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First discovery of colobine fossils from the Late Miocene/Early Pliocene in central Myanmar

Masanaru Takai [a, *], Thaung-Htike [b], Zin-Maung-Maung-Thein [c], Aung Naing Soe [d], Maung Maung [e], Takehisa Tsubamoto [f], Naoko Egi [a], Takeshi D. Nishimura [a], Yuichiro Nishioka [a]

[a] Primate Research Institute, Kyoto University, Inuyama, Aichi 484-8506, Japan
[b] Shwebo University, Shwebo, Myanmar
[c] Mandalay University, Mandalay, Myanmar
[d] Defence Service Academy, Pyin Oo Lwin, Myanmar
[e] Magway University, Magway, Myanmar
[f] Hayashibara Museum of Natural Sciences, Setouchi 701-4212, Japan

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ABSTRACT

Here we report two kinds of colobine fossils discovered from the latest Miocene/Early Pliocene Irrawaddy sediments of the Chaingzauk area, central Myanmar. A left mandibular corpus fragment preserving M_{1-3} is named as a new genus and species, *Myanmarcolobus yawensis*. Isolated upper (M^1?) and lower (M_2) molars are tentatively identified as Colobinae *gen. et sp. indet*. Although both forms are medium-sized colobines, they are quite different from each other in M_2 morphology. The isolated teeth of the latter show typical colobine-type features, so it is difficult to identify their taxonomic position, whereas lower molars of *Myanmarcolobus* have unique features, such as a trapezoid-shaped long median lingual notch, a deeply concave median buccal cleft, a strongly developed mesiobuccal notch, and rather obliquely running transverse lophids. Compared with fossil and living Eurasian colobine genera, *Myanmarcolobus* is most similar in lower molar morphology to the Pliocene *Dolichopithecus* of Europe rather than to any Asian forms. In *Dolichopithecus*, however, the tooth size is much larger and the median lingual notch is mesiodistally much shorter than that of *Myanmarcolobus*. The discovery of *Myanmarcolobus* in central Myanmar is the oldest fossil record in Southeast Asia not only of colobine but also of cercopithecid monkeys and raises many questions regarding the evolutionary history of Asian colobine monkeys.

1. Introduction

Colobine monkeys (Cercopithecidae, Colobinae) are now among the most diversified land mammals in South to Southeast Asia, but their evolutionary history is not well known because of their scarcity in the Asian fossil record. The known fossil record suggests that colobine monkeys originated on the African continent in the Middle Miocene (e.g., Benefit and Pickford, 1986; Nakatsukasa et al., 2010; Fleagle, 2013; Rossie et al., 2013), and some members entered Eurasia as early as the Late Miocene (Delson, 1994). The oldest Eurasian fossil colobine is *Mesopithecus*, a small-to-medium-sized terrestrial monkey, fossils of which have been discovered from the Late Miocene to Late Pliocene in Europe and western Asia (Iran and Afghanistan; e.g., Heintz et al., 1981; Andrews et al., 1996; Jablonski, 2002). Recently, some researchers have suggested that "*Presbytis*" *sivalensis*, which was discovered from the Late Miocene/Early Pliocene of Siwaliks, Indo/Pakistan in the 19th century (Lydekker, 1878), should be included in *Mesopithecus* (Harrison and Delson, 2007). In this paper we use ?*Mesopithecus sivalensis* for this small Siwalik colobine fossil, accepting the opinion of Harrison and Delson (2007). In addition, new specimens of *Mesopithecus* (*M.* cf. *pentelicus*) were discovered from the Late Miocene site in Yunnan Province, southwestern China, extending its geographical distribution as far as East Asia (Jablonski et al., 2011; Ji et al., 2013).

After the appearance of *Mesopithecus*, a large-sized terrestrial colobine, *Dolichopithecus*, occurred in the Early Pliocene in Europe (e.g., Szalay and Delson, 1979; Delson, 1994; Jablonski, 2002). Some authorities consider that *Dolichopithecus* evolved from

* Corresponding author.
E-mail address: takai.masanaru.2s@kyoto-u.ac.jp (M. Takai).

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Mesopithecus by the end of the Miocene (Delson, 1994). Two large-sized colobines, *Parapresbytis* and *Kanagawapithecus*, discovered from the Middle to Late Pliocene of East Asia (Transbaikalia and Japan, respectively) were once considered to be the subgenera of *Dolichopithecus* (Borissoglebskaya, 1981; Kalmykov and Maschenko, 1992; Delson, 1994; Iwamoto et al., 2005), but both are now regarded as independent genera, respectively (Jablonski, 2002; Maschenko, 2005; Egi et al., 2007; Takai and Maschenko, 2009; Nishimura et al., 2012). There is another enigmatic colobine tooth from the Early Pliocene that has been discovered in Yushe, Shaangxi Province, northern China, but no detailed descriptions have been published (Delson, 1996; Williams and Holmes, 2011).

Concerning the phylogenetic relationships of these East Asian fossil colobines, Delson (1994) indicated the close relationships between *Dolichopithecus, Parapresbytis*, and *Kanagawapithecus*. However, a detailed morphological analysis of the cranial specimens using computed tomography (CT) scans revealed that *Kanagawapithecus* was quite different at least in cranial structure not only from *Dolichopithecus* and *Parapresbytis* but also from any extant Asian colobines (Nishimura et al., 2012).

On the other hand, the oldest colobine fossils from Southeast Asia are isolated teeth and/or fragmentary jaws of *Rhinopithecus* discovered from the Early Pleistocene cave sediments of southern China, such as in Guangxi and Guangdong Provinces (Jin et al., 2009). Jablonski (2002) proposed an ancestor–descendant relationship between *Parapresbytis* and extant *Rhinopithecus*, but Takai and Maschenko (2009) disagreed with this hypothesis because no "intermediate" fossils have been discovered from the Pliocene sediments of East Asia to date. Moreover, it is really strange that to date no colobine fossils have been reported from the Pliocene sediments of Southeast Asia, where many extant colobine monkeys are now flourishing. The present colobine fossils from the latest Miocene/Early Pliocene of central Myanmar represent the oldest discovery in Southeast Asia not only in terms of colobines but also of any cercopithecid monkeys.

2. Materials and methods

In Myanmar, it is strictly prohibited to take fossil specimens on loan outside the country, so we made high-resolution silicone molds (Seamless Silicon, Nissin Resin Co., Ltd.) of the fossils in the field. Silicon molds were also taken from the extant colobine specimens at the museums using dental silicon (Exahiflex Injection Type, GC Corp.). After returning to Japan, we made epoxy casts and scanned the surface configuration of tooth casts using a needle scanning system composed of a 3D plotter (MDX-20) and scanning software (Dr. PICZA; Roland DG Corp.), with a resolution of 0.05 mm (Figs. 4–6), and also through a One-shot 3D Measurement Macroscope (VR-3050, Keyence Corp.; Figs. 8–10). The fossil specimens were compared with epoxy casts of other extant and extinct colobine teeth.

2.1. Institutional abbreviations

Institutional abbreviations used here include: AMNH: American Museum of Natural History, New York, USA; BMNH: The Natural History Museum, London, UK; BSM: Bayerische Staatssammlung für Paläontologie, München, Germany; FSL: Laboratoire des Sciences de la Terre, Faculte des Sciences, Universite de Lyon, France; GIN: Geological Institute, Russian Academy of Sciences, Russia; GSI: Geological Survey of India, India; GSP: Geological Survey of Pakistan, Pakistan; IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; JMC: Japan Monkey Centre, Inuyama, Japan; KUPRI: Kyoto University, Primate Research Institute, Inuyama, Japan; LGI: Laboratorul de Geologie, Universitate "Al. I. Cuza," Iasi, Romania; LPB: Laboratorul de Paleontologie, University of Bucharest, Romania; MAFI: Foldtani Inteszet (Geological Seice), Budapest, Huangary; MNHN: Muséum National d'Histoire Naturelle, Paris, France; MP: Musée Perpignan, France; NMB: Naturhistorisches Museum of Basel, Switzerland; NMMP-KU-IR: National Museum of Myanmar, Paleontology–Kyoto University–Irrawaddy specimen, Myanmar; PIN: Paleontological Institute, Russian Academy of Sciences, Russia; and ZRC: Zoological Reference Collection, National University of Singapore (Raffles Museum), Singapore.

2.2. Anatomical abbreviations

Anatomical abbreviations used here include: BL: buccolingual width; prd: protodonid; med: metaconid; end: entoconid; hyd: hypoconid; hyld: hypoconulid; MD: mesiodistal length; tad: talonid; and trd: trigonid.

2.3. Geological setting of Chaingzauk

The present specimens were collected from Neogene Irrawaddy sediments at two sites in Myokhinthar village, Chaingzauk area, Pauk township, Magway Division, central Myanmar in February, 2009 (Fig. 1). The Irrawaddy sediments, mainly composed of fluvial sediments 2,000 to 3,000 m in thickness (Bender, 1983; Wandrey, 2006), have traditionally been subdivided into Lower and Upper Irrawaddy based on the lithological and paleontological criteria. The Lower Irrawaddy overlies the Oligocene to Miocene "Freshwater Pegu Bed" and is correlated mainly to the Dhok Pathan Formation of the Siwalik Group of India/Pakistan, suggesting a Late Miocene to Early Pliocene age based on the mammal fossils (Bender, 1983), whereas the Upper Irrawaddy is overlain by the Middle Pleistocene to Holocene Terrace deposits and is conventionally referred to the Early Pleistocene (Stamp, 1922; Chhibber, 1934; Colbert, 1938, 1943; Bender, 1983).

The Chaingzauk area, located about 10 km northeast of Pauk city, has been known for yielding numerous vertebrate fossils since the 19th century (Lydekker, 1878; Cotter, 1938; Pilgrim, 1939; Matthew, 1929). The geological age of the Chaingzauk fauna was originally proposed to be Late Miocene to Early Pliocene by Pilgrim (1939) and was recently reconfirmed as near the boundary between the Late Miocene and the Early Pliocene by the presence of the combination of the following mammal taxa (Table 1): *Agriotherium myanmarensis* (Ursidae, Carnivora), *Hystrix paukensis* (Hystricidae, Rodentia), *Dorcatherium* cf. *anthracotherioides* (Tragulidae, Artiodactyla), *Microbunodon milaensis* and *Merycopotamus dissimilis* (Anthracotheriidae, Artiodactyla), *Sivachoerus prior* and *Propotamochoerus hysudricus* (Suidae, Artiodactyla), and *Hexaprotodon sivalensis* and *H. iravaticus* (Hippopotamidae, Artiodactyla) (Pickford, 1988; van der Made, 1999; Barry et al., 2002, 2007; Badgley et al., 2008; Thaung-Htike, 2008; Nishioka et al., 2011; Ogino et al., 2011; Zin-Maung-Maung-Thein et al., 2011; Tsubamoto et al., 2012).

The fossil localities of the Chaingzauk area are divided into two regions (or villages), the Chaingzauk (CHZ, northern part) and Myokhinthar (MKT, southern part) villages, although there is no distinct geographical boundary between them. All of the colobine fossils described here were collected in Myokhinthar, but several important, index taxa (*Agriotherium*, *Sivachoerus*, *Propotamochoerus*) and many bovids were discovered from Chaingzauk. Although it is hard to correlate the sediments of the two regions because of the complicated fluvial sedimentary structure (Fig. 2), these two regions are regarded as being almost similar in age based on the mammalian fossils and overall geological setting (Zin-Maung-