

## Environmental change during the Quaternary in East Asia and its consequences for mammals

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**Abstract** – Environmental changes during the Quaternary in eastern Asia had profound impacts on the distributions of mammals. Critical for many taxa were the southward latitudinal shifts of the tropical and subtropical zones, and decreases in the areal extents of these zones. In this study, a geographic information system (GIS) has been used to examine the spatial responses of mammalian genera to environmental changes of the Pleistocene of China. Conditions of increasing seasonality during the Pleistocene favoured the evolution of large and well-insulated morphs in several mammalian families (e.g., Rhinocerotidae, Tapiridae, Elephantidae), but this strategy was not successful (in terms of long-term survival) in many cases.

The spatial responses of members of a single clade, the Catarrhini or Old World higher primates, are of particular interest. The main catarrhine genera of eastern Asia responded individually to conditions of increasing seasonality during the Pleistocene, and these responses reflected the life history parameters of the genera involved. Apes were found to be the most sensitive to conditions of increased seasonality, with large apes (*Pongo*, *Gigantopithecus*) retreating in advance of gibbons (*Hylobates*). Monkeys retreated southward more slowly and to a lesser extent than apes because of their abilities to survive in more highly seasonal environments and to produce offspring on relatively abbreviated reproductive schedules.

These results provide a new basis for predicting the responses of primates and other mammals to future environmental change.

### INTRODUCTION

The record of environmental change during the Pleistocene is rich and is yielding increasing amounts of detailed information, especially as new sources of data, from columns of continuous deposition such as loess sequences and ice cores, are fully explored. These improvements in the palaeoenvironmental record have been enthusiastically welcomed by palaeontologists because it is against these records that organismal evolution can be fully understood. Climate change places myriad stresses on organisms, which differ in their forcing response to these stresses (FAUNMAP Working Group 1996; Parsons 1993a, 1993b; Roy *et al.* 1996; Webb and Bartlein 1992). It is now widely recognized that natural populations respond to climatic change by latitudinal shifts in abundances and/or geographic range boundaries (Huntley and Webb 1989; Roy *et al.* 1996; Webb and Bartlein 1992). The sometimes extreme climatic fluctuations of the Pleistocene tended to destabilize species interactions within communities, and species tended to adjust themselves individually to

such stresses. Pleistocene communities were not just geographically displaced versions of modern ones, they were fundamentally different in their composition because of the differential responses of species to environmental change; hence their name of 'non-analogue' communities (FAUNMAP Working Group 1996).

Environmental changes during the Pleistocene in East Asia were, to an extent, more extreme than in other continents because the local climatic effects of the Qinghai-Xizang (Tibetan) Plateau tended to magnify, for much of eastern Asia, the orbitally induced climatic fluctuations associated with glacials and interglacials worldwide (Webb and Bartlein 1992). Among the most dramatic of these changes was the abrupt increase, at about the Gauss/Matuyama boundary, 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).

In this study, a geographic information system (GIS) has been used to visually superimpose and analyse data concerning environments and

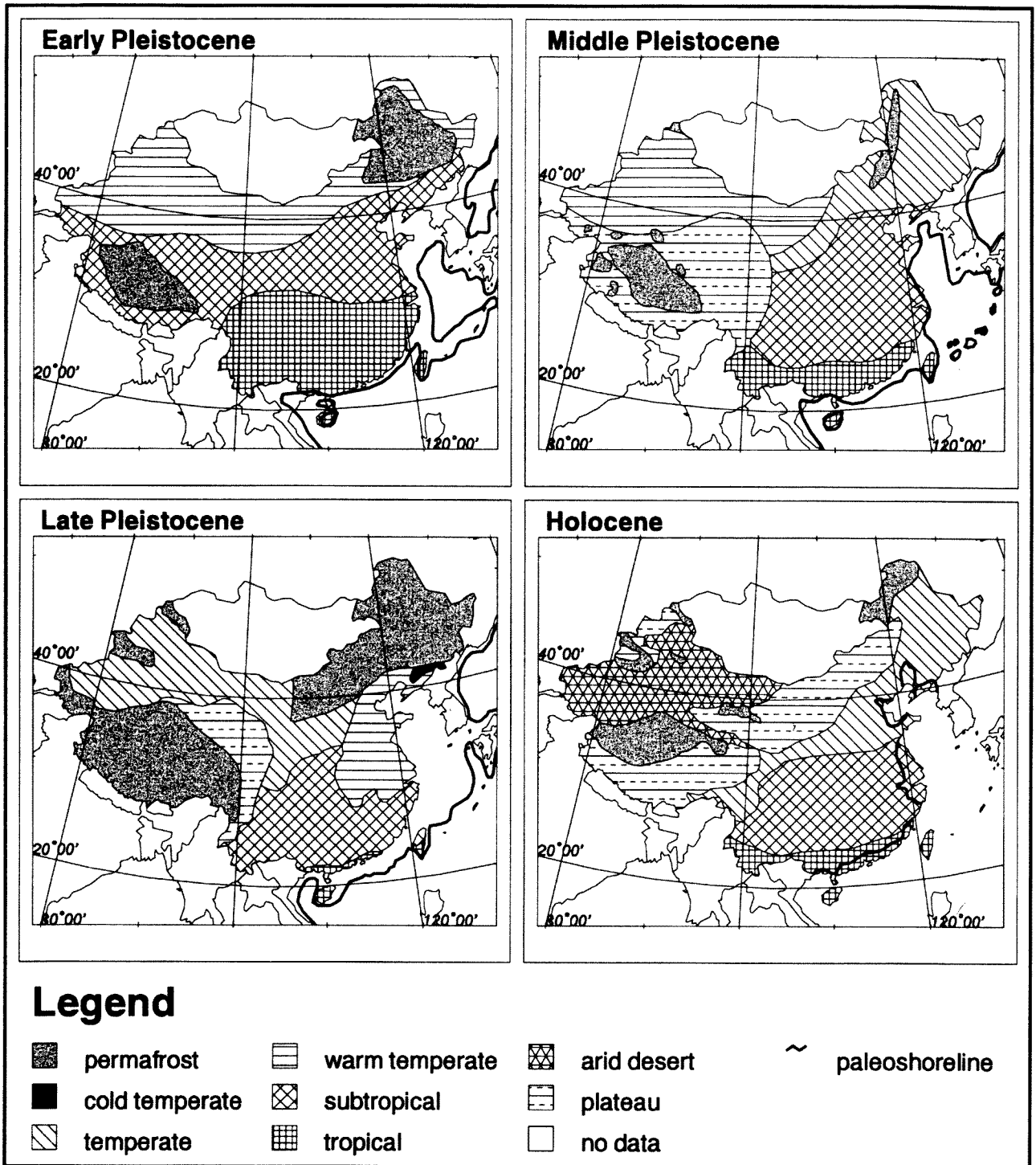


Figure 1 The major environmental zones of China in the Early, Middle, Late Pleistocene and Holocene.

distributions of mammals in the past. Our palaeoenvironmental data have been compiled from several sources and are based mainly on the distribution of vegetation types (as judged mostly from pollen records), soils, permafrost and loess (An *et al.* 1991; Cui and Song 1991; Li 1991; Winkler and Wang 1993; Zhou *et al.* 1991). Our attention in this study was concentrated on China because it displays the highest density and most even distribution of

palaeoenvironmental and palaeontological data. The boundary dates used for the subdivisions of the Pleistocene are those applied by most Chinese geoscientists and by an increasing number of stratigraphers elsewhere, who recognize the Gauss-Matuyama palaeomagnetic reversal at 2.5 Myr as the Plio-Pleistocene boundary (Ding *et al.* 1997; Partridge 1997). The Early Pleistocene is then taken as 2.5 Myr to 780,000 yr, the Middle Pleistocene from 780,000

to 128,000 yr, and the Late Pleistocene from 128,000 to 11,000 yr. The Holocene is taken as the span from 11,000 yr to the present.

### ENVIRONMENTAL BACKGROUND

The Early Pleistocene of China was characterized by generally warmer and more humid environmental conditions of greater homogeneity than those that obtained later in the Pleistocene or in the Holocene. At this time (Figure 1), the subtropical zone covered a broad east-west expanse (including the area over the proto-Tibetan Plateau) and there existed a large tropical zone south of it. There is evidence of permafrost over the Tibetan Plateau and in northeastern China by the later part of the Early Pleistocene (Zhou *et al.* 1991). By the Middle Pleistocene, the subtropical and tropical zones had shifted south- and eastward, and the Tibetan Plateau had emerged as a distinct environmental zone. By the Late Pleistocene the subtropical and tropical zones had migrated even farther southward and were considerably reduced in area, the Loess Plateau (see Figure 3) had increased in size due to more widespread aeolian deposition of loess under cold and dry conditions, and permafrost covered much of Tibet and the northeast. A broad area of continental shelf was also exposed during much of this time, permitting extensive exchanges of mammals between the mainland and the island environments of Hainan and Taiwan. Conditions at the Last Glacial Maximum (not depicted in Figure 1) were even more extreme, with elimination of the tropical zone entirely from the Chinese mainland.

For mammals, 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 Pleistocene environmental changes (Ferguson 1993; Jablonski 1993). The effects of this reorganization were pronounced. The reduction in the size of the subtropical zone was marked. This zone, which had extended across the breadth of the continent in the Tertiary, lost its western flank and was shifted southward over the course of the Pleistocene, with predictable changes in mammalian distributions. This trend became dramatically exaggerated during the climatic fluctuations of the Late Pleistocene, when it appears that the subtropical zone was entirely eliminated from China. In connection with biogeographic corridors, the opening up of new pathways for dispersal of species and the erecting of new physical and climatic barriers to

distribution was another trend which characterized the East Asian Pleistocene. The most famous example here is that of the Qin Ling Mountains, lying directly to the south of the Loess Plateau. Uplift of these mountains from the mid-Pleistocene onward put an end to the north-south exchange of faunas that had occurred up to that time. This barrier not only prevented the southward migration of thermophilic species during glacial phases, but also prevented the northward migration of cryophilic species during interglacials and at the end of the Pleistocene. A further specific important consequence for mammals of the dramatic environmental changes of the late Tertiary and Quaternary was the creation of niches in which archaic taxa could survive and new species could evolve. The most important of these sites for mammals was the Heng Duan Mountains in northeastern Yunnan that, with their deeply dissected north-south trending valleys, provided a last resting place for palaeoendemics and a cradle for diverse neoendemics. The final important consequence — related to the last — was that the Tibetan Plateau itself and adjacent mountain ranges became a refuge for cold-loving species. These areas acted as a staging grounds of sorts for such organisms to invade lower-lying areas in northern China during the colder phases of the Quaternary and to return to during the interglacials. This last point had as important consequences for plants as for animals, because it created numerous local sources of montane plants and animals from which cryophilic species could emigrate during glacials and retreat to during interglacials (Ferguson 1993).

The Holocene amelioration, peaking at 6000 yr BP, saw a major warming and northward re-expansion of the tropical and subtropical zones, the emergence of large tracts of arid desert north and northeast of the Tibetan Plateau, and a marine transgression.

Before we can examine changes in the distributions of mammals against this backdrop, it is important to recognize that there are several factors that affect the potential accuracy of our information on the geographical distribution of fossil taxa, and that will influence the biological conclusions drawn from observed changes in animal distributions through time. Collecting and sampling biases are potentially very significant. In our choice of the relatively well-surveyed country of China as the focus of this study, we have reduced, but not eliminated, these influences. Also potentially important, are various taphonomic biases such as 'non-preserving' or poor-preserving environments such as tropical forests, selective destruction of species or age classes after death, and post mortem removal of animals from the life habitat (Roy *et al.* 1996).

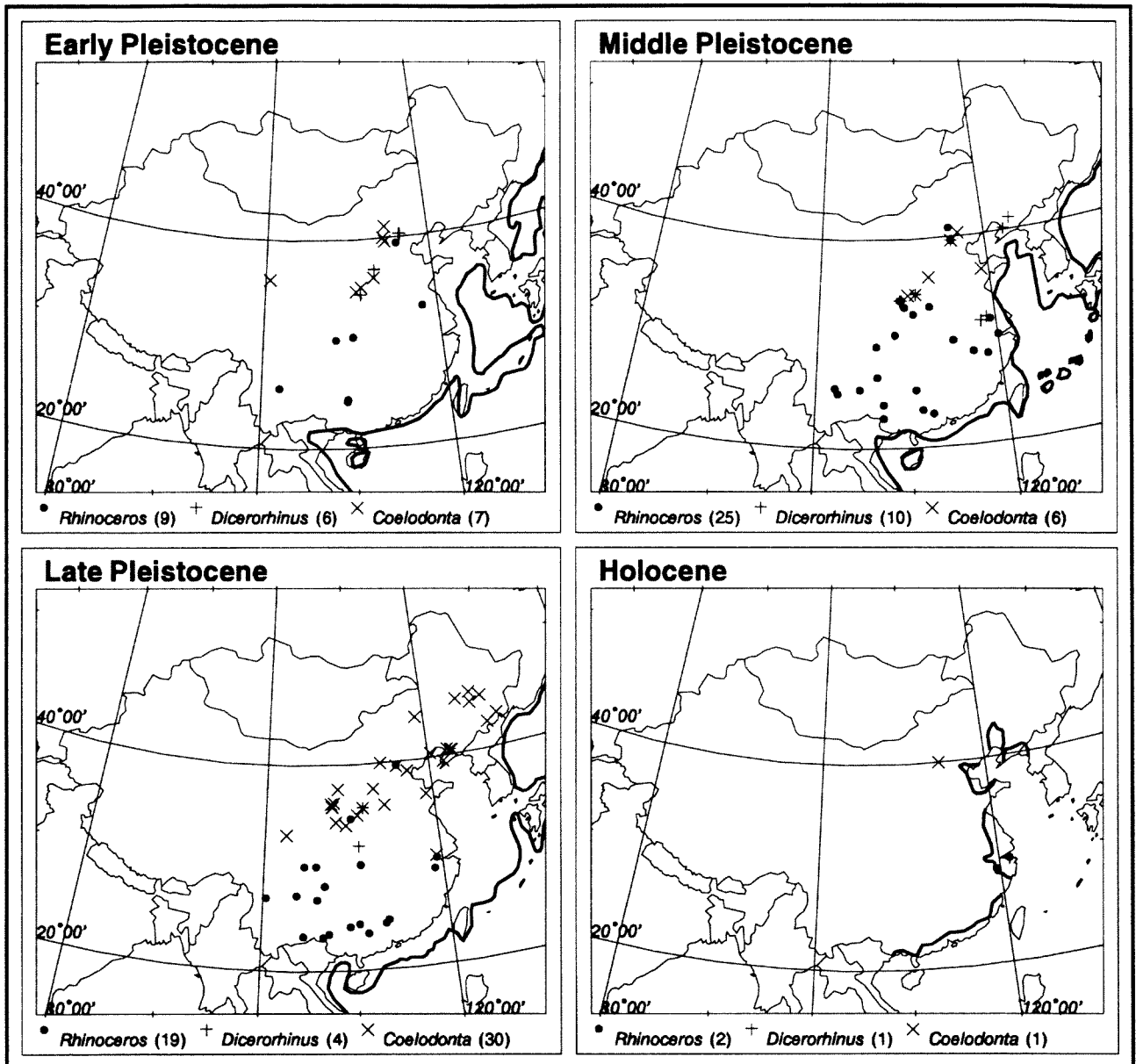


Figure 2 The distributions of *Rhinoceros*, *Dicerorhinus* and *Coelodonta* in the Early, Middle, Late Pleistocene and Holocene.

#### CHANGES IN THE DISTRIBUTIONS OF SELECTED GENERA OF MAMMALS

The environmental changes of the Pleistocene are correlated with a series of profound changes in the diversity and distribution of mammals in China. Interesting individual stories can be told for all genera, but we shall concentrate here on a few illustrative genera of larger, hoofed mammals and the genera of higher primates. Data on the distributions of fossil mammals were drawn from the Eurasian Fossil Mammal Database, which comprises point data for the distribution in time and space for fossil mammal species in Eurasia during the Cenozoic. The database consists, in part, of the location, and geological and numerical age of mammalian fossils. 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'. 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 at a particular time.

The distributions of several large mammals shifted southward and appear to have become less dense during the Late Pleistocene. Looking at the genera of one family, the Rhinocerotidae, we see this pattern followed by *Rhinoceros*, the genus representing the modern Javan rhinoceros (Figure 2). *Dicerorhinus*, another thermophilic

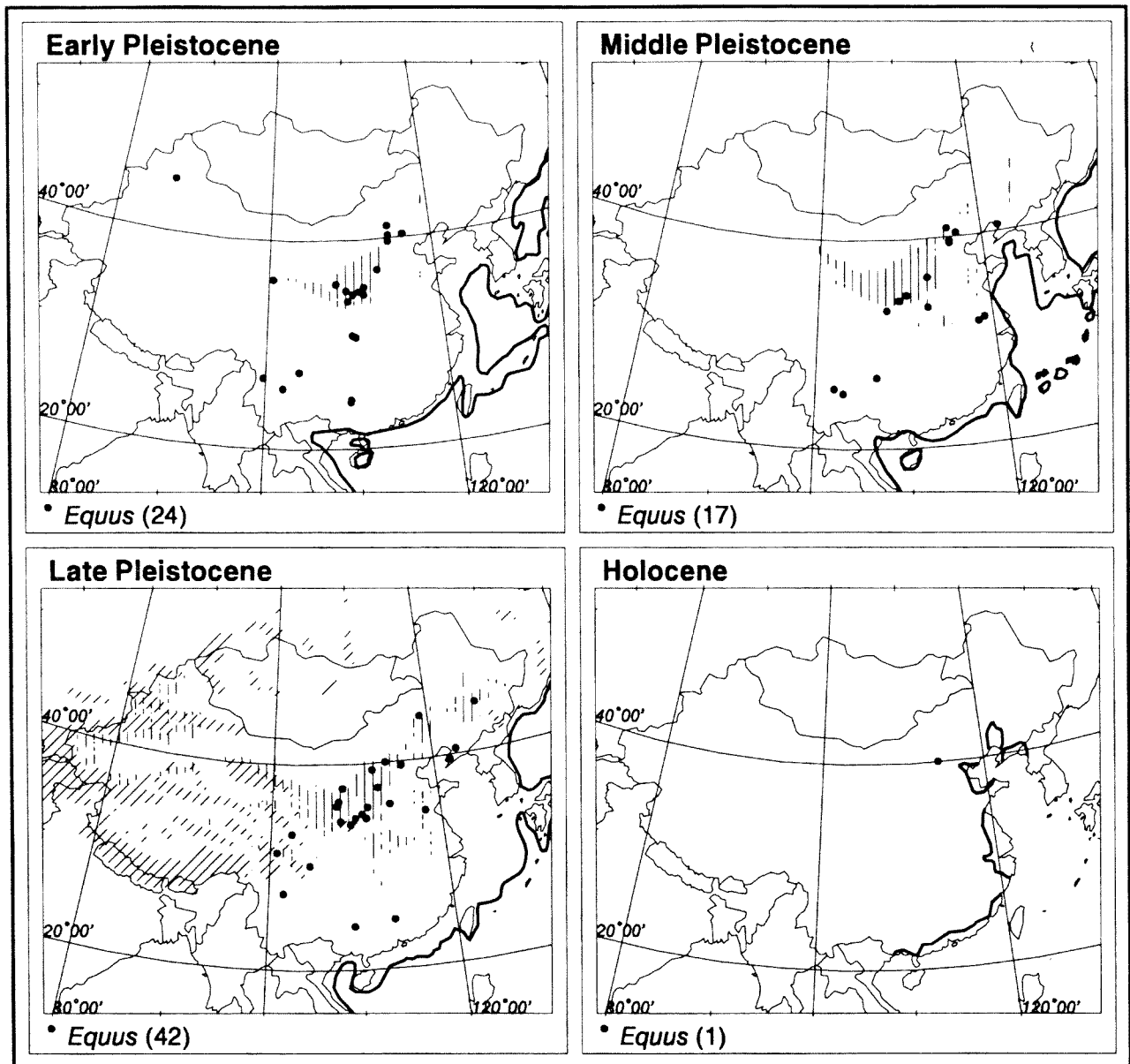


Figure 3 The distributions of *Equus* in the Early, Middle, Late Pleistocene and Holocene plotted relative to loess distribution (vertical hachures) and glacial cover (oblique hachures). Note the strong and consistent association of *Equus* with the grassland environment of the Loess Plateau.

genus of the Rhinocerotidae, met a different fate: its southward migration during the Pleistocene appears to have been blocked by the newly formed Qin Ling Mountains. With its exit blocked, the genus became extinct in China and survived only in those tropical parts of Sundaland, such as Sumatra, where it had previously established itself (Groves 1983; Jablonski unpublished data). (This effect may, in reality, have been less pronounced than it appears. According to C.P. Groves [pers. comm. 1998], *Dicerorhinus* is almost certainly paraphyletic and one of the northerly species representing the genus in Figure 2, "*D.*" *choukoutienensis*, is probably more closely related

to *Coelodonta*.) As was the case in many mammalian lineages, the rhinocerotid genus which most successfully withstood the increasingly intense cold, dry conditions and the heightened seasonality of the later Pleistocene was the giant, well-insulated *Coelodonta*, the woolly rhinoceros. For this genus and other cryophils, their number of occurrences peaked in the Late Pleistocene before they disappeared abruptly from the faunal record in the early Holocene.

Some of the real benefactors of the environmental changes of the Pleistocene of East Asia were the true horses and gazelles which could successfully exploit the newly evolved grassland and steppe niches of the Tibetan and Loess Plateaux (Figure 3).

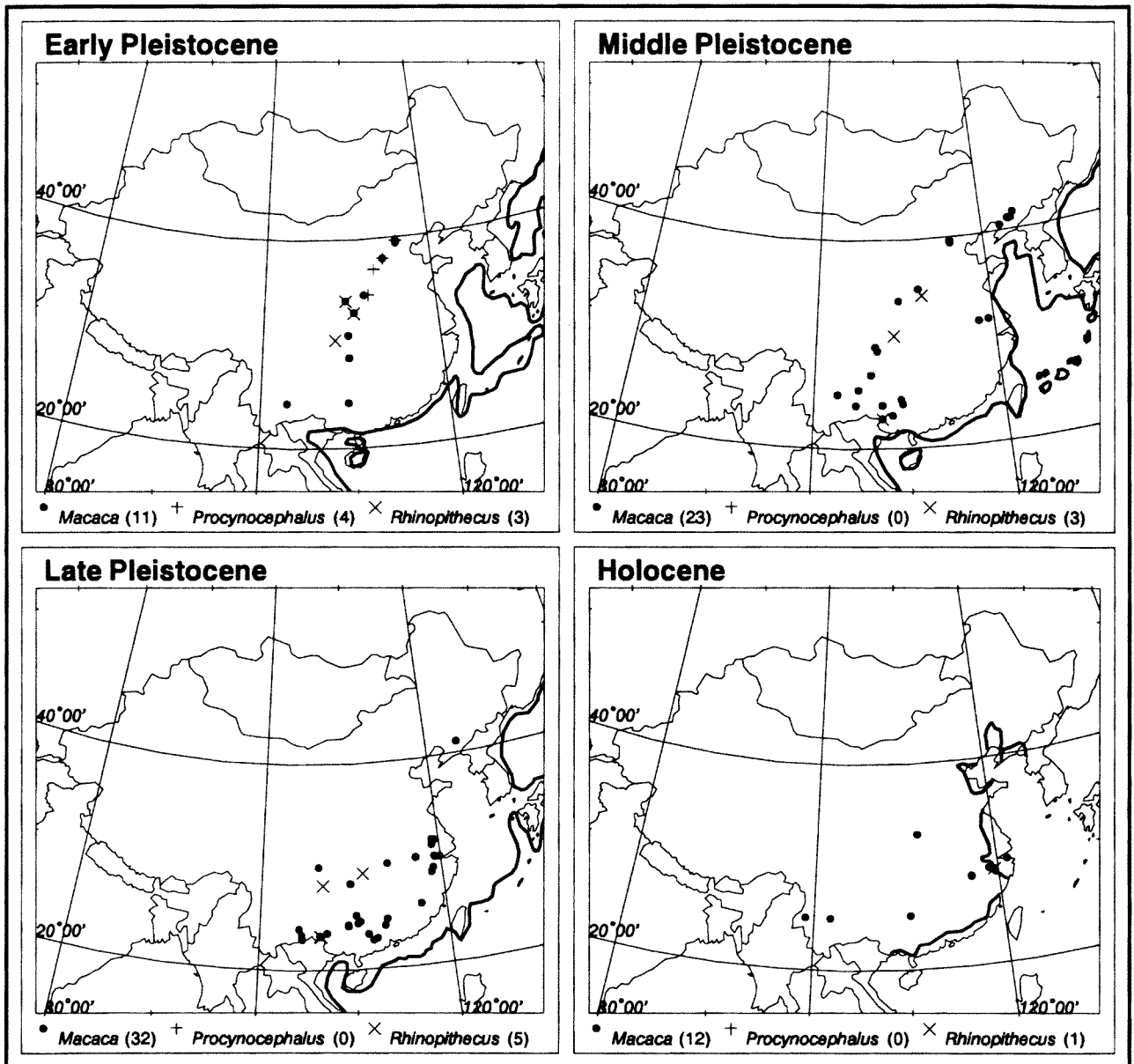


Figure 4 The distributions of *Macaca*, *Procynocephalus*, and *Rhinopithecus* in the Early, Middle, Late Pleistocene and Holocene.

This is best illustrated by the genus *Equus*, which, by Late Pleistocene times, was confined mostly to the Loess Plateau, an area now recognized to have been consistently covered with grasses and herbs for at least the last 100,000 yr, and perhaps longer (Sun *et al.* 1997).

The catarrhine or higher Old World primates present an interesting set of case histories concerning the effects of Pleistocene environmental change, because the entire assemblage comprises both relatively stenotopic and eurytopic genera and is considered part of China's so-called Oriental Fauna. The Old World monkeys of the genera *Macaca*, *Procynocephalus* and *Rhinopithecus* together showed a noticeable south- and eastward shift during the Pleistocene, mirroring the *Rhinoceros*

pattern quite closely (Figure 4). Apes reacted somewhat differently (Figure 5). The so-called lesser apes, the gibbons (genus *Hylobates*), remained quite abundant in the tropical zone throughout the Pleistocene, while the large apes, the orangutan (genus *Pongo*) and *Gigantopithecus*, appeared to retreat southward earlier in the Pleistocene, and were eliminated from China by the end of the Pleistocene. If number of occurrences can be counted as some measure of evolutionary success, the smallest-bodied ape genus, *Hylobates*, was the most successful of all, with distributions maintained in the southern portion of the subtropical zone through the Late Pleistocene, and surviving the Last Glacial Maximum into the Holocene.

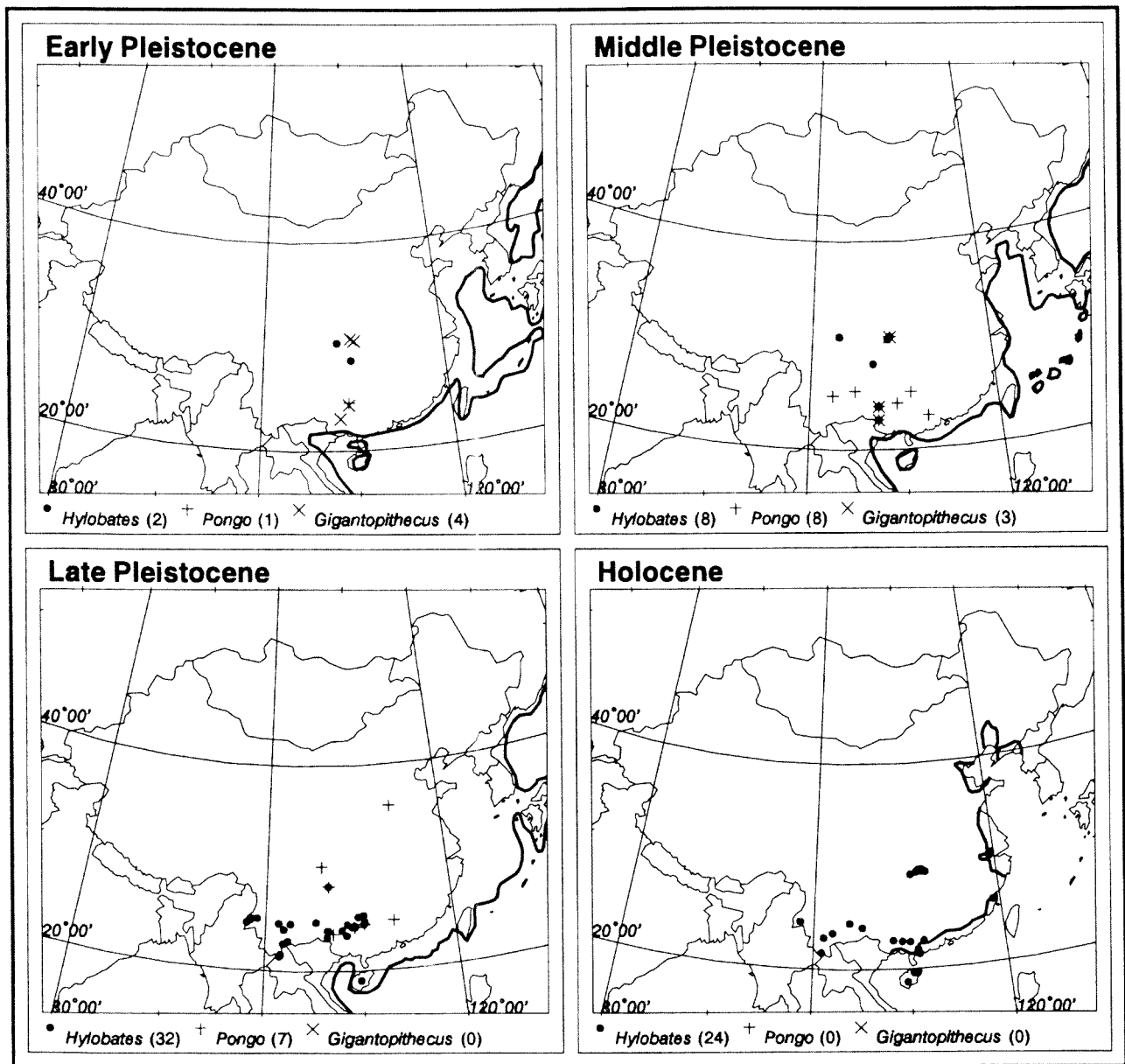


Figure 5 Distributions of *Hylobates*, *Pongo* and *Gigantopithecus* in the Early, Middle, Late Pleistocene and Holocene.

The changing distributions of the cercopithecoid genera *Macaca* and *Rhinopithecus* show a few significant departures from those of the apes. Firstly, the distributions of the monkey genera extend farther northward than those of the apes for all time periods. Interestingly, however, the distribution of monkeys only extends minimally north of the subtropical zone at any time. Secondly, the degree of southward compression of distributions during the Late Pleistocene and Holocene would appear to be less pronounced for monkeys than for apes. In this connection, the contrast between the changing patterns of distribution of *Macaca* and *Hylobates* through time is particularly germane, given that the two genera are of similar body size (approximate range 8–15 kg).

## DISCUSSION

The few examples considered here suggest that mammalian taxa responded individually to the severe environmental fluctuations of the Pleistocene. This is illustrated most clearly by the catarrhine primate genera, whose distributions shifted at different times and at different rates in response to changes in Quaternary environments. This finding is in accord with that of the FAUNMAP Working Group (1996), who showed that mammalian species responded individually to late Quaternary climatic fluctuations in North America. This result also helps to account for observations of living faunas in North America and Australia that indicate that species and communities are individualistic in spatial

distribution and that communities are not restricted to specific combinations of species (Brown and Kurzius 1989; Morton *et al.* 1994). The conclusion that mammalian communities are continually and unpredictably emergent, is one shared by the present study.

The evolution of larger body sizes has occurred in many lineages of mammals living in seasonal or unpredictable climates through time and was one of the most common strategies employed by mammals to contend with the climatic fluctuations of the Pleistocene (Owen-Smith 1988; Zeveloff and Boyce 1988). 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. These factors helped mammals to cope with extreme seasonal fluctuations in food availability such as those that occurred during the Pleistocene.

The differences in patterns of response to environmental change demonstrated by the various primate genera are of great interest because they can be traced to known aspects of the biology of those forms. It is now widely recognized that changes in patterns of climatic seasonality have profound effects on animals and especially on those mammals like primates with long generation times and energy- and time-intensive modes of raising offspring. Among the most interesting findings of this study is that, for apes, evolution of larger body sizes was not a key to evolutionary success as it was, at least temporarily, for many other mammalian lineages. The life history parameters of apes evolved under the relatively predictable and stable climatic regimes of the Miocene and are exquisitely suited to them (Kelley 1997). The animals' life spans are long, their gestation times are long, their interbirth intervals are long, and females begin to reproduce at a relatively advanced age. Apes also possess very large brains relative to their body size, and such metabolically costly organs require nutrient- and energy-rich diets in order to develop and be maintained. The absolutely greater metabolic demands of large body size, coupled with the demands of a large brain, proved too great for *Gigantopithecus* and, to a lesser extent, for *Pongo* under conditions of increasing seasonality during the Pleistocene. The orangutan managed to escape extinction, maintaining its distribution in relatively unseasonal equatorial tropical forests. The

orangutan's strategy has proven not to be an effective formula for survival. With its reliance on regular supplies of high-energy tropical food sources, the species was (and still is) at risk. This risk has been exacerbated by the species' long gestation period and very long interbirth intervals that made it impossible for it to survive in areas with anything but predictable environments with relatively little seasonal fluctuation in availability of easily-digested, energy-rich foods (Jablonski 1997).

The relatively greater success of the monkeys during the Pleistocene had to do with their abilities to exploit a wide variety of plant foods and to produce offspring more quickly, because of shorter gestation times and shorter interbirth intervals.

In the rapidly fluctuating environments of the latest Pleistocene and early Holocene in Asia, the response of catarrhine genera was linked to a complex constellation of factors including niche breadth, gestation time, length of interbirth interval, relative brain size, and other factors still to be elucidated. As we learn more about the life history parameters of other mammalian genera, a more complete understanding of their reactions to environmental change will also be forthcoming. This knowledge will significantly aid our abilities to predict relative levels of species vulnerability in response to the environmental fluctuations of the future.

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