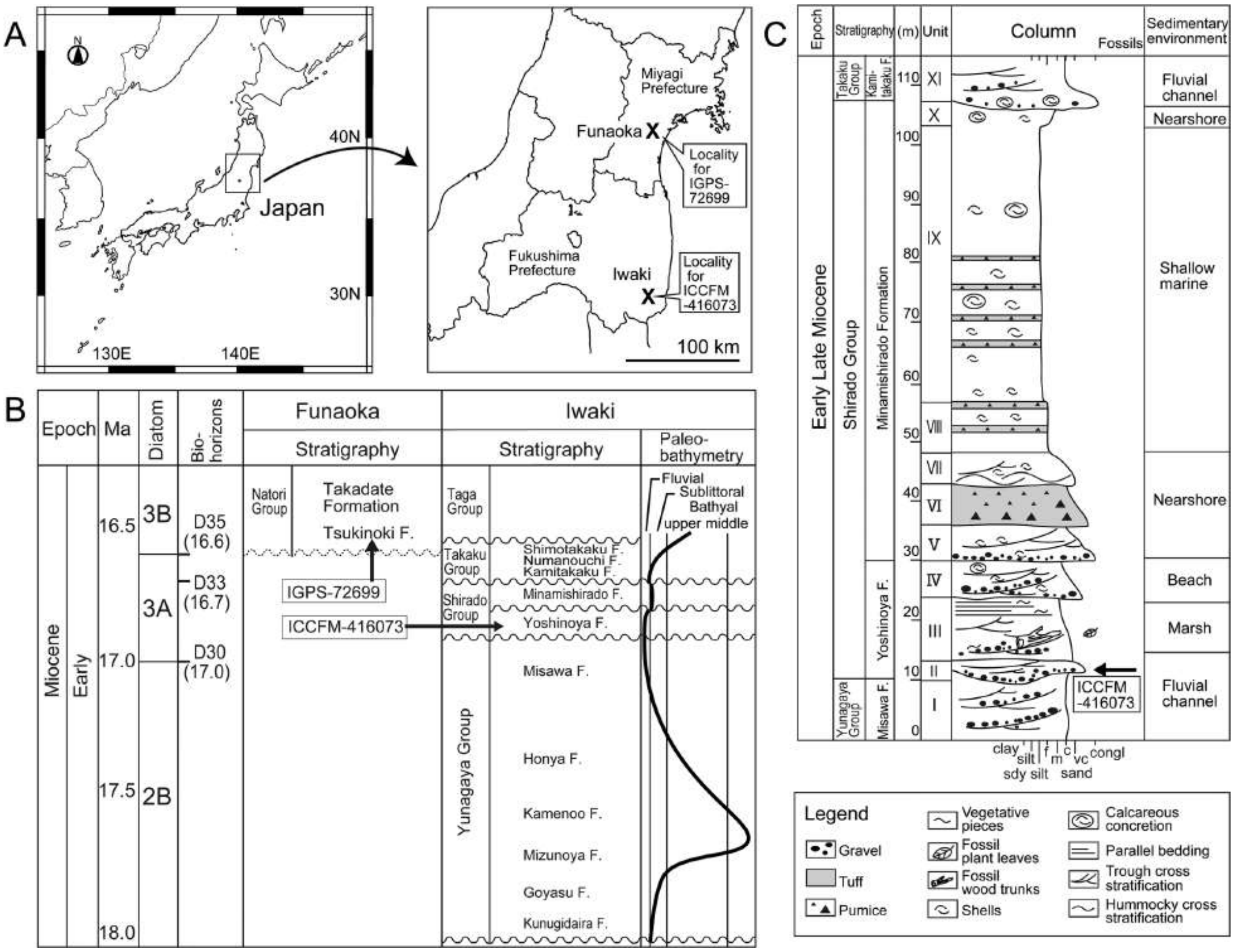

Figure 1. Geological setting of the Miocene *Stegolophodon*-bearing formations in Northeast Japan. **A**, locality map; **B**, lower Miocene stratigraphy of the two studied areas (Funaoka and Iwaki areas, Northeast Japan) based on Okutsu and Muto (1959), Suto *et al*. (2005), Otomo and Kurita (2007), Ando *et al*. (2011), Yanagisawa (2011), and Fujiwara *et al*. (2013); **C**, a part of the geological columnar section indicating the horizon of ICCFM-416073 in the Iwaki area (after Nemoto *et al*., 1998).

comparison of those mandibular morphologies with some other species of *Stegolophodon* and some other genera of the Elephantida, we clarify the characteristics of the mandibular morphology of this species.

Institutional Abbreviations.—AMNH, American Museum of Natural History, New York, USA; CMU, Chang Mai University, Chiang Mai, Thailand; DMR, Department of Mineral Resources, Bangkok, Thailand; ICCFM, Iwaki City Coal and Fossil Museum, Iwaki, Japan; IGPS, Institute of Geology and Paleontology, Tohoku University, Sendai, Japan; INM, Ibaraki Nature Museum, Bando, Japan; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MNHN, Muséum national d'Histoire naturelle, Paris, France; TMM, Texas Memorial Museum, Austin, USA; YUDG; Geological Museum of the University of Yangon, Yangon, Myanmar.

Locality and geological setting

The two mandibles of *Sl. pseudolatidens* described here (IGPS-72699: a syntype, and ICCFM-416073: a new material) occurred in the upper part of the lower Miocene in Northeast Japan. IGPS-72699 is from a tuff bed in the lower part of the Tsukinoki Formation (*ca*. 16.6 Ma) of the Natori Group, Miyagi Prefecture (Yabe, 1956; Okutsu and Muto, 1959; Figure 1A–B). ICCFM-416073 is from a sandstone bed of the lower part (Unit II) of the Yoshinoya Formation (*ca*. 16.9–16.8 Ma) of the Shirado Group, Fukushima Prefecture (Figure 1A–C).

The Tsukinoki Formation is distributed in the Funaoka area, Shibata Town, Miyagi Prefecture. It appears to be

Table 1. List of the comparative specimens used in this study.

Higher taxa	Species	Locality	Geological age	Catalog number	Reference
Elephantida					
Gomphotheriidae					
	Gomphotherium angustidens Cuvier, 1817	Gers, France	middle Miocene	MNHN-F-SEP187	Tassy, 2013
Elephantoidea					
Elephantidae					
	Elephas maximus Linnaeus, 1758	–	Recent	TMM-M-6445	Balanoff, 2003
Stegodontidae					
	Stegolophodon hueiheensis Chow, 1959	Jiangsu, China	early Miocene	IVPP-V2400.1	Chow, 1959; Tobien *et al*., 1988
	Stegolophodon nasaiensis Tassy *et al.*, 1992	Lamphun, Thailand	middle Miocene	DMR-4734a, CMU-4732a	Tassy *et al*., 1992
	Stegolophodon praelatidens Koenigswald, 1959	Lamphun, Thailand	middle Miocene	DMR-TF6271	Chavasseau *et al*., 2009
	Stegolophodon cf. *stegodontoides* Pilgrim, 1913	Magway, Myanmar	late Miocene	YUDG-sbw009	Sein and Thein, 2008
	Stegodon trigonocephalus Martin, 1887	Java Island, Indonesia	Pliocene	INM-4-015283	This study

approximately 16.6 Ma in age, which is near the early–middle Miocene boundary (Figure 1B). This age is based on the occurrence of dinoflagellate species *Spiniferites pseudofurcatus* and *Operculodinium longispinigerum*, which correlate the formation with the *Diphyes latiusculum* dinoflagellate Zone. *D. latiusculum* is indicative of the biohorizon D35 of the lower part of North Pacific Diatom Zone 3B (NPD3B) (Yanagisawa and Akiba, 1998; Otomo and Kurita, 2007; Fujiwara *et al*., 2013).

The Yoshinoya Formation is distributed in Iwaki City, Fukushima Prefecture. The underlying and overlying strata (Misawa and Minamishirado formations, respectively) yield diatoms of the *Crucidenticula kanayae* diatom Zone, which correlates with the lower part of NPD3A and is dated as 17.0–16.7 Ma (Yanagisawa and Akiba, 1998; Suto *et al*., 2005). According to Ando *et al*. (2011, fig. 4) and Yanagisawa (2011, fig. 27), the refined age of the formation is regarded to be the later part of the early Miocene, approximately 16.9–16.8 Ma. The Yoshinoya Formation appears to consist of fluvial deposits with channel scour and fill, judging from the sedimentary facies and structures (Nemoto *et al*., 1998; Figure 1C).

Methods

Comparative material.—The present specimens are compared with the seven species of the four related genera shown in Table 1. We could observe only the specimen of *Stegodon trigonocephalus* Martin, 1887 in Ibaraki Nature Museum, and referred to the published illustrations of the other six species.

Terminology and measurements.—The usage of morphological and anatomical terms for mandibles and molars adopted in this study follows Van Der Merwe *et al*. (1995), Saegusa *et al*. (2005), Saegusa (2008), and Chavasseau *et al*. (2009). Terms for foramina and internal structures of the mandibles follow Ferretti and Debruyne (2011). A total of 23 length parameters and three angle parameters for the mandibles and molars (Table 2; Figure 5) were defined after Beden (1987), Tassy (1996b), Chavasseau *et al*. (2009), Ferretti (2010), and Wang *et al*. (2014). The angle parameters for the mandibles are as follows. Angle *a* is an angle between the left and right condyles at the posterior end of the mandibular symphysis (in the case of the broken condyle, the center of the upper fracture surface of the mandibular ramus is regarded as

Table 2. Mandibular measurements of *Stegolophodon pseudolatidens*, IGPS-72699 and ICCFM-416073. Plus marks (+) indicate minimal length due to the incomplete specimen IGPS-72699. Refer to Figure 5 for the positions of the defined parameters.

no.	parameters	IGPS-72699	ICCFF-416073
1	Maximal length (mm)	530+	738
2	Symphyseal length (mm)	104+	223
3	Maximal depth of ramus (mm)	–	265
4	Maximal width of mandibular corpus (mm)	125	140
5	Alveolar length (mm)	410	316
6	Mandibular width between left and right coronoid processes (mm)	–	401
7	Internal width between posterior alveoli (mm)	–	182
8L	Length of left condyle (mm)	–	49
8R	Length of right condyle (mm)	–	47
9L	Width of left condyle (mm)	–	96
9R	Width of right condyle (mm)	–	87
10	Maximal width of mandible (mm)	–	479
11	Interval width between left and right condyles (mm)	–	294
12	Anterior interval width between left and right alveoli (mm)	–	65
13	Maximal mandibular height at the central axis of condyle (mm)	–	335
14	Depth between angular process and coronoid process (mm)	–	269
15	Height of mandibular corpus (mm)	–	208
16	Ventral length from angular process to anterior edge of symphysis (mm)	–	622
17L	Length of left lower tusk (mm)	–	74
17R	Length of right lower tusk (mm)	–	58
18L	Minor axis of left lower tusk (mm)	–	27
18R	Minor axis of right lower tusk (mm)	–	29
19L	Major axis of left lower tusk (mm)	–	38
19R	Major axis of right lower tusk (mm)	–	32
20L	Transverse diameter of left anterior mental foramen (mm)	–	17
20R	Transverse diameter of right anterior mental foramen (mm)	–	20
21L	Vertical diameter of left anterior mental foramen (mm)	–	12
21R	Vertical diameter of right anterior mental foramen (mm)	–	13
22L	Transverse diameter of left lateral mental foramen (mm)	–	7
22R	Transverse diameter of right lateral mental foramen (mm)	–	6
23L	Vertical diameter of left lateral mental foramen (mm)	–	11
23R	Vertical diameter of right lateral mental foramen (mm)	–	9
Angle *a*	Angle between left and right condyles at posterior end of symphysis (°)	–	47
Angle *b*	Angle between front surface of symphysis and horizontal surface of corpus (°)	–	134
Angle *c*	Angle between frontal ramus wall and posterior horizontal surface of corpus (°)	–	93

the condyle position). Angle *b* is an angle between the dorso-anterior surface of the symphysis and the dorsal horizontal surface of the mandibular corpus. Angle *c* is an angle between the anterior margin of the mandibular ramus and the posterior horizontal surface of the corpus.

Anatomical Abbreviations.—acf, accessory foramen; acmf, accessory lateral mental foramen; acrm3, accessory root of m3; amc, anterior mental canal; amf, anterior mental foramen; arm2, anterior root of m2; arm3, anterior root of m3; coc, coronoid canal; Dp4, upper fourth deciduous premolar; L, left; lmc, lateral mental canal; M1–M3/m1–m3, upper/lower molars; mac, mandibular canal; pc, pulp chamber; pmf, posterior mental foramen; prm2, posterior root of m2; prm3, posterior root of m3; R, right; re, restored part.

Internal structure.—To clarify the internal mandibular structure of the Stegodontidae, transmission imaging of three mandibular specimens (IGPS-72699, ICCFM-416073, and INM-4-015283) was performed using X-ray CT scanners at the same tube voltage of 120 kV. IGPS-72699 (*Sl. pseudolatidens*) was scanned using Xlead (Toshiba Medical Systems Corporation). The images were taken at intervals of 2 mm and saved as DICOM (Digital Imaging and Communications in Medicine) stacks. ICCFM-416073 (*Sl. pseudolatidens*) and INM-4-015283 (*S. trigonocephalus*) were scanned using Aquilion 64 (Toshiba Medical Systems Corporation). The images were taken at intervals of 5 mm and saved as DICOM stacks. The internal mandibular structure of *Elephas maximus* Linnaeus, 1758 (Elephantidae) was sited from Balanoff (2003).

Dental microwear.—The patterns of dental microwear provide some of the best indirect evidence of tooth use in living and extinct species. The occlusal surfaces of molars were observed by digital microscope VHX-5000 (Keyence Corporation). The images of many scratches on left m3 (ICCFM-416073) were taken at 20x magnification.

Systematic paleontology

Order Proboscidea Illiger, 1811
Elephantida Tassy and Shoshani in Shoshani *et al*., 1998
Superfamily Elephantoidea Gray, 1821
Family Stegodontidae Osborn, 1918
Genus ***Stegolophodon*** Schlesinger, 1917

Type species.—*Stegolophodon latidens* (Clift, 1828) Schlesinger, 1917

Stegolophodon pseudolatidens (Yabe, 1950) Takai and Fujii, 1961

Figures 2–7, 8B, 8F, 10A, 10F, Tables 2–3

Material described here.—IGPS-72699, a mandible with right m2–m3 and left m3; and ICCFM-416073, a mandible with left and right lower tusk and m2–m3.

Formation and age.—IGPS-72699 is from the lower Miocene Tsukinoki Formation (*ca*. 16.6 Ma) of the Natori Group; and ICCFM-416073 is from the lower Miocene Yoshinoya Formation (*ca*. 16.9–16.8 Ma) of the Shirado Group (Figure 1; Yabe, 1950; Nemoto *et al*., 1998; Suto *et al*., 2005; Ando *et al*., 2011).

Remarks on the type series.—The syntype series was described by Yabe (1950). There are four specimens: IGPS-7861 (right M3), IGPS-72696 (left m3), IGPS-72698 (an incomplete cranium with left and right M2–M3), and IGPS-72699 (a mandible described here; Figure 2A–B). IGPS-7861 was initially described as right Dp4 or M1 by Matsumoto (1926, pl.5, figs. 1–3). IGPS-72696 was initially described as right m3 by Yabe (1950, figs. 1–3), and it is identified as left m3 in this study based on the direction of the arcuate median sulcus. IGPS-7861 and IGPS-72696 appear to be derived from the same single individual (Yabe, 1950). They were recovered from the lower Miocene Sauramachi Formation, Miyagi Prefecture, Northeast Japan. IGPS-72698 and IGPS-72699 are also likely derived from the different single individual (Yabe, 1950).

Remarks.—Most species of *Stegolophodo*n have the following characteristics: tetralophodont, brachyodont molars with loph(id)s made of four bulbous cusps, the first lophid with fused pretrite conule and pretrite mesoconelets, upper tusks with longitudinal enamel band, and lower tusks ovoid to pyriform in transverse cross-sections (Chavasseau *et al*., 2009). According to Saegusa *et al*. (2005) and Saegusa (2008), *Sl. pseudolatidens* has a fine and pointed mammillae apex in each cusp on molars and is divided into two molar types. A primitive molar type has the character that central conules are on two mesial loph(id)s; and a derived molar type has the following four characters: (1) the second posterior central conule on the upper molar is much reduced, (2) the main pretrite cusp of the lophid is not displaced distally, (3) the first posterior central conule is always present, and (4) the second posterior central conule on the lower molar is absent.

Description

IGPS-72699

The mandible is dorsoventrally compressed during diagenesis posterior to deposition. The preserved parts are the broken left mandibular corpus and the nearly complete right corpus with only the lower part of the right mandibular ramus (Figure 2A–B). Because the deficient parts of both the corpora were restored using plaster, the length of the mandible and the missing alveolar parts

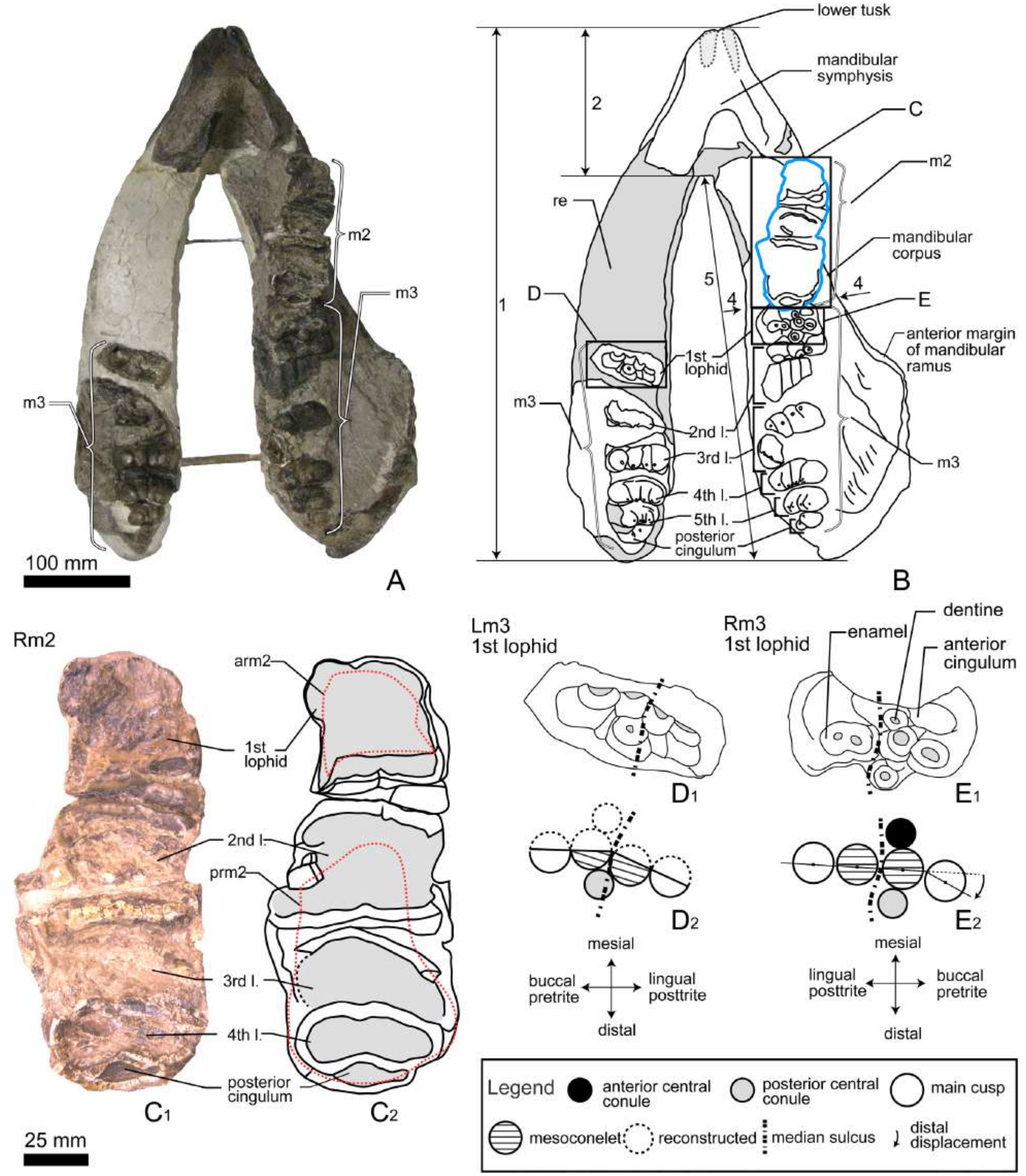

Figure 2. A mandible of *Stegolophodon pseudolatidens*, IGPS-72699 (a syntype of the species) from the lower Miocene of Japan (after Yabe, 1950). **A**, photograph in occlusal view; **B**, line drawing in occlusal view; **C**, right m2 in occlusal view (C_1, photograph; C_2, line drawing); **D**, first lophid of left m3 in occlusal view (D_1, line drawing; D_2, schematic drawing); **E**, first lophid of right m3 (E_1, line drawing; E_2, schematic drawing). Anatomical abbreviations (e.g. m2, also on Figures 3 to 10) are explained in the text. Numbers (1, 2, 4, 5; 1–23 in Figure 5) indicate the morphological parameters defined in Table 2. The upper and lower scales are applied to A–B and C–E, respectively.

appear to be elongated artificially (Figure 2B). Both sides of the lateral mental foramina, the mandibular foramina, the coronoid canals, and foramina are not preserved.

Mandibular canal.—The preserved right mandibular canal is severely damaged. In cross-sectional view, the posterior (Figure 3C_7) to middle (Figure 3C_5) segments are dorsoventrally compressed, and the anterior segment (Figure 3C_2) is elliptical.

Tusk.—The bases of left and right lower tusks (= incisors) are preserved within the mandibular symphysis (Figure 3C_1, 3E_2, 3F_2). The cross-section of the proximal part is ovoid to piriform (Figure 3C_1).

Molar.—The left m2 and left and right m3 are preserved (Figures 2, 3D). The morphological characteristics of m2 are not clear because they are strongly worn and badly preserved (Figure 2C). The first and second lophids of m3 are moderately worn (Figure 2A–B). The enamel thickness of the molars ranges within 5.3–5.9 mm (Table 3). The third lower molar (m3) is pentalophodont with an anterior and a posterior cingulum (Figure 2A–B). The indices of crown height [(maximal height/maximal width) × 100] are 51.8–52.0. The third lower molar is brachyodont (Table 3). Each "cusp" is bunodont, and its apex is subdivided into fine and pointed mammillae. The first lophid of m3 possesses six 'cusps': two main cusps, two central conules, and two mesoconelets. The two main cusps are located on the lingual and buccal sides, with the median sulcus in between. The anterior and posterior central conules are in contact with the pretrite mesoconelets. The buccal main cusp is distally displaced (Figure 2E_1–E_2). The second lophids are broken. Each lophid of the third to fifth lophids contains two main cusps and two mesoconelets. Each mesoconelet is well developed and reaches the same size as the main cusp.

ICCFM-416073

The mandible is almost completely preserved (Figures 4–5). In the occlusal view, the mandibular corpus is massive and buccally inflated. There is a narrow and deep groove on the upper surface of its mandibular symphysis with two accessory foramina. Angle *a* is 47° (Figure 5A; Table 2). In the anterior view, the upper surface of the mandibular symphysis forms a U-shaped valley with two accessory foramina, and the lower tusks are directed anteriorly (Figures 4B, 5B). The upper surface of the mandibular condyle is slightly inclined lingually, and the coronoid process is situated in the significantly lower position than the condyle. In the lateral view, the ventral border of the symphysis is ventrally inclined, and the mandibular corpus is anteroposteriorly elongated (Figures 4C–D, 5C). The outline of the mandibular ramus is trapezoidal and slightly inclined anteriorly. A thin dorsoanterior (rostral) coronoid process is present in ramus. The caudal border of the ramus forms a thin, rounded angular process. The mandibular notch forms a shallow convex arch between the coronoid process and the mandibular condyle. There is a deep semilunar lingual depression just below the notch. This depression forms a masseteric fossa for the attachment of the deep masseteric muscle. Angle *b* is 134°, and Angle *c* is 93° (Figure 5C; Table 2). In the medial view, a semilunar depression lies just below the mandibular notch. The pterygoid fovea is situated dorsally on the mandibular foramen for the attachment of the lateral pterygoid muscle.

Lateral mental foramen.—The anterior and posterior mental foramina with two accessory lateral mental foramina are preserved (Figure 5C). The position of the anterior mental foramen is slightly anterior to the posterior border of the lower tusk inside the symphysis (Figure 6E_2). The position of the posterior mental foramen is below the anterior root of m2 and above the mandibular canal (Figure 6C_4). The transverse diameter of the anterior mental foramen is larger than that of the posterior mental foramen (nos. 20 and 22 of Figure 5B and Table 2).

Mandibular foramen.—The mandibular foramen is well preserved (Figure 5D). The mandibular foramen is situated higher than the occlusal plane and is closer to the posterior border of the mandibular ramus. The relatively small opening of the mandibular foramen faces upward and has a triangular outline in a horizontal cross-section. Its anteroposterior diameter is approximately 20 mm. The linguoid process on the anterior border of the mandibular foramen is not well developed.

Mandibular canal.—The well-preserved mandibular canal traverses the corpus inside and extends from the mandibular foramen to the lateral anterior mental foramen (Figures 5C–D, 6). This canal is divided into three (posterior, middle, and anterior) segments. The posterior segment runs within the intermediate portion of the mandibular ramus and below the tooth roots (Figure 6C_6, 6D_1). The middle segment of the mandibular canal extends through the inside of the mandibular corpus, where the spongy bone tissue becomes buccally thick (Figure 6C_5). The anterior segment of the mandibular canal branches in front of m2. The anterior and lateral mental canal branches lead to the anterior and posterior mental foramina, respectively. Furthermore, the anterior mental canal branches at a somewhat posterior portion of the mandibular symphysis and leads to the anterior mental foramina and accessory lateral mental foramen 1. The lateral mental canal also branches at the anterior tooth root of m2 and leads to the posterior mental foramen and the accessory lateral mental foramen 2. In occlusal view, the mandibular canal extends along the buccal side of the molars (Figure 6E_2). In cross-sectional view, the mandibular canal is rectangularly flattened at the pos-

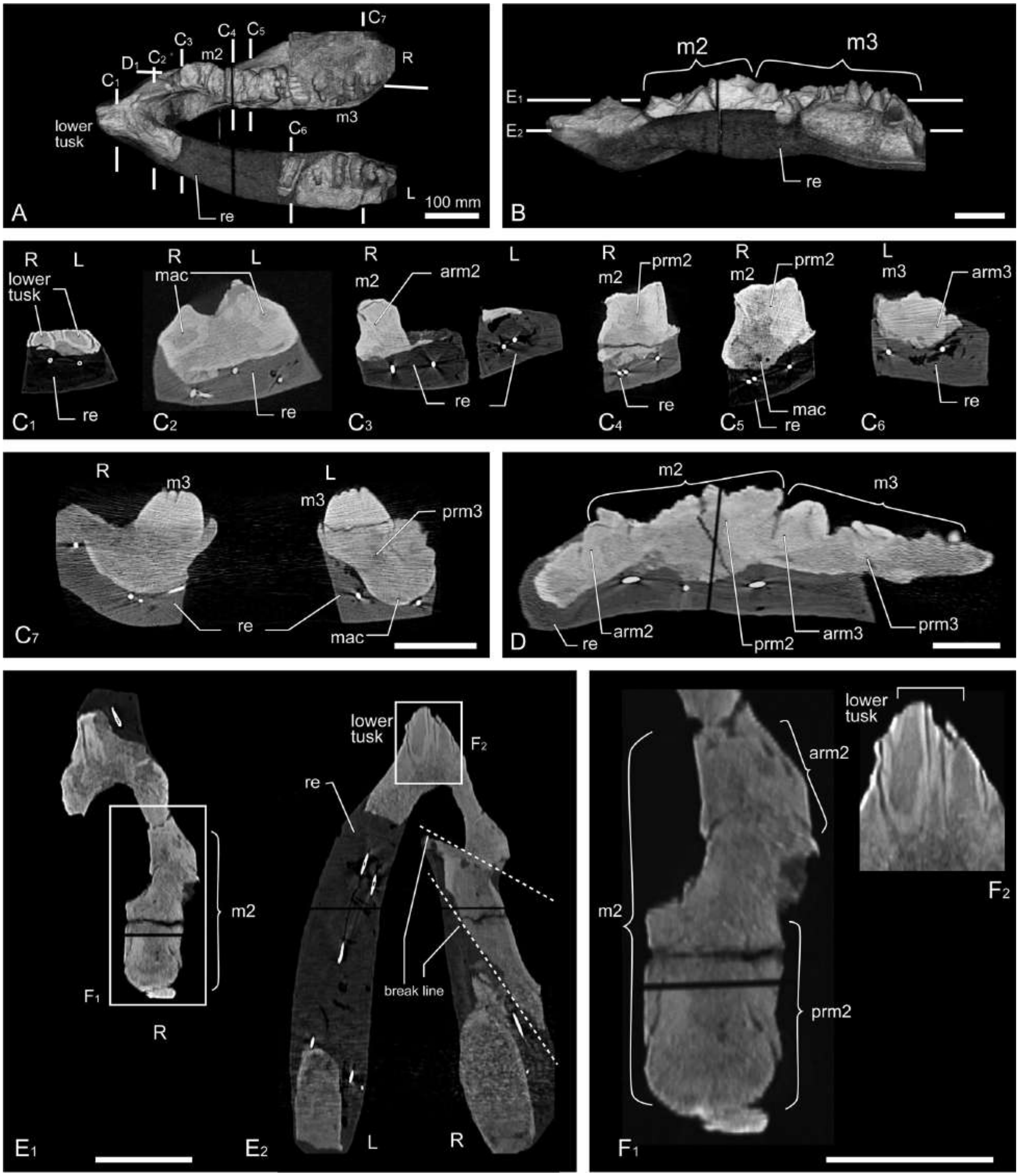

Figure 3. Serially sliced CT images of IGPS-72699 (*Stegolophodon pseudolatidens*). **A**, 3D image of the occlusal view showing the position of each transverse and sagittal slice; **B**, 3D image of the left lateral view showing the position of each horizontal slice; **C**, transverse slices; **D**, sagittal slice; **E**, horizontal slices. Dotted lines indicate the internal fracture surfaces; **F**, close-up of the tooth roots (F_1, anterior and posterior tooth roots of right m2; F_2, left and right lower tusks). Scale = 100 mm.

Table 3. Molar measurements of *Stegolophodon pseudolatidens*, IGPS-72699 and ICCFM-416073. Abbreviations: ET, enamel thickness; MH, maximal height; HI, height index = maximal height / maximal width x 100; ML, maximal length; LF, lophid frequency = number of lophids / maximal length x 100; Lm2, left m2; Lm3, left m3; Rm1, right m1; Rm2, right m2; Rm3, right m3; MW, maximal width; WI, width index = maximal width / maximal length × 100.

specimens / parameters	ML (mm)	MW (mm)	MH (mm)	WI	HI	ET (mm)	LF
Sl. pseudolatidens							
IGPS-72699							
Rm2	–	61.4	–	–	–	5.3	–
Lm3	–	59.7	30.9	–	51.8	5.9	–
Rm3	–	60.2	31.3	–	52.0	5.7	–
ICCFM-416073							
Lm2	120.0	68.3	15.7	56.9	–	5.2	3.3
Rm2	115.2	68.7	19.2	59.6	–	5.5	3.5
Lm3	171.7	75.0	45.3	43.7	60.4	6.0	2.9
Rm3	170.8	77.5	50.1	45.4	64.6	5.9	2.9

terior segment (Figure 6C$_6$) and longitudinally elliptical from the middle (Figure 6C$_5$) to the anterior (Figure 6C$_2$) segments.

Coronoid canal and foramen.—The coronoid canal is ventrally arcuate and extend from the dorsal part of the pterygoid fovea to the posterior part of alveolus within the mandibular ramus (Figures 5D, 6D$_2$). The coronoid foramen is not open because the posterior part of the alveolus is covered by alveolar bone.

Tusk.—The main parts of the left and right lower tusks (= incisors) are broken away. The length of the remaining right lower tusk is slightly shorter than that of the left lower tusk (Figure 4A; no. 17 of Figure 5A and Table 2). Both lower tusks are straight in the occlusal view. Multiple shallow grooves extend along the occlusal surface in the anteroposterior direction (Figures 4A, 5A). The proximal part continues to the vicinity of the posterior border of the symphysis (Figure 6E$_2$). In the lateral view, lower tusks are weakly arcuate into the ventral side (Figure 5C). Their cross-sections of the proximal parts are ovoid to piriform (Figure 6C$_1$). The outer surfaces are covered with cementum, and the inside consists of dentin (Figures 4B, 5B).

Molar.—Left and right m2–m3 are preserved (Figures 4–5, 7). The first to fourth lophids of each m2 are strongly worn. The first and second lophids of each m3 are moderately worn. Many small scratches in a mesial direction are seen on the occlusal surface of the fourth lophid of left m3 (Figure 7C). The enamel thickness of the molars ranges within 5.2–6.0 mm (Table 3). Each "cusp" is bunodont, and its apex is subdivided into fine and pointed mammillae. The m2 is a tetralophodont with an anterior cingulum (Figure 7A). There is a trace of the anterior central conule on the buccal side of the first lophid in each m2 (Figures 5, 7A). A rectangular dent on the mesial edge of each m2's crown is formed as a socket trace for attaching m1 (Figure 5B). The indices of the crown width of m2 are 56.9–59.6 (Table 3). The anterior root of m2 supports only the first lophid, and the posterior root of m2 supports the second to fourth lophids (Figures 6D$_2$, 7A). The m3 is tetralophodont with an anterior and a posterior cingulum. Because it is slightly inclined toward the lingual side, its buccal side tends to wear out earlier. The median sulcus is fine and is slightly curved toward the buccal side (Figure 7B). The indices of crown width are 43.7–45.4 (Table 3). The indices of the crown height are 60.4–64.6 (Table 3). The m3 is brachyodont.

The anterior root of m3 supports only the first lophid. The accessory root of m3 and the posterior root of m3 support the second lophids to the posterior cingulum (Figures 6D$_2$, 7A). The first lophid of m3 possesses six 'cusps': two main cusps, two central conules, and two mesoconelets. The two main cusps are located on the lingual and buccal sides, with the median sulcus in between. The anterior and posterior central conules are in contact with the pretrite mesoconelets. The buccal main cusp is distally displaced (Figure 7B). The second lophid has five 'cusps.' The arrangement of the main cusps and meso-

Figure 4. A mandible of *Stegolophodon pseudolatidens*, ICCFM-416073, from the lower Miocene of Japan. Photographs. **A**, in occlusal view; **B**, in anterior view; **C**, in left lateral view; **D**, in right lateral view.

conelets is the same as that in the first lophids. If the posterior central conule is present, it is located posterior to the pretrite mesoconelet. The buccal main cusp is also distally displaced. Each lophid of the third and fourth lophids contains two main cusps and two mesoconelets. Each mesoconelet is well developed and reaches the same

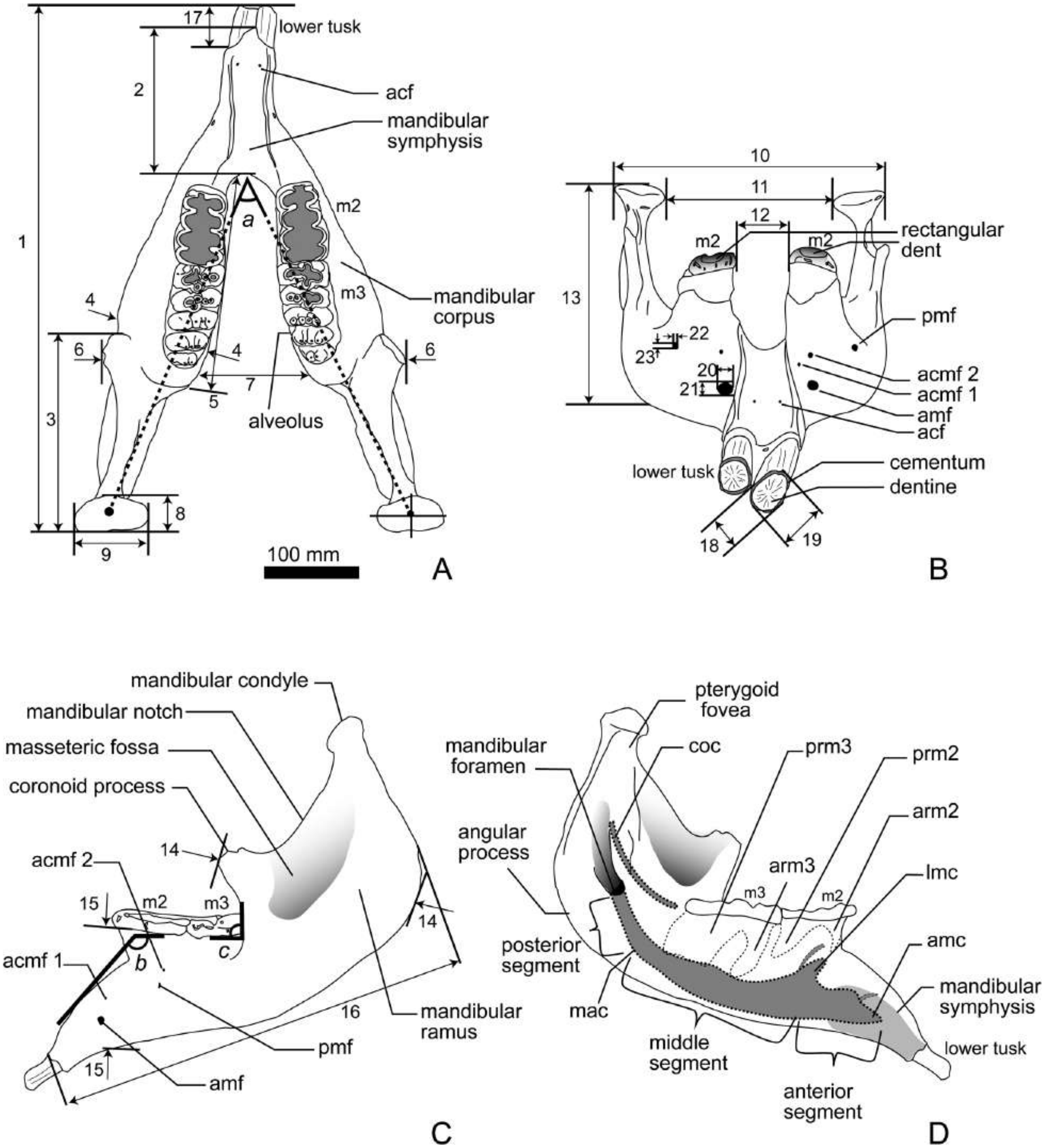

Figure 5. Line drawings of a mandible of *Stegolophodon pseudolatidens*, ICCFM-416073, shown in Figure 4. **A**, in occlusal view; **B**, in anterior view; **C**, in left lateral view; **D**, in left view with the internal structure. Morphological and anatomical terms and their abbreviations are explained in the text (Materials and methods). Parameter numbers 1–23 are defined in Table 2. Mandibular angles (Angles *a*, *b* and *c*) are defined in text and Table 2, and Figure 5.

size as the main cusp.

Comparisons and discussion

Reexamination of the lower teeth in IGPS-72699

Yabe (1950) identified the preserved lower teeth

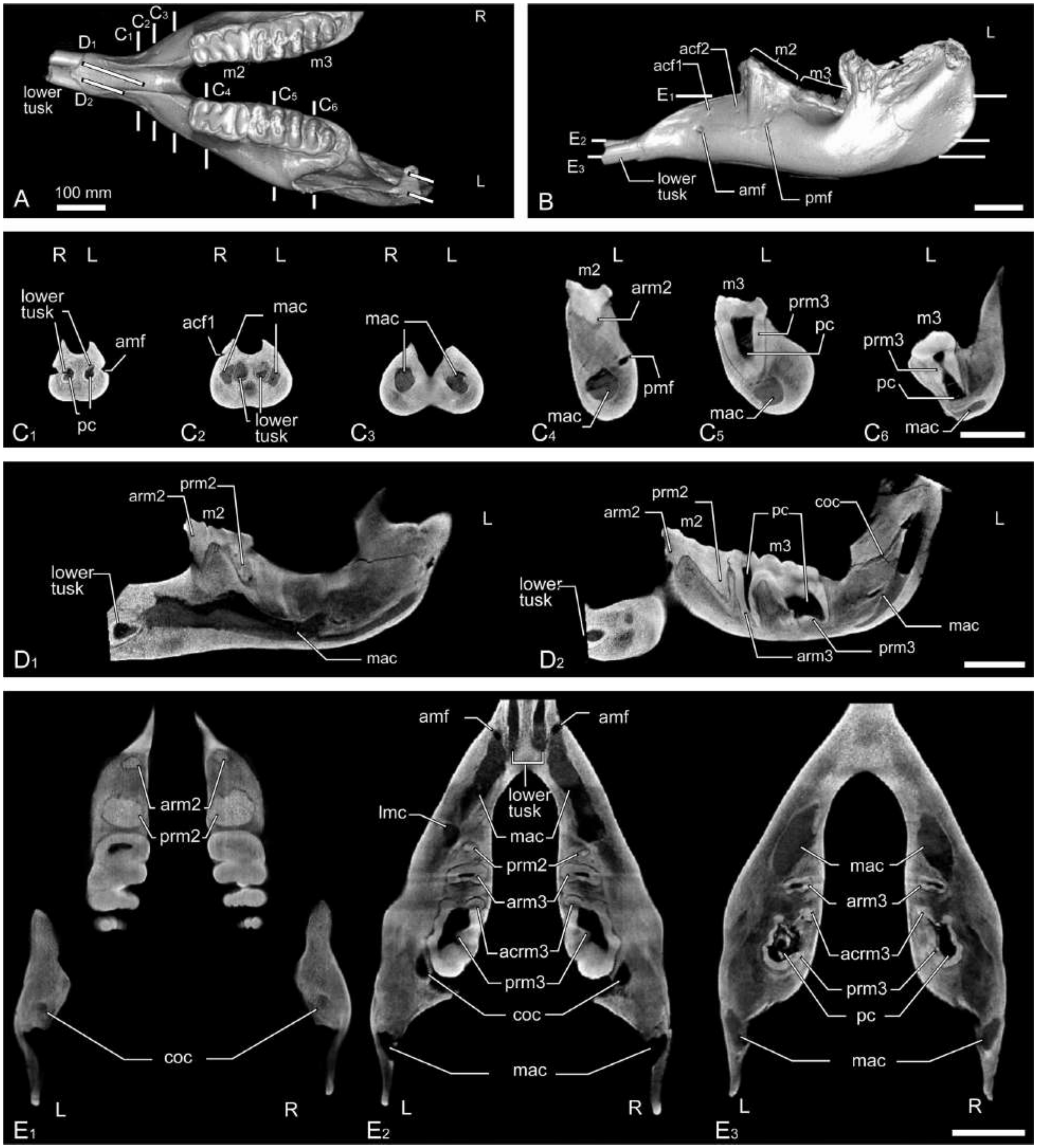

Figure 6. Serially sliced CT images of *Stegolophodon pseudolatidens*, ICCFM-416073. **A**, 3D image of the occlusal view showing the position of each transverse and sagittal slice; **B**, 3D image of the left lateral view showing the position of each horizontal slice; **C**, transverse slices; **D**, sagittal slices; **E**, horizontal slices. Each scale = 100 mm.

in IGPS-72699 as right m1–m3 and left m2–m3 in his original description of *Sl. pseudolatidens*. Later, Saegusa (2002) identified the preserved right lower teeth as m2–m3 lacking m1 based on the external crown observation. We support the Saegusa's (2002) conclusion that the preserved lower teeth of IGPS-72699 are right m2–m3 and left m3 (Figure 2B), as explained below.

On the right mandible, the CT images show no evi-

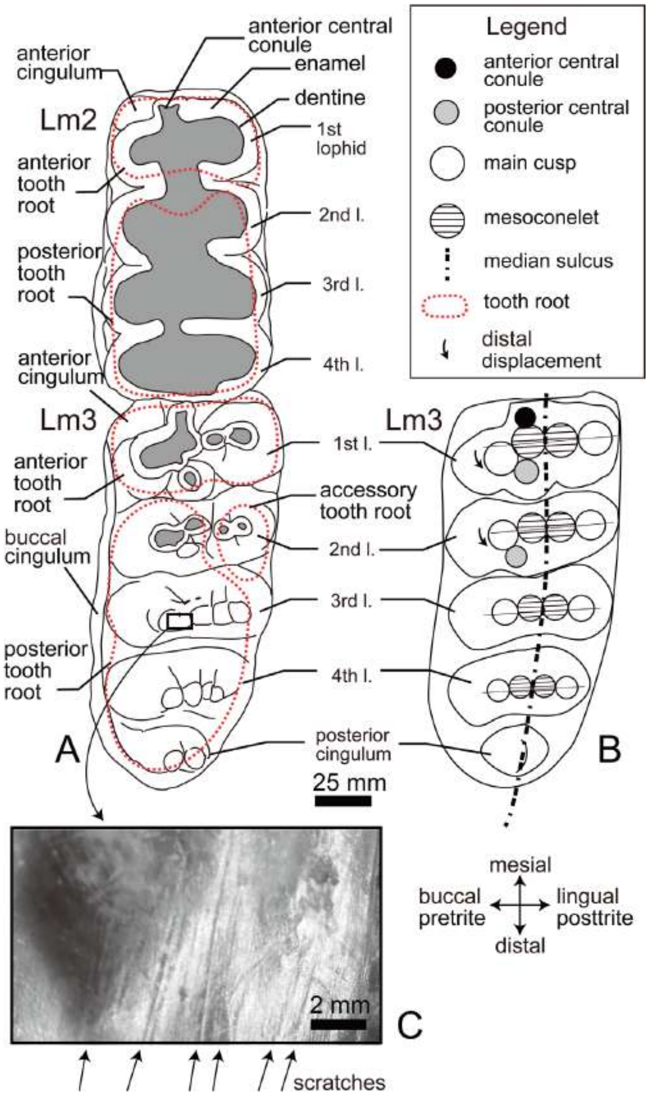

Figure 7. Line drawings of left m2–m3 of *Stegolophodon pseudolatidens*, ICCFM-416073. **A**, left m2–m3; **B**, schematic representation of left m3; **C**, close-up of the 3rd lophid of m3.

dence of any additional tooth poster to the most posterior tooth that can be observed externally (Figure 3D). Both of the posterior and anterior teeth have two main roots (the anterior root of m3 and the posterior root of m3, the anterior root of m2 and the posterior root of m2, respectively) (Figure 3C$_3$, 3D, 3E$_1$–E$_2$, 3F$_1$), indicating the presence of at least two molariforms in the right mandible (Figure 3D).

On the left mandible, an isolated lophid is preserved anterior to the most posteriorly preserved tooth, left m3 (Figure 2D$_1$). This lophid is likely the first or second lophid of m2/m3 because it has a posterior central conule (Figure 2D$_2$). It is less worn than the right m2, and its wear stage is nearly equal to that of left and right m3s (Figure 2A–B). Therefore, this lophid appears to be the first or second lophid of left m3. In stegodontids, the first lophid in m3 is supported by the anterior root, and the second and posterior lophids are supported by the accessory root and the posterior root (Saegusa *et al*., 2005; Saegusa and Haile-Selassie, 2009; Tassy, 2013). This left frontal lophid (Figure 2D$_1$) is independently supported by a root (Figure 3C$_6$), indicating that this lophid is the isolated first lophid of left m3. Therefore, the preserved lower tooth in the left mandible of IGPS-72699 is m3, which consists of five lophids and a posterior cingulum (Figure 2B).

Comparisons with the species of other genera

To elucidate the species variations in the functional morphology of the mandible, we compared and clarified the differences of the mandibular morphology of *Sl. pseudolatidens* with those of the following three species of the Elephantida in Figure 8: a gomphotheriid *Gomphotherium angustidens* Cuiver, 1817, a stegodontid *Stegodon trigonocephalu*s, and an elephantid *Elephas maximus*.

Mandibular angles.—Three indices of the mandible (Angles *a*, *b* and *c* in Figure 5; Wang *et al*., 2014) are useful to understand the evolutionary trend of the Elephantida. Angle *a* and *b* are related to the shortening of the mandible, and the shortening of the mandibular symphysis and development of the alveolus, respectively. Angle *c* is related to the position of the coronoid process. The mandibular morphology of *Sl. pseudolatidens* is likely intermediate between that of *G. angustidens* and [*S. trigonocephalus* + *E. maximus*], as explained below.

Based on the measurements presented (Figure 8), the typical long mandibular gomphotheriid, *G. angustidens* has relatively smaller Angle *a*, and larger Angles *b* and *c*, while *E. maximus* has correspondingly larger Angle *a*, and smaller Angles *b* and *c*. Angle *a* is similar among brevirostrine taxa without lower tusks (*S. trigonocephalus* and *E. maximus*). The stegodontids, *Sl. pseudolatidens* and *S. trigonocephalus* have intermediate Angles *b* and *c* among four species. Thus, the coronoid process is more posterior, and the mandibular corpus is more elongate in *G. angustidens*. The coronoid process is more anteriorly and the dentary deeper in *Sl. pseudolatidens*, *S. trigonocephalus*, and *E. maximus*. These morphological trends in the Elephantida imply the reduction and loss of lower tusks and the shortening of the mandible. The same trend has been observed by Wang *et al*. (2014) among four species of the Elephantida: long mandibular gomphotheriid, *Rhynchotherium shepardi*, brevirostrine taxa without lower tusks, *Sinomastodon jiangnanensis*, *Mammuthus trogontherii*, and *E. maximus*.

The mandibular ramus of *G. angustidens* is more pos-

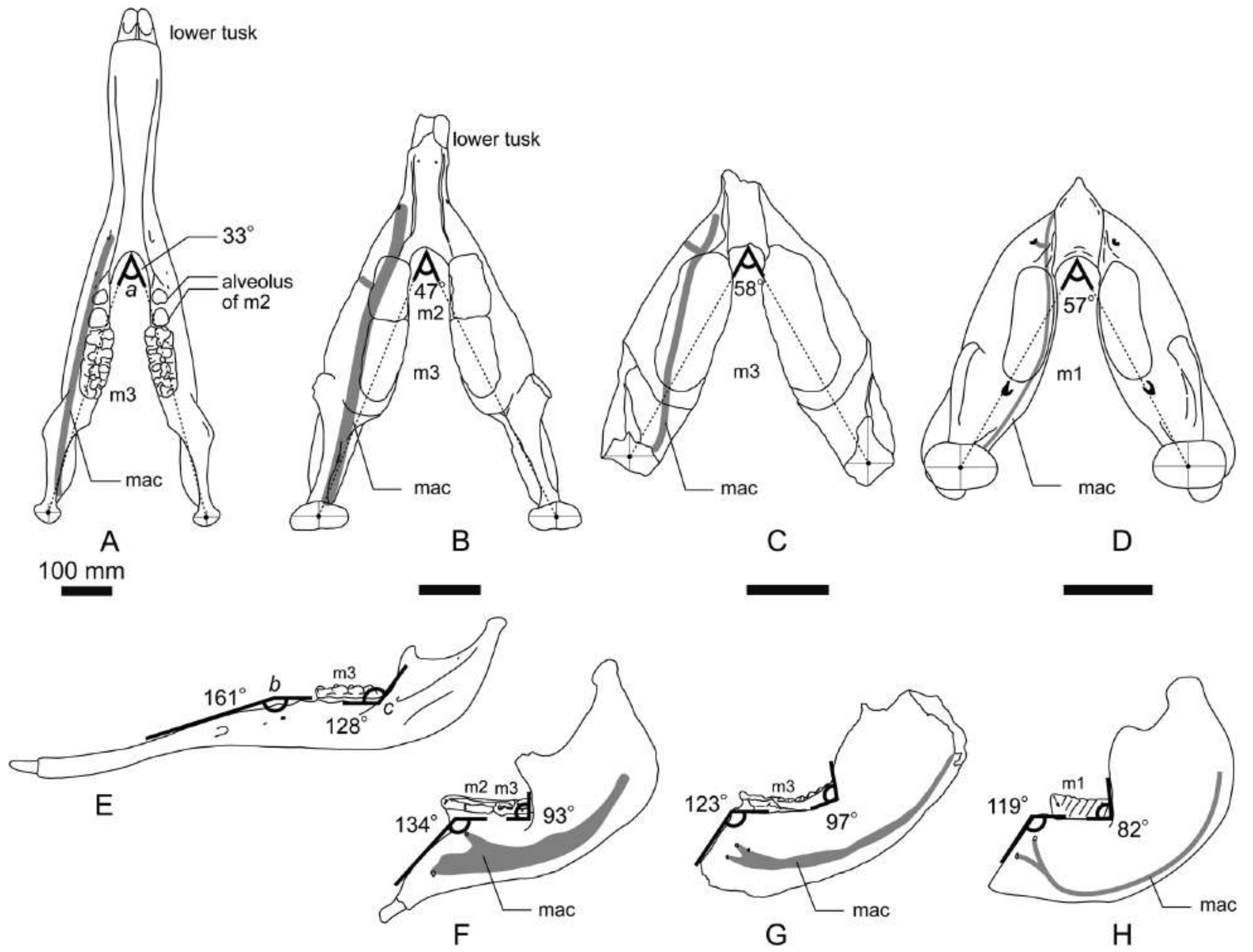

Figure 8. Comparison of the mandibles among four proboscidean species with the location (gray passage) of the left mandibular canal in occlusal and lateral views, and mandibular angles. **A**, **E**, *Gomphotherium angustidens*, MNHN-F-SEP187 (after Tassy, 2013) from the middle Miocene of France; **B**, **F**, *Stegolophodon pseudolatidens*, ICCFM-416073 from the lower Miocene of Japan; **C**, **G**, *Stegodon trigonocephalus*, INM-4-015283 from the Pliocene of Indonesia; **D**, **H**, Recent *Elephas maximus*, TMM-M-6445 (after Balanoff, 2003; Ferretti and Debruyne, 2011).

teriorly inclined than that of *Sl. pseudolatidens*, *S. trigonocephalus*, and *E. maximus*. The anterior surface of the ramus in the latter three is nearly perpendicular to the dorsal horizontal surface of the corpus (Angle *c*). According to Maglio (1970) and Wang *et al*. (2016), the ramal shape, combined with the cranial shape, is correlated with the distribution of jaw-closing muscles, and possibly represents feeding behavior. The difference of Angle *c* (variations in the morphology of the mandibular ramus) in these four species appears to be related to the evolution of the mastication style.

Pattern of mastication.—From the dental microwear observation on the occlusal surfaces of the molars, the jaw movement during mastication of the stegodontids has been considered to be a proal type (Saegusa, 1996a; Koenigswald, 2016). Although it is difficult to determine the direction of the jaw movement from fossil material in stegodontids, the direction can be confirmed with scratches in a mesial direction on the lower m3 fairly often occurring in the erupting part (Koenigswald, 2016). We show the scratches on the third lophid of m3 of *Sl. pseudolatidens* (Figure 7C). The jaw movement of the stegodontids is almost horizontal and is generally in a proal (mesial) direction. According to Koenigswald, (2016), this style is also observed in the Elephantidae, such as *Loxodonta africana* Blumenbach, 1797 and *E. maximus*. Therefore, *Sl. pseudolatidens* had probably acquired a proal jaw movement during mastication because the morphological characteristics of the mandibular ramus and the dental microwear of *Sl. pseudolatidens* are comparable to those of the Elephantidae.

Mandibular canal.—Ferretti and Debruyne (2011)

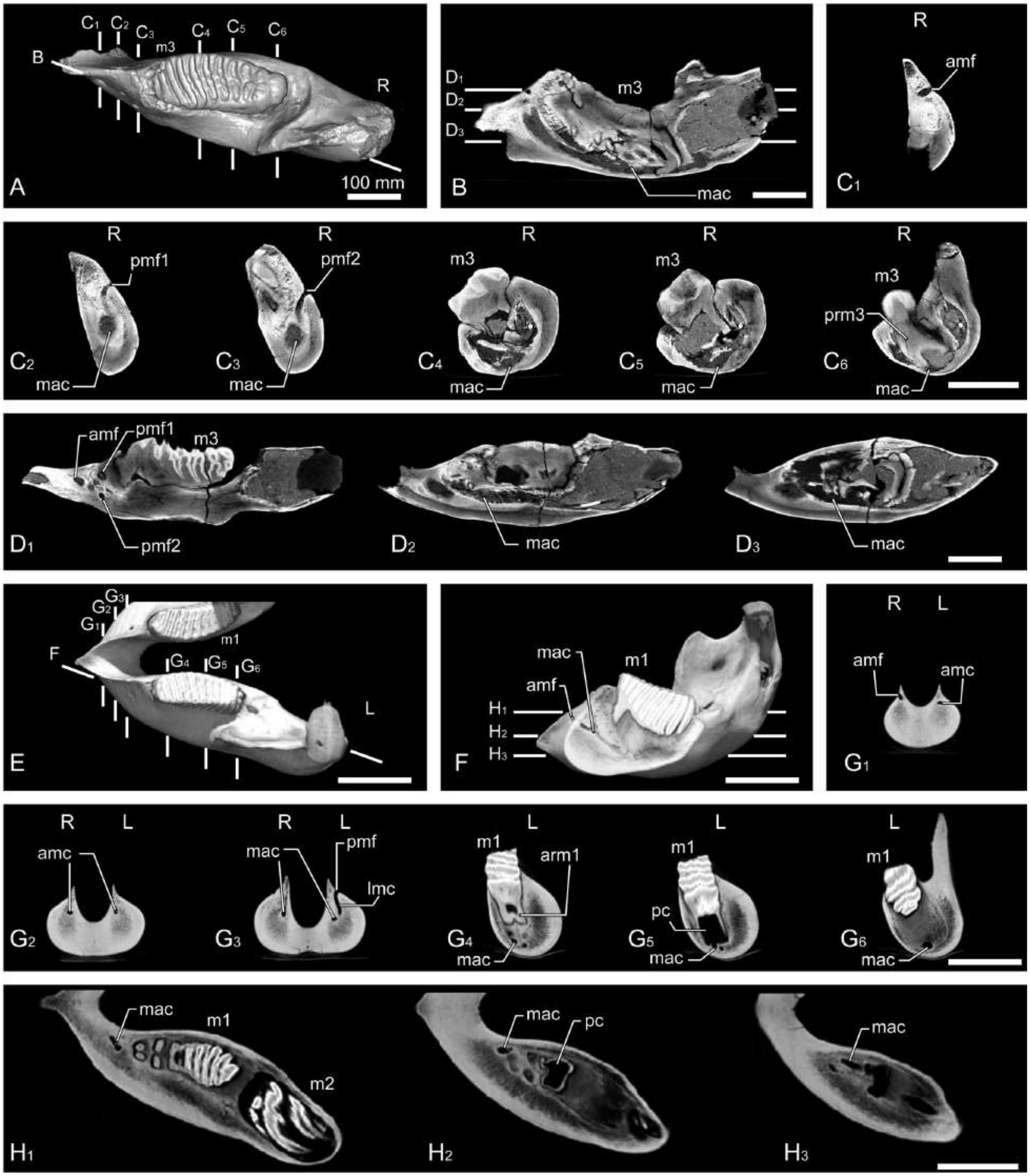

Figure 9. Serially sliced CT images of the mandibles of *Stegodon trigonocephalus* and *Elephas maximus*. **A**, 3D image of *S. trigonocephalus* (INM-4-015283) in the occlusal view showing the position of each sagittal and transverse slice; **B**, sagittal slice of *S. trigonocephalus* (INM-4-015283) showing the position of each horizontal slice; **C**, transverse slices of *S. trigonocephalus* (INM-4-015283); **D**, horizontal slices of *S. trigonocephalus* (INM-4-015283); **E**, 3D image of *E. maximus* (TMM-M-6445) in the occlusal view showing the position of each sagittal and transverse slice, after Balanoff (2003) and Ferretti and Debruyne (2011); **F**, sagittal slice of *E. maximus* (TMM-M-6445) showing the position of each horizontal slice; **G**, transverse slices of *Elephas maximus* (TMM-M-6445); **H**, horizontal slices of *E. maximus* (TMM-M-6445). The images of *S. trigonocephalus* (INM-4-015283) are horizontally inverted for comparison. Scale = 100 mm.

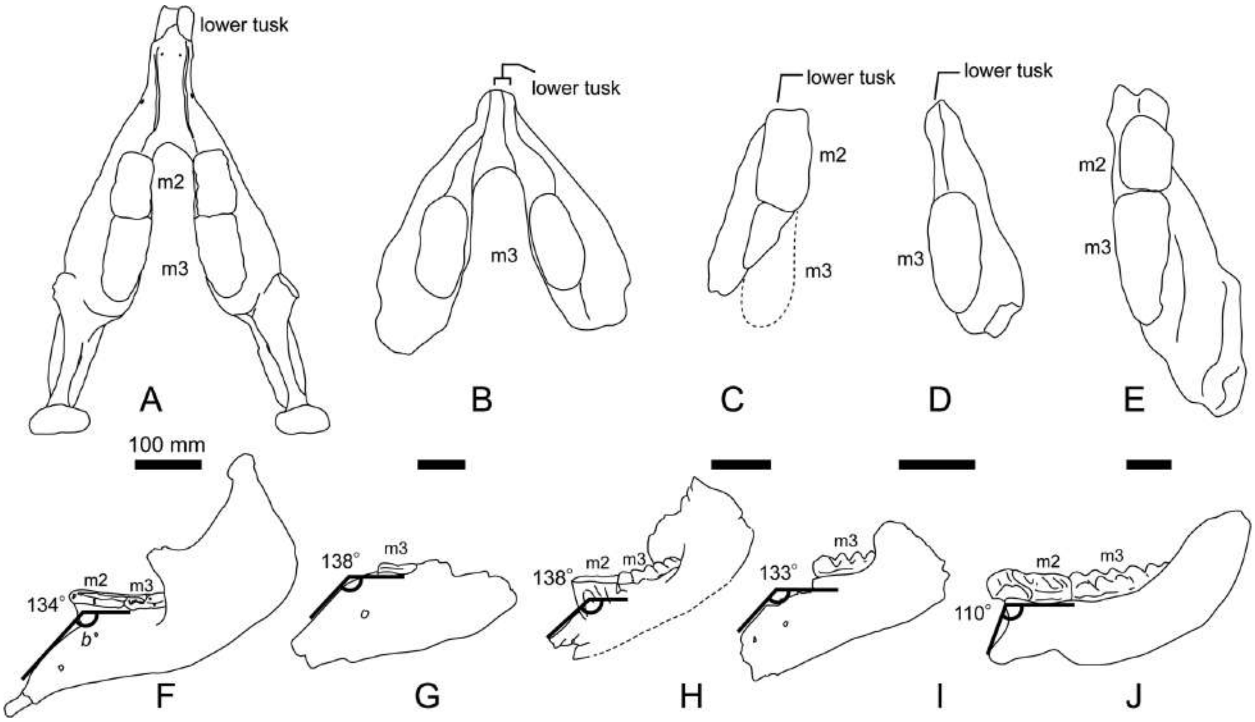

Figure 10. Line drawings for comparison of the mandibles in the genus *Stegolophodon*. **A**, **F**, *Stegolophodon pseudolatidens*, ICCFM-416073 from the lower Miocene of Japan; **B**, **G**, *Stegolophodon hueiheensis*, IVPP-V2400.1 from the lower Miocene of China (after Chow, 1959); **C**, **H**, *Stegolophodon nasaiensis*; (C, DMR-4734a; H, CMU-4732a) from the lower Miocene of Thailand (after Tassy *et al*., 1992); **D**, **I**, *Stegolophodon praelatidens*, DMR-TF6271 from the middle Miocene of Thailand (after Chavasseau *et al*., 2009); **E**, **J**, *Stegolophodon* cf. *stegodontoides*, YUDG-sbw009 from the upper Miocene of Myanmar (after Sein and Thein, 2008). A–E, occlusal views. F–J, lateral (medial) views (I–J, reversed). Scale = 100 mm.

revealed that the morphology of the mandibular canal and foramina reflects the phylogeny in several groups of the Proboscidea. Unfortunately, they did not illustrate that of the stegodontids. Here, we investigate the morphology of the mandibular canal of *Sl. pseudolatidens* and compare it with that of *G. angustidens*, *S. trigonocephalus*, and *E. maximus* (Figures 3, 6, 8–9). Ferretti and Debruyne (2011) showed that the mandibular canal of *G. angustidens* passes through the lateral side to the toothrow (the buccal side in the mandibular corpus) (Figure 8A). The middle segment of the mandibular canal extends along the buccal side in *Sl. pseudolatidens* and *S. trigonocephalus* (Figures 3C$_7$, 6C$_5$–C$_6$, 6E$_3$, 8B–C, 9C$_4$–C$_6$, 9D$_2$–D$_3$) but it does along the lingual side in *E. maximus* (Figures 8D, 9G$_4$–G$_6$, 9H$_2$–H$_3$; Ferretti and Debruyne, 2011). The mandibular canal position may be related to the hypsodonty trend in the proboscideans (Ferretti and Debruyne, 2011). The mandibular canals of *Sl. pseudolatidens* and *S. trigonocephalus* always pass through the buccal side (Figure 8B–C). However, it is located somewhere along the lingual side in *E. maximus* because the hypsodont molars occupy the greater part of the mandibular corpus (Figure 8D).

The presence of lower tusks reflects phylogenetic relationships (Tassy, 1996a). According to Maglio (1973), the decrease in dorsoventral diameters of the mandibular canal is likely related to the evolutionary trend of disappearing the lower tusks in the gomphotheriid-stegodontid-elephantid lineage. *Sl. pseudolatidens* has the lower tusks, but *S. trigonocephalus* and *E. maximus* lack them. The dorsoventral diameter of the mandibular canal in the anterior segment of *Sl. pseudolatidens* is the largest, that of *S. trigonocephalus* is intermediate, and that of *E. maximus* is the smallest (Figures 6, 8F–H, 9).

The mandibular canal morphology of *Sl. pseudolatidens* is likely more primitive than those of *S. trigonocephalus* and *E. maximus*. Our observation of the mandibular canal morphology supports the hypotheses by Ferretti and Debruyne (2011) and Maglio (1973).

Comparisons within the genus *Stegolophodon*

To clarify the species variations in the mandibular morphology among genus *Stegolophodon*, we compared the mandible of *Sl. pseudolatidens* with the following four *Stegolophodon* species: *Stegolophodon hueiheensis*, Chow, 1959; *Stegolophodon nasaiensis*, Tassy *et al*., 1992; *Stegolophodon praelatidens*, Koenigswald, 1959 (Chavasseau *et al*., 2009); and *Stegolophodon* cf. *stegodontoides* Pilgrim, 1913 reported from the upper Miocene of Myanmar by Sein and Thein (2008). We illustrated the outline of the occlusal and lateral (medial) views of the mandibles of these five species in Figure 10 based on figures and photographs in the literature.

Sl. pseudolatidens has a pair of small lower tusks. In *Sl. hueiheensis*, *Sl. nasaiensis*, and *Sl. praelatidens*, the presence of the lower tusks can also be confirmed or estimated (Figure 10A–D; Tobien *et al*., 1988; Tassy *et al*., 1992; Chavasseau *et al*., 2009). In contrast, the lower tusks have never been reported in *Sl. stegodontoides* (Figure 10E; Tassy, 1983; Sein and Thein, 2008; Thasod *et al*., 2011). *Sl. stegodontoides* is likely the most advanced among the genus *Stegolophodon* because the lower third molar shows straightly arranged cusps on the fourth and fifth lophids (Tassy *et al*., 1992; Saegusa *et al*., 2005). Although *Stegotetrabelodon maluvalensis* can be safely allocated to stegodontids (Saegusa *et al*., 2005), we do not mention this species due to the scarcity of the relevant literature and sufficient data.

In the lateral (medial) view, Angle *b* of *Sl. pseudolatidens* (134°) is comparable to that of *Sl. hueiheensis* (138°), *Sl. nasaiensis* (138°), and *Sl. praelatidens* (133°) and is larger than that of *Sl.* cf. *stegodontoides* (110°) (Figure 10F–J). Because a larger Angle *b* indicates a longer mandibular symphysis in primitive proboscideans within the gomphotheriid-stegodontid-elephantid lineage (Maglio, 1973; Wang *et al*., 2014), the shortened symphysis of *Sl.* cf. *stegodontoides* is likely a more advanced condition than that of *Sl. pseudolatidens*.

In sum, the mandibular morphology of *Sl. pseudolatidens* is as primitive as *Sl. hueiheensis*, *Sl. nasaiensis*, and *Sl. praelatidens*, and is more primitive than *Sl.* cf. *stegodontoides*.

Conclusions

The characteristics of the mandibular morphology of *Stegolophodon pseudolatidens* described here are as follows: the lower tusks are present, the ascending mandibular ramus is developed, and the ventral boundary of the mandibular symphysis is inclined ventrally in lateral view. Our CT analysis confirmed the conclusion by Saegusa (2002) that the preserved teeth of IGPS-72699 are right m2–m3 and left m3. *Sl. pseudolatidens* had probably acquired a proal jaw movement during mastication like the Elephantidae because the morphological characteristics of the mandibular ramus and dental microwear are comparable to those of the Elephantidae. Our results support the hypothesis by Ferretti and Debruyne (2011) that the morphology of the mandibular canal and foramina well reflects the phylogenetic relationships in the Proboscidea. Within the genus *Stegolophodon*, the mandibular characters of *Sl. pseudolatidens* are generally comparable to those of other species such as *Sl. hueiheensis*, *Sl. nasaiensis*, and *Sl. praelatidens*, and differs from those of *Sl*. cf. *stegodontoides* from the upper Miocene of Myanmar in having a longer symphysis, which is a primitive condition among the Stegodontidae.

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Author contributions

K. I. initiated the study and is primarily responsible for the observations on the fossils and their taxonomic analysis. K. I. and H. A. wrote the paper. K. S. and Y. K. contributed to anatomy and X-ray CT analysis. All authors contributed to the writing of the paper.