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The influence of life history and diet on the distribution of catarrhine primates during the Pleistocene in eastern Asia

Environmental changes during the Pleistocene in eastern Asia had profound impacts on the distributions of mammalian groups. Critical for many mammals were the southward latitudinal shifts of the tropical and subtropical vegetational zones, and decreases in the areas of these zones. Examination of the responses of members of a single clade, the Catarrhini, indicates that the main catarrhine genera of eastern Asia responded individually to the environmental changes in the Pleistocene. These responses were influenced by the life history parameters and diets of the genera involved. Those animals (macaques, langurs) with shorter gestation times, shorter weaning periods, shorter interbirth intervals, higher intrinsic rates of increase of population, and abilities to survive on a wider variety of vegetation in seasonal habitats were less adversely affected than those (gibbons, orang-utans and the giant extinct hominoid, *Gigantopithecus*) with more protracted reproductive schedules, lower intrinsic rates of population increase and preferences for the higher quality foods (especially ripe fruits) of less seasonal environments. Hominids, while displaying "hyper-ape" life history parameters, increasingly overcame the constraints of these parameters through extrasomatic means not available to other catarrhines. This ability made possible their colonization, by the Late Pleistocene, of highly seasonal habitats such as tundra, which were off-limits to non-culture-bearing catarrhines.

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Introduction

Natural populations of mammals respond to the myriad stresses of climatic change by latitudinal shifts in abundances and/or geographic range boundaries (FAUNMAP Working Group, 1996; Roy *et al.*, 1996).

The sometimes extreme climatic fluctuations of the Pleistocene destabilized species interactions within communities, with the result that species tended to respond individually to environmental stresses because they observed the environment with their own unique suites of life history parameters.

Environmental changes during the Pleistocene in East Asia were more marked than in other parts of the Northern Hemisphere because the local climatic effects of the Himalayas and Qinghai-Xizang (Tibetan) Plateau tended to magnify the orbitally induced climatic fluctuations associated with glacials and interglacials worldwide (Liu *et al.*, 1997). Among the most dramatic of these changes was the abrupt increase, at about the Gauss/Matuyama boundary (2.5 Ma), in aeolian dust deposition occurring on the Loess Plateau due to an apparent northward shift and intensification of the Siberian High (Ding *et al.*, 1997). Marked increases in environmental seasonality at all latitudes, increasing environmental heterogeneity and fragmentation, an increasing potential for physical isolation of populations as a result of habitat fragmentation, and changes in the configuration of biogeographic corridors were the most important consequences of these changes for mammalian populations (Ferguson, 1993; Jablonski, 1993).

Our primary goal in this study is to examine the geographical responses of the genera within a closely related mammalian clade in order to shed light on the factors critical to determining taxon survival and movement during times of environmental stress. The Catarrhini or Old World anthropoids were chosen as the clade of interest because the phylogeny of the group is widely agreed upon and the biology of most of the constituent genera is well known. In their landmark paper, Temerin & Cant (1983) called for empirical evaluation of their hypotheses concerning the evolutionary divergence of Old World monkeys and apes. This study represents an attempt to answer this call with a combination of paleontological and neontological data.

Our secondary goal is to determine if changes may have occurred over time in the pattern of associations between hominids and other mammals. Other workers (e.g.,

Turner, 1992; Reed, 1997) have observed that different genera and species of hominids tend to be associated with distinct assemblages of mammals. The nature of these assemblages changed through time, as environmental conditions changed, as migrations brought hominids into contact with new species, and as shifts in the trophic levels of hominid populations occurred. Here we attempt to examine, through the course of the Pleistocene, the nature of the mammalian communities that included hominids in east Asia to determine if the species that hominids were associated with changed through time.

A geographic information system (GIS) was used to assemble, visually superimpose, and analyze data concerning past environments and animal distributions. Paleoenvironmental data were compiled from the literature as described below and developed into composite coverages representing the environmental situations of the Early, Middle and Late Pleistocene, respectively. On these coverages were plotted data on catarrhine-bearing paleontological localities for the Pleistocene. Our geographical scope was limited to China because paleoenvironmental information and paleontological occurrence data for the country were plentiful and better sampled than for other East Asian countries.

Methods

Paleoenvironmental coverages and data on fossil mammal distributions

Paleoecological data were compiled from the literature and developed into composite paleoenvironmental maps or coverages representing the environmental zones of the Early, Middle and Late Pleistocene, respectively. All coverages were developed using *Arc/Info*[®] GIS software. The sources from which paleoenvironmental data were obtained were as follows: (1) soils, loess, and paleoshorelines: An *et al.*, 1991; Liu & Ding,

1984; (2) vegetation (mostly pollen), mollusks, and lake levels: Liu & Ding, 1984; Winkler & Wang, 1993; and (3) permafrost: Cui & Song, 1991; Zhou *et al.*, 1991. The boundary dates adopted for subdivision of the Pleistocene were: Early Pleistocene: 2.5 Ma–780 ka; Middle Pleistocene: 780–128 ka; and Late Pleistocene: 128–11 ka. The recognition of the Gauss/Matuyama boundary as the Plio-Pleistocene boundary is followed by most geologists in China because it corresponds to the striking contrast between the Red Clay, formed under conditions of more or less continuous warmth, and the loess (Ding *et al.*, 1997). Although the 2.5 Ma age for the Pliocene–Pleistocene boundary is not widely accepted as a standard outside of China, it was used here because the Chinese concept of the “Early Pleistocene” was that used as an approximate age assignment for fossil finds reported in the primary Chinese literature sources consulted in the development of the fossil mammal database. It is recognized that the paleoenvironmental coverages developed for this study represent average situations or generalizations over relatively long periods of time and that they cannot convey details of the major, and sometimes abrupt, climatic changes which occurred during the Pliocene epoch (Roy *et al.*, 1996).

The distributions of the families and genera of catarrhine primates and other mammals presented here were drawn from the Eurasian Fossil Mammal Database developed by the first author. This database comprises points locations described by latitude and longitude and temporal occurrence for the late Tertiary and Quaternary fossil mammal species. The database was compiled from original descriptions of sites and species in the literature. The database consists, in part, of the location, and geological and numerical age of mammalian fossils; for hominids, locality data for paleontological and archaeological occurrences were

entered. In most of the original fossil or geological descriptions consulted, only approximate ages (e.g., “Middle Pleistocene”) were provided for the fossils, based on faunal correlation. Most east Asian Tertiary and Quaternary fossil sites have not been dated to a high level of accuracy due, in large part, to a paucity of sediments of volcanic origin associated with the fossils. The use of electron spin resonance and uranium series dating on sediments and speleothems from some cave sites (e.g., Zhoukoudian) and the implementation of paleomagnetic stratigraphy on sequences of continuous sedimentation (e.g., the Loess Plateau) have made possible the refinement of dates in recent years. The application of these techniques is still not widespread enough, however, to have made possible broad-scale correlations by “absolute” ages. The accuracy of taxonomic assignments and age assessments was carefully checked for all database entries, and amendments were made in these areas as necessary. This work consisted mostly of consulting published updates of age and taxonomic determinations for species from various localities, based on detailed geological and systematic investigations published after the original report. One record in the database consists of the occurrence, at one specific time and place, of one species, and is thus best referred to as a species occurrence. If a species was found to occur in more than one stratum of a specific locality and so represented the occurrence of the species at a different time, the creation of a new record or records was warranted. The number of actual specimens of a species that occurred at a specific time and place did not influence the number of records; the database was designed only to record the occurrence of a particular species at a particular place and a particular time.

Despite the fact that the potentially mammal-bearing fossil localities of Pleistocene age in China have been well sampled,

the possibility of collecting and sampling biases must be recognized. Taphonomic biases such as non-preserving or poor-preserving environments (such as tropical forests), selective destruction of species or age classes and removal from the life habitat must also be noted (Roy *et al.*, 1996). Finally, because the database was compiled on the basis of literature reports in which faunal lists and species descriptions were written by many different investigators with different levels of experience over the course of several decades, an indeterminate amount of interobserver error in the species identifications must be acknowledged.

For purposes of this investigation, changes in catarrhine primate distributions were analyzed at the family level. This treatment served the dual purposes of unifying groups that share similar life history characteristics and of increasing the sample sizes for the groups under consideration. The genera included within the catarrhine families were as follows: Pongidae=*Pongo* and *Gigantopithecus*; Hylobatidae=*Hylobates*; Cercopithecidae=*Procynocephalus*, *Macaca*, *Rhinopithecus*, and *Trachypithecus*; Homi-nidae=*Homo*. The latitude and longitude for all the catarrhine primate species occurrences surveyed are presented, by Pleistocene subepoch, in Table 1.

Spatial statistical analyses

Cluster analyses were conducted in order to determine the relative degree of clustering of locality points for each catarrhine family for each subepoch of the Pleistocene. In other words, these provided an indication of the spread of the overall areas of distribution for each family. The clustering analysis conducted resulted in the calculation of a nearest neighbor index (R). This analysis examines the mean distance, l , between points and their nearest neighbors. The result is based on what would be expected if the process of generating points followed a

Poisson distribution. The expected distance, $l_e = 0.5/(d)^{0.5}$, where the point density, $d = n/\text{area}$, where n = the number of points. The standard error of the expected distance is calculated as $S_{l_e} = 0.26136/(nd)^{0.5}$. If the nearest neighbor index, calculated as $R = l/l_e$, yielded a result of less than one, a tendency to cluster was indicated; a result of greater than one indicated a tendency toward uniform spacing. The significance test for this procedure was calculated using the standard deviation of the mean distance, as follows: $Z\text{-score} = (l - l_e)/S_{l_e}$.

Two methods, the nearest neighbor chi-square and the coefficient of spatial association (CoSA), were used to evaluate evidence of change through time for each of the catarrhine families. Both methods compare the spatial relationships of each data point in the two data sets under consideration. The main advantage of both types of tests are that they permit evaluation of relationships between different numbers of points. The nearest neighbor chi-square statistic, with one degree of freedom, tests for the significance of a spatial relationship and is based on relative distance. The null hypothesis being evaluated is that there is no significant association or segregation between points representing one taxon between two time intervals. If this hypothesis is rejected, then the type of spatial relationship (association or segregation) can be determined by examining the contingency table. The CoSA is a distance method which provides a measure of the extent of the spatial relationship. It considers the average distance to the nearest neighbor between sets (in this case, the point occurrences for any one family from two time periods), the average distance to the nearest neighbor within sets, and calculates the ratio between these to provide the measure of extent. Because the resulting index can lie anywhere between zero and infinity, the CoSA was transformed in order to make the results more easily interpretable. Using

Table 1 Species occurrences of known fossil catarrhines from the Pleistocene of China. (A list of bibliographic and other sources from which this list was compiled is available upon request from the first author)

Family	Genus	Species	Locality	Province	Latitude	Longitude
Early Pleistocene:						
Cercopithecidae	<i>Macaca</i>	<i>anderssoni</i>	Zhoukoudian	Beijing	39 30 00	115 55 00
Cercopithecidae	<i>Macaca</i>	<i>jiangchuanensis</i>	Jiangchuan	Yunnan	24 17 00	102 48 00
Cercopithecidae	<i>Macaca</i>	sp.	Longgupo Cave	Sichuan	30 50 00	109 40 00
Cercopithecidae	<i>Macaca</i>	sp.	Zoukoudian	Beijing	39 41 15	115 55 23
Cercopithecidae	<i>Macaca</i>	sp.	Jingxing	Hebei	38 05 00	114 10 00
Cercopithecidae	<i>Macaca</i>	sp.	Mianchi	Henan	34 40 00	111 40 00
Cercopithecidae	<i>Macaca</i>	sp.	Gongwangling	Shaanxi	34 10 00	109 30 00
Cercopithecidae	<i>Macaca</i>	sp.	Baojing	Hunan	28 40 00	109 40 00
Cercopithecidae	<i>Macaca</i>	sp.	Liuzhou	Guangxi	24 20 00	109 25 00
Cercopithecidae	<i>Macaca</i>	sp.	Gongwangling	Shaanxi	34 10 00	109 30 00
Cercopithecidae	<i>Macaca</i>	sp.	Yunxi	Hubei	33 00 00	110 25 00
Cercopithecidae	<i>Macaca</i>	sp.	Longgupo Cave	Sichuan	30 50 00	109 40 00
Cercopithecidae	<i>Procyonocephalus</i>	<i>wimani</i>	Zhoukoudian	Beijing	39 41 15	115 55 23
Cercopithecidae	<i>Procyonocephalus</i>	<i>wimani</i>	Jingxing	Hebei	38 05 00	114 10 00
Cercopithecidae	<i>Procyonocephalus</i>	<i>wimani</i>	Yushe	Shanxi	37 06 00	112 58 00
Cercopithecidae	<i>Procyonocephalus</i>	<i>wimani</i>	Xinan	Henan	34 40 00	112 10 00
Cercopithecidae	<i>Rhinopithecus</i>	<i>lanitanensis</i>	Gongwangling	Shaanxi	34 10 00	109 30 00
Cercopithecidae	<i>Rhinopithecus</i>	<i>lanitanensis</i>	Xuetangliangzi	Hubei	32 59 00	110 22 00
Cercopithecidae	<i>Rhinopithecus</i>	<i>lanitanensis</i>	Lantian	Shaanxi	34 11 06	109 29 22
Cercopithecidae	<i>Rhinopithecus</i>	<i>tingianus</i>	Wanxian	Sichuan	30 25 00	108 10 00
Cercopithecidae	<i>Semnopithecus</i>	sp.	Jiangchuan	Yunnan	24 20 00	100 50 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Chenjiawo	Shaanxi	34 11 06	109 29 22
Hominidae	<i>Homo</i>	<i>erectus</i>	Shangnabang	Yunnan	25 35 00	101 50 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Longgudong Cave	Hubei	32 58 00	110 57 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Bailongdong Cave	Hubei	32 58 00	110 45 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Gongwangling	Shaanxi	34 15 00	109 25 00
Hominidae	<i>Homo</i>	<i>erectus?</i>	Xihoudu	Shanxi	34 41 00	110 17 00
Hominidae	<i>Homo</i>	<i>erectus?</i>	Xiaochangliang	Hebei	41 13 00	114 40 00
Hominidae	<i>Homo</i>	sp.	Longdong Cave	Hubei	30 38 00	110 04 00
Hominidae	<i>Homo</i>	sp. indet.	Longgupo Cave	Sichuan	30 50 00	109 40 00
Hylobatidae	<i>Hylobates</i>	<i>erectus</i>	Wanxian	Sichuan	30 25 00	108 10 00
Hylobatidae	<i>Hylobates</i>	sp.	Baojing	Hunan	28 42 00	109 40 00
Pongidae	<i>Gigantopithecus</i>	<i>blacki</i>	Longgupo Cave	Sichuan	30 50 00	109 40 00
Pongidae	<i>Gigantopithecus</i>	<i>blacki</i>	Lengchaishan Cave	Guangxi	24 28 00	109 12 00
Pongidae	<i>Gigantopithecus</i>	<i>blacki</i>	Longdong Cave	Hubei	30 38 00	110 04 00
Pongidae	<i>Gigantopithecus</i>	sp.	Wuning	Guangxi	23 10 00	108 18 00

Table 1 (Continued)

Family	Genus	Species	Locality	Province	Latitude	Longitude
Early Pleistocene: <i>Continued</i>						
Pongidae	<i>Pongo</i>	sp.	Liucheng	Guangxi	24 40 00	109 15 00
Middle Pleistocene:						
Cercopithecidae	<i>Macaca</i>	<i>andersoni</i>	Zhoukoudian	Beijing	39 30 00	115 55 00
Cercopithecidae	<i>Macaca</i>	<i>robustus</i>	Anping	Liaoning	41 10 00	123 25 00
Cercopithecidae	<i>Macaca</i>	<i>robustus</i>	Lantian	Shaanxi	34 10 00	109 20 00
Cercopithecidae	<i>Macaca</i>	<i>robustus</i>	Zhoukoudian	Beijing	39 41 16	115 55 23
Cercopithecidae	<i>Macaca</i>	<i>robustus</i>	Jinnitushan	Liaoning	40 36 00	122 20 00
Cercopithecidae	<i>Macaca</i>	<i>robustus</i>	Miaohousshan	Liaoning	41 40 00	124 10 00
Cercopithecidae	<i>Macaca</i>	sp.	Koloshan	Sichuan	29 46 00	106 34 00
Cercopithecidae	<i>Macaca</i>	sp.	Bama	Guangxi	24 10 00	107 15 00
Cercopithecidae	<i>Macaca</i>	sp.	Newshuishan Cave	Guangxi	22 52 00	107 14 00
Cercopithecidae	<i>Macaca</i>	sp.	Wuming	Guangxi	23 10 00	108 18 00
Cercopithecidae	<i>Macaca</i>	sp.	Benxi	Liaoning	41 10 00	123 50 00
Cercopithecidae	<i>Macaca</i>	sp.	Anping	Liaoning	41 05 00	123 30 00
Cercopithecidae	<i>Macaca</i>	sp.	Zhoukoudian	Beijing	39 40 00	115 50 00
Cercopithecidae	<i>Macaca</i>	sp.	Yuanqu	Shanxi	35 15 00	111 40 00
Cercopithecidae	<i>Macaca</i>	sp.	Hexian	Anhui	31 45 00	118 20 00
Cercopithecidae	<i>Macaca</i>	sp.	Koloshan	Sichuan	29 46 00	106 34 00
Cercopithecidae	<i>Macaca</i>	sp.	Heshangpo	Sichuan	29 24 00	106 47 00
Cercopithecidae	<i>Macaca</i>	sp.	Qianxi	Guizhou	27 05 00	106 05 00
Cercopithecidae	<i>Macaca</i>	sp.	Fumin	Yunnan	25 10 00	102 30 00
Cercopithecidae	<i>Macaca</i>	sp.	Liucheng	Guangxi	24 40 00	109 15 00
Cercopithecidae	<i>Macaca</i>	sp.	Liujiang	Guangxi	24 15 00	109 25 00
Cercopithecidae	<i>Macaca</i>	sp.	Heichimlungtsun	Yunnan	24 08 00	104 27 00
Cercopithecidae	<i>Macaca</i>	sp.	Tanyang	Jiangsu	31 50 00	119 24 00
Cercopithecidae	<i>Macaca</i>	sp.	Panxian Dadong	Guizhou	25 37 38	104 44 00
Cercopithecidae	<i>Macaca</i>	sp.	Xinan	Henan	34 40 00	112 05 00
Cercopithecidae	<i>Rhinopithecus</i>	<i>roxellana</i>	Niushuishan Cave	Guangxi	22 52 00	107 14 00
Cercopithecidae	<i>Rhinopithecus</i>	<i>tinganus</i>	Yenchingkuo	Sichuan	30 52 00	108 39 00
Cercopithecidae	<i>Rhinopithecus</i>	<i>tinganus</i>	Zhoukoudian	Beijing	39 40 00	115 55 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Lantian	Shaanxi	34 20 00	109 30 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Dali	Shaanxi	34 47 00	109 55 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Chaoxian	Anhui	31 35 00	117 50 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Hexian	Anhui	31 44 00	118 22 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Xindong	Beijing	39 41 15	115 55 23
Hominidae	<i>Homo</i>	<i>erectus</i>	Yiyuan	Shandong	36 12 00	118 09 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Luonan	Shaanxi	34 07 00	110 10 00

Table 1 (Continued)

Family	Genus	Species	Locality	Province	Latitude	Longitude
Middle Pleistocene: <i>Continued</i>						
Hominidae	<i>Homo</i>	<i>erectus</i>	Nanzhao	Henan	33 28 00	112 41 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Yuanmou	Yunnan	25 35 00	101 50 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Zhoukoudian	Beijing	39 40 00	115 50 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Tangshan	Jiangsu	32 40 00	119 02 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Gongwangling	Shaanxi	34 15 00	109 25 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Zhoukoudian	Shaanxi	34 15 00	109 25 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Miaohoushan	Beijing	39 40 00	115 55 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Miaohoushan	Liaoning	41 40 00	124 10 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Lantian	Liaoning	41 40 00	124 10 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Quyuanhekou	Shaanxi	34 14 05	109 15 07
Hominidae	<i>Homo</i>	<i>erectus?</i>	Cenjiawan	Hubei	32 48 00	110 47 00
Hominidae	<i>Homo</i>	<i>erectus?</i>	Kehe	Hubei	41 13 00	114 40 00
Hominidae	<i>Homo</i>	<i>erectus?</i>	Qianxi	Hubei	34 40 00	110 20 00
Hominidae	<i>Homo</i>	<i>erectus?</i>	Daye	Guizhou	27 05 00	106 05 00
Hominidae	<i>Homo</i>	<i>lantianensis</i>	Lantian	Hubei	30 07 00	114 55 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Jinmushan	Shaanxi	34 10 00	109 20 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Xiazhongjiawan	Liaoning	40 15 00	122 30 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Jinmushan	Liaoning	30 15 00	110 35 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Dali	Hubei	40 36 00	122 20 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Dali	Liaoning	34 47 00	109 55 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Miaohoushan	Shaanxi	34 47 00	109 55 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Miaohoushan	Liaoning	41 40 00	124 10 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Panxian Dadong	Liaoning	41 40 00	124 10 00
Hominidae	<i>Homo</i>	<i>sp.</i>	Newshuishan Cave	Guixhou	25 37 38	104 44 00
Hylobatidae	<i>Hylobates</i>	<i>concolor</i>	Daxin	Guangxi	22 52 00	107 14 00
Hylobatidae	<i>Hylobates</i>	<i>hoolock</i>	Yenchingkuo	Guangxi	22 52 00	107 14 00
Hylobatidae	<i>Hylobates</i>	<i>sericus</i>	Bama	Sichuan	30 52 00	108 39 00
Hylobatidae	<i>Hylobates</i>	<i>sp.</i>	Yanjingkuo	Guangxi	24 10 00	107 15 00
Hylobatidae	<i>Hylobates</i>	<i>sp.</i>	Tongzi	Sichuan	30 35 39	108 25 41
Hylobatidae	<i>Hylobates</i>	<i>sp.</i>	Bama	Guizhou	28 15 00	106 45 00
Hylobatidae	<i>Hylobates</i>	<i>sp.</i>	Bama	Guangxi	24 10 00	107 17 00
Hylobatidae	<i>Hylobates</i>	<i>sp.</i>	Yanjingou	Sichuan	30 50 00	103 00 00
Pongidae	<i>Gigantopithecus</i>	<i>blacki</i>	Bama	Guangxi	24 10 00	107 15 00
Pongidae	<i>Gigantopithecus</i>	<i>blacki</i>	Newshuishan Cave	Guangxi	22 52 00	107 14 00
Pongidae	<i>Gigantopithecus</i>	<i>sp.</i>	Yenchingkuo	Guangxi	22 52 00	107 14 00
Pongidae	<i>Pongo</i>	<i>pygmaeus</i>	Hoshantung Cave	Sichuan	30 52 00	108 39 00
Pongidae	<i>Pongo</i>	<i>pygmaeus</i>	Hsingan	Yunnan	25 12 00	102 22 00
Pongidae	<i>Pongo</i>	<i>pygmaeus</i>	Hsingan	Guangxi	25 30 00	110 43 00

Table 1 (Continued)

Family	Genus	Species	Locality	Province	Latitude	Longitude
Middle Pleistocene: <i>Continued</i>						
Pongidae	<i>Pongo</i>	<i>satyrus</i>	Yenchingkuo	Sichuan	30 52 00	108 39 00
Pongidae	<i>Pongo</i>	sp.	Bama	Guangxi	24 10 00	107 15 00
Pongidae	<i>Pongo</i>	sp.	Newshuishan Cave	Guangxi	22 52 00	107 14 00
Pongidae	<i>Pongo</i>	sp.	Lengchaishan Cave	Guangxi	24 28 00	109 12 00
Pongidae	<i>Pongo</i>	sp.	Zhaoqing	Guangdong	23 12 00	112 25 00
Pongidae	<i>Pongo</i>	sp.	Panxian Dadong	Guizhou	25 37 38	104 44 00
Late Pleistocene:						
Cercopithecidae	<i>Macaca</i>	sp.	Qiubei	Yunnan	24 00 00	104 10 00
Cercopithecidae	<i>Macaca</i>	sp.	Xichou	Yunnan	23 25 00	104 25 00
Cercopithecidae	<i>Macaca</i>	sp.	Maguan	Yunnan	23 00 00	104 30 00
Cercopithecidae	<i>Macaca</i>	sp.	Yinde	Guangdong	24 10 00	113 20 00
Cercopithecidae	<i>Macaca</i>	sp.	Fengkai	Guangdong	23 25 00	111 30 00
Cercopithecidae	<i>Macaca</i>	sp.	Zhaoqing	Guangdong	23 00 00	112 25 00
Cercopithecidae	<i>Macaca</i>	sp.	Yunfu	Guangdong	22 50 00	112 00 00
Cercopithecidae	<i>Macaca</i>	sp.	Shuang Cave	Guangdong	24 48 00	113 35 00
Cercopithecidae	<i>Macaca</i>	sp.	Zhaicun Cave	Guangxi	24 30 00	110 26 00
Cercopithecidae	<i>Rhinopithecus</i>	sp.	Du'an	Guangxi	23 17 00	106 30 00
Cercopithecidae	<i>Rhinopithecus</i>	sp.	Tongzi	Guizhou	28 15 00	106 45 00
Cercopithecidae	<i>Rhinopithecus</i>	<i>tingianus</i>	Tongzi	Guizhou	28 15 00	106 45 00
Cercopithecidae	<i>Rhinopithecus</i>	<i>tingianus</i>	Cili	Hunan	29 20 00	111 10 00
Cercopithecidae	<i>Rhinopithecus</i>	<i>erectus</i>	Du'an	Guangxi	23 20 00	106 25 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Tongzi	Guizhou	28 15 00	106 45 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Dingcun	Shanxi	35 49 45	111 25 10
Hominidae	<i>Homo</i>	<i>erectus</i>	Duleyan	Guangxi	24 15 00	109 20 00
Hominidae	<i>Homo</i>	<i>erectus</i>	Zhoukoudian	Beijing	39 40 00	115 55 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Antu	Jilin	42 40 00	128 15 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Du'an	Guangxi	23 17 00	106 30 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Wuguidong Cave	Zhejiang	29 20 00	119 05 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Xujiayao	Shanxi	40 06 00	113 59 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Shizifeng Hill	Guangdong	24 45 00	113 30 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Xiaohui Cave	Guizhou	26 40 00	105 50 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Chengguan	Liaoning	41 20 00	119 30 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Zhoukoudian	Beijing	39 41 15	115 55 23
Hominidae	<i>Homo</i>	<i>sapiens</i>	Shiyu	Shanxi	39 25 00	112 21 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Dagouwan	Nei Mongol	37 43 56	108 31 47
Hominidae	<i>Homo</i>	<i>sapiens</i>	Tongtianyan	Guangxi	24 15 00	109 25 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Qilinshan Hill	Guangxi	23 40 00	109 05 00

Table 1 (Continued)

Family	Genus	Species	Locality	Province	Latitude	Longitude
Late Pleistocene: <i>Continued</i>						
Hominidae	<i>Homo</i>	<i>sapiens</i>	Huangshanxi	Sichuan	30 10 00	104 30 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Xianrendong Cave	Yunnan	23 30 00	104 25 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Yangxi	Yunnan	26 46 00	100 17 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Maomao Cave	Guizhou	25 10 00	105 02 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Xiacaowan	Jiangsu	33 13 00	118 12 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Wuzhutai	Shandong	35 55 00	117 45 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Qingliu	Fujian	26 10 00	116 50 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Fengkai	Guangdong	111 20 00	111 20 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Zhaotong	Yunnan	27 20 00	103 40 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Tiandong	Guangxi	23 35 00	107 08 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Kunming	Yunnan	24 49 00	102 49 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Jingchuan	Gansu	35 10 00	107 30 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Huanglong	Shaanxi	35 37 00	109 50 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Dingcun	Shaanxi	35 49 45	111 25 10
Hominidae	<i>Homo</i>	<i>sapiens</i>	Ghangyang	Hubei	30 15 00	110 50 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Jiande	Zhejiang	29 20 00	119 05 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Qingshantou	Jilin	45 20 00	124 30 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Zhoujia Youfang	Jilin	44 53 00	127 10 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Xuedian	Heilongjiang	45 10 00	128 00 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Antu	Jilin	42 35 00	128 15 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Jienping	Liaoning	41 52 00	119 45 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Xujiayao	Shanxi	40 06 00	113 59 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Xujiayao	Shanxi	40 06 00	113 59 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Honglui He	Nei Mongol	37 10 00	108 10 58
Hominidae	<i>Homo</i>	<i>sapiens</i>	Xiaonanhai	Henan	36 05 00	114 15 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Zhoukoudian	Beijing	39 41 15	115 55 23
Hominidae	<i>Homo</i>	<i>sapiens</i>	Ziyang	Sichuan	30 10 00	104 30 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Tongliang	Sichuan	28 55 00	106 03 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Xiachuan	Shanxi	35 28 00	112 01 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Xiachuan	Shanxi	35 28 00	112 01 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Xueguan	Shanxi	36 23 00	110 57 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Jalainur	Nei Mongol	49 34 00	117 26 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Hutouliang	Hebei	40 00 00	114 11 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Miaohoushan	Liaoning	41 40 00	124 10 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Chenggong	Yunnan	24 54 00	102 48 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Chenggong	Yunnan	24 54 00	102 48 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Chenggong	Yunnan	24 54 00	102 48 00

Table 1 (Continued)

Family	Genus	Species	Locality	Province	Latitude	Longitude
Late Pleistocene: <i>Continued</i>						
Hominidae	<i>Homo</i>	<i>sapiens</i>	Zhoukoudian	Beijing	39 40 00	115 55 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Zhoukoudian	Beijing	39 40 00	115 55 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Zhoukoudian	Beijing	39 40 00	115 55 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Zhoukoudian	Beijing	39 40 00	115 55 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Zhoujiayoufan	Jilin	44 53 00	127 10 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Zhoujiayoufan	Jilin	44 53 00	127 10 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Zhoujiayoufan	Jilin	44 53 00	127 10 00
Hominidae	<i>Homo</i>	<i>sapiens</i>	Dingcun	Jilin	35 49 45	111 25 10
Hominidae	<i>Homo</i>	<i>sapiens</i>	Salawusu	Shaanxi	36 54 00	108 10 00
Hominidae	<i>Homo</i>	sp.	Yuci	Shaanxi	37 40 30	112 50 10
Hominidae	<i>Homo</i>	sp.	Xiaozhan	Shaanxi	40 06 15	113 12 50
Hominidae	<i>Homo</i>	sp.	Guanyindong Cave	Guixhou	26 55 00	105 55 00
Hominidae	<i>Homo</i>	sp.	Sanmenxia	Henan	34 45 00	111 15 00
Hominidae	<i>Homo</i>	sp.	Zhangjiawan	Shaanxi	34 35 00	110 20 00
Hominidae	<i>Homo</i>	sp.	Henancun	Shaanxi	35 20 00	111 40 00
Hominidae	<i>Homo</i>	sp.	Nanhaiyu	Shaanxi	35 20 00	111 40 00
Hominidae	<i>Homo</i>	sp.	Fanjiazhuang	Shaanxi	37 35 00	112 10 00
Hominidae	<i>Homo</i>	sp.	Licunxigou	Shaanxi	35 45 00	111 35 00
Hominidae	<i>Homo</i>	sp.	Gezidong Cave	Liaoning	41 15 00	119 50 00
Hominidae	<i>Homo</i>	sp.	Jiangjiawan	Gansu	35 35 00	107 20 00
Hominidae	<i>Homo</i>	sp.	Rejuqu	Xizang	28 45 00	87 21 00
Hominidae	<i>Homo</i>	sp.	Xibajianfang	Liaoning	41 19 00	119 30 00
Hominidae	<i>Homo</i>	sp.	Shibazhan	Heilongjiang	52 25 00	125 35 00
Hominidae	<i>Homo</i>	sp.	Zhaocun	Hebei	39 55 00	118 40 00
Hominidae	<i>Homo</i>	sp.	Lamawan	Nei Mongol	40 03 00	110 35 00
Hominidae	<i>Homo</i>	sp.	Shuidonggou	Ningxia Hui	38 10 00	106 40 00
Hominidae	<i>Homo</i>	sp.	Loufangzi	Gansu	36 20 00	107 40 00
Hominidae	<i>Homo</i>	sp.	Huohuoxili	Qinghai	35 25 00	93 15 00
Hominidae	<i>Homo</i>	sp.	Bailiandong Cave	Guangxi	24 15 00	109 20 00
Hominidae	<i>Homo</i>	sp.	Shangsong	Guangxi	23 55 00	106 25 00
Hominidae	<i>Homo</i>	sp.	Fulin	Sichuan	29 23 00	102 42 00
Hominidae	<i>Homo</i>	sp.	Banqiao	Yunnan	24 40 00	103 35 00
Hominidae	<i>Homo</i>	sp.	Shandongyidong Cave	Shandong	35 05 00	118 15 00
Hominidae	<i>Homo</i>	sp.	Pratapapur	Orissa	32 04 40	86 38 30
Hyalobatiidae	<i>Hyalobates</i>	<i>concolor</i>	Lingyan Cave	Guangxi	24 15 00	109 25 00
Hyalobatiidae	<i>Hyalobates</i>	<i>concolor</i>	Liujiang	Sichuan	24 15 00	109 25 00

Table 1 (Continued)

Family	Genus	Species	Locality	Province	Latitude	Longitude
Late Pleistocene: <i>Continued</i>						
Hylobatidae	<i>Hylobates</i>	<i>concolor</i>	Guilin	Guangxi	25 14 00	110 17 00
Hylobatidae	<i>Hylobates</i>	<i>concolor</i>	Yangshuo	Guangxi	24 43 00	110 29 00
Hylobatidae	<i>Hylobates</i>	<i>concolor</i>	Lipu	Guangxi	24 30 00	110 24 00
Hylobatidae	<i>Hylobates</i>	<i>concolor</i>	Shanglin	Guangxi	23 27 00	108 34 00
Hylobatidae	<i>Hylobates</i>	<i>concolor</i>	Baise	Guangxi	23 55 00	106 38 00
Hylobatidae	<i>Hylobates</i>	<i>concolor</i>	Baoshan	Yunnan	25 05 00	99 05 00
Hylobatidae	<i>Hylobates</i>	<i>concolor</i>	Jingdong	Yunnan	24 35 00	102 39 00
Hylobatidae	<i>Hylobates</i>	<i>concolor</i>	Shuangbai	Yunnan	24 38 00	101 25 00
Hylobatidae	<i>Hylobates</i>	<i>concolor</i>	Xinping	Yunnan	24 02 00	101 57 00
Hylobatidae	<i>Hylobates</i>	<i>concolor</i>	Jiangcheng	Yunnan	22 40 00	101 53 00
Hylobatidae	<i>Hylobates</i>	<i>concolor</i>	Luchun	Yunnan	22 55 00	102 23 00
Hylobatidae	<i>Hylobates</i>	<i>concolor</i>	Mengla	Yunnan	21 27 00	101 30 00
Hylobatidae	<i>Hylobates</i>	<i>concolor</i>	Shangyong	Yunnan	21 38 00	101 38 00
Hylobatidae	<i>Hylobates</i>	<i>concolor?</i>	Qiongzong	Hainan	19 05 00	109 50 00
Hylobatidae	<i>Hylobates</i>	<i>concolor?</i>	Du'an	Guangxi	23 17 00	106 30 00
Hylobatidae	<i>Hylobates</i>	<i>hooleck</i>	Yingjiang	Yunnan	24 40 00	97 58 00
Hylobatidae	<i>Hylobates</i>	<i>hooleck</i>	Lianghe	Yunnan	24 55 00	98 20 00
Hylobatidae	<i>Hylobates</i>	<i>hooleck</i>	Tengchong	Yunnan	25 04 00	98 27 00
Hylobatidae	<i>Hylobates</i>	<i>hooleck</i>	Baoshan	Yunnan	25 05 00	99 05 00
Hylobatidae	<i>Hylobates</i>	<i>hooleck</i>	Lipu	Guangxi	24 30 00	110 24 00
Hylobatidae	<i>Hylobates</i>	sp.	Yishan Cave	Guangxi	24 30 00	108 40 00
Hylobatidae	<i>Hylobates</i>	sp.	Tongzi	Guizhou	28 15 00	106 45 00
Hylobatidae	<i>Hylobates</i>	sp.	Liuzhou	Guangxi	24 20 00	109 26 00
Hylobatidae	<i>Hylobates</i>	sp.	Du'an	Guangxi	23 57 00	108 06 00
Hylobatidae	<i>Hylobates</i>	sp.	Bose	Guangxi	23 56 00	106 34 00
Hylobatidae	<i>Hylobates</i>	sp.	Longlin	Guangxi	24 45 00	105 20 00
Hylobatidae	<i>Hylobates</i>	sp.	Shanzhongmen	Guangxi	24 15 00	109 10 00
Hylobatidae	<i>Hylobates</i>	sp.	Baojijian	Guangxi	25 13 00	109 50 00
Hylobatidae	<i>Hylobates</i>	sp.	Taipingyan	Guangxi	25 22 00	110 24 00
Hylobatidae	<i>Hylobates</i>	sp.	Xichou	Guangxi	24 22 00	109 25 00
Hylobatidae	<i>Hylobates</i>	sp.	Thung Lang	Ha Nam Ninh	30 10 00	106 01 00
Pongidae	<i>Pongo</i>	<i>pygmaeus</i>	Tiangdong	Guangxi	23 35 00	107 08 00
Pongidae	<i>Pongo</i>	sp.	Liujiang	Guangxi	24 15 00	109 25 00
Pongidae	<i>Pongo</i>	sp.	Tongzi	Guizhou	28 15 00	106 45 00
Pongidae	<i>Pongo</i>	sp.	Xiaonanhai	Henan	36 02 28	114 05 42
Pongidae	<i>Pongo</i>	sp.	Shuang Cave	Guangdong	24 48 00	113 35 00
Pongidae	<i>Pongo</i>	sp.	Zhaicun Cave	Guangxi	24 30 00	110 26 00

the formula, Transformed CoSA = $(\text{CoSA} - 1)/(\text{CoSA} + 1)$, values were produced that were symmetrically distributed around 0, with a minimum of -1 and a maximum of $+1$. In none of the cases evaluated for the catarrhine families was a positive spatial association found between the two sets of points from different time periods. This means that some level of change in the distribution occurred. In sum, these analyses examined whether or not points of a distribution occupied the same or similar regional space from one time period to the next. If the points did occupy the same space, association was found; and if the points occupied different spaces from one time period to the next, spatial segregation was found. The CoSA is particularly useful at demonstrating the extent of association or segregation and allowing one to see the trend of the statistical results in the associated maps.

The same procedures (nearest neighbor chi-square and transformed CoSA) that were applied to evaluating change in the distribution of single families through time were used to compare the points of spatial occurrence between the genus *Homo* and other selected mammalian genera during the time periods under consideration. The question here was, do the points of distributions of the two genera concerned occupy the same space or not? The ranks reported indicate the strength of spatial association between *Homo* and other genera, with lower ranks indicating stronger association and higher ones indicating degrees of segregation.

Results

The environmental changes of the East Asian Pleistocene were associated with major changes in the distributions of catarrhine families. These shifts, for the most part, tracked the southeastward contractions of the tropical and subtropical zones (Figure

1), the zones showing the least pronounced seasonality. In many cases, latitudinal shifts were accompanied by more pronounced clustering of locality points, indicating that distributions were contracting. In the Early Pleistocene, the apes (Families Pongidae and Hylobatidae) were confined to the tropical zone; the monkeys (Cercopithecidae) and hominids were more broadly distributed, but still restricted to the tropical and subtropical zones [Figure 1(a)].

By the Middle Pleistocene [Figure 1(b)] the relative area of the tropical zone had decreased considerably. During that interval, the latitudinal range for all catarrhine families remained similar to that of the Early Pleistocene, but a moderate trend toward increased southward clustering of the non-hominid catarrhines was observed (Tables 2 and 3). This trend was registered more strongly by the Pongidae and Hylobatidae than by the other families. The results of a nearest neighbor index (R) cluster analysis for the Middle Pleistocene showed that the Hylobatidae exhibited the greatest clustering tendency (Tables 2 and 3). The near elimination of the tropical zone and the continued southeastward contraction of the subtropical zone in the Late Pleistocene of China contributed to a wider and greater range of reactions by the catarrhine families than those seen earlier in the epoch [Figure 1(c)]. By this time, the largest of the pongids, *Gigantopithecus*, was extinct and the distribution of most of the remaining apes had collapsed into the southern subtropical zone. The distribution of monkeys was compressed southward by approximately ten degrees of latitude. Hominids, in contrast, expanded their range during the Late Pleistocene, and were seen to occupy the subtropical, warm temperate, temperate, cold temperate, plateau and tundra (permafrost) zones. The distributions of the catarrhine families showed no statistically significant changes between the Early and

(a)

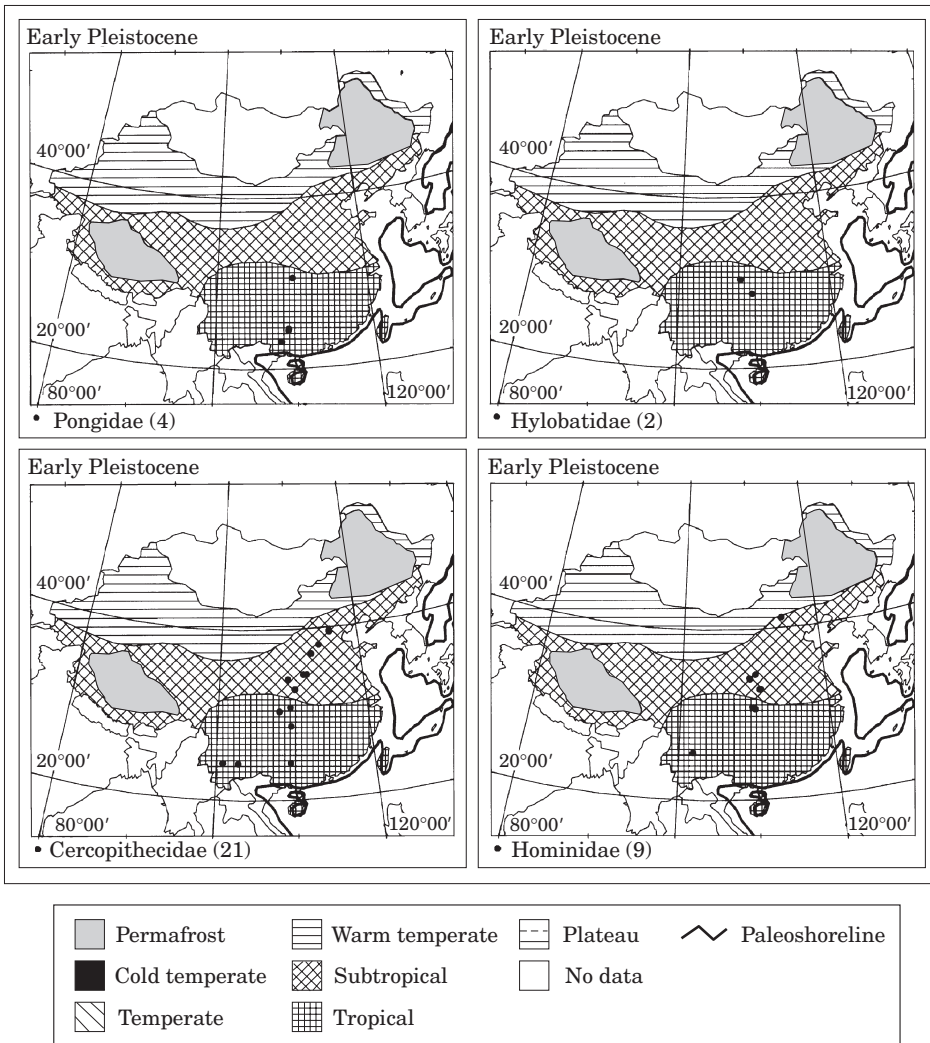


Figure 1. Distribution of catarrhine primate fossil occurrences in China during the Pleistocene. Localities for Hominidae include archaeological occurrences. The numbers enclosed in parentheses following the Family name indicate the total number of locality occurrences for that Family for that subepoch: (a) Early Pleistocene; (b) Middle Pleistocene; and (c) Late Pleistocene. The boundary dates adopted for the subdivision of the Pleistocene were: Early Pleistocene: 2.5 Ma–780 ka; Middle Pleistocene: 780–128 ka; and Late Pleistocene: 128–11 ka. The genera included within the catarrhine families were as follows: Pongidae=*Pongo* and *Gigantopithecus*; Hylobatidae=*Hylobates*; Cercopithecidae=*Procynocephalus*, *Macaca*, *Rhinopithecus*, *Trachypithecus* and *Pygathrix*; Hominidae=*Homo*.

Middle Pleistocene, but all except the Pongidae showed such changes between the Middle and Late Pleistocene (Table 3). The most significant change was registered by the Hylobatidae, which underwent severe

range compression between the Middle and Late Pleistocene. The range expansion undergone by hominids during the same interval constituted the next most significant change.

(b)

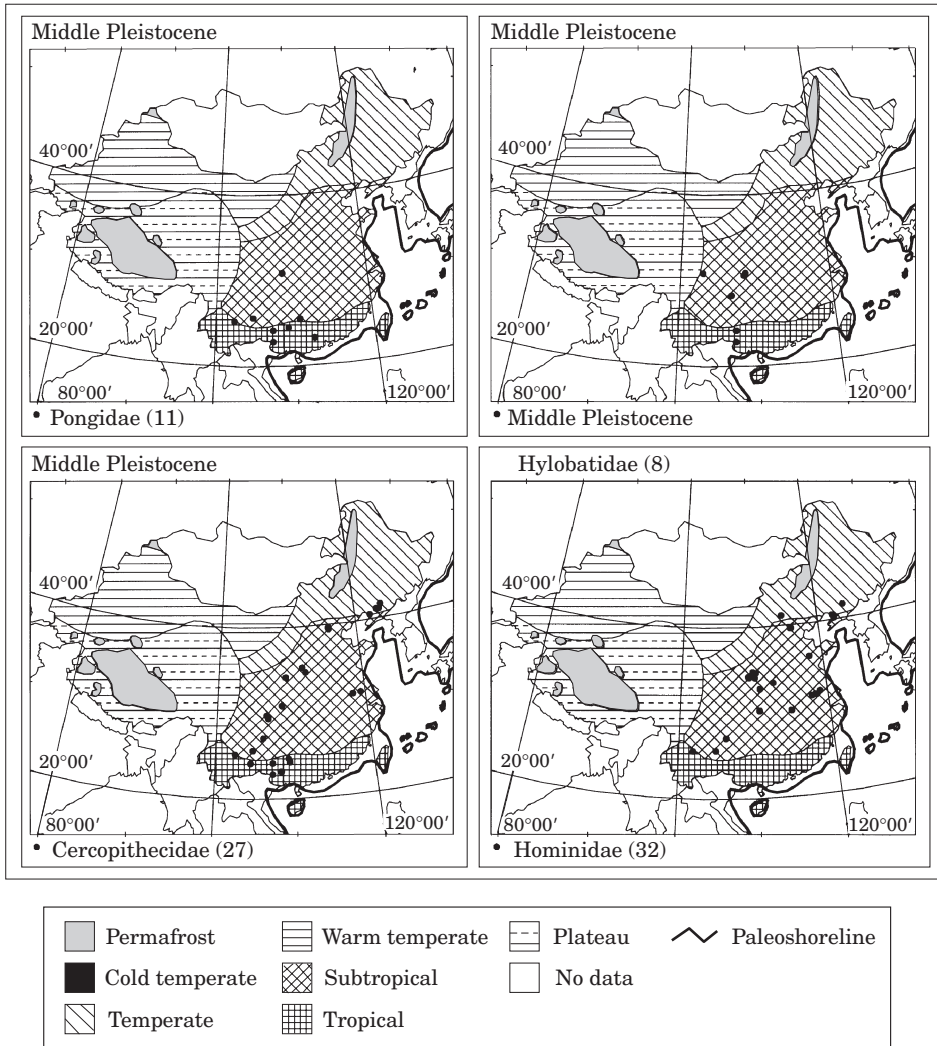


Figure 1. (Continued)

The spatial response of hominids to the environmental changes of the Late Pleistocene motivated us to pursue the question of whether the patterns of association of hominids with other elements of the medium to large-sized mammalian fauna might also have changed through the Pleistocene. These associations revealed what appear to be significant changes in patterns of spatial association between hominids and

other mammals. In the Early Pleistocene, the strongest spatial associations between *Homo* and other genera were with *Macaca*, *Hyaena* and *Ursus*, while the strongest evidence of segregation was seen relative to *Mammathus*, *Pongo*, *Panthera* and *Bos* (Table 4). By the Middle Pleistocene, the genus *Canis* was most positively associated with *Homo*, followed by *Felis* and *Macaca*. The strongest spatial segregation was

(c)

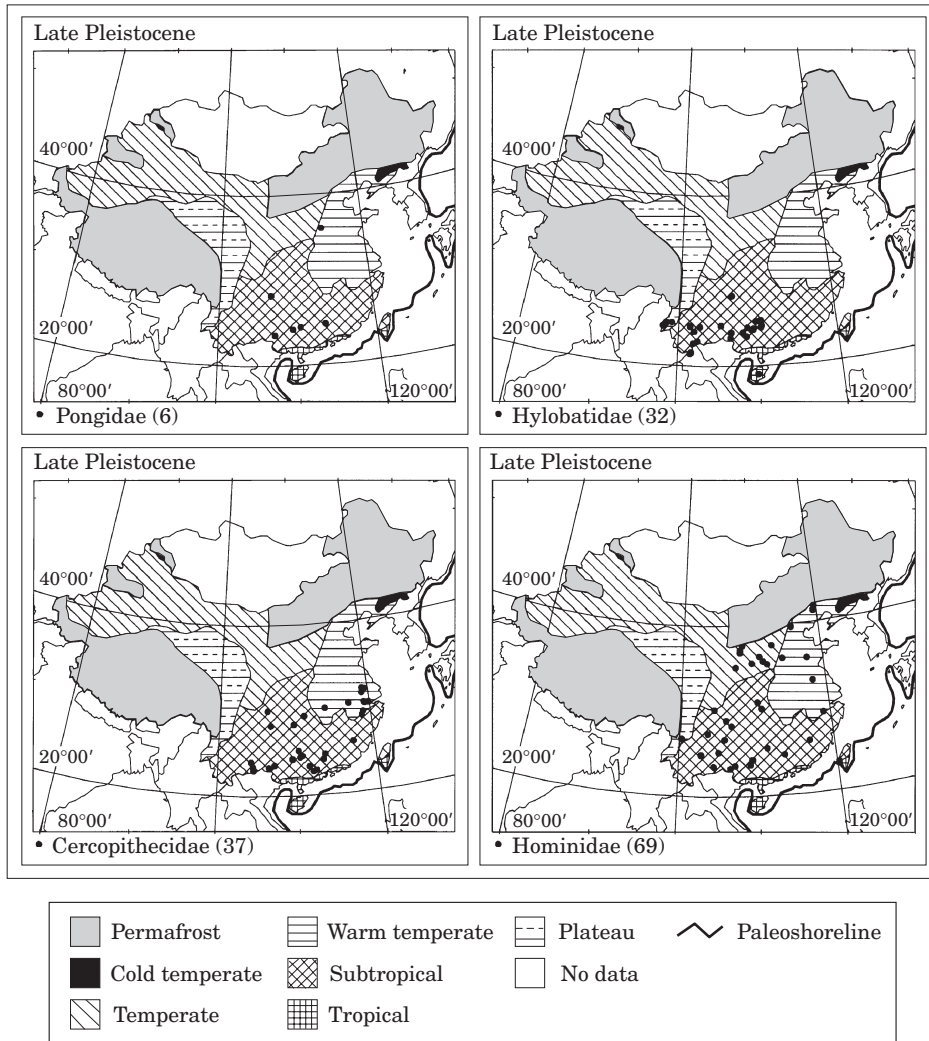


Figure 1. (Continued)

relative to other apes, *Hylobates*, *Gigantopithecus* and *Pongo*. The Late Pleistocene saw *Crocota* most strongly associated with *Homo*, followed by *Canis* and *Ursus*, while the snub-nosed monkey, *Rhinopithecus*, and *Hylobates* were the most strongly segregated. *Macaca*, which was strongly associated with *Homo* earlier in the Pleistocene, was by the Late Pleistocene moderately segregated from it.

Discussion

Examination of the life history parameters and diets of the catarrhines in question sheds light on their varying patterns of spatial response to environmental change. The Pleistocene catarrhines of China, except for *Gigantopithecus*, are represented by living species in China or southeast Asia. The existence of data on the life history

Table 2 Results of nearest neighbor index (R) cluster analyses

Family	R value	Meaning	Z-score	Sig. (0.05)	Rank
Early Pleistocene					
Cercopithecidae	0.21297	Cluster	-6.89974	✓	2
Hylobatidae	0.21265	Cluster	-2.13017	✓	1
Pongidae	0.27820	Cluster	-2.76169	✓	3
Middle Pleistocene					
Cercopithecidae	0.27576	Cluster	-7.19934	✓	3
Hylobatidae	0.11871	Cluster	-4.38985	✓	1
Pongidae	0.22418	Cluster	-4.92256	✓	2
Late Pleistocene					
Cercopithecidae	0.35904	Cluster	-7.45865	✓	2
Hylobatidae	0.22630	Cluster	-8.37296	✓	1
Pongidae	0.61793	Cluster	-1.79038	✓	3
Holocene					
Cercopithecidae	0.29074	Cluster	-5.42748	✓	1
Hylobatidae	0.31307	Cluster	-6.43795	✓	2
Pongidae	—	—	—	—	—

Table 3 Examination of the significance of the change of distribution for the four Asian catarrhine families from the Early to Middle Pleistocene and from the Middle to Late Pleistocene using chi-square nearest neighbor and coefficient of spatial association analyses*

Family	χ^2 with Yeats Correction	P-value	Sig. (0.05)	Transformed CoSA	Rank
Early Pleistocene to Middle Pleistocene					
Cercopithecidae	3.0476	0.0809	—	-0.41422	3
Hylobatidae	0.0298	0.863	—	-0.46669	4
Pongidae	0.1918	0.6615	—	-0.13874	1
Hominidae	3.1536	0.0758	—	-0.35942	2
Middle Pleistocene to Late Pleistocene					
Cercopithecidae	9.5381	0.002	✓	-0.34594	2
Hylobatidae	19.7939	0	✓	-0.64951	4
Pongidae	0.0111	0.9159	—	-0.01951	1
Hominidae	36.3302	0	✓	-0.40817	3

*The chi-square (χ^2) statistic was computed using the Yeats Correction for small sample sizes and the coefficient of spatial association is reported as the transformed coefficient of spatial association (Transformed CoSA). The negative values for the Transformed CoSA in all cases indicate spatial segregation (as opposed to association) between occurrences of individual families from one time period to the next. The degree of segregation identified by the transformed CoSA is indicated by the rank in the far right column: the lowest number shows the least spatial segregation (i.e., the least difference between distributions from one time interval to the next), highest number shows the most.

parameters of these species (Table 5) permitted us to explore the nature of the relationship between spatial responses to Pleistocene environmental change and life histories. Methods for estimating the life history parameters of extinct forms from fossil remains were not applied because of

practical limitations of specimen availability. We feel confident, however, that the acknowledged stability (Read & Harvey, 1989) of these parameters validates our application of data from extant to Pleistocene forms. Parameters such as length of the gestation period and the age of

Table 4 Examination of evidence of spatial association of *Homo* with other mammalian genera during the Early, Middle and Late Pleistocene using chi-square (χ^2) nearest neighbor and coefficient of spatial association analyses (11)

Genus	χ^2 with Yeats Correction	P-value	Sig. (0.05)	Transformed CoSA	Rank
Early Pleistocene					
<i>Ailuropoda</i>	1.8591	0.1727	—	-0.36813	19
<i>Bos</i>	0.0391	0.8433	—	-0.55312	20
<i>Canis</i>	0.5	0.4795	—	-0.10866	10
<i>Coelodonta</i>	0.5469	0.4596	—	-0.05288	6
<i>Crocota</i>	0.5022	0.4785	—	-0.35474	18
<i>Dicerorhinus</i>	2.625	0.1052	—	-0.26782	14
<i>Elephas</i>	0.0064	0.9364	—	-0.08787	8
<i>Equus</i>	1.2882	0.2564	—	-0.08948	9
<i>Felis</i>	2.8538	0.0912	—	-0.07825	7
<i>Gazella</i>	2.0939	0.1479	—	0.03190	5
<i>Gigantopithecus</i>	1.0714	0.3006	—	-0.32199	16
<i>Hyaena</i>	0.0084	0.9269	—	0.17724	2
<i>Hylobates</i>	0.0391	0.8433	—	-0.28874	15
<i>Macaca</i>	0.0153	0.9014	—	0.25614	1
<i>Mammuthus</i>	4.7266	0.0297	✓	-0.75467	23
<i>Megatapirus</i>	0.5022	0.4785	—	-0.35474	18
<i>Panthera</i>	∞	N.A.	N.A.	-0.57163	21
<i>Pongo</i>	1.7227	0.1894	—	-0.61283	22
<i>Rhinoceros</i>	0.5124	0.4741	—	-0.18032	12
<i>Rhinopithecus</i>	0.2339	0.6286	—	0.11474	4
<i>Stegodon</i>	0.3067	0.5797	—	-0.34518	17
<i>Tapirus</i>	0.0023	0.9621	—	-0.24380	13
<i>Ursus</i>	0.0335	0.8548	—	0.12326	3
Middle Pleistocene					
<i>Ailuropoda</i>	3.1509	0.0759	—	-0.52466	15
<i>Bos</i>	1.3414	0.2468	—	-0.59898	17
<i>Canis</i>	0.4083	0.5228	—	0.13584	1
<i>Coelodonta</i>	0.1644	0.6851	—	-0.50533	12
<i>Crocota</i>	1.6549	0.1983	—	-0.15923	5
<i>Dicerorhinus</i>	0.0718	0.7888	—	-0.29079	9
<i>Elephas</i>	0.0889	0.7655	—	-0.12429	4
<i>Equus</i>	1.5995	0.206	—	-0.17487	6
<i>Felis</i>	3.6196	0.0571	—	0.03049	2
<i>Gazella</i>	0.6912	0.4058	—	-0.51668	14
<i>Gigantopithecus</i>	6.9344	0.0085	✓	-0.76270	21
<i>Hyaena</i>	0.4681	0.4939	—	-0.19861	7
<i>Hylobates</i>	19.1868	0	✓	-0.78330	22
<i>Macaca</i>	0.4003	0.5269	—	-0.07542	3
<i>Mammuthus</i>	∞	—	—	—	—
<i>Megatapirus</i>	0.0225	0.8806	—	-0.45320	11
<i>Panthera</i>	6.796	0.0091	✓	-0.64073	19
<i>Pongo</i>	7.8834	0.005	✓	-0.71302	20
<i>Rhinoceros</i>	0.3453	0.5568	—	-0.30335	10
<i>Rhinopithecus</i>	0.6912	0.4058	—	-0.60261	18
<i>Stegodon</i>	1.9874	0.1586	—	-0.51552	13
<i>Tapirus</i>	2.4021	0.1212	—	-0.57515	16
<i>Ursus</i>	1.9060	0.1674	—	-0.25234	8
Late Pleistocene					
<i>Ailuropoda</i>	0.8263	0.3633	—	-0.72435	18
<i>Bos</i>	12.8796	0.0003	✓	-0.28838	5
<i>Canis</i>	0.1685	0.6814	—	-0.25186	2

Table 4 (*Continued*)

Genus	χ^2 with Yeats Correction	<i>P</i> -value	Sig. (0.05)	Transformed CoSA	Rank
Late Pleistocene (<i>Continued</i>)					
<i>Coelodonta</i>	4.5329	0.0332	✓	-0.41740	8
<i>Crocota</i>	1.0153	0.3136	—	-0.03339	1
<i>Dicerorhinus</i>	11.7852	0.0006	✓	-0.68159	16
<i>Elephas</i>	3.8177	0.0507	—	-0.52284	10
<i>Equus</i>	38.5436	0	✓	-0.27130	4
<i>Felis</i>	17.3706	0	✓	-0.29819	6
<i>Gazella</i>	14.8851	0.0001	✓	-0.49511	9
<i>Gigantopithecus</i>	∞	N.A.	N.A.	N.A.	N.A.
<i>Hyaena</i>	0.0937	0.7595	—	-0.65582	15
<i>Hylobates</i>	41.3078	0	✓	-0.81309	21
<i>Macaca</i>	19.7179	0	✓	-0.55797	11
<i>Mammuthus</i>	35.116	0	✓	-0.80129	20
<i>Megatapirus</i>	0.0111	0.9162	—	-0.69981	17
<i>Panthera</i>	4.509	0.0337	✓	-0.58456	12
<i>Pongo</i>	0.0416	0.8385	—	-0.61907	14
<i>Rhinoceros</i>	0.1265	0.7221	—	-0.37371	7
<i>Rhinopithecus</i>	12.421	0.0004	✓	-0.81839	22
<i>Stegodon</i>	0.0671	0.7956	—	-0.58949	13
<i>Tapirus</i>	0.3893	0.5327	—	-0.73999	19
<i>Ursus</i>	10.925	0.0009	✓	-0.25781	3

The ranks reported correspond to the values for the Transformed CoSA, with the lowest numbered ranks indicating strongest spatial association, the highest indicating the strongest spatial segregation.

females at first reproduction are extremely conservative and slow to change because alterations in them require alterations in so many integrated physiological and behavioral systems (Partridge & Sibly, 1991). Because of this, the life history parameters of the living catarrhine species under consideration are likely to be extremely similar to those of their Pleistocene relatives and the extrapolation of one to the other is fully defensible.

Hominoids differ markedly from cercopithecoids in their life history parameters (Table 5). Apes and hominids are characterized by an advanced age for onset of reproduction, long gestation periods, long weaning periods and long interbirth intervals. This is an extreme version of the “K-selection” reproductive strategy, in which high parental investments in low numbers of offspring per lifetime yield a low intrinsic rate of increase of population. It

is now clear that this pattern evolved under the more stable environmental conditions of the early and middle Miocene in Eurasia (Kelley, 1997), characterized by low to moderate levels of seasonality and more highly predictable regimes of forest productivity (Janis, 1993). Study of growth lines in the tooth germs of *Sivapithecus parvada* from the middle Miocene of Pakistan (Kelley, 1997) indicates that this species matured at approximately the same rate as living apes. The life history parameters of apes thus appear to have become established early in the Miocene, when extensive belts of low-seasonality forests were widespread throughout the Old World (Janis, 1993). The most widespread distributions and highest levels of diversity of ape species were attained when Miocene forests reached their areal maxima, approximately 12–17 m.y.a.; it remains unclear as to whether any ape species (apart from, perhaps, pre-hominids) significantly

Table 5 Life history parameters of selected species of catarrhine primates from China and southeast Asia.

Species	Adult mass ♂ (g)	Adult mass ♀ (g)	Neonatal mass (g)	Age at 1st birth	Gestation (days)	Weaning age (years)	Interbirth interval (years)
<i>Macaca arctoides</i>	9130	7100	500	4.9	176	0.5-1.25	1.43
<i>M. fascicularis</i>	5190	3410	347	3.8	167	0.75-1.5	1.07
<i>M. mulatta</i>	7883	4743	475	4.0	167	0.5-1.0	1.0
<i>M. thibetana</i>	18,300*	12,800*	550	—	—	0.5	—
<i>Semnopithecus entellus</i>	16,300†	13,000†	500	3.5-4.0	22	1-1.25	1.4
<i>Hylobates lar</i>	5940	5303	389	10	199-215	—	2.0-4.0
<i>H. syndactylus</i>	10,913	10,600	537	—	230-235	—	2.0-3.0
<i>Pongo pygmaeus</i>	74,483	37,143	1750	12.0-15.0	244	3.0-4.0	7.0-8.0
<i>Homo sapiens</i>	54,260	48,260	3250	12.0-14.0‡	259	0.5-3.0	2.25§

Data were collected from the literature on adult body mass (Hiernaux & Boedhi Hartono, 1980; Roonwal, 1981; Leigh, 1994; Zhao, 1996), neonatal body mass (Hayssen *et al.*, 1993; Geissmann & Orgeldinger, 1995); age at first birth (Hayssen *et al.*, 1993), gestation periods (Winkler *et al.*, 1984; Galdikas & Woods, 1990; Hayssen *et al.*, 1993; Markham, 1994); weaning age (Hayssen *et al.*, 1993), and interbirth intervals (Galdikas & Woods, 1990; Hayssen *et al.*, 1993).

*Species weight in the late spring, a close approximation of the mean species weight over one year.

†Species weight based on a population from northern India reported by Roonwal (1981).

‡Age range for menarche.

§Average figure based on naturally lactating mothers.

utilized nonforest habitats (Andrews, 1992; Kelley & Pilbeam, 1986). This does not mean that apes inhabited only tropical rain forests; significant evidence now attests to Miocene apes surviving well in other types of forest environments, including more deciduous and somewhat more seasonal forests (e.g., Proconsulidae from Rusinga Island, Kenya), wet subtropical forests of low seasonality (e.g., *Dryopithecus* from central Europe), in closed forest developed in swamp conditions (e.g., *Oreopithecus* from Baccinello, Italy) and in subtropical seasonal forests (e.g., *Griphopithecus* at Paşalar, Turkey) (Andrews *et al.*, 1997). It is worth speculating that the critical shared characteristic of these diverse Miocene forests will prove to be the presence of trees which produced juicy fruits on a regular basis, even if they were widely separated. Anatomical evidence now strongly suggests that at least three groups of Miocene apes (as well as all extant apes) utilized suspensory postures and locomotion, an adaptation that has been interpreted as one promoting the harvesting of widely separated, high quality food items (Andrews *et al.*, 1997).

Monkeys exhibit an earlier age for onset of reproduction, shorter gestation times, shorter weaning periods, short interbirth intervals and, overall, a capacity for a much higher intrinsic rate of increase of population. Importantly, these parameters permit monkeys, even in highly seasonal habitats, to time their breeding and birth schedules so that infants are born in time to take advantage of mid-spring weather conditions and can be semi-independent by the beginning of the next winter (Bishop, 1979; Kirkpatrick, 1996). Among Tibetan macaques living along a broad altitudinal gradient on Mt Emei, Sichuan, onset of breeding and birth of infants occurs earliest in the higher altitude populations, a phenomenon hypothesized to increase the likelihood of conception and to meet the extra energy needs of pregnancy and lactation

(Zhao, 1994). Although Old World monkeys and their attendant life history parameters were established early in the Miocene (Benefit, 1993), the diversification of the group appears to have been limited throughout this epoch, possibly because available niches were occupied by apes. Their major evolutionary "break" appears to have occurred at the end of the Miocene, when the areas occupied by tropical forests in the Old World contracted, and areas once occupied by such forests gave way to more open and highly seasonal habitats.

Apes and monkeys also differ in their food preferences, reflecting an ancient divergence in their respective adaptive strategies (Temerin & Cant, 1983). Although considerable variation in dietary composition exists from one species to another, apes generally prefer ripe fruit, which is easily digested and rich in energy due to its high content of simple sugars and nonstructural carbohydrate (e.g., Chivers, 1984; Hamilton & Galdikas, 1994; Conklin-Brittain *et al.*, 1998). When ripe, pulpy fruit is scarce or not available, apes fall back on other energy-rich foods when these are available. For some apes, such as the community of *Pan troglodytes verus* at Bossou, Guinea, the animals depend heavily on fruit pulp derived from several tree species (Yamakoshi, 1998). When this resource is in short supply, the animals depend heavily on other, highly energy-rich "keystone resources" including oil palm nuts and pith (Yamakoshi, 1998). For this community, the presence of high-quality backup foods means that the animals do not have to feed on many different items of lower quality or of higher secondary compound content when their preferred food is not available (Yamakoshi, 1998). Although the Bossou chimpanzee community is particularly well supplied with high-quality plant foods throughout the year, other chimpanzees show similar trends in food consumption, notably, low intakes of unripe fruits, seeds

or leaves throughout the year, even when fruit pulp is scarce (Conklin-Brittain *et al.*, 1998).

Eastern and western lowland gorillas (*Gorilla gorilla graueri* and *G. g. gorilla*) prefer fruit when it is available, but marked seasonal changes in fruit resources demand that the animals depend on continuously available keystone resources (Nishihara, 1995; Tutin & Fernandez, 1985; Watts, 1998). Herbaceous and vine foods are eaten throughout the year, and are used, along with bark, as backup foods when fruit abundance is low (Nishihara, 1995; Watts, 1998). Mountain gorillas (*G. g. beringei*) are at the low variance end of the spectrum of seasonal variation in ecology among gorilla populations, relying on perennially available food leaves, pith, and stems, which are abundant, high in protein and easily digested (Watts, 1998).

For some ape species, however, high-quality backup foods are not available when ripe fruit is scarce. For *Pongo pygmaeus* in Gungung Palung National Park in West Kalimantan, Indonesia, diet varies tremendously according to fluctuations in the availability of pulpy fruit (Knott, 1998). When fruit is available, the animals consume it in large quantities, considerably in excess of their baseline metabolic requirements. Consumption during a mast fruiting can be so great that orang-utans can gain as much as 0.66 kg per day (Knott, 1998). During periods of low fruit availability, however, the orang-utans depend heavily on bark, a backup food of significantly lower quality in terms of caloric yield (Knott, 1998; Wheatley, 1982). The production of ketones—products of fat metabolism—during periods of fruit scarcity, indicate that under such conditions the animals lose weight and are energetically stressed (Robinson, 1980; Knott, 1998).

Because of their preference for ripe fruit, large apes are at a particular disadvantage during periods of heightened or prolonged

seasonality when fruits are unusually scarce. Under these conditions, fat reserves would be quickly depleted because of the high energetic demands of a relatively large brain. This situation departs strongly from that seen in clades of other herbivores, in which larger body size (but without increased encephalization) insures to some extent against the vicissitudes of increased environmental seasonality (Zevuloff & Boyce, 1988). The evolution of larger body sizes has occurred in many lineages of mammals living in seasonal or unpredictable climates and was one of the most common strategies employed by mammals to cope with the climatic fluctuations of the Pleistocene. A larger body is more efficient in its utilization of food energy because its smaller surface area relative to volume makes possible less loss of energy through dissipation of heat at the body's surface. Larger herbivores tend to eat less food or lower quality food per day, as a proportion of body mass, than small herbivores, and large animals lose condition more slowly on a submaintenance diet than do smaller animals (Owen-Smith, 1988). Finally, stored fat reserves become a greater fraction of body mass as size increases (Owen-Smith, 1988). These factors help mammals to cope with extreme seasonal fluctuations in food availability, such as those which occurred during the Pleistocene. Wheatley (1982) argued persuasively that large body size in the orang-utan reflected the evolutionary importance of an increased capacity for energy storage in environments in which fruiting and flowering were unpredictable. This is true, but in the orang-utan and other large apes the benefits of large body size are offset to some extent by the high energetic demands of a large brain. The beneficial consequences of large body size did not enhance the survival of large apes during the extreme environmental fluctuations of the Pleistocene because of the animals' preference for high energy food sources coupled with the high energetic

demands of large brain size. This would appear to have held true even for the largest known Asian catarrhine, *Gigantopithecus*.

The molar and mandibular dimensions of *Gigantopithecus* indicate that it was a large ape, but just how large is not known. Judging from its dental microwear, *Gigantopithecus* appears to have been an eclectic feeder, showing a pattern of molar scratch and pit features closer to that seen in *Pan* than *Gorilla* (Daegling & Grine, 1994), suggestive of a diet consisting of a broad range of fruits and fibrous materials. If one uses a regression based on molar dimensions of Plio-Pleistocene megadont hominids, *Gigantopithecus* would have approximated the size of a modern male gorilla (Gerrell Drawhorn, personal communication). The known Pleistocene distribution of *Gigantopithecus* (Table 1) in China was limited to regions of moist subtropical forests with moderate levels of seasonality. A *Gorilla*-sized ape subsisting on a *Pan*-like diet probably existed fairly well under those conditions at low densities, because sufficient quantities of relatively high quality foods (some fruits, young bamboo shoots, and leaf flush) would have been available at intervals throughout the year to sustain adults and developing young. Under conditions of increasing dryness and seasonality, however, many of the animal's hypothesized food plants would have shifted southward in their distribution or would have become locally extinct. The limited ability of apes to engage in food-switching in response to shortages of preferred food items would have meant that populations of *Gigantopithecus*, by the Late Pleistocene, were stretched beyond their energetic limits and reduced to densities too low to sustain successful reproduction.

In contrast to apes, monkeys are more eclectic feeders and can subsist on generally lower quality foods, when quality is defined in terms of easily realized energy yield (e.g., Bennett & Davies, 1994; Oates, 1994;

Temerin & Cant, 1983; Wheatley, 1980; Wrangham *et al.*, 1998). Cercopithecines and colobines differ in their dietary preferences and their tolerance of antifeedants, so discussion of each group is warranted.

Cercopithecine monkeys possess simple stomachs like apes, and thus lack the capacity to undertake fermentative foregut digestion (Bauchop, 1978). Despite this similarity, cercopithecines generally consume a diet that is much more diverse than apes throughout the year (Conklin-Brittain *et al.*, 1998; Wrangham *et al.*, 1998). It is also a diet that is lower in quality in terms of its water-soluble carbohydrate (simple sugar) content and in its concentrations of antifeedants (Conklin-Brittain *et al.*, 1998; Wrangham *et al.*, 1998). In habitats such as the Kibale National Park, Uganda, where cercopithecines and chimpanzees are sympatric, both groups will consume ripe fruit when it is available. But while chimpanzees will concentrate almost exclusively on ripe fruit at those times, monkeys will consistently consume unripe fruits, leaves and flowers in addition to the ripe fruit (Wrangham *et al.*, 1998). In times of fruit scarcity, ape and cercopithecine diets diverge markedly, with monkeys turning to plant parts such as unripe fruits and seeds which are rich in tannins and other secondary compounds and apes relying on more vegetative matter such as leaves and piths (Andrews, 1981). Although cercopithecines lack the microbial symbionts in the forestomach that help colobines to neutralize some antifeedants, it is possible that some microbial inactivation of secondary compounds occurs during microbial fermentation in the cecum of the cercopithecine hindgut (Toshitaka Iwamoto, personal communication). In sum, cercopithecines can accommodate a more diverse diet and appear more tolerant of the presence of antifeedants in their foods than are hominoids (Andrews, 1981).

Colobine monkeys are also eclectic feeders, but can afford to eat lower quality

vegetation than cercopithecines and apes because they are equipped with a capacity for the fermentation of cellulose and hemicellulose in the forestomach. For colobines, the main energy sources are not simple sugars, but volatile fatty acids, which are the main products of microbial fermentation in the gut. Colobine diets are highly diverse, but for most species include leaves, seeds, winter buds and unripe fruits (e.g., Bennett & Davies, 1994; Oates, 1994). Species with more capacious guts and an ability for prolonged retention of foodstuffs during fermentation (e.g., *Pygathrix nemaeus*) concentrate more exclusively on leaves (Chivers, 1994). Colobines do not tolerate the simple sugars in ripe fruits because of their adverse effects on gut pH and the activity of cellulolytic bacteria (Kay & Davies, 1994). They generally avoid pulpy fruits even when available. Microbial activity in the colobine gut not only breaks down the cellulose and hemicellulose of plant cell walls, it also is responsible for the partial breakdown of certain toxic constituents of the diet, including some alkaloids, amines and organic acids (Kay & Davies, 1994). This capacity permits colobines to utilize a variety of seeds and leaves (including mature leaf stock) that are off-limits to cercopithecines and apes.

For cercopithecoids, then, the combination of eclectic diets and life history parameters which allowed populations to be reproductively successful in seasonal environments rendered them much better prepared biologically for the environmental insults of the Pleistocene than hominoids. Apes are poorly equipped for survival under conditions of extreme seasonality. Compared to monkeys, they generally show little ability to engage in food-switching in response to shortages in preferred food items (van Schaik *et al.*, 1993). Further, in times of food shortage, age of first reproduction is delayed and interbirth intervals increase (Wrangham, 1975).

Of all the apes, the smaller bodied gibbons appear to have the most flexibility in terms of abilities to survive periods of environmental change and withstand increases in seasonality. While hylobatids managed to maintain distributions in marginal subtropical environments throughout the Pleistocene, pongids did not. This is borne out by the evidence of historical and modern distributions of both families. Pongids “pay the metabolic penalty” of a combination of larger body size and encephalization by not being able to survive in forests in which seasonality has become extreme. If fruitings become so irregular and widely spaced that animals cannot maintain body weight and first female reproduction is greatly delayed, chances of survival are slim. Gibbons are able to avoid the same problem because of a smaller body mass (lower absolute caloric requirement) and because their highly energy-efficient mode of locomotion allows them to cover plenty of ground and get to whatever high-quality foods might be available. Populations of *Hylobates concolor* inhabiting evergreen broadleaf forests in southwestern Yunnan, China, prefer fruits when they are available, but become nearly exclusively folivorous when they are not. Of great interest is the fact that their ability to undertake some food-switching permits these populations to inhabit the higher altitudes of evergreen broadleaf forests (at approximately 1000–2000 m), but not the higher coniferous forests, which, in northwestern Yunnan, are inhabited by snub-nosed colobine monkeys. Of all the hominoids, gibbons succeed in environments where others fail, but in habitats of moderate altitude (>1500 m) their populations are stressed and are no match for monkeys of equal body size. Among the gibbons (*Hylobates lar*) of Khao Yai, Thailand, populations at higher altitudes exhibit lower densities, delayed onset of reproduction and longer interbirth intervals than those at lower

altitudes (W. Brockleman, personal communication).

Hominids display an extreme form of the ape pattern of life history parameters. If these criteria had been the sole determinants of their evolutionary success, they might have been expected to follow the declining course of the apes during the Pleistocene. The archaeological record abundantly attests, however, to the fact that this was not the case, and that—taxonomic assignment of Asian fossil hominids notwithstanding—increasingly sophisticated modes of extrasomatic adaptation were permitting hominid survival in and expanding exploitation of highly seasonal environments (Wang *et al.*, 1997).

Our data on patterns of association between *Homo* and other genera of mammals during the Pleistocene in China also suggest that these patterns changed as the epoch progressed. Throughout the Pleistocene, hominids in China were associated with members of the scavenger and carnivore community, and this association appears to have become stronger through time. The spatial relationship of hominids with other catarrhines underwent a marked shift. The association of *Homo* with macaques from the Early through the Middle Pleistocene was strong, but significantly diminished by the Late Pleistocene. That some ecological separation of *Homo* from other apes had occurred by the Early Pleistocene is supported by the finding of moderate segregation between *Homo* and the apes in the spatial association analyses. This separation became extreme in the Middle and Late Pleistocene. Taken together, these findings indicate an increasing contrast through the course of the Pleistocene between *Homo* and all other catarrhines in the range of habitats preferred and tolerated. They also suggest that, as *Homo* fell out of ecological phase with its close relatives it fell closer into phase with members of the scavenger and predator communities (Turner, 1992).

Implications, summary and conclusions

The major shifts in the distributions of catarrhine families during the Pleistocene of China were related to profound changes in the distribution of the subtropical zone. Examination of the patterns of spatial response among these primates to the environmental changes of the Pleistocene in Asia indicates that life history parameters and dietary selectivity are strong predictors of the type and magnitude of response on the part of individual taxa. Apes (even small-bodied forms) are more sensitive to environmental change than are monkeys because of their more protracted reproductive schedules and preference for the ripe fruits more regularly found in tropical forests. In contrast to other apes, hominids expanded their range in the Late Pleistocene to extend into highly seasonal environments with less predictable food supplies. The ecological association of hominids with other catarrhines was strong in the Early Pleistocene, but became weaker through time as culture permitted hominid range expansion into habitats off limits to other catarrhines for most of the year.

It is interesting to note, in conclusion, that these same parameters also determined the relative successes of anthropoid species during the Holocene amelioration. Although the early Holocene (~9000 yr B.P.) in China saw a return to warmer and wetter summers, cold, dry winters persisted (Winkler & Wang, 1993). Thus, the so-called amelioration did not coincide with a lessening of seasonality, at least at first. These conditions tended to inhibit the re-expansion of plants and animals that preferred relatively nonseasonal conditions (Winkler & Wang, 1993), while favoring the expansion of those (especially Gramineae) that could thrive under highly seasonal conditions. At ~6000 yr B.P. in China, summer warmth and wetness remained and

winters warmed, yielding a net reduction in seasonality (Winkler & Wang, 1993). It is during this time in China that the greatest expansion of plants and animals (including humans) occurred. Judging from their modern distributions (Corbet & Hill, 1992), monkeys were able to take full advantage of the two-stage Holocene amelioration and re-expand their range because of their ability to live successfully in highly seasonal ecosystems. The apes, however, could not. When less seasonal conditions, ~6000 yr B.P., finally did favor their re-colonization of re-expanded southern subtropical and tropical forests, they probably faced stiff competition from well-established monkeys and their closest relatives, humans. For orang-utans, the picture was further complicated by the fact that when appropriate environmental conditions on the Asian mainland were reinstated, elevated sea levels (Winkler & Wang, 1993) precluded re-dispersal along the once-exposed Sunda Shelf. For these reasons, the orang-utan appears never to have re-established itself outside of island southeast Asia, and gibbons have never reclaimed much of their Middle Pleistocene distribution. The apparent severity of the range compression and population declines suffered by these animals in the recent geological past renders them highly vulnerable to anthropogenic or other environmental disturbances in the future. The expansion of post-Pleistocene hominid populations was dramatic, eventually leading to the development of agriculture and the increasing extirpation of environments inhabited by their catarrhine relatives.

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