New hominoid mandible from the early Late Miocene Irrawaddy Formation in Tebingan area, central Myanmar

Masanaru Takai1*, Khin Nyo2, Reiko T. Kono3, Thaung Htike4, Nao Kusuhashi5, Zin Maung Maung Thein6

1Primate Research Institute, Kyoto University, 41 Kanrin, Inuyama, Aichi 484-8506, Japan
2Zaykabar Museum, No. 1, Mingaradon Garden City, Highway No. 3, Mingaradon Township, Yangon, Myanmar
3Keio University, 4-1-1 Hiyoshi, Kouhoku-Ku, Yokohama, Kanagawa 223-8521, Japan
4University of Yangon, Hlaing Campus, Block (12), Hlaing Township, Yangon, Myanmar
5Ehime University, 2-5 Bunkyo-cho, Matsuyama, Ehime 790-8577, Japan
6University of Mandalay, Mandalay, Myanmar

Received 14 August 2020; accepted 13 December 2020

Abstract A new medium-sized hominoid mandibular fossil was discovered at an early Late Miocene site, Tebingan area, south of Magway city, central Myanmar. The specimen is a left adult mandibular corpus preserving strongly worn M2 and M3, fragmentary roots of P4 and M1, alveoli of canine and P3, and the lower half of the mandibular symphysis. In Southeast Asia, two Late Miocene medium-sized hominoids have been discovered so far: Lufengpithecus from the Yunnan Province, southern China, and Khoratpithecus from northern Thailand and central Myanmar. In particular, the mandibular specimen of Khoratpithecus was discovered from the neighboring village of Tebingan. However, the new mandible shows apparent differences from both genera in the outline of the mandibular symphysis section. The new Tebingan mandible has a well-developed superior transverse torus, a deep intertoral sulcus (= genioglossal fossa), and a thin, shelf-like inferior transverse torus. In contrast, Lufengpithecus and Khoratpithecus each have very shallow intertoral sulcus and a thick, rounded inferior transverse torus. The characteristic morphology of the mandibular symphysis in the Tebingan specimen suggests a different taxon from Khoratpithecus. In central Myanmar at least two kinds of medium-sized hominoids were likely present in the early Late Miocene.

Key words: hominoid, Ponginae, mandibular symphysis, Southeast Asia

Introduction

Since the first Asian hominoid fossil was discovered from the Siwalik sediments of India/Pakistan in the 19th century (Lydekker, 1879), numerous hominoid fossils have been discovered and described as various taxa by early workers (e.g. Pilgrim, 1915, 1927; Gregory et al., 1935; Pilbeam et al., 1990; Pilbeam, 1997; Ward, 1997; Kelley, 2002, 2005). Their classification has long been disputed among researchers because most of these specimens are isolated teeth and/or fragmentary jaw materials showing large variation in size and morphology. It is now widely recognized that they consist of two genera: the large-sized Indopithecus (formerly known as Gigantopithecus), including the single species, I. giganteus; and the medium-sized Sivapithecus, including three species, S. indicus, S. sivalensis, and S. parvada (Kelley, 2002, 2005). Some researchers also propose another, smaller species, S. hysudricus (or S. simonsi) (Kay, 1982; Pickford, 2010; Bhandari et al., 2018). To date, the localities of Sivapithecus fossils are limited to South Asia, from northeastern Pakistan through northwest India to western Nepal (Munthe et al., 1983; Kelley, 2002). Although some Late Miocene hominoids discovered in southern China and west Asia had once been assigned to Sivapithecus (Andrews and Tekkaya, 1980; Wu and Oxnard, 1983), they are now recognized as different genera, Lufengpithecus and Ankara-pithecus, respectively (Alpagut et al., 1996; Begun and Güleç, 1998; Kelley, 2002; Kappelman et al., 2003). Regardless of distribution, Sivapithecus has been considered as the ancestral form of extant Pongo (orangutan), mainly based on the strong similarity in facial morphology. However, several postcranial bones of Sivapithecus, especially humerus and carpals, are not similar to those of extant Pongo, suggesting differences in their positional behavior (Pilbeam et al., 1990; Pilbeam, 1997; Richmond and Whalen, 2001; Madar et al., 2002; Begun, 2015).

Recently a new fossil hominoid, Khoratpithecus, including the two species K. chiangmuanensis and K. piriyai, was discovered at the early Late Miocene sites in northern and northeastern Thailand (Chaimanee et al., 2003, 2004, 2006). In particular, the almost complete mandible of Khorat-pithecus piriyai, discovered from the Late Miocene site of...
Nakhon Ratchasima Province (Khorat), shows strong similarity to that of extant *Pongo*, suggesting a close relationship between *Khoratpithecus* and *Pongo* (Chaimanee et al., 2004, 2006). In addition, the discovery of *Khoratpithecus aveyarwadyensis* from the lower Upper Miocene near Magway, central Myanmar, expanded the distribution of *Khoratpithecus* westward to Myanmar (Jaeger et al., 2011).

The new hominoid mandible we introduce here was discovered from the early Late Miocene sediments in the Tebinggan area, south of Magway, that neighbors the Yinseik area where an isolated molar of *Khoratpithecus* was collected (Figure 1, Jaeger et al., 2011). The precise stratigraphic correlation between strata of the two areas has yet to be well established. The lithological analysis suggests that the fossil-yielding horizon in the Yinseik area may be slightly lower than in the Tebinggan area (see below for details).

**Materials and Methods**

The present mandibular specimen was scanned with computed tomography (CT) using a microfocal X-ray CT system (TXS320-ACTIS; TESCO, Tokyo, Japan). The original scans were taken at 204 kV and 0.2 mA with a 0.5-mm-thick copper plate prefilter to lessen beam-hardening effects. The scanned images were reconstructed into a 512 × 512 matrix of 0.2-mm pixel size with 0.2-mm slice interval and thickness. The mandible and its dentition were segmented from the CT scan image stack, and then their polygon surfaces were generated and visualized using Avizo Lite version 9.0.1 software (FEI, Thermo Fisher Scientific, Waltham, MA, USA).

The surface configurations of casts of Late Miocene hominoids were scanned using a one-shot three-dimensional (3D) measurement macroscope (VR-3050; Keyence, Osaka, Japan) and an all-direction 3D scanner (VL-300; Keyence).

**Institutional abbreviations**

MZKB-K, Zaykabar Museum, Yangon, Myanmar.
NMMP-KU-IR, National Museum of Myanmar, Paleontology–Kyoto University–Irrawaddy specimen, Myanmar.

**Geological Setting and Tebingan Mammal Fauna**

The present mandibular specimen was collected by a villager during farm work in December 2016 at the SMG1 site, near Sanmagyi village, Tebingan area, about 50 km southeast of Magway city (Figure 1; the Tebingan area described in this paper includes several villages: Tebingan, Inbingan, Alebo, and Sanmagyi). The authors confirmed the SMG1 site in the presence of the discoverer in March 2018. The strata of the Tebingan area generally dip slightly northeast and almost horizontally around the SMG1 site (Figure 1; Supplementary Figure 1). The horizons of the SMG1 site correspond to the lowermost part of the Irrawaddy Formation (Figure 2).

The Irrawaddy Formation consists of Late Miocene to Early Pleistocene non-marine sediments widely distributed along the Ayeyarwaddy (= Irrawaddy) and Chindwin rivers in central Myanmar. It has been traditionally subdivided into lower and upper parts based on paleontological and lithological criteria (Stamp, 1922; Pilgrim, 1937, 1939; Colbert, 1938, 1943; Bender, 1938, 1943; Colbert, 1938, 1943; Bender, 1983; Nishioka et al., 2015; Zin Maung Maung Thein et al., 2017). The lower part of the formation is correlated to the Nagri and Dhok Pathan formations in the

![Image](image_url)
Middle Siwaliks, and possibly to the uppermost part of the Chinji Formation in the Lower Siwaliks. Accordingly, the Lower Irrawaddy fauna are dated between the latest Middle Miocene and the Early Pliocene (Colbert, 1938; Chavasseau et al., 2006, 2013; Zin Maung Maung Thein et al., 2011; Takai et al., 2015, 2016; Naing Maw Than et al., 2017). The upper part of the Irrawaddy Formation is correlated with the Upper Siwaliks, which is dated from the Late Pliocene to the Early Pleistocene (Colbert, 1938, 1943; Bender 1983; Zin Maung Maung Thein et al., 2011, 2017).

In the Tebingan area, the fluvial Irrawaddy Formation overlies the shallow marine Obogon Formation (mainly tidal deposits) of the Pegu Group. Although the former formation is generally considered to unconformably overlie the latter (Zin Maung Maung Thein et al., 2008, 2011, 2017; Chit Sein et al., 2009, 2011, 2017), the two formations are conformable in this area (Figure 2; Supplementary Figure 2). The lithological succession in the area shows that tidal deposits grade upward into fluvial deposits, with the transition zone characterized by interbedded tidal and fluvial deposits. Most of the Tebingan vertebrate fossils are likely collected from the lowermost part of the Irrawaddy Formation (Figure 2), and some of them are likely from upper parts of the Obogon–Irrawaddy transition zone. Unfortunately, no volcaniclastic sediments providing reliable numerical depositional age have been discovered in the area. For this reason, the age of Tebingan vertebrate fossils is estimated from the combination of several mammal genera with well-established chronological distributions in the Siwalik deposits in northern Pakistan (Table 1, Barry et al., 2002). Namely, the presences of *Hipparion cf. theobaldi* (Equidae, Perissodactyla), *Anisodon* sp. (Chalicotheriidae, Perissodactyla), *Bramatherium megacephalum* (Giraffidae, Artiodactyla), and *Hippopotamodon sivalense* and *Tetraconodon* spp. (Suidae, Artiodactyla) suggest 10–8 Ma for the Tebingan sediments. In addition, the absence of *Hexaprotodon* (Hippopotamidae, Artiodactyla) and *Sivachoerus* (Suidae, Artiodactyla) supports this age because both genera are supposed to have appeared in the late Late Miocene (Barry et al., 2002; Zin Maung Maung Thein et al., 2011; Nishioka et al., 2015; Thaung Htike and Takai, 2016).

Jaeger et al. (2011) reported two *Khoratpithecus* specimens, a right M² (MFI 89, described as *Khoratpithecus* sp.) and a left mandible (MFI-K 171, described as *Khoratpithecus ayeyarwadyensis*), discovered from the Magway area (Jaeger et al., 2011). The former was collected by the Myanmar–French Paleontological Team at the YS1 site in Yinseik, about 30 km northwest of SMG1 (Figure 1), but the exact locality of the latter, *K. ayeyarwadyensis*, is uncertain (Jaeger et al., 2011; Chavasseau et al., 2013). The YS1 site of MFI 89 lithologically corresponds to the Obogon–Irrawaddy transition zone, suggesting it is possibly stratigraphically slightly lower than the SMG1 site of MZKB-K-001. The Tebingan and Yinseik mammal fauna (Table 1, Table 2) show strong similarity to each other, except for the lack of *Bramatherium* (Giraffidae) in Yinseik, which is one of the most abundant fossils in the Tebingan area.

### Systematic Paleontology

**Order Primates Linnaeus, 1758**

**Family Hominidae Gray, 1825**

**Subfamily Ponginae Elliot, 1913**

**Ponginae gen. et sp. indet.**

**Specimen:** Adult left mandibular corpus preserving M₂–3, fragmentary M₁, root of P₃, and alveoli of C–P₃, MZKB-K-001 (Figure 3, Figure 4).

**Locality:** SMG1 (N 19°51.356'E 95°54.2'), Sammagyi village, Alebo Township, (referred to as the Tebingan area in this paper), Magway Region, central Myanmar (Figure 1).

**Age:** early Late Miocene (about 10–8 Ma).

**Description of the material**

An almost complete left mandibular corpus, preserving M₂–3, fragmentary roots of P₃–M₁, and alveoli of C–P₃. The posterior part of the corpus is broken about 1 cm posterior to M₁, lacking the mandibular ramus and angle. Incisal alveoli are likely missing around the mandibular symphysis, and in particular, the I₁ alveolus is completely missing. The hori-
The horizontal section of the lower canine root is almost ovoid, with the buccal side wider than the lingual side. Judging from the preserved alveolus, P3 is double rooted: the mesiobuccal root is much smaller than the posterior root and located just buccal to the lower canine. There is no distinct diastema between the lower canine and P3. P4–M3 are all double-rooted (Figure 5).

The crowns of M2 and M3 are heavily and flatly worn. Because of this wear, enamel crenulations are not observed in the present specimen. Although the crown enamel is lacking at the mesiolingual corner and buccal side on M1 and the mesiobuccal and distolingual corners on M2, the original crown outlines of both teeth are likely oval without waisting at the midpoint. As for the crown area, M2 is almost the same size as M3, and M1 is much smaller than M2, although the tooth crown of M1 is broken. The crown sizes of M2 and M3 fall within the range of medium-sized Sivapithecus (S. indicus and S. sivalensis) and Khoratpithecus, although only four specimens of Khoratpithecus have been reported (two of them belong to the same individual) (Figure 6, Table 3, Supplementary Table 1).

The heavily worn molars indicate an adult, and the canine alveolus is too poorly preserved to allow determination of the individual’s sex. At the symphyseal section, both superior and inferior transverse tori are well developed with a deep intertoral sulcus (= genioglossal fossa or genial fossa). The posterior end of the inferior transverse torus protrudes as posteriorly as P4, forming a shelf-like structure (Figure 4, Figure 7). A small but distinct foramen is open just lateral to the fracture surface of the intertoral sulcus (Figure 4e). The mandibular corpus becomes slightly shallow posteriorly. On the buccal side of the mandible, the single mental foramen is open below P3, at about half of the corpus height, and a shallow mandibular buccal depression is present below P4 to M1. The base of the mandibular ramus is well inflated buccally, and the buccinator groove between the anterior ridge of the

| Table 1. Tebingan mammal fauna. |
|---------------------------------|
| PRIMATES                        |
| Ponginae                        |
| gen. et sp. indet.              |
| CARNIVORA                       |
| Amphicyonidae                   |
| Amphicyoninae gen. nov.         |
| Ursiidae                        |
| Indarctos sp.                   |
| Felidae                         |
| Amphimachairodus sp. indet.     |
| gen. et sp. indet.              |
| PROBOSCIDEA                     |
| Mammutidae                      |
| Mammut sp.                      |
| Gomphotheriida                  |
| Tetralophodon cf. xiaohensis    |
| Tetralophodon sp. indet.        |
| Stegodontidae                   |
| Stegolophodon stegodontoides    |
| Stegolophodon sp. indet.        |
| PERISSODACTYLA                  |
| Equidae                         |
| Hipparion cf. theohaldi         |
| Chalicotheriida                 |
| Anisodon sp.                    |
| Rhinocerotidae                  |
| cf. Rhinoceros sp.              |
| Brachytherium perimense         |
| Brachytherium fatehjangense     |
| ARTIODACTYLA                    |
| Anthracotheriida                |
| Merycopotamus medioximus         |
| Microbunodon milaensis          |
| Bovidae                         |
| Selenoportax sp. indet.         |
| Pachyportax latidens            |
| Pachyportax giganteus           |
| Suidae                          |
| Tetraconodon irrmedius          |
| Tetraconodon irragnamus         |
| Hippopotamodon sivalensis       |
| Propotamochoerus hysudricus     |
| Propotamochoerus cf. wui        |
| Giraffidae                      |
| Bramatherium megacephalum       |

| Table 2. Yinseik mammal fauna (from Jaeger et al., 2011). |
|---------------------------------|
| PRIMATES                        |
| Hominidae                       |
| Khoratpithecus ayeyarwadyensis  |
| CARNIVORA                       |
| Fam. gen. et sp. indet.         |
| PROBOSCIDEA                     |
| Stegolophodon/Tetralophodon sp. |
| PERISSODACTYLA                  |
| Equidae                         |
| Hipparion (s.l.) sp.            |
| Chalicotheriida                 |
| gen. et sp. indet.              |
| Rhinocerotidae                  |
| gen. et sp. indet.              |
| ARTIODACTYLA                    |
| Suidae                          |
| Tetraconodon minor              |
| cf. Hippopotamodon sivalensis   |
| Propotamochoerus cf. hysudricus |
| Palaeochoerida                  |
| Schizochoerus sp.               |
| Tragulidae                      |
| gen. et sp. Indet. (medium-sized)|
| Bovidae                         |
| Antilopini indet.               |
| gen. et sp. indet.              |
| gen. et sp. indet. 2            |
| Anthracotheriida                |
| Merycopotamus medioximus         |

ing at the mesiolingual corner and buccal side on M1 and the mesiobuccal and distolingual corners on M2, the original crown outlines of both teeth are likely oval without waisting at the midfoot. As for the crown area, M2 is almost the same size as M3, and M1 is much smaller than M2, although the tooth crown of M1 is broken. The crown sizes of M2 and M3 fall within the range of medium-sized Sivapithecus (S. indicus and S. sivalensis) and Khoratpithecus, although only four specimens of Khoratpithecus have been reported (two of them belong to the same individual) (Figure 6, Table 3, Supplementary Table 1).

The heavily worn molars indicate an adult, and the canine alveolus is too poorly preserved to allow determination of the individual’s sex. At the symphyseal section, both superior and inferior transverse tori are well developed with a deep intertoral sulcus (= genioglossal fossa or genial fossa). The posterior end of the inferior transverse torus protrudes as posteriorly as P4, forming a shelf-like structure (Figure 4, Figure 7). A small but distinct foramen is open just lateral to the fracture surface of the intertoral sulcus (Figure 4e). The mandibular corpus becomes slightly shallow posteriorly. On the buccal side of the mandible, the single mental foramen is open below P3, at about half of the corpus height, and a shallow mandibular buccal depression is present below P4 to M1. The base of the mandibular ramus is well inflated buccally, and the buccinator groove between the anterior ridge of the
ramus and M₃ is rather wide. At the lingual side of the mandible, a distinct mylohyoid line extends straight from about 1 cm below M₃ to the inferior transverse torus of the mandibular symphysis (Figure 4c, Figure 5b, Figure 8). In the
occlusal view, M₂–M₃ are located in almost a straight line, and the tooth-row of C–P₄ curves gradually lingually.

**Comparisons with Extant and Extinct Taxa**

**Structure of mandibular symphysis**

In studies of Miocene hominoids, the midsagittal outline shape of the mandibular symphysis has been considered important for classification (Smith-Woodward, 1914; Simons and Chopra, 1969; Kelley and Pilbeam, 1986; Ward and Brown, 1986; Brown and Ward, 1988; Brown, 1989, 1997; Daegling, 1993, 2001; Daegling and Jungers, 2000; Sherwood et al., 2005; Jaeger et al., 2011). In MZKB-K-001, although the upper part of the mandibular symphysis is broken, the reconstructed CT image and the sagittal sections of the preserved part indicate that the superior transverse torus is very thick and strongly developed, the intertoral sulcus (= genial fossa or genioglossal fossa) is deep, and the inferior transverse torus is thin and shelf-like, extending posteriorly (Figure 7, Figure 9a). In *Sivapithecus*, although there is considerable variation, the mandibular symphysis is characterized by well-developed superior and inferior tori and a deep intertoral sulcus, but the posterior margin of the inferior transverse torus is thick and rounded (Figure 9b). In *K. piriya* (RIN 765, an almost complete mandibular specimen), the mandibular symphysis inclines more anteriorly than in *Sivapithecus* and *Lufengpithecus*, the superior transverse torus is not distinct, the geniofossa is quite shallow, and the inferior transverse torus is dorsoventrally thick and rounded (Chaimanee et al., 2004, 2006; Jaeger et al., 2011) (Figure 9c2). In *K. ayeyarwadyensis* (MFI-K171), although the real mandibular symphyseal section is broken, the outline of the fracture surface suggest that the superior transverse torus is not strongly developed, the genial fossa is quite shallow, and the inferior transverse torus is thick and rounded without protruding posteriorly as was the case in *K. piriya* (Figure 9c1). In *Lufengpithecus*, the superior transverse torus is indistinct, the genial fossa is shallow, and the inferior torus is dorsoventrally quite thick and bulbous (Figure 9d). However, the basal margin of the mandibular symphysis does not protrude inferoposteriorly but instead looks ‘truncated’ below the inferior torus (Figure 9d). In *Indopithecus*, both superior and inferior transverse tori are indistinct, and the inferior transverse torus does not extend posteriorly (Figure 9e). In *Ankarapithecus*, both superior and inferior transverse tori are distinct, and the inferior torus protrudes posteriorly, but the superior transverse torus is positioned much lower than in *Sivapithecus* and MZKB-K-001 (Begun and Güleç, 1998; Kappelman et al., 2003) (Figure 9f). In the extant *Pongo*, the mandibular symphysis inclines 50°–60° anteriorly, and both superior and

---

Table 3. Dental and mandibular measurements of MZKB-K-001. Parentheses show the estimated values because of the partially broken tooth.

| M₂ | M₃ | Mandibular corpus |
|----|----|------------------|
| BL | BL | Height | Width |
| MD | trd | tad | | P₄ | M₁ | M₂ | M₃ | P₄ | M₁ | M₂ | M₃ |
| MZKB-K-001 | 13.90 (12.30) | 11.30 | 14.65 (13.00) | 12.20 | 39.88 | 39.34 | 37.54 | 37.02 | 20.54 | 19.05 | 18.28 | 23.81 |
inferior transverse torus are well developed with moderately deep genial fossa. The inferior transverse torus extends posteriorly to \( P_4 - M_1 \), although with considerable shape variations between individuals (Figure 9g). Sherwood et al. (2005) reported low sexual dimorphism in the symphyseal outline shape of extant \textit{Pongo}.

Thus, concerning its mandibular symphyseal outline shape, MZKB-K-001 differs from the pattern seen in the two extinct Southeast Asian hominoids, \textit{Khoratpithecus} and
Lufengpithecus. However, it shows some similarity to Sivapithecus and extant Pongo in having well-developed superior and inferior transverse tori and a deep genioglossal fossa. The variation pattern seen in extinct hominoids suggests that the development of the superior transverse torus and the deepening of the genioglossal fossa may correlate to each other (Daegling, 1993).

Distinct impressions or fossae for the anterior digastric muscle are usually observed at the base of mandibular symphysis in humans and African great apes. These are not seen in the Asian great apes (Pongo) because their anterior digastic muscle is absent (Smith-Woodward, 1914; Brown and Ward, 1988; Brown, 1989). In fossil taxa the digastric fossae are not observed in the two mandibles of Khoratpithecus (Chaimanee et al., 2004, 2006; Jaeger et al., 2011) but are reported in Lufengpithecus (Schwartz, 1997; Xu and Lu, 2008), Ankarapithecus (Begun and Güleç, 1998; Kappelman et al., 2003), and in many specimens of Sivapithecus (Ward and Brown, 1986; Brown and Ward, 1988; Brown, 1989). In MZKB-K-001 no distinct impressions are observed at the basal lingual surface of the inferior transverse torus (Figure 3d, Figure 4e), suggesting the lack of an anterior digastic muscle in this individual, as in extant Pongo. However, there is only one sample of the Tebingan hominoid at present.

**Dentition, dental arcade, and mandibular corpus**

Among the Middle to Late Miocene Asian hominoids, including Sivapithecus, Khoratpithecus, Lufengpithecus, Indopithecus, and Ankarapithecus, the lower canine and premolars are usually positioned more laterally than M1 and M2 in the cheek tooth row, and the major axis of M3 often rotates distolaterally (Figure 10a, e–g). Therefore, the straight or buccally concave cheek tooth row is retained in most specimens of Sivapithecus (e.g. GSP4622, GSP6160, GSP15000, GSP16077, AMNH 19412), Khoratpithecus (RIN765 and MFI-K171) (Chaimanee et al., 2004, 2006; Jaeger et al., 2011), Lufengpithecus (PA580, PA948) (Xu and Lu, 2008), Indopithecus (CYP359/68) (Simons and Chopra, 1969), and Ankarapithecus (AS95-500) (Kappelman et al., 2003) (Figure 11). It is notable that some of them are considered female specimens based on the size and shape of canine and/or P3: namely, Sivapithecus (GSP6160), Lufengpithecus (PA580), and Indopithecus (CYP359/68). In contrast, MZKB-K-001 preserves a buccally convex cheek tooth row because the alveoli of canine and premolars are situated more medially than molars and M3 does not rotate distolaterally (Figure 3c). Interestingly, one female Gigantopithecus mandibular specimen (Mandible I, PA77) shows a parabolic dental arcade with relatively small lower incisors as seen in MZKB-K-001 (Zhang and Harrison, 2017, figure 3D). In Figure 11, several patterns of the synthetic dental arcade of MZKB-K-001 are presented using the mirror image. The left and right corpora are arranged more distally diverged in a3 and b3 than in a1 and b1. In the a1–a3 models the corpora are arranged adjacent to each other, because the inferior mesiolingual corner of the symphyseal section protrudes distally, suggesting the presence of the midline ridge at the mandibular symphysis (indicated by the arrows in Figure 4b and Figure 8a1). The space between the lower canines might be too small for lower four incisors in these models, however, and therefore in the b1–b3 models, the corpora are arranged more widely separated to ensure space for lower incisors. In these models the assumption is that a relatively large midline ridge would be present at the symphyseal part of the mandible (Figure 11).

Judging from the preserved space of the incisor alveoli, the lower incisors of MZKB-K-001 would have been relatively small, although the incisal alveolar region is missing. Even in the widely separated models (Figure 11b), the presumed space for lower incisors is very narrow, in compari-
son with the almost complete mandible of K. piriya\textit{i}. The narrow incisor space in MZKB-K-001 is probably caused by the buccally convex tooth row.

The canine external rotation, the typical feature of \textit{Sivapithecus}, is not clearly observed in MZKB-K-001 because only the basal part of the canine alveolus is preserved. Compared with \textit{K. piriya\textit{i}} (RIN765), however, the major axis of the lower canine alveolus of MZKB-K-001 is more externally rotated in any synthetic dental arcade model (Figure 11). Note that lower canine alveoli of MZKB-K-001 (a, b) show more external rotation than in \textit{K. piriya\textit{i}} (c). The reconstructed 3D image was obtained using a 3D scanner. Not to the same scale.

In MZKB-K-001, M\textsubscript{1}–M\textsubscript{3} are double rooted, and all roots except the distal root of M\textsubscript{1} are buccolingually wide and tabular shaped (Figure 5). The M\textsubscript{1} distal root forms a trigonal pyramid. The tooth roots of M\textsubscript{2,3} are relatively long, extending as deep as half of the mandibular corpus. The M\textsubscript{1} roots are slightly shorter than those of M\textsubscript{2,3} in MZKB-K-001, as in two mandibles (RIN765 and MKI-K171) of \textit{Khoratpithecus} (Chaimanee et al., 2006; Jaeger et al., 2011). In contrast, the tooth roots of M\textsubscript{1} are much shorter than those of M\textsubscript{2,3} in \textit{Sivapithecus} (Brown, 1997). In a female \textit{Gigantopithecus} mandibular specimen (Mandible No. 1, PA77), the roots of M\textsubscript{1} and M\textsubscript{2} are almost the same length, and those of P\textsubscript{4} are slightly longer than those of lower molars (Kupczik and Dean, 2008). In extant great apes M\textsubscript{1} roots are much shorter than those of M\textsubscript{1} and M\textsubscript{2}, and P\textsubscript{4} roots are slightly shorter than those of M\textsubscript{1} and M\textsubscript{2} in \textit{Gorilla} and \textit{Pongo} but slightly longer in \textit{Pan} (Kupczik and Dean, 2008). In MZKB-K-001, P\textsubscript{4} retains double roots, which are slightly longer than those of M\textsubscript{1} (Figure 5). On M\textsubscript{1}, the anterior root is slightly shorter than the posterior one, whereas the anterior root is longer on P\textsubscript{4}.

**Discussion**

MFI-K171 (\textit{K. ayeyarwadyensis}) and MZKB-K-001 are left mandibular corpora of the medium-sized hominoids discovered from neighboring areas of Yinsen and Tebingan, respectively (the exact locality of MFI-K171 is uncertain, but it is treated here as being discovered in Yinsen). Therefore, an initial, natural inference would be that MZKB-K-001 belongs to the same genus as MFI-K171, \textit{Khoratpithecus}. However, as noted, the mandibular symphysis of MZKB-K-001, despite the unfortunate absence of the upper part, shows quite a different pattern from that of \textit{Khoratpithecus}. MZKB-K-001 retains a well-developed thick superior transverse torus, a deep genioglossal fossa, and a posteriorly extending labiogingually thin, shelf-like inferior transverse torus (Figure 9a). In contrast, two mandibular specimens of \textit{Khoratpithecus}, RIN765 (= TF 6223, K. piriya\textit{i}) and MFI-K171 (\textit{K. ayeyarwadyensis}), display the same pattern of symphysis section outline shape: the former is an almost complete male mandible without deformation at the symphysis, discovered from northern Thailand, and the latter is the hemimandible discovered probably from Yinsen as mentioned above. The mandibular symphysis section of \textit{K. piriya\textit{i}} (RIN765) has a weak superior transverse torus, a shallow genioglossal fossa, and a thick, rounded, inferior transverse torus (Chaimanee et al., 2004; Figure 9c2). In \textit{K. ayeyarwadyensis} (MFI-K171), despite damage to the posterior part of the symphysis, a weak superior transverse torus, shallow genioglossal fossa, and thick, rounded inferior transverse torus are reconstructed (Jaeger et al., 2011). Although MFI-K171 has a much shorter symphysis than RIN765, the similar pattern of the symphysis section seen in both specimens suggests a stable morphological condition in this genus (Figure 9c).

A possible hypothesis to explain morphological differences between the two \textit{Khoratpithecus} specimens and MZKB-K-001 is sexual dimorphism, because both RIN765 and MFI-K171 are considered adult male specimens (Chaimanee et al., 2004, 2006; Jaeger et al., 2011). Could the symphysis section outline of the MZKB-K-001 repre-
sent a female feature of *Khoratpithecus*? Plenty of mandibular specimens of *Sivapithecus* discovered to date do not support this hypothesis: the combination of the well-developed superior and inferior transverse tori and deep intertoral sulcus is observed in some male specimens (e.g. GSP9564, GSP15000). Therefore, sexual dimorphism of *Khoratpithecus* is implausible as an explanation for the morphological difference between MZKB-K-001 and RIN765. The Tebingan hominoid MZKB-K-001 is likely to be a different taxon from *Khoratpithecus*, although we still have just one mandibular specimen and far from a reliable identification for it.

If the Tebingan hominoid belongs to a different genus from *Khoratpithecus*, another question is now on the table regarding the distribution of early Late Miocene hominoids in central Myanmar. As noted, Yinseik and Tebingan are regarding the distribution of early Late Miocene hominoids from it.

For it.

Identification of the taxonomic position of the Tebingan hominoid MZKB-K-001 is likely to be a different taxon from *Khoratpithecus*, although we still have just one mandibular specimen and far from a reliable identification for it. This question requires additional specimens preserving the complete or almost complete mandibular symphysis for identification of the taxonomic position of the Tebingan hominoid.

Acknowledgments

We are grateful to Mr. U Khin Shwe, the director of Zaykabar Museum, Yangon, for allowing us to study the present hominoid specimen. We also thank the staff of the Department of Archaeology and National Museum for their help in our paleontological research in Myanmar, and all Japanese research members who participated in the fieldwork in Myanmar. We thank Dr. Jay Kelley of Arizona State University for his precious advice and for graciously providing access to the casts and original specimens of *Sivapithecus* at their respective institutions. We also thank Dr. Pratueung Jintasakul, Director of the Northeastern Research Institutes of Petrified Wood and Mineral Resources, Nakhon Ratchasima Rajabhat University, for providing us with the cast of *K. priyai* (RIN 765). This study was partly supported by JSPS Grant-in-Aid for Scientific Research (#26304019 to MT).

References

Alpagut B., Andrews P., Fortelius M., Kappelman J., Temizsoy I., Çekibi H., and Lindsay W. (1996) A new specimen of *Ankarapithecus meteai* from the Sinap Formation of central Anatolia. Nature, 382: 349–351.

Andrews P. and Tekkaya I. (1980) A revision of the Turkish Miocene hominoid *Sivapithecus meteai*. Palaeontology, 23: 85–95.

Barry J.C., Morgan M.E., Flynn L.J., Pilbeam D.R., Behrensmeyer A.K., Raza S.M., Raza M., Khan I.A., Badgley C., Hicks J., and Kelley J. (2002) Faunal and environmental change in the Late Miocene Siwaliks of northern Pakistan. Palaeobiology, 28(3): 1–71.

Begun D.R. (2015) Fossil Record of Miocene Hominoids. In: Henke W., Tattersall I., (eds), Handbook of Paleoanthropology, Vol. III. Springer, Berlin, pp. 1261–1332.

Begun D.R. and Güleç, E. (1998) Restoration of the type and palate of *Ankarapithecus meteai*: taxonomic and phylogenetic implications. American Journal of Physical Anthropology, 105: 279–314.

Bender F. (1983) Geology of Burma. Gebrüder Bortraeger, Berlin.

Bhandari A., Kay R.F., Williams B.A., Tiwari B.N., Bajpai S., and Hominonymus T. (2018) First record of the Miocene hominoid *Sivapithecus* from Kutch, Gujarat state, western India. PLoS One, 13(11): e0206314.

Brown B. (1989) The mandibles of *Sivapithecus*. PhD thesis, Kent State University, OH.

Brown B. (1997) Miocene hominoid mandible: functional and phylogenetic perspectives. In: Begun D.R., Ward C.V., and Rose M.D., (eds.), Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum Press, New York, pp. 153–171.

Brown B. and Ward S.C. (1988) Basicranial and facial topography in *Pongo* and *Sivapithecus*. In: Schwartz J.H. (ed.), Orangutan Biology. Oxford University Press, New York, pp. 247–260.

Chaimanee Y., Jolly D., Benammi M., Tafforeau P., Duzer D., Moussa I., and Jaeger J.-J. (2003) A Middle Miocene hominoid from Thailand and orangutan origins. Nature, 422: 61–65.

Chaimanee Y., Suteethorn V., Jintasakul P., Vidhyayanon C., Marandat B., and Jaeger J.-J. (2004) A new orangutan relative from the Late Miocene of Thailand. Nature, 427: 439–441.

Chaimanee Y., Yamee C., Tian P., Khawisiset K., Marandat B., Tafforeau P., Nemoz C., and Jaeger J.-J. (2006) *Khoratpithecus priyai*, a late Miocene hominoid of Thailand. American Journal of Physical Anthropology, 131(3): 311–323.

Chavasseau O., Chaimanee Y., Soe-Thura-Tun, Aung-Naing-Soe, Barry J.C., Marandat B., Sudre J., Marivaux L., Ducrocq S., and Jaeger J.-J. (2006) Chaungtha, a new Middle Miocene mammal locality from the Irrawaddy Formation, Myanmar. Journal of Asian Earth Sciences, 28: 354–362.

Chavasseau O., Aung Aung Kyaw, Chaimanee Y., Coster P., Emonet E.-G., Aung Naing Soe, Rugumburung M., Soe Thura Tun, and Jaeger J.-J. (2013) Advances in the biochronology and biostratigraphy of the continental Neogene of Myanmar. In: Wang X., Flynn L.J., and Fortelius M. (eds.), Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology. Columbia University Press, New York, pp. 461–474.

Chit Sein, van der Made J., and Rössner G. (2009) New material of *Propotamochoros* (Suidae, Mammalia) from the Irrawaddy Formation, Myanmar. Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, 251: 17–31.

Colbert E.H. (1938) Fossil mammals from Burma in the American Museum of Natural History. Bulletin of the American Museum of Natural History, 74: 255–436.

Colbert E.H. (1943) The fauna of the Late Miocene of Thailand. American Journal of Physical Anthropology, 13(11): e0206314.
EARLY LATE MIocene HOMINOID MANDIBLE FROM MYANMAR

Chaivnanich K., Tafforeau P., and Chaimane Y. (2011) First hominoid from the Late Miocene of the Irrawaddy Formation (Myanmar). PLoS One, 011; 6: e17065.

Kappelman J., Richmond B.G., Seifert E.R., Maga A.M., and Ryan T.M. (2003) Hominoida (Primates). In: Fortelius M., Kappelman J., Sen S., and Bernor R.L. (eds.), Geology and Paleontology of the Miocene Siwalik Formation, Turkey. Columbia University Press, New York, pp. 90–124.

Kay R.F. (1982) Sivapithecus simonis, a new species of Miocene hominoid, with comments on the phylogenetic status of the Ramapithecinae. International Journal of Primatology, 3: 113–174.

Kelley J. (2002) The hominoid radiation in Asia. In: Hartwig W. (ed.), The Primate Fossil Record. Cambridge University Press, Cambridge, pp. 369–384.

Kelley J. (2005) Twenty-five years contemplating Sivapithecus taxonomy. In: Smith R.J., Kelley J., and Lieberman D.E. (eds.), Interpreting the Past: Essays on Human, Primate, and Mammal Evolution in Honor of David Pilbeam. Brill Academic, Boston, MA, pp. 123–143.

Kelley J. and Pilbeam D.R. (1986) The Dryopithecines: taxonomy, comparative anatomy, and phylogeny of Miocene large hominoids. In: Swindler D. and Irwin J. (eds.), Comparative Primate Biology, Vol. I: Systematics, Evolution, and Anatomy. Alan R. Liss, New York, pp. 361–431.

Kupczik K. and Dean M.C. (2008) Comparative observations on the tooth root morphology of Gigantopithecus blacki. Journal of Human Evolution, 54: 196–204.

Lu Q. (1998) Dental sexual dimorphism and chewing efficiency of anthropoid ape from Keiyuan, Yunnan Province. Memoirs of the Geological Survey of India, New Series, 16: 1–26.

Pilgrim G.E. (1937) Siwalik antelopes and oxen in the American Museum of Natural History. Bulletin of American Museum of Natural History, 72: 729–874.

Pilgrim G.E. (1939) The fossil Bovidae of India. Palaeontologia Indica, 26: 1–356.

Qi G. and Dong W. (2006) Lufengpithecus hudiensis site. Science, 311: 217–219.

Richmond B.G. and Whalen M. (2001) Forelimb function, bone curvature, and phylogeny of Sivapithecus. In: de Bonis L., Koufos G., and Andrews P. (eds.), Phylogeny of the Neogene Hominoid Primates of Eurasia. Cambridge University Press, Cambridge, pp. 326–348.

Schwartz J.H. (1997) Lufengpithecus and hominoid phylogeny: problems in delineating and evaluating phylogenetically relevant characters. In: Begun D., Ward C., and Rose M. (eds.), Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum Press, New York, pp. 363–388.

Sherwood R., Hlusko L.J., Duren D.L., Emch V.C., and Walker A. (2005) Mandibular symphysis of large-bodied hominoids. Human Biology, 77(6): 735–759.

Simons E.L. and Chopra S.R.K. (1969) Gigantopithecus (Pongidae, Hominoidae) a new species from North India. Postilla, Yale Peabody Museum, 1968: 1–18.

Smith-Robertson A. (1960) On the lower jaw of an anthropoid ape (Dryopithecus) from the upper Miocene of Lerida (Spain). Quarterly Journal of the Geological Society, 70: 316–320.

Stamp L.D. (1922) An outline of the tertiary geology of Burma. Geological Magazine, 59: 481–501.

Takai M., Thaug-Htike, Zin Maung Maung Thein, Soe A.N., Maung Maung, Tsabamoto T., Egi N., and Nishimura T.D. (2015) First discovery of colobine fossils from the Late Miocene/Early Pliocene of central Myanmar. Journal of Human Evolution, 84: 1–15.

Takai M., Nishioka Y., Thaug Htike, Maung Maung, Kyaw Khang, Zin Maung Maung Thein, Tsabamoto T., and Egi N. (2016) Late Pliocene Semnopithecus fossil from central Myanmar: rethinking of the evolutionary history of cercopithecid monkeys in Southeast Asia. Historical Biology, 28: 171–187.

Thaug Htike and Takai M. (2016) Reevaluation of the phylogeny and taxonomy of the Asian fossil hominoids. Universities Research Journal, 8(1): 171–177.

Tsung Aung (1980) Geological Map of Central Myanmar Basin. Myanmar Oil and Gas Enterprises.

Ward S. (1997) The taxonomy and phylogenetic relationships of Sivapithecus revisited. In: Begun D., Ward C., and Rose M. (eds.), Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum Press, New York, pp. 269–290.

Ward S. and Brown B. (1986) The facial skeleton of Sivapithecus indicus. In: Swindler D.R. and Erwin J. (eds.), Comparative Primate Biology, Vol. I: Systematics, Evolution, and Anatomy. Alan R. Liss, New York, pp. 413–452.

Woo R. (1957) Dryopithecus teeth from Keiyuan, Yunnan Province. Vertebrae PalAsiatica, 1: 25–31, plate 1.

Woo R. (1958) New materials of Dryopithecus from Keiyuan, Yunnan. Vertebrae PalAsiatica, 2: 38–42, plate 1.

Wu R. and Oxnard C.E. (1983) Ramapithecines from China: evidence from tooth dimensions. Nature, 306: 258–260.

Xu Q. and Lu Q. (2008) Lufengpithecus lufengensis: an early member of Hominidae. Science Press, Beijing.

Zhang Y. and Harrison T. (2017) Gigantopithecus blacki: a giant ape from the Pleistocene of Asia revisited. American Journal of Physical Anthropology, 162: 153–177.

Zin Maung Maung Thein, Takai M., Tsabamoto T., Thaug Htike, Egi N., and Maung Maung (2008) A new species of Dicerorhinus (Rhinocerotidae) from the Plio-Pleistocene of Myanmar. Palaeontology, 51: 1419–1433.

Zin Maung Maung Thein, Takai M., Uno H., Wynn J.G., Egi N., Tsabamoto T., Thaug-Htike, Aung Naing Soe, Maung Maung Maung Maung Thein, Takai M., Uno H., Wynn J.G., Egi N., and Maung Maung (2008) A new species of Sivapithecus from Keiyuan, Yunnan Province. Vertebrata PalAsiatica, 2: 38–42, plate 1.
Maung, Nishimura T., and Yoneda M. (2011) Stable isotope analysis of the tooth enamel of Chaingzauk mammalian fauna (late Neogene, Myanmar) and its implication to paleoenvironment and paleogeography. Palaeogeography, Palaeoclimatology, Palaeoecology, 300: 11–22.

Zin Maung Maung Thein, Thaung Htike, Aung Naing Soe, Chit Sein, Maung Maung, and Takai M. (2017) A review of the investigation of primate fossils in Myanmar. In: Barber A.J., Khin Zaw, and Crow M.J. (eds.), Myanmar: Geology: Resources and Tectonics. Geological Society, London, Memoirs, 48: 185–206.