<table>
<thead>
<tr>
<th>Title</th>
<th>Parapresbytis eohanuman: the northernmost colobine monkey from the Pliocene of Transbaikalia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Author(s)</td>
<td>Takai, Masanaru; Maschenko, Evgeny N.</td>
</tr>
<tr>
<td>Citation</td>
<td>Asian paleoprimatology (2009), 5: 1-14</td>
</tr>
<tr>
<td>Issue Date</td>
<td>2009</td>
</tr>
<tr>
<td>URL</td>
<td><a href="http://hdl.handle.net/2433/199778">http://hdl.handle.net/2433/199778</a></td>
</tr>
<tr>
<td>Type</td>
<td>Departmental Bulletin Paper</td>
</tr>
<tr>
<td>Textversion</td>
<td>publisher</td>
</tr>
</tbody>
</table>

Kyoto University
Parapresbytis eohanuman: the northernmost colobine monkey from the Pliocene of Transbaikalia

Masanaru Takai* and Evgeny N. Maschenko

Abstract

Parapresbytis eohanuman (Borissoglebskaya, 1981) is the northernmost colobine monkey discovered from the middle to late Pliocene sediments in Transbaikalia area, southern Siberia. Although most of the specimens are isolated teeth, three premaxillary/maxillary fragments, some cranial fragments, and two nearly complete mandibles are also included. Some researchers regard it the close relative to Dolichopithecus, the Pliocene colobines in Europe, while others insist that it is an ancestral taxon of Rhinopithecus, snub-nosed monkey, which is presently distributed in southern China and northern Vietnam. However, the phyletic position of P. eohanuman has not yet been established because of the scarcity of fossil evidences in the northern East Asia in the Late Pliocene.

Introduction

Although there is no non-human primates distributed in northern Eurasia at present, a fossil monkey, Parapresbytis eohanuman, has been discovered from the two middle to late Pliocene localities, Udunga and Shamar (= Shaamar), Transbaikalia area. P. eohanuman was originally described as Presbytis eohanuman by Borissoglebskaya (1981) on the basis of the mandibular specimen discovered from the late Pliocene sediments in Shamar, northern Mongolia. The type specimen is a nearly complete mandibular corpus preserving all lower dentition. The dental morphology obviously indicates that it is not cercopithecine but colobine monkey. Another poorly crushed mandibular corpus preserving most lower dentition, and two postcranial fragments (distal end of left humerus and nearly complete right ulna lacking distal end) have also been collected from the same locality (Kalmykov and Maschenko, 1992 1995; Maschenko, 2005; Kalmykov et al., 2005).

In the end of 1990s to the beginning of 2000s several additional specimens were discovered from the middle Pliocene deposits in Udunga, which is located at the southeast of Baikal Lake and about 140 km north of the Shamar (Kalmykov and Maschenko, 1992). The geological age of the Udunga fauna corresponds to the boundary of late Ruscinian and
early Villafranchian ages (Kalmykov, 1992; Maschenko, 2005) or to the MN 16a (mammal zone) by the small and large mammals (Vislobokova et al., 1995, 2003; Ervajeva et al., 2003). Based on the new materials together with the type specimens from Shamar, Kalmykov and Maschenko (1992) revised “Presbytis” eohanuman to the new genus, Parapresbytis eohanuman, mainly because of its much larger size and incisor morphology. In 1995 the diagnosis of Parapresbytis was added with some characters of dental and facial morphology (Kalmykov and Maschenko, 1995). Their revision on the Siberian monkey is now widely accepted by most paleontologists (e.g. Jablonski, 2002).

On the other hand, the phylogenetic position of Parapresbytis is still being discussed by several workers (e.g. Delson, 1988, 1994; Iwamoto et al., 2005). Delson (1988, 1994) argued that Parapresbytis is not significantly distinct from Dolichopithecus, which has been widely distributed in the Pliocene Europe, such as France, Spain, Germany, Greece, Hungary, Romania, Bulgaria, and Ukraine (Ardito & Mottura, 1987; Andrews et al., 1996; Delson, 1973, 1974, 1994; Delson et al., 2005; Doukas & Bruijin, 2002; Maschenko, 1991), and regard it as a species of Dolichopithecus (Delson, 1994). On the other hand, Jablonski (2002) indicates the morphological similarity between Parapresbytis and some Asian colobine monkeys, such as Semnopithecus and Rhinopithecus, suggesting close relationships among

Table 1. The specimens of Parapresbytis eohanuman. L, left; R, right.

<table>
<thead>
<tr>
<th>locality</th>
<th>no.</th>
<th>side</th>
<th>description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shaamar</td>
<td>PIN 3381-235</td>
<td>R/L</td>
<td>distorted mandible with right I1-M3, and left C1-M3</td>
</tr>
<tr>
<td>Shaamar</td>
<td>PIN 3381-236</td>
<td>R/L</td>
<td>nearly complete mandible with full dentition</td>
</tr>
<tr>
<td>Shaamar</td>
<td>PIN 3381-210</td>
<td>L</td>
<td>distal end of left humerus</td>
</tr>
<tr>
<td>Shaamar</td>
<td>PIN 3381-211</td>
<td>R</td>
<td>proximal part of right ulna</td>
</tr>
</tbody>
</table>
Prapresbytis from Transbaikalia

In this article we shortly present a number of additional specimens and discuss the morphological features and evolutionary history of Siberian colobine monkeys comparing with some fossil and living Asian colobine monkeys.

**Abbreviations:** GIN U, Geological Institute Siberian Branch, Russian Academy of Science; PIN, Paleontological Institute, Russian Academy of Science; Udg, Udunga fossil number; MNHN-P PER, Muséum National d’Histoire Naturelle, Paris, Perpignan; KPM, Kanagawa Prefectural Museum, Japan; NWU, Northwestern University, China.

**Description of the fossil materials**

**Dentition and mandibular corpus**

Both upper and lower incisors of *Parapresbytis* are very robust and labiolingually thick. There are basal lingual conule on the strong lingual cingulum of upper incisors, so the occlusal outline of I1 is nearly triangular or pentagonal. Labial enamel crenulation is very strong both in I1 and I2. Both in upper and lower incisors the crown is not protruding anteriorly but...
inclined slightly lingually.

One of the most impressive feature of *Parapresbytis* is the largeness and heavy wearing of anterior teeth, incisors and canines. Compared with other living and fossil colobine monkeys, the upper incisor size of *Parapresbytis* is much larger than that of any colobine mokeys. In GIN U 987/878(1) and 987/878(2) upper incisor and canines are so strongly worn that the dental area is widely exposed at the apex of teeth. Especially in GIN U 987/878(1), both I¹ and I² are so strongly worn that the two third of the crown height has been lost. The lower incisors (GIN U 986/38(1), (2), (8), (9)) also show the strong wearing. The wearing conditions in these teeth indicate the heavy using of anterior teeth for feeding of the hard food, such as siliceous vegetation.

The molars show the typical pattern of colobine monkeys: bilophodonty, relatively low crown, and high relief of molariform teeth. The upper cheek tooth row is nearly straight, but the premolars are slightly more lingualy positioned than molars. There is a variation in the size and morphology of the distal lobe of M₃: it is relatively smalland situated buccally in some specimens (Figure 4 and %) but large with an extra cusp (6th cusp) in a large individual (Figure 6), very small retaining a small hypoconulid, which is situated slightly buccally.

In living colobine monkeys there is sexual dimorphism observed in canines and lower P₃. In the *Parapresbytis* specimens distinct sexual dimorphism is not confirmed. Most of the specimens preserving canines and/or P₃ are likely to be female individual. There are slight morphological difference between two mandibular specimens collected from Shamart, PIN 3381-235 and PIN 3381-236. Lower canine is slightly larger and higher and P₃ retains lightly longer mesiobuccal flange in the former than in the latter, but the difference is not so
distinct but looks like individual variation. If there is actually sexual dimorphism in upper/lower canines and P₃, it would be very small. However, more typical male-type specimen is necessary to identify the sexual dimorphism in *Parapresbytis*.

To date, two mandibular corpi (PIN 3381-235 and 3381-236) of *Parapresbytis* have been collected from Shamar, northern Mongolia. The former is a bilaterally crashed mandible preserving moth lower dentition, while the latter has a distinct mandibular fossa at the buccal face of the corpus below P₃-4, which is not analogous of mandibular fossa in cercopithecinae but often seen in living *Rhinopithecus* mandible.
Cranial fragments

To date the fragments of skull roof (GIN U 987/493, Figure 7-8), occipital part (GIN U 987/493(2), and parietal part (GIN U 987/493(3)) have been discovered from Udunga. Especially the crushed fragment of skull roof preserves the supraorbital torus, temporal lines, and superior part of the interorbital septum, providing some important cranial characters. In *Parapresbytis* the supraorbital torus is so developed, forming a continuous ridge, that there is a distinct supratoral concavity, which is bordered laterally by temporal lines, and both supraorbital tori runs posterolaterally in dorsal view (Figure 7). In anterior view right and left tori run slightly downward laterally and contact to each other at the mid line, and the midpoint of the supraorbital torus is slightly concave (Figure 8). There is no supraorbital foramen observed. The size of the cranial roof of *Parapresbytis* is almost same as that of living *Rhinopithecus* (Figure 8).

Delson (1994) indicated the morphological similarity between *Parapresbytis* and *Dolichopithecus* and regarded them as congeneric taxa. *Dolichopithecus* is a moderately large-bodied colobine monkey with a rather long face, relatively narrow interorbital width (Figure 8), and considerable sexual dimorphism (Delson, 1996; Jablonski, 2002), whereas *Parapresbytis* has moderately wide interorbital pillar (Figure 8), relatively short face, and no distinct sexual dimorphism. According to these morphology, there is no reason to classify them in the same genus.
Although there are two famous cranial specimens of *Dolichopithecus* known so far, both are so poorly distorted that it is hard to observe the exact direction of the supraorbital torus (Figure 9).

**Postcranials**

Two postcranial specimens, the distal end of left humerus (PIN 3381-210, Figure 10) and proximal part of right ulna (PIN 3381-211, Figure 11), have been discovered from Shamar. Originally Borissoblebskaya (1981) said that these postcranial specimens belong to the different individuals. Egi et al. (2007) examined these specimens carefully and also concluded that they don’t belong to the same individual mainly based on the size difference of the elbow joint. Therefore there are at least two, probably three or four individuals in Shamar. As for the locomotion/positional behavior, the comparative morphological analysis of the humerus and ulna using principal components analysis (PCA) suggests that *Parapresbytis* is not terrestrial but rather arboreal monkey, though some previous researchers considered *Parapresbytis* is a terrestrial monkey as is *Dolichopithecus* (Szalay and Delson, 1979; Delson, 1994; Jablonski, 2002). *Parapresbytis* was likely adapted to the arboreal habitat in the Udung forest.

On the other hand, the elbow morphology of *Parapresbytis* suggest the phylogenetic closeness neither to *Dolichopithecus* nor to any particular arboreal colobines (Egi et al., 2007). Strasser and Delson (1987) also suspended their decision on the taxonomic allocation of *Dolichopithecus*.

**Discussion**

---

*Figure 10.* Left humerus (PIN 3381-210): anterior (A) and posterior (B) views.

*Figure 11.* Right ulna (PIN 3381-211): lateral (A), anterior (B), medial (C), and posterior (D) views.
Comparisons with fossil colobine monkeys from Eastern Asia

As mentioned above, several workers have pointed out the morphological similarity and close affinity between Parapresbytis and Dolichopithecus from the Pliocene of Europe (e.g. Delson, 1988, 1994; Iwamoto et al., 2005). Dolichopithecus is a moderately large-bodied colobine monkey with a rather long face, relatively narrow interorbital width, and considerable sexual dimorphism (Figure 9, Delson, 1996; Jablonski, 2002). In Parapresbytis, however, the interorbital pillar is moderately wide, the face is relatively short, and no distinct sexual dimorphism have been recognized to date. In addition, the lower postcanine teeth of Parapresbytis show moderate bunodonty in contrast to the relatively high, sharp cusps and very deep relief in Dolichopithecus. Although both Delson (1996) and Jablonski (2002) insist that Dolichopithecus is a highly terrestrial monkey, the morphological analysis of the elbow joint of Parapresbytis indicates not terrestrial but arboreal adaptation (Egi et al., 2008). In dental morphology, moreover, Dolichopithecus has much smaller upper incisors relative to upper molars among living/fossil colobine monkeys (Table 3, Figure 12). In cranial morphology the supraorbital torus is not so developed in Dolichopithecus, whereas it is strongly developed forming the supratoral groove in Parapresbytis. The combination of these morphological differences suggests the relatively far phyletic relationship between Parapresbytis and Dolichopithecus.

In eastern Asia another fossil colobine cranium has been discovered from the late Pliocene Nakatsu Group (ca. 2.5 Ma), Kanagawa Prefecture, central Japan (Figure 14, Iwamoto et al., 2005; Delson, 1994). This facial part of skull (KPM-N NC 005802) was originally named as Dolichopithecus (Kanagawapithecus) leptopostorbitalis, that is the subgenus of Dolichopithecus (Iwamoto et al., 2005), but the detailed analysis of the inner structure of the cranium revealed that it is quite different from that of Dolichopithecus.
Prapresbytis from Transbaikalia

Therefore, we treat this cranium as the different, independent genus, *Kanagawapithecus*, in this paper.

*Kanagawapithecus* is as large as *Parapresbytis* in the size of upper cheek teeth (Table 2, Figure 14), so we tried to compare the size of upper incisors, which is very large relative to upper cheek teeth in *Parapresbytis*. Unfortunately, there is no upper incisors preserved in the *Kanagawapithecus* skull, but it is possible to reconstruct the approximate size of the upper incisors in Kanagawapithecus by comparing the *Parapresbytis* specimens directly (Figure 14). It is apparent that *Kanagawapithecus* and *Parapresbytis* are quite different at least in the upper incisor size, though they show minimal differences in the morphology of supraorbital torus and in the relatively wide interorbital pillar (Kalmykov et al., 2005).

Thus, three Pliocene colobine taxa discovered from Eurasia, *Dolichopithecus*, *Parapresbytis*, and *Kanagawapithecus*, are different from one another in the craniodental morphology. There is no definitive characters uniting any two of these taxa, suggesting the complicated evolutionary history of the Pliocene colobine monkeys in East Asia.

**Comparisons with fossil and living Rhinopithecus of China**

Several workers now consider that *Parapresbytis* could be an ancestral group to living *Rhinopithecus* and its relatives, because *Rhinopithecus* is the oldest colobine fossil from East Asia (Jablonski, 2002). For example, Jablonski (2002) says that *Parapresbytis* is most similar to some Asian colobine monkeys, such as *Semnopithecus* and *Rhinopithecus* in having broad interorbital distance, shelf-like supraorbital torus, pronounced ophyronic groove (= supratoral concavity), molar morphology, molar dimensions, and postcranial robustness. As above mentioned, however, Egi et al. (2007) concluded that the morpholog of the elbow joint of *Parapresbytis* does not show special phylogenetic closeness to any particular arboreal colobine. In addition, although both *Rhinopithecus* and *Parapresbytis* retain strongly developed shelf-like supraorbital torus, it runs upward laterally in *Rhinopithecus* (Figure 13 right) but runs horizontally or rather downward laterally in *Parapresbytis* (Figure 8) and in living *Presbytis* and *Trachypithecus* (Figure 13 left). In the angle of the supraorbital torus...
Parapresbytis resembles Presbytis and/or Trachypithecus rather than Rhinopithecus.

Many fossil specimens of Rhinopithecus have been reported from the late Pleistocene sediments of northern China. However, there is chronological and geographical gap between Parapresbytis from the middle Pliocene of Transbaikal area and the oldest Rhinopithecus fossil from the middle Pleistocene of central China (Hu & Qi, 1978; Gu & Hu, 1991; Jablonski, 1993). In order to support the Parapresbytis-Rhinopithecus hypothesis it is necessary to find an intermediate fossil specimen from the late Pliocene/early Pleistocene sediments of Mongolia and/or Inner Mongolia.

The first fossil record of Rhinopithecus may be R. lantianensis (including "Megamacaca") from the later Early Pleistocene sites of north-central China (Pan and Jablonski, 1987; Jablonski and Pan, 1988; Jablonski, 1991, 1998): such as Gongwangling (Lantian, Shaanxi Province, Jablonski and Gu, 1991), Quyuan River Mouth Site (Yunxian, Hubei Province, Li et al., 1994; Li and Feng, 2001), and Sanhe Cave (Chongzuo, Guangxi Province, Jin et al., 2009). Among these early Pleistocene localities, Gongwangling is one of the oldest and geographically northernmost site, about 34°N, while the Trasbaikal localities are located 50-51°N (Figure 15). There is a large geographical hiatus for the colobine fossil localities between Gongwangling and Udunga/Shamar. This wide range corresponds to Mongolia and Inner Mongolia, where is many Pliocene localities producing plenty of land mammals. If Parapresbytis is actually the ancestral group to living Rhinopithecus, the intermediate forms from the late Pliocene of this area have to fill this geographical hiatus.

One of the candidates for the intermediate form is the isolated teeth of "Macaca" discovered from the early Pliocene sediments of Yushe, Shanxi Province (Delson, 1996). In a short abstract Delson (1996) mentioned the specimens belong to Macaca, but one of the isolated teeth, a relatively large M3, is obviously of colobine monkey. If this specimen actually belong to Colobinae, it may be the "missing link" between Parapresbytis and Rhinopithecus.

Recently, some Rhinopithecus specimens were reported from the early Pleistocene cave sediments of Guangxi Province, southern China (Jin et al., 2009). The discovery of
Prapresbytis from Transbaikalia

Rhinopithecus fossil from the early Pleistocene of southern China likely suggest that the genus may have originated in the southern rather than in northern China. It is necessary to examine the colobine fossils discovered from the early Pleistocene of China.

On the other hand, one nearly complete infant cranium and some fragmentary specimens of Rhinopithecus have been discovered from the middle to late Pleistocene limestone fissure sediments of Yenchingkou (Matthew and Granger, 1923; Colbert and Hooijer, 1953), but all these materials are nearly identical to living species. Some subfossils of Rhinopithecus are also reported from the late Pleistocene of Fujian Province, southeast China, but there is no morphological description in the paper (You and Cai, 1996).

Anyway, in order to make clear the evolutionary history of Asian colobine monkeys including Parapresbytis, we must discover more fossil specimens. However, it is hard to expect the new findings from the Latest Pliocene of Mongolia and Inner Mongolia because these areas were already in the very arid condition of Central Asia. However, the piedmont regions of Central and Southwest China should be most important for the prospecting missing links for the evolutionary history of the Asian colobine monkeys. The classification

---

**Figure 15.** Index map of the localities of living and fossil colobine monkeys in East Asia. Open squares indicate middle to late Pliocene sites (Udunga, Shamar, and Nakatsu). Open triangles indicate late Pliocene/early Pleistocene localities of Rhinopithecus or colobine fossils in China: 1, Yushe (Shanxi); 2, Gongwangling (Lantian, Shaanxi); 3, Yunxi (Hubei); 4, Yunxian (Hubei); 5, Longquodong Cave (Jianshi, Hubei); 6, Sanhe Cave (Chongzuo, Guangxi). Open circles indicate the middle/late Pleistocene localities of Rhinopithecus fossils in China: 7, Xin’an (Henan); 8, Yenchingkou (Wanxiang, Sichuan); 9, Jiandu Hill (Cili County, Hunan); 10, Yanhuidong (Tongzi County, Guizhou); 11, Guanyindong (Qianxi County, Guizhou); 12, Jiandaqian (Fujian); 13, Luohang (Qujiang, Guangdong); 14, Luoding (Guangdong); 15, Julengshan (Du’an, Guangxi); 16, Heidong (Daxin, Guangxi). Small filled marks indicate the distribution of living Rhinopithecus: filled circles, *R. roxellanae*; filled square, *R. brelichi*; filled triangles, *R. bieti*. Data of living Rhinopithecus localities are from Zhang et al. (2002), and of the fossil localities are from Matthew and Granger (1923), Colbert and Hooijer (1953), Jablonski and Pan (1988), Jablonski (1998), Gu and Hu (1991), Hu and Qi (1978), Gu et al. (1996), Li et al., 1994, Li and Ma (2001), Li and Feng (1986), Han (1982), Zheng, S. (2004), Zhang et al. (1988), and Jin et al. (2009).
and phyletic relationships of living and fossils colobine monkeys have not yet been well established.

For example, concerning the phyletic relationships among three fossil taxa in Eastern Asia (Kanagawapithecus and Parapresbytis and Rhinopithecus), the present two authors still have different opinions. In spite of the morphological differences among them, E.N.M. believes, based on the combination of morphological characters, that the three taxa should be unite into the "rhinopithecemorph" (not systematic unit) in the Pliocene and Pleistocene colobines (Maschenko, 2003). On the other hand, M.T. regards these three East Asian colobine monkeys and European Dolichopithecus have no special close relationships among them, but some of them, such as Kanagawapithecus, may be closely related to the African colobines. Only additional specimens of colobine monkeys in East Asia would solve this controversy.

Acknowledgements

We are deeply grateful to Prof. N.P. Kalmykov of the Southern Scientific Centre, Russian Academy of Sciences for providing us with useful fossil specimens of the Udunga fauna. We are also grateful to the following people: Drs. T. Nishimura and N. Egi of Primate Research Institute, Kyoto University; Prof. M. Nakatsukasa of Kyoto University; Dr. H. Taru of Kanagawa Prefectural Museum of Natural History; Dr. T. Takano of Japan Monkey Center; Dr. E. Delson of American Museum of Natural History; Dr. B. Senut of Museum National d’ Histoire Naturelle, Paris; Dr. J. de Vos and Mr. R. van Zelst of National Natuurhistorisch Museum, Leiden; Dr. R. Kruszynski of Natural History Museum, London; Dr. G. Engesser of Naturhistorisches Museum Basel, Basel, Switzerland; Prof. Li Baoguo of Northwest University, Xi-an, China; Prof. Jin Changzhu of Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing. This research was supported by JSPS (Japan Society for the Promotion of Science) and RFBR (Russian Foundation for Basic Research) under the Japan- Russia Research Cooperative Project (to M.T., Grant 840064200002 and to E.N.M., Grant 060491469).

References


