

## ***Parapresbytis eohanuman*: the northernmost colobine monkey from the Pliocene of Transbaikalia**

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### **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).

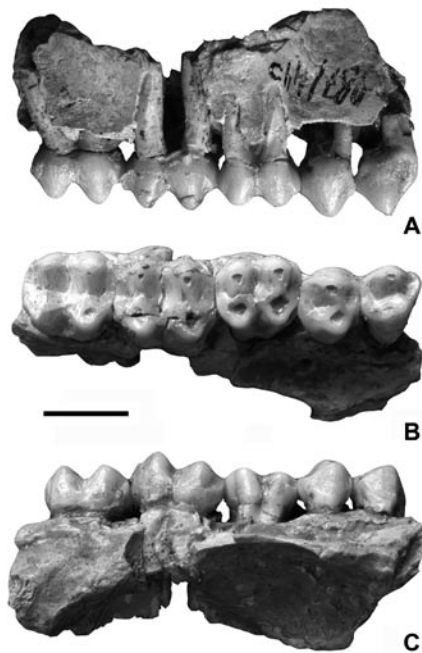
In the end of 1990s to the beginning of 2000s several additional specimens were discovered from the middle Pliocene deposits in Udunga, which is located at the southeast of Baikal Lake and about 140 km north of the Shamar (Kalmykov and Maschenko, 1992). The geological age of the Udunga fauna corresponds to the boundary of late Ruscinian and

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

locality	no.	side	description
	GIN U 987/493(1)	R	skull roof
	GIN U 987/493(2)		occipital fragment
	GIN U 987/493(3)	?	parietal fragment
	GIN U 987/878(1)	L	left premaxilla with I <sup>1</sup> -C <sup>1</sup>
	GIN U 987/878(2)	R/L	premaxilla with right I1 and left I <sup>1-2</sup>
	GIN U 987/445	R	right maxilla with P <sup>3</sup> -M <sup>3</sup>
	GIN U 986/38(1)	R	isolated I <sub>1</sub>
	GIN U 986/38(2)	R	isolated I <sub>2</sub>
	GIN U 986/38(3)	R	isolated C <sub>1</sub>
	GIN U 986/38(4)	R	isolated P <sub>4</sub>
	GIN U 986/38(5)	R	isolated M <sub>1</sub>
	GIN U 986/38(6)	R	isolated M <sub>2</sub>
	GIN U 986/38(7)	R	isolated M <sub>3</sub>
	GIN U 986/38(8)	L	isolated I <sub>1</sub>
	GIN U 986/38(9)	L	isolated I <sub>2</sub>
	GIN U 986/38(10)	L	isolated C <sub>1</sub>
Udunga	GIN U 986/38(11)	L	isolated P <sub>4</sub>
	GIN U 986/38(12)	L	fragment of M <sub>2</sub>
	GIN U 986/38(13)	L	fragment of M <sup>2</sup> ?
	GIN U 987/378	L	fragment of M <sup>3</sup> ?
	No.1	L	maxillary fragment with M <sup>2-3</sup>
	No.2	R	maxillary fragment with M <sup>2-3</sup>
	No.3	L	isolated M <sup>1</sup>
	No.4	L	isolated M <sup>2</sup>
	No.5	L	isolated I <sup>1</sup>
	No.6	L	isolated I <sup>2</sup>
	No.7	L	isolated I <sub>2</sub>
	No.8	L	isolated M <sub>3</sub>
	No.9	L	isolated M <sub>1</sub>
	No.10	R	isolated P <sub>4</sub>
	No.11	R	isolated M <sub>3</sub>
	No.12	L	isolated M <sub>2</sub>
	No.13	R	isolated M <sub>1</sub>
	No.14	L	isolated P <sub>4</sub>
Shaamar	PIN 3381-235	R/L	distorted mandible with right I <sub>2</sub> -M <sub>3</sub> and left C <sub>1</sub> -M <sub>3</sub>
	PIN 3381-236	R/L	nearly complete mandible with full dentition
	PIN 3381-210	L	distal end of left humerus
	PIN 3381-211	R	proximal part of right ulna

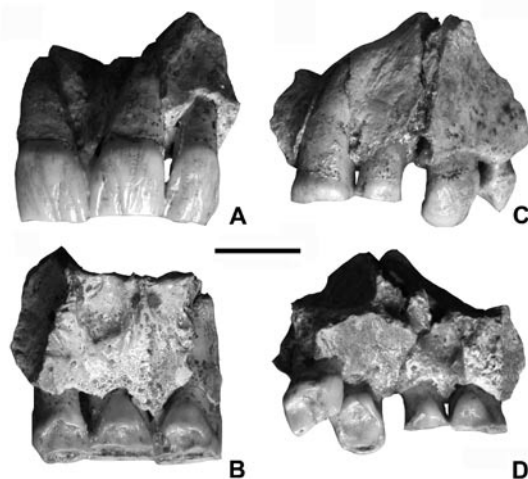
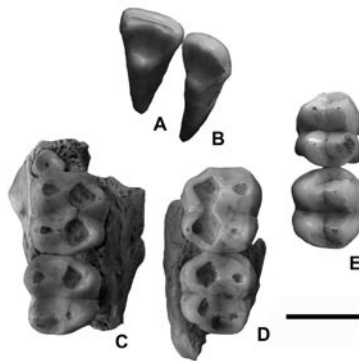
early Villafranchian ages (Kalmykov, 1992; Maschenko, 2005) or to the MN 16a (mammal zone) by the small and large mammals (Vislobokova *et al.*, 1995, 2003; Ervajeva *et al.*, 2003). Based on the new materials together with the type specimens from Shamar, Kalmykov and Maschenko (1992) revised “*Presbytis*” *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



**Figure 1.** Right maxilla preserving P<sup>3</sup>-M<sup>3</sup> (GIN U 987/445). Buccal (A), occlusal (B), and lingual (C) views. Scale bar, 1 cm.

**Figure 3.** Upper dentitions. Isolated right I<sup>1</sup> (A, No. 5) and I<sup>2</sup> (B, No. 6); right maxilla with M<sup>2-3</sup> (C, No.2); left maxilla with M<sup>2-3</sup> (D, No.1); isolated left M<sup>1</sup> and M<sup>2</sup> (E, No. 3 and 4). Scale bar, 1 cm.



**Figure 2.** Labial (A) and lingual (B) views of premaxilla with left I<sup>1-2</sup> and right I<sup>1</sup> (GIN U 987/878(2)). Labial (C) and lingual (D) views of left premaxilla and maxilla with I<sup>1</sup>-P<sup>3</sup> (GIN-U 987/878(1)). Scale bar, 1 cm.

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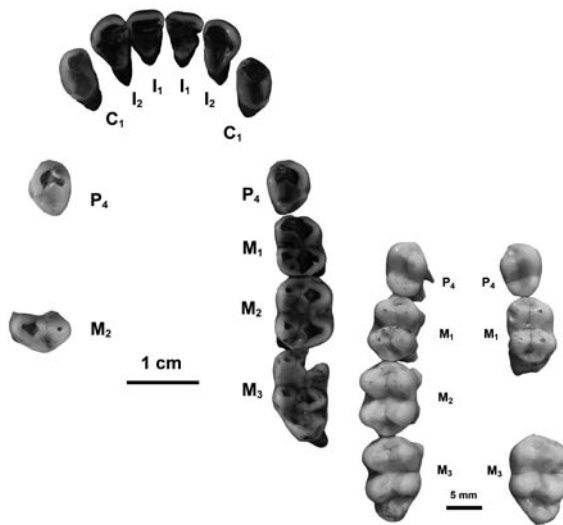
In this article we shortly present a number of additional specimens and discuss the morphological features and evolutionary history of Siberian colobine monkeys comparing with some fossil and living Asian colobine monkeys.

**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 I<sup>1</sup> is nearly triangular or pentagonal. Labial enamel crenulation is very strong both in I<sup>1</sup> and I<sup>2</sup>. Both in upper and lower incisors the crown is not protruding anteriorly but



**Figure 4.** Isolated lower teeth (GIN U 986/38 (1-12)) probably of the same individual.

**Figure 5.** Isolated lower teeth. Left P<sub>4</sub> (No.14), M<sub>1</sub> (No.9), M<sub>2</sub> (No.12), M<sub>3</sub> (No. 8), right P<sub>4</sub> (No. 10), M<sub>1</sub> (No. 13) and M<sub>3</sub> (No. 11).



**Figure 6.** Crushed mandibular corpus (PIN 3381-236) in occlusal view. Scale bar, 1cm.

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 I<sup>1</sup> and I<sup>2</sup> 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 lingually positioned than molars. There is a variation in the size and morphology of the distal lobe of M<sub>3</sub>: it is relatively small and 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 P<sub>3</sub>. In the *Parapresbytis* specimens distinct sexual dimorphism is not confirmed. Most of the specimens preserving canines and/or P<sub>3</sub> are likely to be female individual. There are slight morphological difference between two mandibular specimens collected from Shamar, PIN 3381-235 and PIN 3381-236. Lower canine is slightly larger and higher and P<sub>3</sub> retains lightly longer mesiobuccal flange in the former than in the latter, but the difference is not so

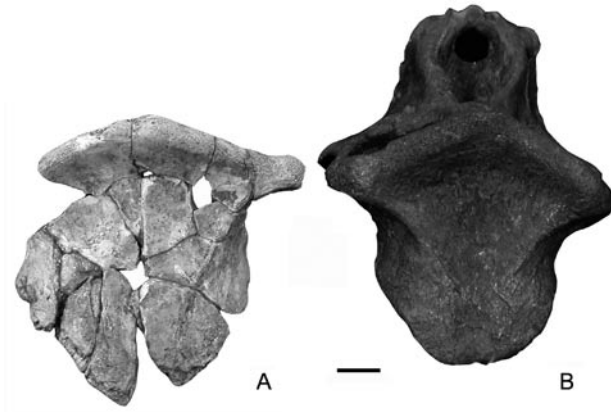
*Prapresbytis* from Transbaikalia

**Table 2.** Dental measurements (mm) of *Parapresbytis eohanuman*. Upper (**A**) and lower (**B**) dentitions. L, left; R, right; MD, mesiodistal length; BL, buccolingual width; mand depth. Data of Kanagawapithecus and Dolichopithecus are from Iwamoto et al. (2005) and Delson (1973). Data in parentheses are number of samples.

(A) upper teeth		I <sup>1</sup>		I <sup>2</sup>		C <sup>1</sup>		P <sup>3</sup>		P <sup>4</sup>		M <sup>1</sup>		M <sup>2</sup>		M <sup>3</sup>					
		MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL				
<i>Parapresbytis</i> (Udunga)																					
GIN U 987/878(2)	R	8.66	9.15																		
GIN U 987/878(2)	L	8.56	8.78	7.31	8.65																
GIN U 987/878(1)	L	7.57	8.59	5.80	7.59	8.82	8.19	6.77	8.03												
GIN U 987/445	R							7.21	7.91	6.82	8.73	9.76	9.13	11.47	10.58	11.01	10.58				
GIN U 986/38(13)	L												10.84	10.12							
GIN U 986/678	L																9.15				
No.1	L																10.65	10.25	10.47	9.65	
No.2	R																10.55	10.33	10.45	9.84	
No.3	L											9.70	8.94								
No.4	L													10.54	9.76						
No.5	L	8.06	8.71																		
No.6	L			6.84	8.13																
<i>Kanagawapithecus</i> (Nakatsu)																					
KPM-N NC005802	R					9.5	8.5			7.0	9.0	10.0	9.5	11.0	11.0	10.5	10.5				
KPM-N NC005802	L													10.5	10.0	10.5	10.5				
<i>Dolichopithecus ruscinensis</i> (Perpignan)						12.67	9.45			7.12	8.31	8.96	8.63	10.31	9.66	9.77	9.15				
(Delson, 1973)						(4)	(4)			(7)	(7)	(10)	(9)	(10)	(10)	(9)	(9)				
(B) Lower teeth		I <sub>1</sub>		I <sub>2</sub>		C <sub>1</sub>		P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>					
		MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL				
no.	side											trd	tad								
<i>Parapresbytis</i> (Udunga)																					
GIN U 986/38(1)	R	5.17	7.12																		
GIN U 986/38(2)	R			5.4	8																
GIN U 986/38(3)	R					5.1	7.5														
GIN U 986/38(4)	R							7.6	7												
GIN U 986/38(5)	R									8.49	6.51	6.84									
GIN U 986/38(6)	R												10	8.07	8.29						
GIN U 986/38(7)	R																12.5	7.62			
GIN U 986/38(8)	L	5.19	7.37																		
GIN U 986/38(9)	L			5.5	8.1																
GIN U 986/38(10)	L					7.3	4.8														
GIN U 986/38(11)	L									7.7	6.2										
GIN U 986/38(12)	L																8.65				
No.7	L			5.09	5.55																
No.8	L																	12.80	8.60		
No.9	L									9.57	7.26	7.23									
No.10	R							7.66	6.17												
No.11	R																13.11	8.40			
No.12	L												10.89	8.34	8.53						
No.13	R									9.40	7.06	7.18									
No.14	L							7.86	6.00												
<i>Parapresbytis</i> (Shaamar)																					
PIN 3381-236	R			6.18	9.11	5.86	8.96	10.38	5.68	8.38	7.03	10.05	7.63	7.85	10.61	9.02	9.34	13.91	9.22		
PIN 3381-236	L					5.94	9.13	10.78	5.79	8.62	7.81	10.02	7.72	7.99	10.80	8.72	9.29	14.06	9.15		
PIN 3381-235	R																				
PIN 3381-235	L																				

distinct but looks like individual variation. If there is actually sexual dimorphism in upper/lower canines and P<sub>3</sub>, 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 most lower dentition, while the latter has a distinct mandibular fossa at the buccal face of the corpus below P<sub>3,4</sub>, which is not analogous of mandibular fossa in cercopithecinae but often seen in living *Rhinopithecus* mandible.



**Figure 7.** Dorsal view of the skull roofs of *Parapresbytis* (A, GIN U 987/493) and *Kanagawapithecus* (B, KPM-N NC005802). Scale bar, 1 cm.



**Figure 8.** Anterior view of the skull roof of *Parapresbytis* (above, GIN U 987/493(1)), comparing with the skull of *Rhinopithecus roxellanae* (NWU-7100093). Note the difference in the angles of the supraorbital tori between them.

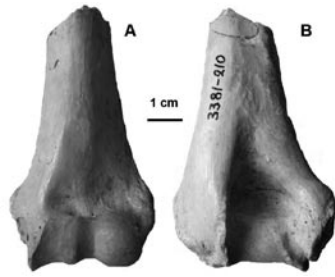


**Figure 9.** Femal skull of *Dolichopithecus ruscinensis* (MNHN-P PER 001) from Perpignan, France. Note that the skull is apparently distorted, forming different angles of the supraorbital tori between right and left sides.

### 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.



**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.

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

**Table 3.** Statistics of the crown area of upper incisors and upper M<sup>1</sup> and M<sup>2</sup> (mesiodistal length\*buccolingual width, in mm<sup>2</sup>). SD, standard deviation; CV, coefficient of variation; min, minimum value; max, maximum value; N, number of samples. Data of *Victoriapithecus* is from Benefit (1994), and some data of *Rhinopithecus* are from Jablonski and Pan (1991). Data of upper incisors and upper molars are not always of the same individual.

	I <sup>1</sup>	I <sup>2</sup>	M <sup>1</sup>	M <sup>2</sup>		I <sup>1</sup>	I <sup>2</sup>	M <sup>1</sup>	M <sup>2</sup>
<i>Rhinopithecus</i>					<i>Dolichopithecus</i>				
mean	31.2	25.3	66.3	84.5	mean	27.7	28.4	80.2	103
SD	5.13	4.01	8.54	13.9	SD	3.07	0.2	4.93	3.81
CV	0.16	0.16	0.13	0.16	CV	0.11	0.01	0.06	0.04
min	21.8	20.6	46.2	60.8	min	24.5	28.3	75.9	99.6
max	38.9	32.6	82.7	122	max	30.6	28.6	87.1	109
N	12	12	21	16	N	3	3	5	5
<i>Presbytis</i>					<i>Victoriapithecus</i>				
mean	16.2	12.8	36.8	46	mean	21	14.3	40.7	58.7
SD	1.56	0.85	2.83	14	N	1	1	1	1
CV	0.1	0.07	0.08	0.3	<i>Libypithecus</i>				
min	14.4	12.2	33.8	34.8	mean	22.4	23.5	48.9	58.9
max	17.3	13.7	40.3	75.2	SD	1.9	1.37	2.97	3.78
N	3	3	6	7	CV	0.08	0.06	0.06	0.06
<i>Parapresbytis</i>					min	21.1	22.6	46.8	56.3
mean	72.4	54.3	87.9	111	max	23.8	24.5	51	61.6
SD	6.15	9.67	1.69	7.75	range	2.69	1.94	4.2	5.35
CV	0.08	0.18	0.02	0.07	N	2	2	2	2
min	65	44	86.7	103	<i>Nasalis</i>				
max	79.2	63.2	89.1	121	mean	29	23.3	49.1	62.5
N	4	3	2	4	SD	-	-	3.85	5.34
<i>Mesopithecus</i>					CV	-	-	0.08	0.09
mean	24.6	20.4	50.3	60.3	min	29	23.3	46.4	58.7
SD	2.24	2.33	3.55	4.43	max	29	23.3	51.8	66.2
CV	0.09	0.11	0.07	0.07	N	1	1	2	2
min	21.7	16.1	44	51.1	<i>Pygathrix</i>				
max	28.4	23.2	57.2	67.2	mean	28.3	27.8	47.2	53.8
N	9	10	19	19	N	1	1	1	1

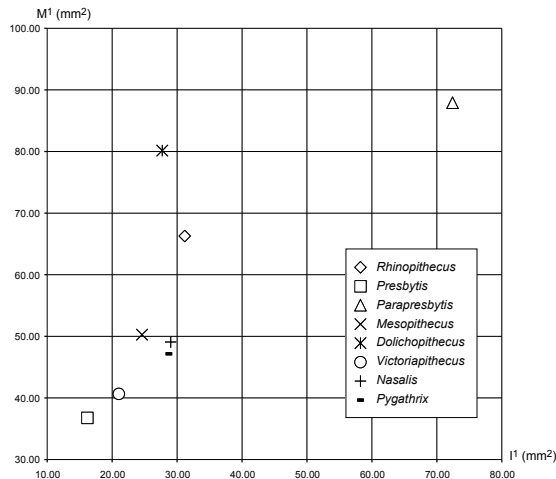
### Comparisons with fossil colobine monkeys from Eastern Asia

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 supratral 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



**Figure 12.** Bivariate plot of the crown size of I¹ against M¹. Note that *Dolichopithecus* retains much smaller I¹ relative to M¹, differing from other colobine monkeys including *Parapresbytis*. Data from Table 3.

(Nishimura et al., in preparation). 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



**Figure 13.** Comparison of the skulls of *Presbytis francoisi* (left, NWU 82005) and *Rhinopithecus roxellanae* (right, NWU 8007). Note the difference in the angles of the supraorbital tori between them. It runs horizontally or rather downward laterally in *Presbytis*, whereas it runs upward laterally in *Rhinopithecus*.



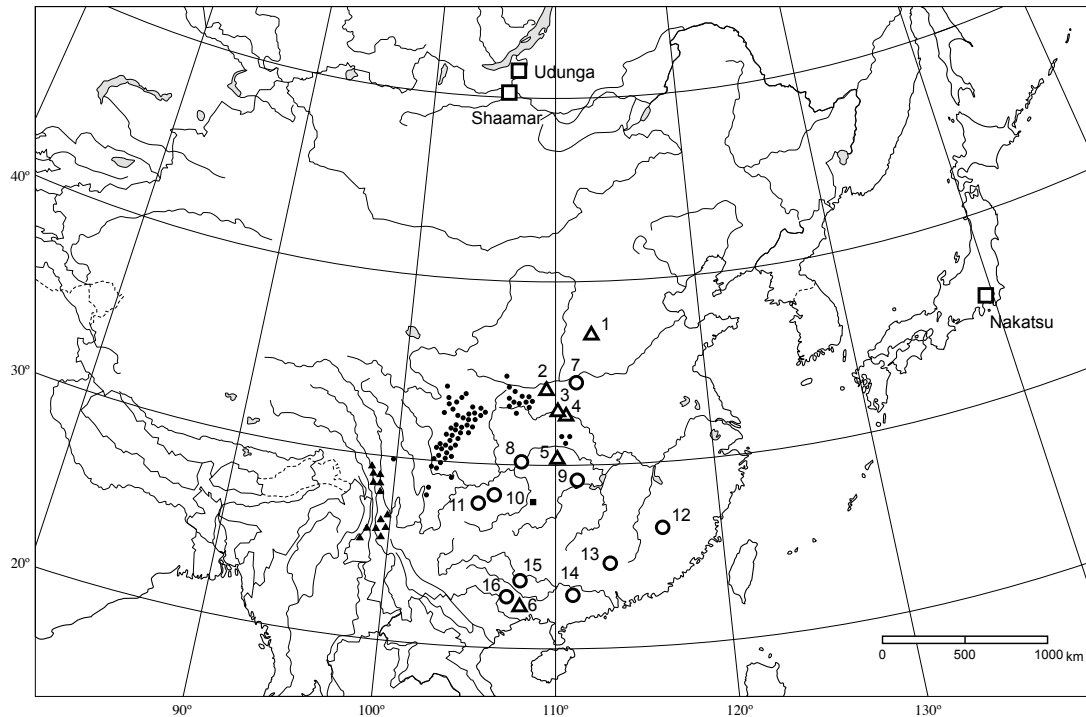
**Figure 14.** Comparison of *Kanagawapithecus* (above, male specimen) and *Parapresbytis* (below, GIN U 987/445 and 987/878(2)): right lateral (left) and anterior (right) views. Note much larger size of upper incisors in *Parapresbytis* despite almost same size of the cheek teeth between them.

*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 Transbaikal 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 M<sub>3</sub>, 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



**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, Shaamar, 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, Longguodong 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, Jiandau Hill (Cili County, Hunan); 10, Yanhuidong (Tongzi County, Guizhou); 11, Guanyindong (Qianxi County, Guizhou); 12, Jiandaoqian (Fujian); 13, Luohang (Qujiang, Guangdong); 14, Luoding (Guangdong); 15, Jiulengshan (Du'an, Guangxi); 16, Heidong (Daxin, Guangxi). Small filled marks indicate the distribution of living *Rhinopithecus*: filled circles, *R. roxellanae*; filled square, *R. brelichii*; 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 and Gu (1991), 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).

*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

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 united into the "rhinopithecomorph" (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.

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