Available online at www.sciencedirect.com
ScienceDirect
Quaternary International 179 (2008) 108–119

Phylogenetic relationships and biogeographic history of *Paradolichopithecus sushkini* Trofimov 1977, a large-bodied cercopithecine monkey from the Pliocene of Eurasia

Masanaru Takai[a,*], Evgeny N. Maschenko[b], Takeshi D. Nishimura[c], Tomoko Anezaki[d], Tomoki Suzuki[a]

[a]*Primate Research Institute, Kyoto University, Inuyama 484-8506, Japan*
[b]*Paleontological Institute, Russian Academy of Science, Profsoyuznaya Street 123, 117995 Moscow, Russian Federation*
[c]*Laboratory of Physical Anthropology, Kyoto University, Kyoto 606-8502, Japan*
[d]*Gunma Museum of Natural History, 1674-1 Kamikuroiwa, Tomioka, Gunma 370-2345, Japan*

Available online 22 October 2007

Abstract

Paradolichopithecus sushkini Trofimov 1977 is a cercopithecine monkey discovered from the late Pliocene of Kuruksay, southern Tajikistan. Despite the baboon-like appearance of the skull, detailed analysis of the inner structure of the rostrum with computed tomography revealed that *P. sushkini* has a maxillary sinus, which occurs only in macaques among the living cercopithecoids. This observation suggests that *Paradolichopithecus* may belong to the lineage of the macaques rather than to that of the baboons. This fact and the fossil records of Eurasian cercopithecines together suggest that *Paradolichopithecus* diverged from European *Macaca* as early as the early Pliocene, and then dispersed into eastern Eurasia. Although the dispersal route of the Asian cercopithecines, *Macaca*, has so far been discussed only in the context of South Asian geographical changes, the distribution pattern of the *Paradolichopithecus* fossil localities may indicate a more northern dispersal route, such as via Central Eurasia rather than a southern route, such as via South Asia.

1. Introduction

Paradolichopithecus is the largest representative of the fossil cercopithecines, which were distributed in Europe and western Asia from the middle Pliocene to the early Pleistocene. Two species have been described in Europe, *Paradolichopithecus arvernensis* Depéret 1929 and *P. geticus* Necrasov 1961, although *P. geticus* is sometimes regarded as a subspecies of *P. arvernensis* (e.g. Eronen and Rook, 2004).

Outside Europe, another species, *Paradolichopithecus sushkini*, has been reported from the late Pliocene site of Kuruksay, southern Tajikistan (Trofimov, 1977). The fossil material consists of skulls, mandibles, and some isolated teeth, all of which were collected at the same locality by joint expeditions of the Paleontological and Geological Institutes, of the USSR Academy of Sciences, Moscow, during the 1977–1979 field seasons (Maschenko, 1994, 2005). The Kuruksay mammalian fauna contains both forest and open-terrain dwellers, and is correlated with the MN17 European Mammal Unit, of about 2.4–2.2 million years ago (Table 1, Vangengeim et al., 1988; Sotnikova et al., 1997; Maschenko, 2005).

There is some controversy regarding the phyletic position of *Paradolichopithecus* within the Cercopithecinae (Fig. 1). Many authorities have insisted that, based on cranial features, *Paradolichopithecus* is more closely related to the macaques than to the baboons, despite the baboon-like terrestrial features in postcranial bones or elements (Jolly, 1967; Simons, 1970; Delson, 1973; Szalay and Delson, 1979; Groves, 2000, 2001; Jablonski, 2002). This interpretation is supported by a geometric morphometric analysis of craniofacial specimens from France and Romania (Delson and Frost, 2004). In contrast, morphological analysis of the nearly complete and incomplete crania and mandibles from Kuruksay has prompted the suggestion that *P. sushkini* be reassigned to the genus

*Corresponding author. Tel.: +81 568 63 0533; fax: +81 568 63 0536.
E-mail address: takai@pri.kyoto-u.ac.jp (M. Takai).

1040-6182/$ - see front matter © 2007 Elsevier Ltd and INQUA. All rights reserved.
doi:10.1016/j.quaint.2007.10.012

Table 1
The list of Kuruksay mammalian fauna (2.4–2.2 Ma, MN17)

Lagomorpha	Perissodactyla
Leporinae gen. indet.	Rhinocerotidae
Rodentia	*Dicerorhinus* sp.
Hystrix trofimovi	Equidae
Ellobius sp.	*Equus stenonis*
Promimomys cf. *basckirica*	Artiodactyla
Primates	Camelidae
Cercopithecidae	*Paracamelus prebactrianus*
Paradolichopithecus sushkini	Cervidae
Carnivora	*Axis flerovi*
Canidae	*Elaphurus eleonorae*
Nyctereutes megamastoides	*Elaphurus* sp.
Canis kuruksaensis	*Sinomegaceros tadzhikistanis*
Canis ex. gr. *lepophagus*	*Libralces* cf.*gallicus*
Ursidae	Giraffidae
Ursus sp.	*Sogdianotherium kuruksaense*
Hyaenidae	*Sivatherium* sp.
Chasmaporthetes lunensis	Bovidae
Pachycrocuta perrieri	*Gazella parasinensis*
Felidae	*Anthilospira* sp.
Lynx ex gr. *issiodorensis*	*Gazellospira gromovae*
Acinonyx sp.	*Protoryx paralatipes*
Megantereon megantereon	*Protoryx* sp.
Homotherium crenatidens	*Damalops palaeindicus*
Hemimachairodus sp.	
Proboscidea	
Mastodontoidea	
fam.et gen indet.	
Elephantidae	
Archidiskodon cf.*gromovi*	

Data was adopted from Vangengeim et al. (1988), Sotnikova et al. (1997) and Maschenko (2005).

Papio, which contains the modern baboons (Maschenko, 1994, 2005).

Extant macaques and baboons (including *Papio* and *Theropithecus*) are closely related groups within the tribe Papionini, which consists of the two lineages (subtribes) Macacina and Papionina: the former includes the extant macaques, and the latter includes the baboons, mandrills, mangabeys, and geladas (see Delson, 2000). Among living species, it is very easy to distinguish baboons from macaques. In the baboons, the muzzle is very long relative to the cranium; the anteorbital "drop" or concavity is very steep; the maxillary and mandibular fossae are distinctive; and the lacrimal fossa is situated in the lacrimal bone and has no contact with the frontal process of the maxilla. However, in fossil taxa such as *Paradolichopithecus*, which is likely to be a primitive member of Papionini, such morphological features are expected to be less stereotypical than those seen in living species and to appear intermediate, at least superficially.

The maxillary sinus is an inner structure of the rostrum and is noted for its value in the phylogenetic analysis of the anthropoid primates (see reviews by Rae and Koppe, 2004; Nishimura, 2006). This sinus communicates with the middle meatus of the nasal cavity through a narrow ostium, from which it develops postnatally to invade the region in which the cancellous bone of the maxilla is resorbed (Cave, 1967; Weiglein, 1999; Witmer, 1999; Maier, 2000; Rossie, 2006). This sinus is shared by extant hominoids (Koppe and Ohkawa, 1999; Rae and Koppe, 2000), stem hominoids, and stem catarrhines (Rossie, 2005), and by most extant platyrrhines (Koppe et al., 1999, 2005; Nishimura et al., 2005; Rossie, 2006). Whereas extant macaques have a small maxillary sinus pneumatizing a part of the maxillary body (Koppe and Ohkawa, 1999; Koppe et al., 1999), other extant cercopithecoids and the stem cercopithecoid *Victoriapithecus* have no maxillary sinus (Fig. 1; Koppe and Ohkawa, 1999; Rae et al., 2002). Instead, their maxillary body is filled with dense cancellous bone (Fig. 2a; Koppe and Ohkawa, 1999; Rae et al., 2002), except in the baboons, which have a negligible cancellous region in the maxillary body (Fig. 2c; Koppe and Ohkawa, 1999).

Here, we examine the dental measurements, a distinct superficial feature, in the Kuruksay skull specimens. Then, we analyze a computed tomography (CT) study of the presence/absence of the maxillary sinus in the specimens (Nishimura et al., 2007), and evaluate the phyletic position of *P. sushkini*. We also examine the distribution pattern of *Paradolichopithecus* fossils in eastern Eurasia, and discuss the dispersal route of this monkey from Europe to East Eurasia.

2. Materials and methods

Two fossil crania of *P. sushkini* (PIN 3120-523 and 3120-524) from Kuruksay are examined here. Both are housed at the Paleontological Institute (PIN) of the Russian Academy of Sciences in Moscow. PIN 3120-523, the adult female type specimen in which left I^2 and P^3–M^3 and right C^1, P^3?, and M^{1-3} are preserved, is slightly distorted facially, but the surface features are well preserved (Figs. 3a–c). The other specimen, PIN 3120-524, is a badly distorted facial part of a subadult male (Figs. 3d–f. Both the left and right C–M^3 are preserved, although the upper canines and M^3s are not fully erupted, suggesting a subadult age. The dental measurements of fossil specimens were compared with data collected from the skeletal specimens of living *Macaca* and *Papio* housed at the Kyoto University Primate Research Institute (KUPRI) and the Japan Monkey Center (JMC) (Table 2, Fig. 4).

The crania were scanned using helical CT scanners, and the inner structures of the facial crania were evaluated on serial coronal CT images and on sagittal and axial images reformatted from the serial coronal images (Nishimura et al., 2007).

3. Results from analysis of dental proportions and evaluation of CT images

P. sushkini is as large as other *Paradolichopithecus* species and *Procynocephalus* Schlosser, 1924, another large