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Dental Agenesis as Evidence of Possible Genetic Isolation in the Colobine Monkey, *Rhinopithecus roxellana*

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ABSTRACT. In a sample of 24 skulls of the rare colobine monkey of China, *Rhinopithecus roxellana*, agenesis of the permanent upper third premolar was observed in 8 specimens (33%). Two of the individuals (8% of the sample) showed unilateral agenesis, while six (25%) showed bilateral agenesis. All of the affected individuals appear to have originated from two areas in central Sichuan Province in China, Moupin (Baoxing) and Wen Chuan, that lie approximately 120 km apart on the western rim of the Sichuan Basin. In this species agenesis of the upper third premolar was generally accompanied by rotation of the upper fourth premolar, but not by any other observable variation in tooth size, morphology, or number. Further, dental agenesis in this species appears to have had no effect craniofacial morphology. In certain human populations, a high prevalence of dental agenesis has been associated with small population effects and genetic isolation. Premolar agenesis in *R. roxellana* can probably be traced to a similar origin. Reconstruction of the evolutionary history of the species indicates that a severe reduction of the geographic range of the species occurred as a result of climatic deterioration during the Late Pleistocene. Although large numbers of populations appear to have become extinct, others survived to give rise to the modern populations of the species that inhabit China today. The two populations showing a high prevalence of premolar agenesis appear to have originated from one that passed through a population bottleneck and suffered the consequences of founder effect in the Late Pleistocene. This interpretation is supported by evidence of dental agenesis in a population of an insectivore species from the same region and by the fact that premolar agenesis is not found in any of the other species of *Rhinopithecus*. There is no evidence to support the interpretation that dental agenesis in *R. roxellana* is due to natural selection, mutation or an evolutionary force other than a small population effect.

Key Words: Dental agenesis; Hypodontia; *Rhinopithecus roxellana*; Geographic isolation; Founder effect.

INTRODUCTION

Variations in tooth number in the primate dentition have long been of interest to primatologists, anthropologists, and geneticists. High frequencies of molar, and particularly third molar, agenesis (or hypodontia) have been documented for several human populations (LAVELLE & MOORE, 1973). This phenomenon has been thought to be related to the shortening of the jaws observed in the course of hominid evolution (LAVELLE & MOORE, 1973) or associated with the gradual trend toward reduction of dental size related to the decreased importance of dental preparation of foods in Late Pleistocene and Post-Pleistocene populations (BRACE et al., 1987). Compared to humans, nonhuman primates tend to show a lower incidence of dental agenesis and the phenomenon does not appear to be concentrated in the molar region (LAVELLE & MOORE, 1973).

In this report an unusual pattern of dental agenesis in the golden monkey of China, *Rhinopithecus roxellana*, is discussed. The golden monkey or golden snub-nosed langur, *R. roxellana*, is one of four known extant species of the colobine genus *Rhinopithecus*.

All the species of *Rhinopithecus* are extremely rare in the wild and their remains are very poorly represented in institutional collections in China and elsewhere.

In his well known work entitled *Variations and Diseases of the Teeth of Animals*, COLYER (1936) reported that he had encountered no cases of numerical variations in the teeth of the 17 specimens of the colobine monkey, *Rhinopithecus*, that he had examined in museums in Britain, Europe, and the U.S. In 1952, HOOIJER (1952), however, noted that 2 out of the 12 adult or subadult specimens of the golden monkey or snub-nosed langur, *Rhinopithecus roxellana*, that he had examined at the National Museum of Natural History in Washington D.C., United States showed bilateral absence of the permanent upper third premolar. This account was followed some years later by another (HYLANDER & KAY, 1975) in which variations among 17 specimens, including most if not all of HOOIJER's original sample, were reported. HYLANDER and KAY (1975) indicated that a total of 6 of the 17 specimens (35%) showed absence of the upper third premolar, with 5 specimens showing bilateral agenesis and one showing unilateral agenesis.

HOOIJER speculated that the causes of premolar agenesis in *Rhinopithecus* could be attributed to "an evident tendency toward reduction of the number of the dental elements, just as is the case in man..." (1952, p. 259), while HYLANDER and KAY (1975) suggested that this deviation in tooth number might be restricted to a particular subspecies (*R. r. roxellana*). Recent evidence now suggests that neither interpretation is entirely correct and that insights into the etiology of dental agenesis in *R. roxellana* can be gained from careful examination of the evolutionary history of *Rhinopithecus* (JABLONSKI, 1991).

MATERIALS AND METHODS

As mentioned above, specimens of *Rhinopithecus* species are extremely rare in institutional collections. For purposes of this study every effort was made to examine as many skulls of *Rhinopithecus roxellana* as possible, but the total number investigated was still relatively small. Twenty-four skulls of adult or subadult *Rhinopithecus roxellana* were examined in collections at the following institutions: National Museum of Natural History (NMNH), Washington D.C. ($N=9$); Field Museum of Natural History (FMNH), Chicago ($N=5$); British Museum (Natural History) (BMNH), London ($N=3$); Museum National d'Histoire Naturelle (MNHN), Paris ($N=4$); Kunming Institute of Zoology (KIZ), Yunnan, China ($N=2$); and Institute of Zoology, Beijing (BIZ), China ($N=1$). Variations in tooth number, size, position, and morphology were noted, as was the provenance of the specimen when this information was available. Unfortunately, it was not possible to take radiographs of specimens exhibiting unusual morphologies.

RESULTS

Agenesis of one or more of the upper third premolars was observed in 8 of the 24 specimens of *R. roxellana* examined (33%). A detailed breakdown of the frequency of premolar agenesis in the various samples of the species is presented in Table 1. It should be noted that all occurrences of agenesis of the upper third premolar were accompanied by rotation of the upper fourth premolar to lesser or greater degrees. In specimens exhibiting premolar agenesis, no difference in tooth size was observed in any of the remaining teeth of the upper dental arcade as compared to unaffected specimens. Premolar agenesis did not noticeably

Table 1. Agenesis of permanent upper third premolars in *Rhinopithecus roxellana*, listed according to provenance of specimens (institutional collection and original locality).[1)]

Institution[2)]	*N*	Unilateral	Bilateral	Locality
NMNH	9	0	2 (F)	Wen Chuan, Sichuan
FMNH	5	1 (F)*	2 (F)	Moupin, Sichuan
MNHN	4	0	1 (M)	Moupin, Sichuan
BMNH	3	0	0	Moupin, Sichuan
KIZ	2	1 (F)	1 (M)	Not known
BIZ	1	0	0	Not known

1) The sex of affected specimens is indicated in parentheses in the appropriate columns; 2) see Materials and Methods for abbreviations of the names of institutional collections. F: female; M: male. * In this individual the left upper third premolar was missing and the right displayed an unusual morphology.

alter the craniofacial morphology of affected specimens.

From the compilation in Table 1, it is evident that all the specimens showing agenesis originated from the localities of Moupin (now known as Baoxing, 30°24′N; 102°50′E) or Wen Chuan (31°15′N; 103°20′E) in central Sichuan Province, People's Republic of China.

DISCUSSION

Numerous studies of human family pedigrees have demonstrated that dental agenesis has a significant heritable component (e.g. GRABER, 1978; Grahnén, 1956; SUAREZ & SPENCE, 1974). Further, in humans, elevated prevalence estimates for dental agenesis appear to be associated with genetic isolation and inbreeding (JOHR, 1934; KIRVESKARI et al., 1978; MAHANEY et al., 1990; THOMSEN, 1953). High prevalence estimates of dental agenesis have been documented for population isolates such as the Hutterite Brethren of Western Canada (MAHANEY et al., 1990), the Skolt Lapps of Finland (KIRVESKARI et al., 1978), and the natives of Tristan de Cunha (THOMSEN, 1953), which have small effective population sizes due to restrictive marriage practices or severe population declines in the past. The results of this study combined with information on the evolutionary history of the genus *Rhinopithecus* suggest that the premolar agenesis observed in *R. roxellana* can probably be attributed, as in the case of the human populations cited, to a population bottleneck. This dramatic reduction in effective population size was due to environmental deterioration in the Late Pleistocene (JABLONSKI & GU, 1991; JABLONSKI & PAN, 1988). Evidence that the species passed through a population bottleneck and suffered from founder effect is strong.

The geographic distribution of fossil forms of *Rhinopithecus* extends farther eastward than does that of the living species of the genus (COLBERT & HOOIJER, 1953; JABLONSKI & PAN, 1988; JABLONSKI & GU, 1991). COLBERT and HOOIJER (1953) suggested that the ranges of the modern species of *Rhinopithecus* were the remnants of an earlier continuous distribution that extended over the greater portion of Sichuan. The results of recent paleontological, geological, and paleoenvironmental studies indicate that the original range of the common ancestor of *Rhinopithecus* and its close relative *Pygathrix* (the genus to which the douc langur of Vietnam belongs) extended over a large area of central and southeastern China (JABLONSKI & GU, 1991). During the Pliocene (approximately 5 to 2 million years ago), this range appears to have undergone fragmentation because of geomorphological changes associated with the uplifting of the Qinghai/Xizang (Tibetan) Plateau. This result-

ed firstly in the splitting of the *Rhinopithecus-Pygathrix* lineage and, later, in the fragmentation of the distribution of the ancestral *Rhinopithecus* species (JABLONSKI & GU, 1991). By Pleistocene times, climatic deterioration in central and southwestern China brought about by the elevation of the Tibetan Plateau was heightened by the effects of episodic glaciations that covered large areas of northern Asia. During the latter Pleistocene, extinctions of large and small mammalian species, including species of *Rhinopithecus* in northern and central China, were widespread (JABLONSKI & GU, 1991; JABLONSKI & PAN, 1988) and China lost a large proportion of its biodiversity.

The localities of Moupin (Baoxing) and Wen Chuan, from which the specimens of *Rhinopithecus roxellana* examined for this study originated, are located in the valleys of the Qingyi and Min Rivers, respectively, on the western perimeter of the Sichuan Basin. Even during the height of the Pleistocene glaciations, the Sichuan Basin appears to have been spared the worst environmental deterioration because of its low altitude (50 – 200 m), and the survival of *R. roxellana* near the basin's perimeter can be attributed to its ameliorating climatic effects. The finding of high prevalence estimates of premolar agenesis in both the Moupin and Wen Chuan populations suggests that they originated from a single, very small population that survived in the Sichuan Basin during the Late Pleistocene.

Populations of *R. roxellana* occur today not only in Sichuan Province, but also in areas of Shaanxi, Gansu, and Hubei Provinces. Because specimens of *R. roxellana* originating outside of Sichuan could not be examined for this study due to logistical problems, it is not known whether these populations of the species also exhibit a high prevalence of agenesis of the permanent upper third premolar. At present, fossil and other evidence does not permit us to determine whether the populations of the species now found in several provinces in central and western China derive from one or several populations that were isolated in the Late Pleistocene. The differences in coat colour between the various provincial populations of the species would suggest that more than one population survived the most severe depredations of the Late Pleistocene. Further investigations will reveal whether populations of *R. roxellana* other than those from Moupin and Wen Chuan exhibit this unusual dental phenomenon.

The hypothesis that dental agenesis in *R. roxellana* can be traced to a small population effect caused by an environmentally induced population collapse near the Sichuan Basin during the Late Pleistocene is supported by other evidence. Firstly, there is no evidence of a similar phenomenon in any of the other species of *Rhinopithecus*. Although the severe climatic deterioration of the Late Pleistocene is thought to have had an effect on all *Rhinopithecus* species living in temperate or subtropical environments, *R. roxellana* was probably the most severely affected because its distribution extends farther northward than any of the other species of the genus (JABLONSKI, 1991). Secondly, there is no evidence to date that premolar agenesis in *R. roxellana* is due to any other evolutionary force such as natural selection, mutation, or gene flow. Dental agenesis in humans has been attributed to a founder effect following a catastrophic collapse in population size (e.g. THOMSEN, 1953) and to genetic isolation, small population size, and apparent genetic drift (KIRVESKARI et al., 1978; MAHANEY et al., 1990). Strong circumstantial evidence that populations of *R. roxellana* have suffered a population collapse in the relatively recent geological past supports the interpretation that premolar agenesis in the species is due to a founder effect. Thirdly, there are other anatomical features of *R. roxellana* that cannot be explained satisfactorily by natural selection or by any other evolutionary force. These include apparently non-adaptive traits like its brilliant golden pelage and bright blue face, which are not seen in any other species of its genus (CHAPLIN & JABLONSKI, in prep.).

Perhaps the most compelling piece of supporting evidence for this interpretation, however, is the observation of a similar phenomenon in another mammalian species from the same locality. OSGOOD (1937) reported great variation in tooth number in the dentition of the shrew-like insectivore, *Uropsilus sorices*, collected from central Sichuan Province. He noted "greatest instability" (OSGOOD, 1937, p. 367) in the upper third premolar and lower third incisor, but also observed variation in the lower third premolar. He contrasted the highly variable condition of the dentitions in the Sichuan populations to those of populations in Yunnan Province and Kachin Province of Burma in which no variations in tooth number occurred and concluded that a trend toward dental reduction appeared to be occurring in west-central Sichuan. It is now clear that the highly variable populations he examined, from the localities of "Luan Shih Go and Lu Ting Shan, about halfway between Mouping [Moupin] and Tatsienlu" (OSGOOD, 1937, p. 365) were close to or sympatric with the populations of *Rhinopithecus roxellana* discussed here. Founder effects are random events, and there can be no direct connection between the apparent founder effects experienced by the insectivore and golden monkey species. On the other hand, the discovery of the consequences of apparent founder effects in these populations is not coincidental, and is best explained by the insectivore and monkey species having experienced the environmental same pressures at the same time. The insectivore populations described by OSGOOD appear to have been subjected to the same environmental and population effects that left their mark on the golden monkeys.

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