БИОЛОГИЧЕСКАЯ АНТРОПОЛОГИЯ
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FOUNDATION AND FRONTIER – CENTENARY PATH OF DENTAL ANTHROPOLOGY IN CHINA

Introduction. *Dental anthropology has been developed for 100 years in China. In this paper, the author reviews the articles on dental anthropology related to Chinese materials in the past one hundred years and briefly introduces the issues involved such as human evolution, and the interaction of different populations in historical periods.*

Results and discussion. *The work of foreign scholars has been the foundation of Chinese paleoanthropology and dental anthropology since the discovery of the Hetao human teeth and the Zhoukoudian site. Since then, dental anthropology in China has gone through a phase of material accumulation, a phase of introducing the American ASUDAS in the 1990s, and a phase of prosperity in the last 30 years. The numerous discoveries and the application of new techniques have brought Chinese dental anthropology to an international level.*

Until now, there are more than 70 human fossil sites in China, over 60 of which contain human dental remains. Less material has been found from the early Pleistocene, and there is some controversy on whether they belong to the genus Homo. While early Middle Pleistocene Homo erectus teeth show primitiveness and some special features, the late Middle Pleistocene human teeth show greater variability, and mosaic features, and there is some controversy on whether some fossils belong to early Homo sapiens or other taxa. The Late Pleistocene human dentition is related to the question of how and when early modern human appeared in China and the evolution of early modern humans. However, due to the incompleteness of the material, the question of human origins is a matter of multidisciplinary and comprehensive interpretation.

About 10 sites were studied from Neolithic to modern human dentition using the American ASUDAS. These results show the consistency of non-metric traits in teeth and skulls, display differences between northern and southern Chinese populations, and reveal the exchange between northwestern chinese and western populations. Some of these results have been confirmed by paleogenomics.

Conclusion. *Anthropologists began to pay more attention to the morphology of modern human teeth. In the future, the application of new methods and the collection of modern human materials will help us better understand the evolution of ancient humans, population interaction.*

Keywords: Dental Anthropology; Human evolution; Pleistocene; diversity and mosaic evolution; China

Introduction

As a branch of physical anthropology, Dental Anthropology uses teeth of fossil, ancient and modern human, non-human primates as materials, through the study of morphological and metrical characteristics, teeth growth and development, wear patterns, and isotopic analysis to answer anthropological questions.

Dental anthropology in China has a unique path due to following reasons: Firstly, modern physical anthropology did not originate in China. The early research on physical anthropology was completely dominated by foreign researchers. Secondly, the frontier field of physical anthropology that under fastest-growing is Paleoanthropology which is rooted deeply in paleontology and geology, and these disciplines have an international cooperation environment from the very beginning. After the end of the Sino-Japanese War, anthropology in China went through a stage of recovery, during which many new materials were collected. China has also gradually formed its domestic research team. Benefiting from the rich fossil discoveries, archaeological findings, the application of new technologies, and efforts of several generations, nowadays this field has been developed rapidly in China and has reached a certain level in the world.

Dental Anthropology comes to its centenary in China this year. Now it is obligate to review this unique path of dental anthropology in China. In this paper, two basic aspects, morphology and metrics, are discussed within the view of human evolution.

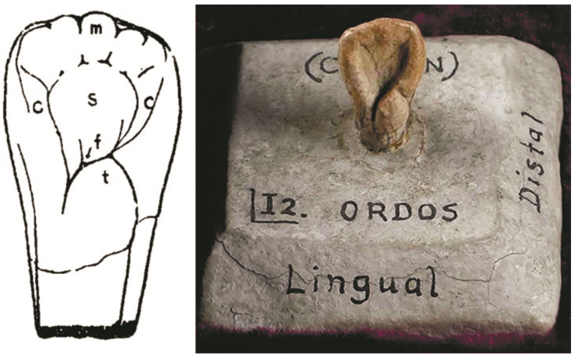

Figure 1. Lingual view of the "Ordos teeth" (Hetao Man) [Licent, 1926 and URL: http://www.uux.cn/viewnews-103782.html, Accessed: 20.10.2022
Рисунок 1. Лингвальный вид "зуб Ордоса" (человек Хэтао)

图 1. "鄂尔多斯牙齿"（河套人牙）舌侧面线图及模型。

Materials and methods

Foundation of Paleoanthropology in China (1920s–1940s)

The discovery of human fossil in China can be traced back to 1922 when French priest and naturalist Emilie Licent found an incisor of a child dated to the late Pleistocene by stratigraphy in Salawusu of Inner Mongolia. Canadian anatomist and anthropologist Davidson Black published the description of this tooth in 1926, named it as "the Ordos tooth" (Fig. 1) (Note: now also known as Hetao man), in which he described its morphology of "shovel-shape" in detail, and ever since it has been accepted as the earliest reliable record of human fossil in China [Licent, 1926].

In 1926, Johan Gunnar Andersson published two Middle Pleistocene hominin teeth discovered from 1921 to 1923 at Locality 1 in Zhoukoudian, Beijing [Wong, 1927]. In 1927, Davidson Black (Fig. 2) led an excavation in Zhoukoudian and he found a lower molar [Black, 1927], in 1929, Pei Wenzhong discovered the first skull of Sinanthropus "Peking Man" [Black, 1929]. The above events

Figure 2. Davidson Black (1884–1934) (URL: Davidson Black – Wikispecies (wikimedia.org), Accessed: 20.10.2022.
Рисунок 2. Дэвидсон Блэк (1884–1934)

图 2. 步达生（1884-1934）

signify the birth of Paleoanthropology in China [Du, 2013]. (Note: D. Black firstly named it *Sinanthropus pekinensis*, and after that, it has been given a popular name "Peking Man", now mostly we use "*Homo erectus pekinensis*" or "Zhoukoudian *Homo erectus*", in this paper, we use the abbreviation ZKD in the following paragraph, to represent these materials.) These numerous specimens unearthed in the Zhoukoudian, represent the most abundant hominin material in China and even East Asia. The discovery of Zhoukoudian has established the evolutionary status of *Homo erectus*. Among them, human teeth fossils are rich materials.

German anthropologist Franz Weidenreich (Fig. 3) led the research of ZKD after Davidson Black, in the following years he published several monographs related to the physical characters of ZKD fossils, including odontological studies. From a very detailed description and comparison of a great number (147) of Peking Man's teeth, he concluded that these teeth were not "specialized", they do represent a transitional type between modern human and our ancient ancestors, especially, some characters in skulls and teeth such as "shovel-shaped" incisor implied close link with modern mongoloid [Weidenreich, 1937].

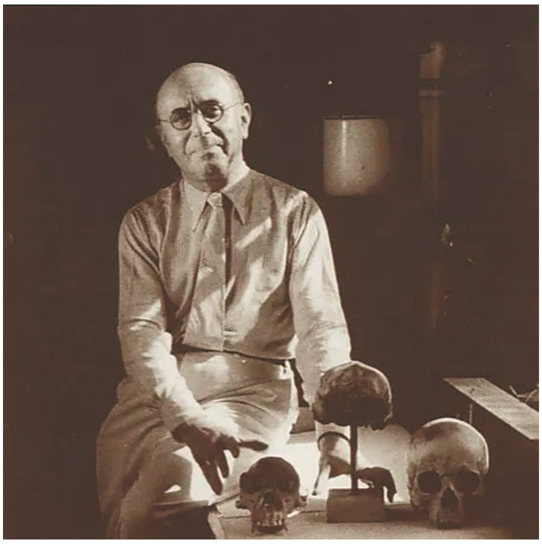

Figure 3. Franz Weidenreich (1873–1948) (URL: https://alchetron.com/Franz-Weidenreich, Accessed: 20.10.2022.
Рисунок 3. Франц Вейденрейх (1873–1948)

图 3．魏敦瑞（1873-1948）

Unfortunately, most of ZKD fossils were lost during the Pacific War. There are still a small number of specimens and models preserved, and research reports for reference. In particular, the work represented by Franz Weidenreich provides an example of paleoanthropology in China and even worldwide. Before the founding of the People's Republic of China, foreigners had been leading the research, and most articles were published in geological journals in English. At that time there were no Chinese who studied human fossil in China.

Accumulation of new materials (1950s–1980s)

After the founding of New China, anthropology experienced a prosperous period of development. During the 1950s to 1980s, a large number of paleolithic sites were discovered that contain human fossils, and rich archaeological materials were accumulated [Wu, 1999]. Some scholars also collected data on modern human teeth.

Under the guidance of anthropologist Wu Rukang (Fig. 4) (Note: Wu Rukang (1916–2006) the first Chinese paleoanthropologist who studied human fossils), a team of paleoanthropologists restarted the excavation in Zhoukoudian in the 1950s and rediscovered the remains of *H. erectus*, including five teeth [Woo et al., 1954: Wu, Jia, 1954; Wu, Zhao, 1959]. Liujiang skull was published in 1959 [Wu, 1959]. Lantian mandibles [Woo, 1964] and Yuanmou teeth [Hu, 1973; Zhou, Hu, 1979] were discovered in the 1960s. Xindong tooth was discov-

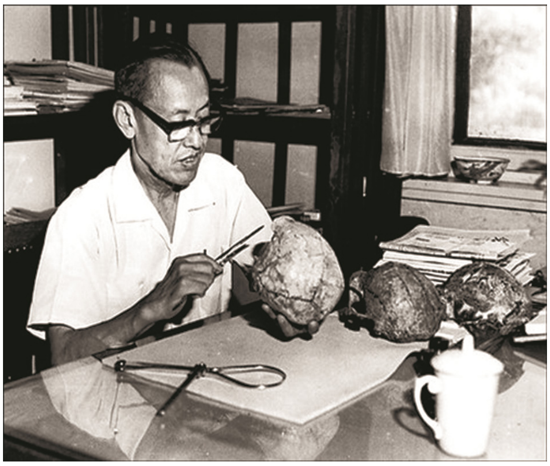

Figure 4. Wu Rukang (1916–2006) (URL: https://news.dmu.edu.cn/info/1033/10252.htm, Accessed: 20.10.2022.
Рисунок 4. У. Жуканг (1916–2006)

图 4．吴汝康（1916-2006）

ered at Locality 4 in Zhoukoudian in the 1970s [Gu, 1978], and other important fossils from Hexian [Wu, Dong, 1980; Huang et al., 1982], Yunxian [Wu, Dong, 1980], Xujiayao [Wu, 1980], Xichuan [Wu, 1982], Tongzi [Wu, 1984], Chaoxian [Xu et al., 1986] Yiyuan [Lv Zun'e et al., 1989], etc. were published in the 1980s.

Dental anthropology has been developed in China for decades, but it has not exceeded Weidenreich's method, and the conclusions of separately published reports of fossils are mostly descriptive and conjectural. We can see from the subsequent studies in the following decades, that Chinese paleoanthropologists used Weidenreich's work as a sample to describe the specimens. However, the accumulated large amount of fossil materials provided vital basics for the later research of human evolution.

For the historical materials, there was study of teeth unearthed in Anyang of Yin Dynasty [Mao, Yan, 1959], and the research on skulls unearthed from Yin Xu in Anyang also includes odontological content [Yang, 1985]. However, the dental research conducted by archaeologists was focused on pathological aspects such as dental caries.

Regarding the research on modern human, dentists represented by Wang Huiyun collected more than 150,000 teeth during the 1950s to 1960s and made statistics on the dental size measurement and morphological variation [Wang, 1965]. The measurements are widely adopted by anthropologists. In addition, the morphological observation of teeth has been noticed in anthropometrics. For example, the "Anthropometric Handbook" edited by Shao Xiangqing from Fudan University in the 1980s briefly recorded the anatomical characteristics of teeth and some non-metric traits, such as shovel-shaped incisors, Carabellis' cusp, groove type of molars, etc. [Shao, 1985].

Wei Boyuan summed up dental anthropology in 1987: Compared with paleo-odontology, there is limited research on modern teeth in China. For example, compared with foreign countries, we have almost no research on teeth calcification, sex differences, and phenotype expression on teeth, only a few studies focus on the relationship between wear and age [Woo, 1965], the relationship between the pulp cavity and age, differences of teeth in different populations, and individual level [Wei, 1983, 1984, 1987].

Zhu Hong [Zhu, 1990; Zhu et al., 1993] has made the first measurements and observations of human teeth excavated from historical archaeological sites, with materials from Xia dynasty in Shanxi and Neolithic site (Miaozigou) in Inner Mongolia. The observation and measurement methods are from Wang Huiyun and Shao Xiangqing, and the observed non-metric traits are few, the conclusions were merely statistical because no other materials are available for comparison.

Adoption of American ASUDAS

In the 1990s, the American school of dental anthropology ASUDAS (Arizona State University Dental Anthropology System) was introduced to China. After studying non-metric traits of human teeth of East Asian populations, Turner proposed that the teeth of these groups (Mongoloid), can be divided into two types, Sundadont and Sinodont [Turner, 1987, 1989, 1990]. Eight traits differ significantly between the two groups: Shovel-shaped and double-shoveling incisor, one rooted upper first premolar, enamel extensions on upper first molar, missing-pegged-reduced upper third molar, deflecting wrinkles on lower first molar, and three rooted lower first molar are more common in Sinodont, while the four-cusped lower second molar has a lower frequency.

Sundadonty is more conservative, typified by trait retention rather than elaboration, while Sinodonty is more intensified and specialized. Sundadonty was firstly formed in Southeast Asia, and during the process of spreading in the late Paleolithic, a population with Sinodonty in Northeast Asia was formed. This is Turner's "Sundadonty hypothesis of the origin of modern humans in northeast Asia" [Turner, 1997].

However, Chinese anthropologists Han Kangxin and Pan Qifeng [1984] argued that similarities between neolithic populations in northern and southern China, were related to the similar natural environment and these southern physical characteristics were remnants of the transition to modern humans and were the result of microevolution but not migration. Yang Ximei [1985] suggested that whether Turner's hypothesis can be supported by fossil evidence, would require more materials from the late Paleolithic and Neolithic.

Zhang Zhenbiao [1993] began to use Turner's method to study the morphological variation of human teeth from the Bronze Age in Changyang and the Northern Wei Dynasty in Datong. Concordance was found by comparing non-metric traits of skulls and teeth, implying the teeth, like skulls, can be used to analyze biological relationships in populations. The dentition of Changyang and Datong belong to Sinodont, but the Changyang group has some characteristics of Sundadont. This is consistent with Hanihara's [1990] view that Sinodonty and Sundadonty have some overlap.

Liu Wu [Liu, 1995; Liu, Zhu, 1995] studied dental morphology of skeletal human remains from two Neolithic sites from Miaozigou and Xiawanggang, the results verified Turner's classification of Sundadont and Sundadont, which are indeed reflected in Chinese materials. Miaozigou and Xiawanggang groups are similar to the group of Bronze Age Anyang Yinxu in northeastern Asia but quite different from those in Southeast Asia. Liu Wu and Zeng Xianglong [1996] studied the morphological characteristics of human teeth from the Warring States Period in Longxian, Shaanxi Province, and believed that this group is similar to the modern North population with typical Mongoloid characteristics.

Liu Wu [1997] compared morphological traits of fossil and modern teeth from China, and concluded that 7 non-metric traits can be traced back to the *Homo erectus*, they represent the continuity of human evolution in China, because these traits maintained a high frequency through the early *Homo sapiens*, to modern Mongoloid. These features are shovel-shaped incisor, double-shoveling incisor, interruption groove in upper incisor, deflecting wrinkles on lower molar, three-rooted lower first molar, 5-cusped lower second molar, and degenerated third molar. Wu Xinzhi [1998] believed that the continuity of these traits' frequency in China is strong evidence that can support the multi-regional origin theory of modern human. The author of present paper suggest that the Tomes' root may also contribute to the continuum features [Lin et al., 2019].

Li Fajun and Zhu Hong [2006] studied the Neolithic group of Jiangjialiang, from Yangyuan, Hebei province, and believed that this group belonged to Sinodonty. Compared with the groups from Miaozigou and Xiawanggang, Jiangjialiang and Miaozigou are consistent in both teeth and skull characteristics. The characteristics of the Neolithic group of the Liyudun in Guangdong Province are similar to Sundadonty, however the number of individuals selected for this study is small [Li et al., 2009].

Li Fajun and others [Li et al., 2008] studied the human teeth preserved in the tombs of the Ming and Qing dynasties in Tianjin. He suggested that the differences in teeth between the pre-Qin period and the modern population were indeed the result of microevolution. However, the reason and mechanism are still unclear. Li Fajun believes that the South China group and the Hong Kong group are on the dividing line between the above Sinodonty and Sundadonty types. More evidence is needed, especially the earlier human dental materials, which may help to draw a more detailly picture of this transitional area.

Besides the dental morphological differences between north and south China, some scholars have analyzed the population of northern Eurasian in recent years. For example, Han Kangxin [2019] in the monograph “Yanghai Cemetery in Xinjiang” reported that the Yanghai group has a simplified dental pattern, the occurrence rate of various features is similar to the western Eurasian population, and the morphological distance of many features is also the smallest with the western Eurasian population [Han, 2008, 2019]. A dental system similar to the Western Eurasian population emerged at least 3000 BP. Contemporaneous group from the Jilintai cemetery in Xinjiang is found to be closest to Yanghai group [Zhang, Zhu, 2013]. Jilintai group also shows interaction with other ancient surrounding populations.

Zhang Xu and others [Zhang et al., 2014] analyzed the non-metric traits of human teeth from the Bronze Age in the Liushui cemetery, Yutian County, Xinjiang province, the result revealed that the Liushui group has closer affinities to people from southern Siberia and the Black Sea area. Population migrations from the west to east can be traced back to as early as 3000 BP in southwestern Xinjiang. Recently, paleogenomics confirmed the exchange between Eastern and Western populations during the Bronze Age [Vikas et al., 2022]. This indicates the prospective and credibility of dental morphological studies.

In addition to permanent teeth, a small number of studies on deciduous teeth have revealed the same value in anthropological identification, and some traits on deciduous teeth are even more distinct [Liu, Wang, 1998; Lei, Chen, 2021]. In the future, hopefully there will be more studies on deciduous teeth.

Japanese scholars have collaborated with Chinese to explore the relationship between various ancient inhabitants of Japan and China from the perspective of dental anthropology, although many of questions remain unanswered, they can serve as an example of the international cooperation in dental anthropology [Zhang, 2008; Manabe, Rokoten, 2000, Manabe et al., 2003; Oyamada, Rokotenda, 2000]. At present, Chinese scholars have not collaborated with foreigners besides Japanese to conduct research using the American ASUDAS.

Nowadays Dental Anthropology in China
(In the perspective of human evolution)

(Note: In this section “Ma” and “ka” refer the geological time “million years ago” and “thousand years ago” separately)

In the last 30 years, anthropology has developed rapidly in China. In 1982, the Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences publicated the first issue of “Acta Anthropologica Sinica”. So far, human fossils have been unearthed in more than 70 sites in China, of which more than 60 contain teeth [Liu et al., 2014]. In many sites, there were no skulls or post-cranial bones preserved, but only teeth. Therefore, the study of dental anthropology is particularly important for revealing human evolution. Especially in the last decade, many discoveries have emerged one after another. A new generation of anthropologists has adopted new technologies such as geometric morphometry and high-resolution CT to explore the significance of the internal and external morphology of teeth in human evolution. In the following paragraphs, the main issues of human evolution related to dental anthropology, new research, and controversies of scientific opinion are briefly outlined.

Early Pleistocene

It has been generally accepted that the earliest representative of *Homo* in China is Yuanmou (1.7 Ma) [Zhu et al., 2008]. However, there are some earlier fossils still under debate. For example, whether the mandible with attached teeth fragment (2 Ma) from Longgupo belongs to genus *Homo* or *Lufengpithecus* [Huang, 1995; Schwartz, Tattersall, 1996; Wang, 1996; Wu, 2000; Etler et al., 2001; Etler, 2009]. The teeth from Longgu Cave of Jianshi, Hubei Province are believed to belong to *Australopithecus* or *Meganthropus*, and some scholars believe that they do not exceed the variation range of *Homo erectus* in China (2.42-1.80Ma in the early Early Pleistocene) [Gao, 1975; Liu et al., 2010]. In any case, according to archaeological evidence, stone artifacts dated to 2.12 Ma were found in China [Zhu et al., 2018], even earlier than the Dmanisi site in Georgia, so there were indeed human activities in China before Yuanmou.

Middle Pleistocene

Weidenreich gave the following description of dental materials of ZKD, these features are considered to be characteristic of typical *Homo erectus* in China: Upper central Incisors are shovel-shaped and have strongly developed basal tubercle (tuberculum dentale) with finger-like prolongations. Upper canines have complicated lingual surfaces. Premolars are asymmetrical, especially the upper first premolar, buccal surface of premolar projects with vertical grooves. Transverse crests with accessory ridges are present on the occlusal surface of premolar. Most lower molars have the pattern of Dryopithecus Y5-Y6, and some have deflecting wrinkles. All teeth roots are robust, especially in lower molars, so-called “taurodontism” etc [Weidenreich, 1937].

So far, 17 sites of *Homo erectus* fossils have been found in China [Liu et al., 2014; Zhao et al., 2018]. Liu Wu believes that some of these (Yuanmou (Fig. 5 a, b), Yunxian, Hexian (Fig. 5 i, j, k, l, o)) are more primitive than the morphology of Zhoukoudian and can be treated as a more primitive type of *Homo erectus*, while others have similar morphological patterns and have been classified as typical *Homo erectus*, such as Xichuan (Fig. 5 g, h), Yiyuan [Liu et al., 2015b].

Liu Wu studied the expression of Carabelli’s cusp in Chinese hominins on enamel and EDJ surface (Fig. 5 m,n). The result shows that the Carabelli’s cusp present in Chinese hominins with a high frequency (27.6%~62.5%), could be a remnant or primitive feature. Especially, Chimpanzees and African early hominins usually have a cingulum-protocone crest and lingual horizontal groove called “shelf-like Carabelli’s cusp”, which is also present in some Chinese hominins (Fig. 5 n) [Liu et al., 2018].

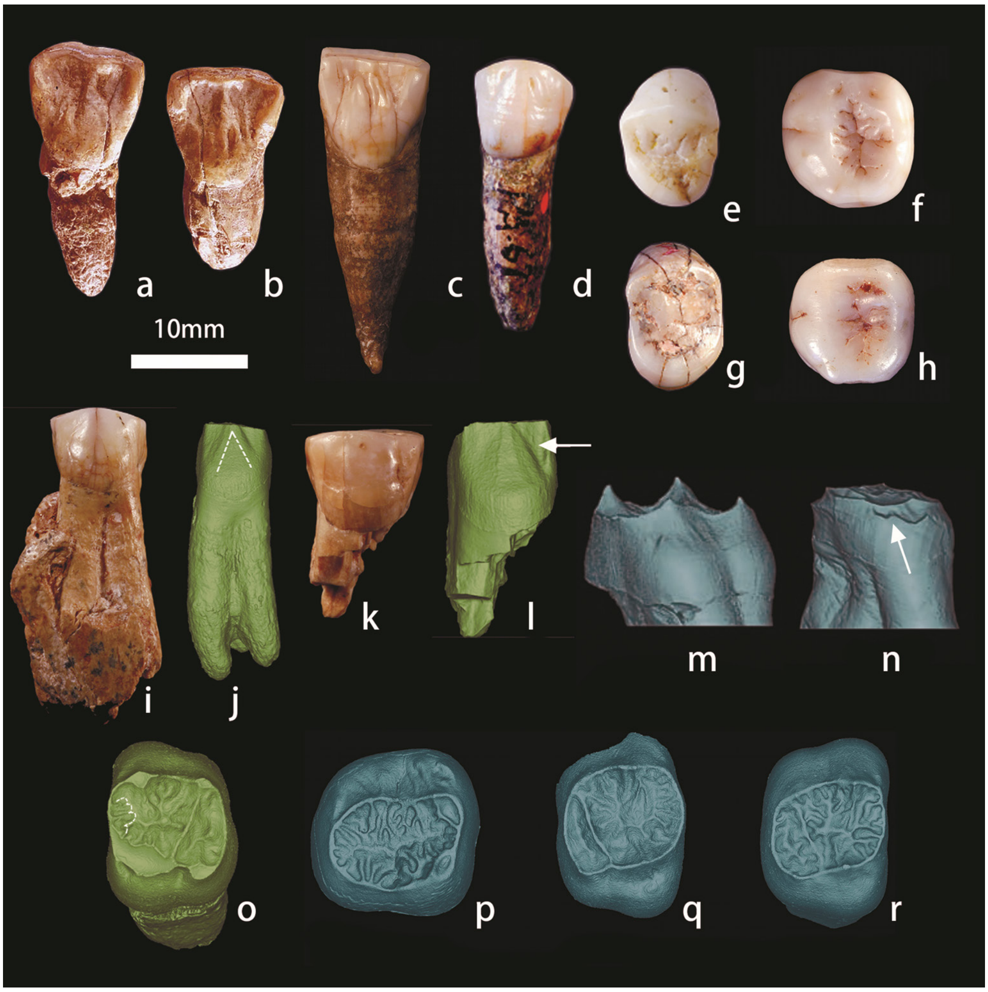

*Figure 5. Fossil teeth from earlier-Middle Pleistocene and early period of Pleistocene (Yuanmou: **a** – right upper I1, **b** – left upper I1; ZKD: **c** – left upper I1; **e,d** – right upper P1, **f** – left lower M2 ; Xichuan: **g** – left upper P2, **h** – left lower M2; Hexian: **i,j** – right upper P1 and EDJ; **k,l** – left upper P1 and EDJ, **o** – EDJ of left upper M1 (dotted line indicate trangular swelling, arrow indicate the vertical groove); Yunxian, **m** – left upper M1, Jianshi, **n** – left upper M1, Carabelli's cusp in EDJ level, arrow indicate the "shelf-like Carabelli's cusp" and "cingulum-protocone crest"); Dendrite-like EDJ, ZKD **p** – left lower M2, Hexian **q** – right upper M2, Yiyuan **r** – right upper M1) (Modified from the articles mentioned above)*

*Рисунок 5. Ископаемые зубы из раннего средне-плейстоцена и раннего плейстоцена (Юаньмоу: **a** – правый верхний I1, **b** – левый верхний I1; Чжоукоудянь: **c** – левый верхний I1, **e,d** – правый верхний P1, **f** – левый нижний M2 ; Сичуань: **g** – левый верхний P2, **h** – левый нижний M2; Хэсянь: **i,j** – правый верхний P1 и EDJ; **k,l** – левый верхний P1 и EDJ, **o** – левый верхний M1 EDJ (пунктирная линия указывает на трангулярную припухлость, стрелка указывает на вертикальную борозду); Юньсянь: **m** – левый верхний M1; Цзяньши: **n** – левый верхний M1, бугорок Карабелли на уровне EDJ, стрелкой указаны "бугорок Карабелли типа ласточкино гнездо" и "цингулюм-протоконусный гребень"); дендритная структура EDJ, ZKD **p** – левый нижний M2, Хэсянь: **q** – правый верхний M2, Июань **r** – правый верхний M1) (Изменено из статей, указанных выше)*

图 5. 早更新世和中更新世早期的人类牙齿化石 (元谋: a 右上 I1, b 左上 I1; 周口店: c 左上 I1, e,d 右上 P1, f 左下M2 ; 淅川: g 左上P2, h 左下M2; 和县 i,j 右上 P1 和 EDJ, k,l 左上 P1 和 EDJ ,o 左上 M1 EDJ (虚线处为三角形隆起，箭头示意垂直沟); 郧县, m 左上 M1, 建始, n 左上 M1, 在 EDJ 水平的卡式尖，箭头所指为屋檐状卡式尖和齿带原尖脊结构); 雪花状 EDJ, ZKD p 左下 M2, 和县 q 右上 M2, 沂源 r 右上 M1) (根据以上文献修改而成)

The EDJ surface of earlier-Middle Pleistocene hominins is primitive presented by complicated furrows, ridges, and accessory cusps, and in particular a vertical groove on the buccal side of both lower and upper premolars. the occlusal EDJ surface is highly crenulated, so-called ‘dendrite-like’ EDJ (Fig. 5 p, q, r), and some researchers suggest this may be a derived feature specific to earlier-Middle Pleistocene East Asian because only found in Chinese materials [Xing et al., 2015a, 2016, Song, 2018, 2019; Liu et al., 2019].

Hominins in later-Middle Pleistocene were previously known as early *Homo sapiens*, now called archaic *Homo sapiens*, representative fossils include Chaoxian (Fig. 6 a, b), Panxian Dadong (Fig. 6 e, f), Xujiayao (Fig. 6 g, h, i), Tongzi (Fig. 6 d), Jinniushan, and Changyang (Fig. 6 c). Previously, these teeth have been described as smaller in size and less complicated. However, recent findings reveal that the morphological variability of this group is greater than *Homo erectus*. For example, Xujiayao presents a mosaic pattern [Xing et al., 2015b], Chaoxian has more primitive traits with large dental size [Bailey, Liu, 2010], Panxian Dadong presents more derived traits, and some teeth have modern contour and smaller size, although the upper central incisor is still primitive with basal tubercle, finger-like projections and strong shove shape (Fig. 6 e, f) [Liu et al., 2013]. Tongzi upper first premolar has a similar contour to late Pleistocene members (Fig. 6 d) [Song et al., 2019]. Some believe that these mosaic features are the result of continuous evolution, and diversity is the consequence of interactions of populations and complex natural environments [Liu et al., 2019; Liu, Wu, 2022]. With new discoveries of Denisovan’s mandible (Fig. 6 j) and DNA trace in Xiahe on the Tibetan Plateau, [Chen et al., 2019; Zhang et al., 2020], some believe that there are still Denisovans among the fossils that have been found in China [Bergström et al., 2021]. Ni Xijun comments that the connection between the mandible of Xiahe and the Denisovans of Altai is not clear, because among the six collagen sequences extracted from Xiahe mandible for systematic analysis, only one locus of Single Amino Acid Polymorphism (SAP) is consistent with the Denisovans, and this locus became key evidence to support the connection, but there is another locus in the Xiahe mandible that is not present in Denisovans [Ni, 2022]. According to Liu Wu, Xiahe mandible and teeth do not have morphological expressions that distinguish them from other Middle Pleistocene hominins in China [Liu, Wu, 2022]. Teeth Xiahe are similar to Penghu (Fig. 6 k) due to the complex morphology of the crown,such as protostylid at EDJ level of lower M2 and the robust roots [Chen et al., 2019; Liu et al., 2022].

Ni Xijun named a new taxa *Homo longi* by a fossil skull found in Haerbin (Fig. 6 l) [Ji et al., 2021; Shao et al., 2021; Ni et al., 2021], and he proposed a hypothesis of multi-directional “shuttle dispersal model” for the evolution of *Homo* by phylogenetic and biogeographic analyses, which present the Jinjiushan, Hualongdong, Dali, Xiahe, and *Homo Longi* belong to a monophyletic group and have been separated with Homo sapiens around 948.73ka. Liu Wu propose that, it may be a proper way to treat the late Middle Pleistocene hominin fossils with combined or mosaic morphological features as uncleared taxa before totally understand their morphological diversities [Liu, Wu, 2022].

From the metric point of view, the overall evolutionary trend is the size of teeth decreases from *Homo erectus* to modern humans. The total dental area of *Homo erectus* (ZKD) is 1632.3 mm^2, which decreased to 1282.8 mm^2 in the late *Homo sapiens* (or early modern human), and the average total dental area of modern Chinese is 1210.0 mm^2 [Liu, Yang, 1999].

Liu Wu [Liu et al., 2015b] explained that the large variation in teeth size of *Homo erectus* in China may be related to complex evolutionary processes such as isolation. Zhang Yinyun [1986, 1999; Zhang, Liu, 2002] discussed the coincidence of *Homo erectus* and archaic (early) *Homo sapiens* with chronological data, and he found that it is difficult to distinguish *Homo erectus* and archaic (early) *Homo sapiens* except for the size of the buccal-lingual diameter of the central incisors. Therefore, some scholars support the classification *of Homo erectus* and *Homo sapiens* as one species [Kramer, 1993; Wolpoff et al., 1994; Tobias, 1995], but others have objections. The key to this question is that if archaic (or early) *Homo sapiens* in East Asia is represented by Denisovans or *Homo longi*, then it is not reasonable to simply compare the sizes of all fossil teeth and depict a trend of decreasing teeth size in a linear pattern.

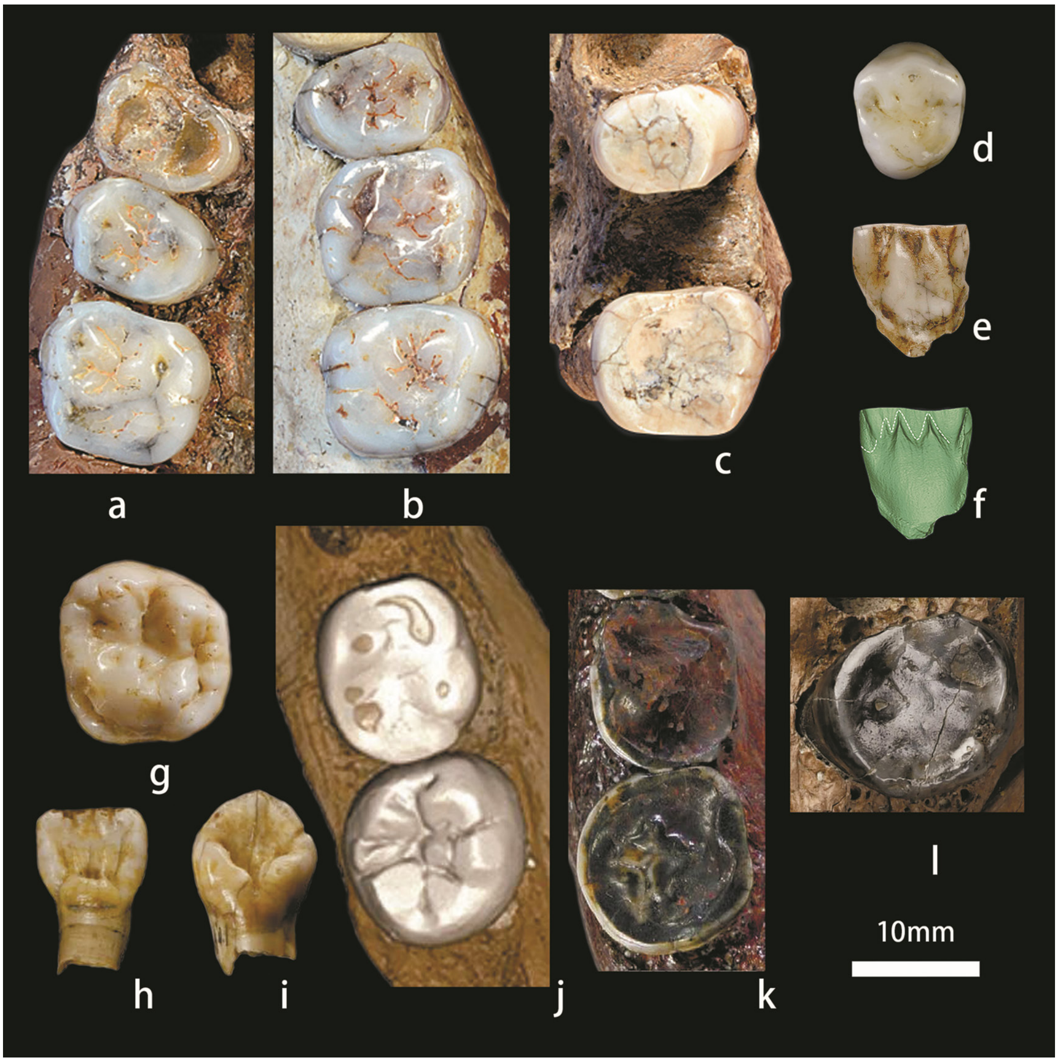

*Figure 6. Fossil teeth from late-Middle Pleistocene (Chaoxian: **a –** right upper P1-M1, **b –** left upper P2-M2; Changyang: **c –** left upper P1, M1 ; Tongzi: **d** – left upper P1 ; Panxian Dadong: **e** – right upper I1, **f –** EDJ ; Xujiayao: **g –** left upper M1, **h** – left upper I1, **l –** left upper C ; Xiahe: **j –** right lower M1-2; Penghu: **k** – right lower M1-2; Homo longi: **l –** left upper M2) (Modified from the articles mentioned above)*

*Рисунок 6. Ископаемые зубы из позднего средне-плейстоцена (Чаосянь: **a –** верхний правый P1-M1, **b** – левый верхний P2-M2; Чанъян: **c** – левый верхний P1, M1; Тунцзы: **d** – левый верхний P1; Паньсянь Да Дун: **e** – правый верхний I1, **f** – EDJ ; Сюйцзяяо: **g** – левый верхний M1, **h** – левый верхний I1, **i** – левый верхний C ; Сяхэ: **j** – правый нижний M1-2; Пэнху: **k** – правый нижний M1-2; Homo longi: **l** – левый верхний M2)(Изменено из статей, указанных выше)*

图 6. 中更新世晚期的人类牙齿化石 (巢县, a 右上 P1-M1 b 左上 P2-M2; 长阳 c 左上 P1, M1 ; 桐梓 d 左上 P1 ; 盘县大洞 e 右上 I1 f EDJ ; 许家窑 g 左上 M1 h 左上 I1 i 左上 C ; 夏河 j 右下 M1-2; 澎湖 k 右下 M1-2; *Homo longi* l 左上 M2)(根据以上文献修改而成)

Late Pleistocene

Human fossils from the late Pleistocene are vital key to understand the origin of modern human, the two main hypotheses “multiregional origin” and “Recent African Origin” have been debated for more than 30 years. Fossil maxilla with teeth from Israel (Misliya-1) which dated 177–194 ka has challenged the time of the first wave of *H. sapiens* out of Africa which is supposed by genetics [Hershkovitz et al., 2018].

Similarly, modern feature also observed in Chinese materials, the "double-shoveling" upper incisor from Huanglongdong (Fig. 7 a, b) represent the earliest record (81–101ka), this trait has not been observed in other fossil hominin except *Homo sapiens*. A good number of modern teeth have been unearthed in several sites, with a chronological frame of more than 100ka, such sites include Daoxian (Fig. 7 c–j) [Liu et al, 2015a], Bijie Mawokou (Fig. 7 k–o) [Zhao et al, 2016], Guangxi

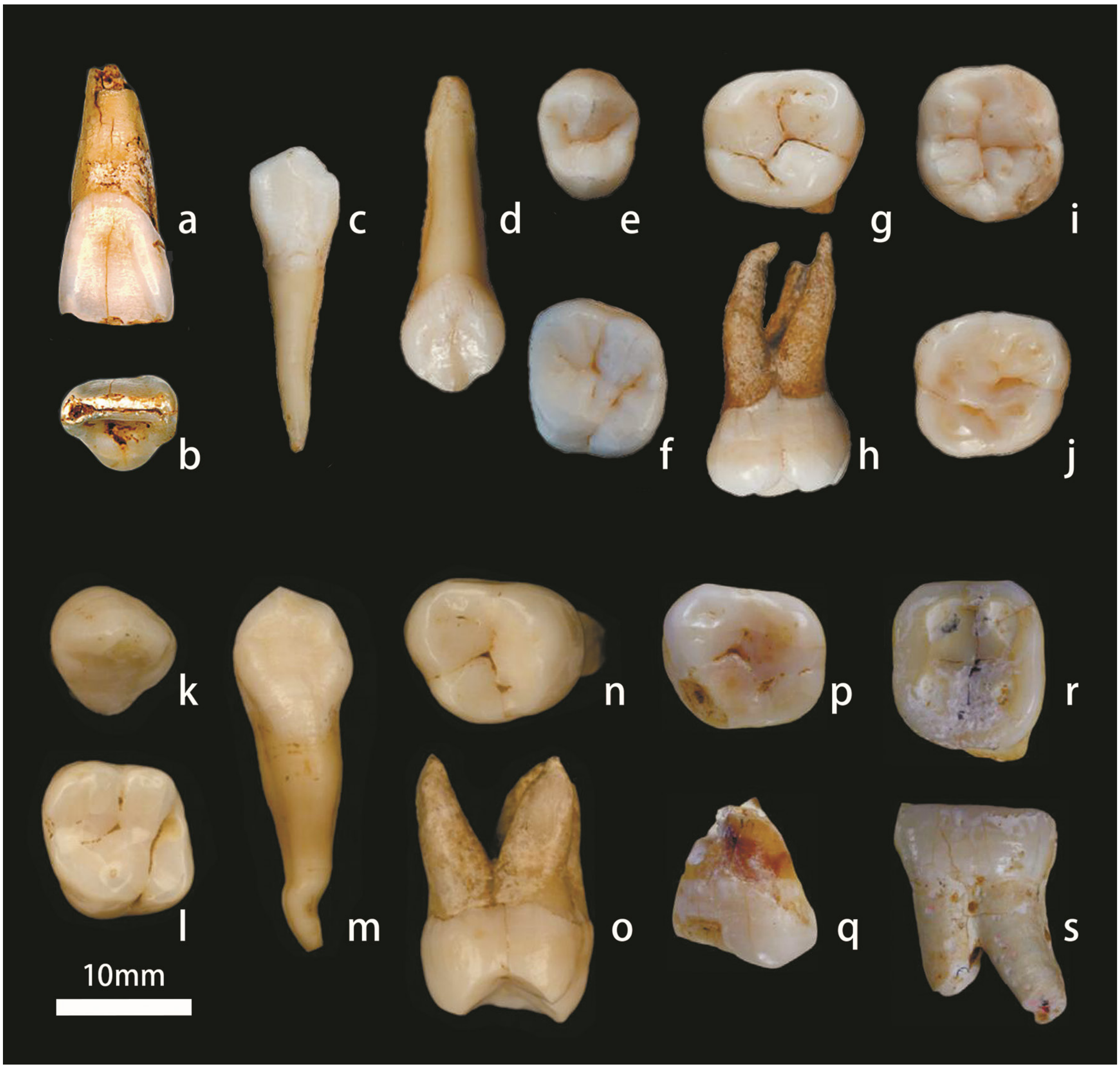

*Figure 7. Fossil teeth from late Pleistocene (Huanglongdong: **a, b** – right upper I1; Daoxian: **c** – right lower C, **d** – right upper C, **e** – left upper P1, **f** – left upper M1, **g, h** – left upper M2, **i** – right lower M3, **j** – left upper M1; Mawokou: **k, m** – left upper C, **l** – left upper M1, **n, o** – right upper M2; Luna cave: **p, q** – left upper M2, **r, s** – right lower M2) (Modified from the articles mentioned above)*

*Рисунок 7. Ископаемые зубы из позднего плейстоцена (Хуанлун Дун: **a, b** – правый верхний I1; Даосянь: **c** – правый нижний C, **d** – правый верхний C, **e** – левый верхний P1, **f** – левый верхний M1, **g, h** – левый верхний M2, **i** – правый нижний M3, **j** – левый верхний M1; Мавокоу Дун: **k, m** – левый верхний C, **l** – левый верхний M1, **n, o** – правый верхний M2; Лу На Дун: **p, q** – левый верхний M2, **r, s** – правый нижний M2). (Изменено из статей, указанных выше)*

图 7. 晚更新世的人类牙齿化石(黄龙洞 a b 右上 I1; 道县 c 右下 C, d 右上 C, e 左上 P1, f 左上 M1, g h 左上 M2, i 右下 M3, j 左上 M1; 麻窝口洞 k m 左上 C, l 左上 M1, n o 右上 M2; 陆那洞, p q 左上 M2, r s 右下 M2)(根据以上文献修改而成)

Luna cave (Fig. 7 p–s) [Bae et al., 2014]. Some researchers believe these teeth with modern morphology proved that *H. sapiens* appeared in China long before the “out of Africa” theory, therefore according to the above, the morphological continuity of fossils from different periods, should support the “multiregional origin with hybridization” theory. However, scholars who disagree, argue that this is the result of human migration rather than continuous evolution [Denell, 2010; Véronique et al., 2016]. Some scholars doubt that the dating of human teeth is not accurate due to the complicated geological deposition in the karst cave [Sun et al., 2019].

More interestingly, scientists found not only modern teeth in the early period but also primitive teeth in the late period. For example, the teeth of Dushan cave from Guangxi province [Liao et al., 2019] (15Ka) have large dental size and various primitive features such as “crown buccal vertical groove complex”, which are different from most of the early modern human (Fig. 8). The author called Dushan fossil "atypical *Homo sapiens*" and offered two explanations. First, this reflects a high degree of regional variation, or these mosaic and primitive features may be the result of introgression from late-surviving archaic population.

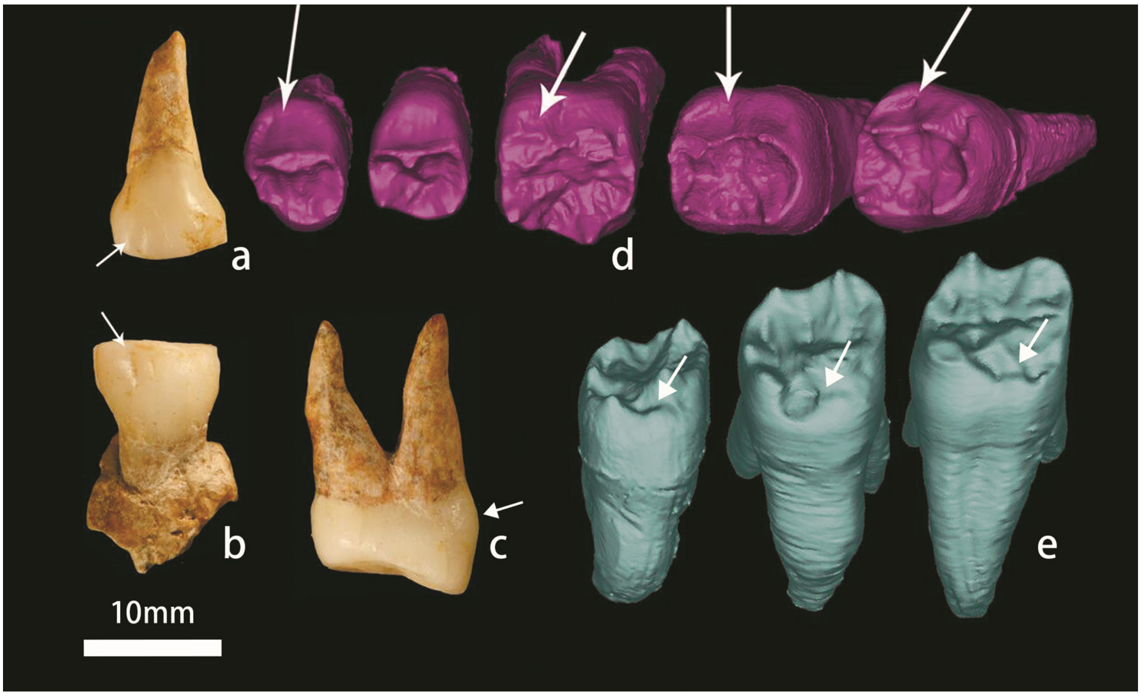

*Figure 8. Fossil teeth of atypical Homo sapiens from Dushan (**a** – right upper P2, **b** – left lower P1, **c** – right upper P1, arrows indicate buccal vertical groove and basal bulging; **d** – EDJ surface of lower dentition P1-M3, arrows indicate buccal vertical groove and cingulum-like protostylid; **e** – EDJ surface of upper dentition M1-M3, arrows indicate cingulum-like carabelli’s cusps) (Modified from the articles mentioned above)*

*Рисунок 8. Ископаемые зубы атипичного Homo sapiens из Душана (**a** – правый верхний P2, **b** – левый нижний P1, **c** – правый верхний P1, стрелками указаны вестибулярня вертикальная борозда и базальная выпуклость; **d** – EDJ поверхность нижних P1-M3, стрелками указаны буккальная вертикальная борозда и цингулоподобный протостилид; **e** – EDJ поверхность верхних M1-M3, стрелками указаны цингулоподобные бугорки Карабелли). (Изменено из статей, указанных выше)*

图 8 独山洞非典型智人牙齿化石 (a 右上 P2, b 左下 P1, c 右上 P1，箭头所指颊侧垂直沟与基底部隆起; d 下齿列 P1-M3 的 EDJ 结构，箭头所指颊侧垂直沟与齿带状原副尖； e 上齿列 M1-M3 EDJ 结构，箭头所指为齿带状卡式尖) (根据以上文献修改而成)

The Maludong skull (MZR) from Yunnan which is dated at 14,5–11,5 ka has a mixture of modern and primitive features, which may represent a late-surviving archaic population, or prior dispersal into Eurasia from Africa than modern humans [Curnoe et al., 2012; Xueping et al., 2013]. Recent paleogenetic studies have shown that MZR represents diversified modern humans who are closely related to the ancestry that formed the first native Americans [Xiaoming et al., 2022]. The paleogenetic data present the connection between modern DNA and primitive physical feature, which shows the diversity of Late Pleistocene population.

The complex evolution of *H. sapiens* in the Late Pleistocene and its mosaic, variable morphology, and disputable chronological problems have made East Asia a hot spot for discussing the origin of modern human.

Conclusion

Dental anthropology and paleoanthropology have been developing together for 100 years in China. Although it has not formed its independent school of dental anthropology in China, through the efforts of several generations, Chinese dental anthropology has a significant position in the international academic world today.

There is still much controversy about human evolution and other issues involved in this discipline. How to interpret the measurement and morphological variations observed in teeth is the key to understand human evolution. For example, whether early hominins existed before *Homo erectus* in China, how to interpret the unique dental characteristics of early Middle Pleistocene hominin teeth, whether late Middle Pleistocene hominins are transitional types of continuous evolution or represent different species of *Homo*, the polymorphism exhibited on late Pleistocene human teeth, and the origin of modern humans are questions that require multidisciplinary collaborative research.

The current study using the American ASUDAS involves ten archaeological sites, and although there are some sites with too little material or few observations to yield particularly clear results, we have been able to discern microevolutionary processes in the evolution of human teeth, differences between northern and southern populations and introgression between eastern and western populations. The consistency of non-metric traits in teeth and skulls, and the recent paleogenomic confirmation, indicate the prospective and important significance of dental anthropology. Palaeogenomics is increasingly flourishing, but there is still much uncertainty and difficulty in obtaining samples, especially from the Paleolithic.

Dental morphology has provided us with convenient materials for observation, and Chinese scholars are experimenting with new research methods. It is worth mentioning that Alexander Zubov is the founder of the Russian school of dental anthropology, has also proposed some features specific to the Mongoloid race [Зубов, 2006], which overlap with American ASUDAS, especially his method of odontoglyphics [Зубов, 2006; Zubov, 1977], which till now has not been applied to Chinese materials.

For modern humans and human teeth excavated from historical and Neolithic archaeological sites, the study is far less meticulous than that of paleoanthropology, which some paleoanthropologists have realized and carried out in recent years from the study of the morphology of modern human teeth [Xing, Liu, 2009; Xing et al., 2010; Zhou et al., 2013; Zhou et al., 2016]. With the discovery of new materials, more studies on the internal structure of the teeth of modern populations are needed in the future and can help us better understand the morphological variation and evolutionary trends on teeth of modern and fossil human.

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СТОЛЕТНИЙ ПУТЬ ОДОНТОЛОГИИ В КИТАЕ

Введение. *Одонтология развивается в Китае уже 100 лет. В данной работе автор анализирует статьи по одонтологии, связанные с китайскими материалами за последние сто лет, и кратко описывает статьи, посвященные такими вопросами, как эволюция человека и взаимодействие различных популяций в исторические периоды.*

Результаты и обсуждение. *Работы иностранных ученых стали основой китайской палеоантропологии и одонтологии с момента обнаружения зубов человека из Хэтао и местности Чжоукоудянь. С тех пор одонтология в Китае прошла этап накопления материала, этап внедрения американской ASUDAS в 1990-х годах и этап процветания в последние 30 лет. Многочисленные открытия и применение новых методов вывели китайскую одонтологию на международный уровень.*

В настоящее время в Китае насчитывается более 70 мест с ископаемыми останками человека, более 60 из которых содержат одонтологический материал. Для периода раннего плейстоцена было найдено меньше материалов, и существуют некоторые разногласия по поводу их принадлежности к роду Homo. Ранние среднеплейстоценовые одонтологические находки, принадлежащие Homo erectus демонстрируют примитивность и имеют некоторые особенности. Для поздних среднеплейстоценовых одонтологических находок характерна бо́льшая изменчивость и наличие мозаичных черт. Существуют споры о том, принадлежат ли некоторые окаменелости ранним Homo sapiens или другим таксонам. Обнаружение одонтологических находок в позднем плейстоцене поднимает вопросы о том, как и когда ранний современный человек появился в Китае, а также каковы особенности его эволюции. Однако из-за неполноты материала вопрос о происхождении человека требует междисциплинарного и всестороннего подхода.

С помощью американской ASUDAS были изучены одонтологические находки (от неолитических до современных) примерно из 10 археологических памятников. Эти результаты показывают согласованность одонтологических и краниологических описательных признаков, выявляют различия между северными и южными китайскими популяциями, показывают существование обмена между северо-западными китайцами и западными популяциями. Некоторые из этих выводов были подтверждены результатами по палеогеномике.

Заключение. *Антропологи стали уделять больше внимания морфологии зубов современного человека. В будущем применение новых методов и сбор материалов современного человека помогут нам лучше понять эволюцию древних людей, взаимодействие популяций.*

Ключевые слова: одонтология; эволюция человека; плейстоцен; разнообразие и мозаичная эволюция; Китай

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摘要：

牙齿人类学在中国已有百年的发展历程。本文作者回顾了百年来有关中国牙齿人类学的文献，并从人类演化，历史时期不同人群互动的角度简述了牙齿人类学的相关问题。

自从河套人牙齿化石和周口店遗址的发现以来，外国学者的工作一直是中国古人类学和牙齿人类学的基础。自此之后，牙齿人类学在中国经历了材料积累期，1990 年代引入美国 ASUDAS 方法时期，以及近 30 年的繁荣期。众多发现和新方法的应用使得中国牙齿人类学列位世界前沿。至今在中国已有 70 余处古人类化石遗址，其中 60 多处包含了人类牙齿化石。早更新世的材料较少，对于这些材料是否属于人属（*Homo*）还存在一些争议。中更新世早期的直立人（*Homo erectus*）牙齿展现出原始性和独特特征，中更新世晚期的古人类牙齿则展现出更大的变异范围和镶嵌性特征，对于其中一些化石是否属于早期智人还存在一些争议。晚更新世的人类牙齿与早期现代人在中国的出现和演化问题有关。然而由于化石保存的不完整性，人类起源的问题还要依靠多学科综合性分析。

新石器时代至现代人的材料大约有 10 余处遗址采用了 ASUDAS 方法进行了研究。其结果证实了牙齿同头骨的非测量性状有一致性，中国南北方人群的差异性和中国西北地区与西方人群的交流等。其中一些结论已经得到了古基因组学的证实。人类学家开始关注现代人的牙齿形态学问题。在将来，新方法的应用和现代人新材料的积累会有助于我们理解古人类的演化和人群之间的互动问题。

关键词：牙齿人类学，人类演化，更新世，多样性与镶嵌演化，中国。