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Research Article

Catarrhine Evolution in China

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Abstract

Cattrthrines (humans and nonhuman primates) in Asia experienced similar migrating routes from Africa to East Asia but with different time frames during the Miocene and Early Pliocene. They dispersed and radiated in East and Southeast Asia during the Pliocene and Pleistocene so that one's experiences of evolutionary development and biodiversity changes can mutually be interpreted for the others. Thus, it is necessary to jointly explore the issues in mainland China, the major part of East Asia. Their regional fossil diversity profiles during Pliocene, Pleistocene, and Early Holocene and extant distribution patterns of the primates are analyzed in this study. The results indicate that primate diversity reached the climax before the Early Holocene, which has unfortunately been shrunken gradually in the following Holocene, especially during the most recent Chinese history, so that many taxa are on the edger of extinction. That fossil age in Eastern and Central China is older than in Western China clarifies that, instead of from Africa, the modern human (*Homo sapiens*) evolved directly from *H. erectus* in the regions.

Keywords: Primate and human evolution in China; Human impacts on primates; Origin of modern humans

Introduction

Among the primates in China, fossil records of the earliest primitive primates unearthed in Hunan and Hubei provinces about 55 mya imply that prosimians originated in China [1-3]. That is more impressive considering numerous archaeological sites bearing primates and hominins have been found in China, including 103 for macaques (*Macaca*) alone, and more than 70 for hominins (*Homo erectus* and *H. sapiens*), and more than 1,000 for Palaeolithic cultural remains. As for the catarrhines, including Old World monkeys (Macaques and Colobines), and apes (gibbons and great apes), and archaic humans, their ancestors came from Africa during the Miocene, Pliocene, and the Early Pleistocene [4-8]. China has provided a unique mainland for their further evolutionary development in East and Southeast Asia through dispersion, speciation, and radiation, especially regarding early archaic human development involving *Homo erectus* and early *H. sapiens* [9-11]. In other words, China can provide one of the ideal regions in this globe to analyze the relationship between humans and nonhuman primates (primates thereafter), and clarify some controversial issues in their evolution, biodiversity, phylogeny, natural selection, and environmental adaptation [12-15].

Unfortunately, those studies have not been conclusively and integrally analyzed by focusing on primates and humans simultaneously. Thus, with fossil data of archaic humans and primates, and that of the extant primates, this study aims to explore the evolutionary coexistence between the two groups; identify when and how primate diversity has significantly changed, and clarify whether the modern human (*H. sapiens*) evolved from China proposed by different anthropologists. Such an effort is critically required to fully understand the evolutionary development and diversity changes of the catarrhines in East Asia.

Material and Methods

Fossil records are used to explore paleo-regional diversity disparity (Western, Central, and Eastern China). Since such records for the colobines and apes are scarce, those of the macaques found in the Pliocene, Pleistocene, and the Early Holocene, are used to represent paleo-diversity profiles of the primates in China. Database of the archaic humans (Pleistocene and Early Holocene) are utilized to study the scenarios of *Homo erectus* and *H. sapiens*. Fossil databases were collected from journal publications. Another database containing the extant primates (macaques, colobines, and gibbons) from Dr. Zhigang Jiang is used to illustrate China's contemporary primate diversity scenarios.

SPSS Version 20 are used to illustrate the regional diversity disparity of the primates and humans schematically.

Results

Primates

Fossil diversity profile (a proportion of the total recorded sites bearing *Macaca*) uncovered in China during the Pliocene,

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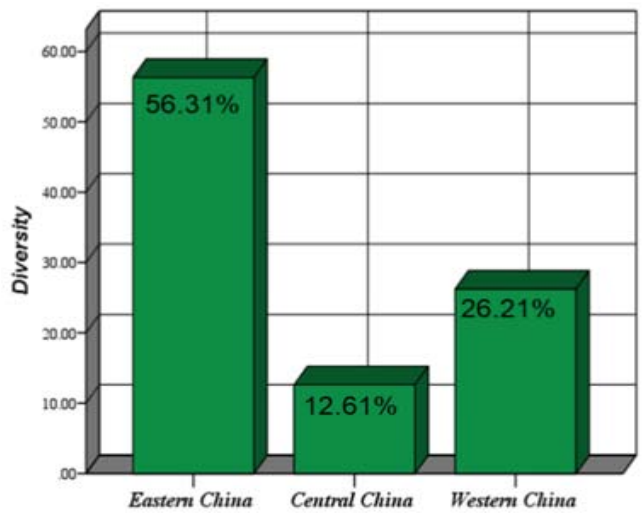

Figure 1: A diversity profile of fossil macaques uncovered in the Pliocene, Pleistocene, and early Holocene in China, based on the database from [62]. Eastern China: Hebei, Beijing, Liaoning, Shandong, Guangdong, Jiangsu, Guangxi, and Zhejiang; Central China: Hubei, Shanxi, Anhui, Shanxi, Henan, Shanxi and Anhui; and Western China: Inner Mongolia, Yunnan, Shaanxi, Sichuan, and Guizhou.

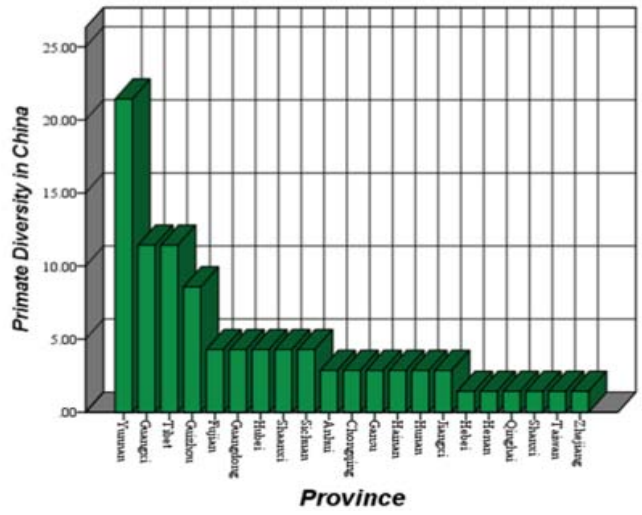

Figure 2: Extant primate diversity in China is progressively decreased from Western China, characterized by the plateaus and high mountains, to the coastlines in Eastern China.

Pleistocene, and the Early Holocene is illustrated in Figure 1. Eastern China maintained the highest diversity (56.31%), followed by Western China (26.2%). Central China had the lowest diversity (12.61%). Their current diversity profile is illustrated in Figure 2. It is clear that Western China, particularly Yunnan, Guangxi, Tibet, and Guizhou, maintain the most remarkable diversity, which is gradually diminished from Central to Eastern China.

Archaic humans

Their diversity patterns are presented in Figure 3. As for the *H. erectus*, its fossil locations are dominant in Western China. Central and Eastern China show about the same level. However, that of the *H. sapiens* is quite different - its diversity gradually decreases from

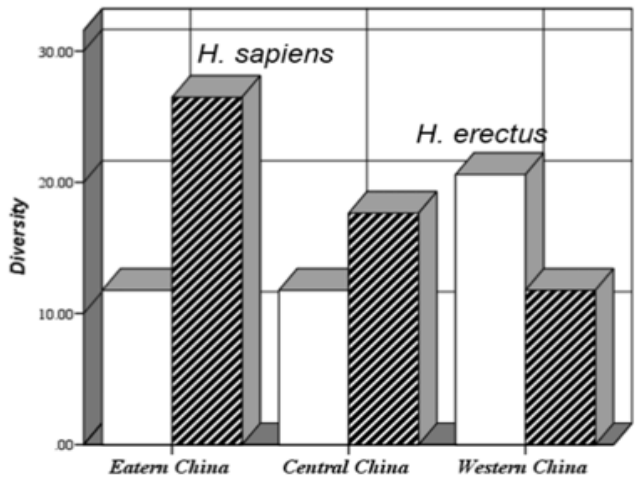

Figure 3: Archaic human diversity during the Pliocene, Pleistocene, and the Early Holocne in China, data from [52,55,63].

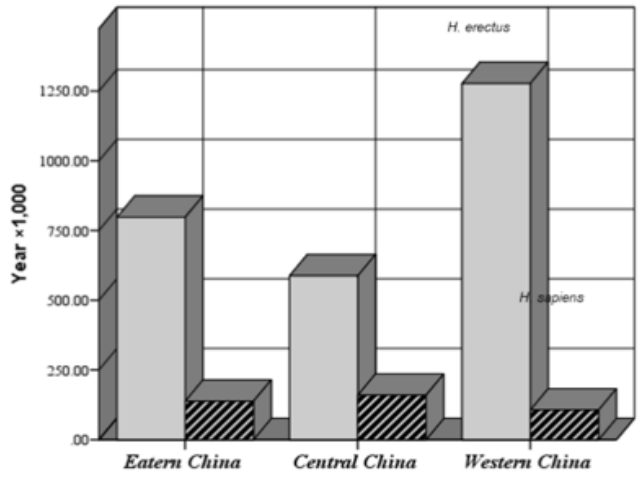

Figure 4: Age variation of the archaic humans in China, data from [52,55,63].

Eastern to Western China. Regional fossil age differentiation of the archaic *Homo* is provided in Figure 4. The age of the *H. erectus* in Western China is older than that in Eastern and Central China. As for the age of *H. sapiens*, Western China has the youngest fossils compared with the other two regions.

Discussion

Primate evolution

As for the Old World monkeys, macaques and colobines separated about 14 mya [4] or before ten mya [5] in Africa, then migrated through Eurasia to enter Western China at different times, based on which they completed further dispersion and radiation in East and Southeast Asia [6-8].

Macaques

According to [9], Mediterranean-Eurasia species, or ancestors of the Barbary macaques now living in northern Africa, started their long journey in the Miocene about 10 mya. They might have entered an area covering the southeast Qinghai-Tibet Plateau and Mts.

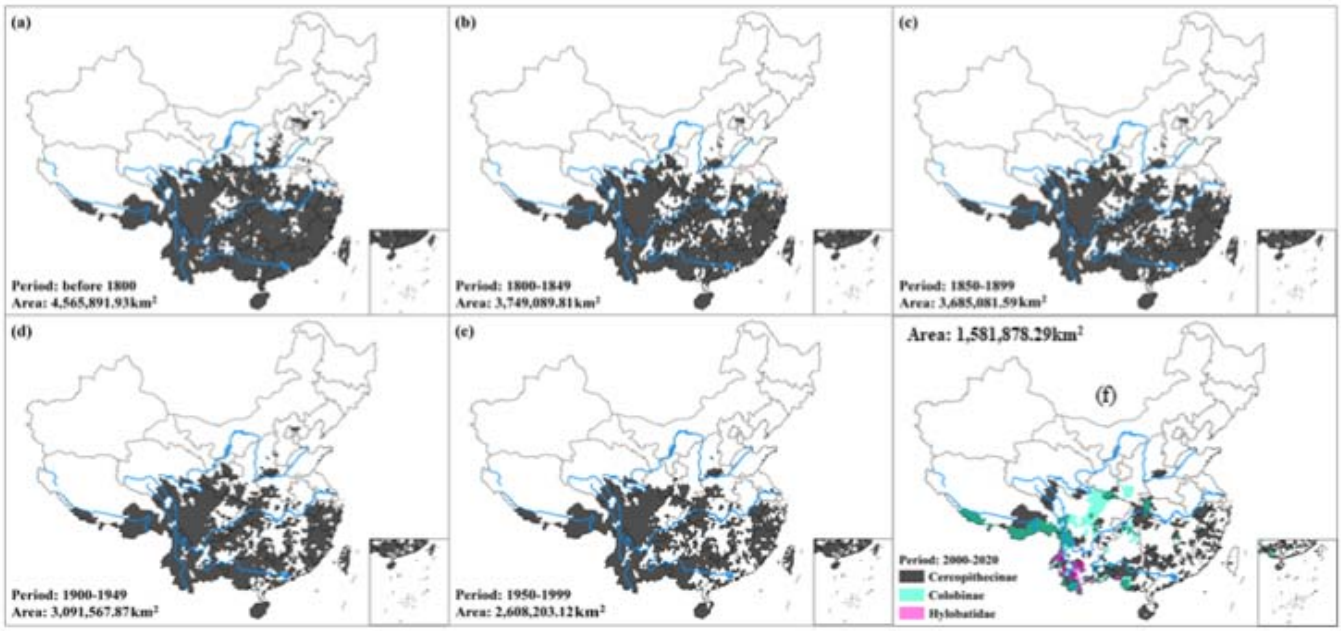

Figure 5: Historically reduced primate diversity in China since 1175, cited from [45] with permission.

Hengduan in China and northern Myanmar in the late Pliocene [8], then widely radiated in East and Southeast Asia, including Taiwan, Korea, and Japan. Nineteen species were derived in the same genus (*Macaca*) during the evolutionary development - eight of them are now allocated in mainland China and Twain, namely, *M. leonina*, *M. arctoides*, *M. assamensis*, *M. thibetana*, *M. mulatta*, *M. cyclopis*, *M. leucogenys*, and *M. munzala*, e.g. [8,10-14]. The related fossils have been found in China, South Korean, and Taiwan (*M. anderssoni*, *M. robusta*, and *M. jiangchuanensis*).

Colobines

The extant taxa in China include 12 species: *Pygathrix nemaeus* (extirpated recently), *Trachypithecus francoisi*, *Trachypithecus leucocephalus*, *Trachypithecus shortridgei*, *Trachypithecus crepusculus*, *Trachypithecus pileatus*, *Trachypithecus phayrei*, *Semnopithecus schistaceus*, *Rhinopithecus bieti*, *Rhinopithecus brelichi*, *Rhinopithecus roxellana*, and *Rhinopithecus strykeri* [14]. They may have reached Western China in the Late Miocene, e.g., [15]. The oldest colobine fossil record was *Mesopithecus* in Europe, western and eastern Asia [15-17]. A most recent proposition on the formation of Asian colobines was provided based on mt DAN evidence [18]: they approached East Asia in the Late Miocene, and some species radiated to alternative regions in Southeast Asia, such as the ancestors of the odd-nosed forms (*Rhinopithecus, Nasalis* and *Pygathrix*) and the langurs (*Trachypithecus*/*Presbytis* and *Semnopithecus*), leading to the extant taxa in Bangladesh, India, Burma, China, and Sundaland [7].

Apes

Apes in Eurasia appeared approximately 17 million years ago [19]. They may have arrived in Western China during the middle and late Miocene (12-6 mya) [20]. Fossil Asian great apes (*Pongo, Gigantopithecus*, and *Lufengpithecus*) and lesser apes (Hylobates) were unearthed in the late Miocene and Pleistocene in southern China [20-22]. The ancestors of the great apes include *Lufengpithecus* in the Late Miocene (12.0-6.0 mya) at five localities of Yunnan in Western China [20,23,24].

The distribution of great apes appears to retreat southward during the early Pleistocene, around 2.0 mya [25], followed by the shifts of lesser apes (Hylobates) that remained relatively abundant in the tropical zone in the Pleistocene. Such a significant shift was caused by climate change accelerated since the Late Pleistocene [26]. Despite their success for about 10 million years, the larger-bodied great apes *Lufengpithecus* taxa went extinct in China in the Late Miocene (6.0 mya). *Gigantopithecus* disappeared by the end of the Pleistocene, whereas gibbons, the smallest-bodied ape, survived in the southern subtropical zone through the Late Pleistocene and Holocene [27,28].

Given the incomplete nature of understanding ape fossil records in East Asia, their origin and dispersal patterns remain poorly understood [29]. The primary debate is whether gibbons and great apes are part of an ancient lineage, evolved in the middle Miocene in Africa (around 10 mya), or gibbons originated independently in Asia [30,31]. DNA evidence indicates that gibbons split from great apes before the African and Asian great ape divergence in Africa some 13.1 to 9.8 mya [29] or Eurasia between 14-16 ma [32,33]. Assuming a Eurasian origin for gibbons, they may have gotten into Western China in the late Miocene or early Pliocene. Gibbon-related fossils, such as *Dionypithecuss huangouensis* were found in Jiangsu in Eastern China, and *Laccopithecus robustus* in Lufeng, Yunnan in Western China, dated the Late Miocene [30]. They were regarded as being associated with the extant species, *Nomascus concolor*, in Southern China. Another fossil species (*Bunopithecus sericus*) found in Chongqing in Western China in the Pleistocene deposit is considered close to the extinct crown hylobatid and the one possibly representing a sister taxon to Hoolock [34]. Based on the studies of molecular data, it appears that gibbon radiation is relatively recent and rapid, either as a vicariant event or extremely fast radiation [35-37]. Some southeast

and western China regions, such as Yunnan, Jiangsu, Sichuan, Inner Magnolia, and Guangdong, Guangxi, and Hainan, appear to have played an essential role in gibbons' origins and dispersal [30,38-42].

What is illustrated in Figure 1 and 2 indicate that primates in China have experienced quite different evolutionary development before and after the Early Holocene. They reached every corner of mainland China and Taiwan, indicated by Eastern China's highest abundance (56.31%) in Figure 1. That Western China, where primates initiated the continental dispersion and radiation, does not show the highest diversity, must be associated with the violent tectonic movements of the region since the Late Miocene or Early Pliocene, particularly regarding the Qinghai-Tibet Plateaus and Yun-Gui Plateau [43] so that many animal fossils were buried during the uplift [44,45]. That Central China remains a minor proportion must be associated with the fact that the region had been remarkably impacted since the Late Pleistocene, following the appearance of archaic humans in the region [45] (please see below). Figure 2 presents the current primate diversity profiles in China; unlike Figure 1, it illustrates a gradually decreased diversity from Western to Eastern China, indicating that most of the populations/taxa in Eastern and Central China have disappeared, and Western China is the place remaining most of the taxa and populations. This phenomenon corresponds to what has been revealed based on available historical records: primate extirpation and geographic reduction in China appeared about 850 ago [45] (Figure 5). They started shrinking from north to south and from east to west, and a significant disappearance was accelerated since the second half of the last century (Figure 5e and 5f). So that more than 84.4% of gibbons' distribution has been lost [14,46]. Among 25 species of primates in China today, 80% are threatened. A modeling expectation indicates that the agricultural expansion to the end of this century could result in about 51 to 87% of China's primates disappeared by 2100 [14]. Thus, primates in China are primarily on the verge of extinction unless tangible conservation strategies and tactics and forceful managerial means must be implemented sooner rather than later.

Dreadful diversity reduction of the primates in China could have started about 50-70,000 years ago, caused by further extension and occupation of modern humans (*Homo sapiens*) [45]. Many archaeological records from Henan, Shanxi, Hubei, Chongqing, Zhejiang, Guizhou, and Guangxi indicate that early modern humans occupied continental China 50 or 100 kyr ago in Central and Eastern China [47,48]. Thus, the first measurable impact of modern humans on China's primates and other animals may begin some 7,000-9,000 years ago following more sophisticated tool technology [14,49,50]. Beginning about 2,000-3,000 years ago, China's first dynastic rulers resulted in significant changes to the landscape, deforestation due to increased human population size, followed by sizeable mammalian population extinction [51], particularly the shrunken gibbons' distribution areas [46].

Archiac Homan evolution

Chinese prehistory may have started about 2.12 mya at Shangcun, Lantian in Shaanxi province, considering the oldest Palaeolithic recognizable tools [52] or 1.36 or 1.7-1.6 mya in the Nihewan Basin, next to Beijing [53,54]. That indicates that tool-making early *Homo* had reached the area during the Later Pliocene or Early Pleistocene, 2.12 Ma [52].

What is presented in Figure 3 indicates that Western China shows the most remarkable diversity for *H. erectus*, which is quite different from the scenario of the primates represented by the macaques (Figure 1). That must be related to the fact that this species arrived in Western China about 2.12 mya, referring to Palaeolithic tools [52] or 1.36 or 1.7-1.6 mya based on the fossil records aforementioned [53,54]. That was much later than the macaques, colobines, and apes did. Thus, it is likely that fewer fossil sites of *H. erectus* were buried by the violent tectonic movement in Western China. In Yuanmou, Western China, Hominin species include the taxa of African *H. erectus* and *H. habilis*, dated about 1.9-1.66 ma. They were proposed to have used the stone artifacts made with Oldowan technology [55]. Their followed eastern and southern dispersions resulted in numerous hominin sites in China and other parts of Asia. Two are at Nihewan Basin and Zhoukoudian, Northern China, next to Beijing [56-58]. That explains why *H. erectus* in Western China is older than those found in the other two regions (Figure 4).

As for the appearance of modern humans (early *H. sapiens*) in China, there have been two hypotheses: 'Out of Africa,' implying that it first appeared in Africa, then migrated to Eastern Asia in the Late Pleistocene (126,000 ± 5,000 years ago). That is evidenced by their fossilized remains and cultural/technological inventory (stone tools) found in China (e.g., Yuanmou, Dali, Maba, Peking, etc.) and India (Narmada) [59]. Another hypothesis is multiregional development: modern humans in China and other parts of Southeast Asia were derived from regional *H. erectus*, which is supported by the evidence found in Dali in Shaanxi Provinces, Zhoukoudian, Daoxin in Hunan, Zhirendong in Guangxi, Yunxian in Hubei - they are located in Eastern and Central China [60]. Such a regional origin proposition can be backed up by the diversity profile illustrated in Fig.3, in which East China is prosperous with fossil *H. sapiens* than Central China. Western China, however, shows fewer fossil sites, which is different from the scenario of its ancestor (*H. erectus*) in the same figure. That matches what is illustrated in Figure 4 - the fossils of *H. sapiens* found in Eastern and Central China are older than those found in Western China. Another newly named human species, *Homo longi*, found in the Middle Pleistocene in Harbin City, Heilongjiang Province, is considered closely associated with *H. sapiens* in Central China [61]. Thus, what is provided in Figure 3 and 4 clarify the hypothesis that *H. sapiens* appeared in China came from the same continent.

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