**Habitat, climate and potential plant food resources for the late Miocene
Shuitangba hominoid in Southwest China: Insights from carpological remains**

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Abstract: The late Miocene is a sub-epoch when hominoids became rare worldwide but managed to survive in a few refugia. Investigating the living conditions of the late Miocene hominoids is therefore crucial for a better understanding of how they survived in those refugia. In this study, we present relevant palaeobotanical evidence regarding the habitat, climate and possible plant food resources for the Shuitangba hominoid (*Lufengpithecus cf. lufengensis*) from the late Miocene Zhaotong Basin, Southwest China. Totally 14 plant taxa were recognized from carpological remains newly recovered from the Zhaotong Basin, among which ten taxa were not reflected in the previous pollen record. These new plant taxa expand our knowledge of the flora and indicate how diverse the ecosystem in the late Miocene Zhaotong Basin was. Based on our carpological taxa, we hypothesize that the Shuitangba hominoid lived in a stratified mixed forest composed of trees, shrubs, lianas, herbs and grasses, near a lake occupied by various aquatic plants. The quantitative palaeoclimate reconstruction using the Coexistence Approach (CoA) indicates that the late Miocene Zhaotong Basin had a mean annual temperature (MAT) of 11.3–17.6 °C and a mean annual precipitation (MAP) of 1042–1547 mm, suggesting a mildly warm and humid climate for the Shuitangba hominoid. It also indicates that the hominoid had warm and wet summers but cool and dry winters, under the influence of the Asian monsoon. Edible and nutritious fruits and seeds of a considerable size, e.g., nuts of *Carya* and *Corylus*, fruits of *Euryale* and *Trapa*, were possibly exploited by the Shuitangba hominoid. The harder fruits, e.g., nuts of *Carya* and *Corylus*, might have benefited the hominoid as a

reserve in the winter when foods were scarce.

Key words: Fossil carpology; palaeoclimate reconstruction; palaeoenvironment; diet; Zhaotong Basin

1. Introduction

The late Miocene is a sub-epoch when hominoid primates (apes and humans) perished worldwide after their temporary success during the mid-Miocene climate optimum (Begun, 2002; Ward and Duren, 2002). They disappeared in many regions especially in Europe by the late Miocene (Agustí et al., 1997; Bernor et al., 2004), but continued to survive in East Africa, West Africa and Southeast Asia (Qiu and Qiu, 1995; Ward and Duren, 2002; Harrison, 2006; Bonnefille, 2010). Because the environment had a profound impact on the survival or extinction of early hominoids (Bonnefille et al., 2004; Elton, 2008; Wood and Harrison, 2011; Potts, 2013; Maslin et al., 2014), investigating their living conditions is particularly informative for a better understanding of their survival in those refugia during the late Miocene.

Southwest China on the southeastern margin of the Tibetan Plateau served as an important refugium for the late Miocene hominoids (Harrison, 2006). As revealed by their fossils, at least three hominoid species attributed to the genus *Lufengpithecus* lived in Southwest China during the late Miocene: *Lufengpithecus hudianensis* from the Yuanmou Basin (Zhu et al., 2005; Qi et al., 2006), *Lufengpithecus lufengensis* from the Lufeng Basin (Yue et al., 2004), and *Lufengpithecus* cf. *lufengensis* from the Zhaotong Basin (Ji et al., 2013). Among them, *Lufengpithecus* cf. *lufengensis* from the Zhaotong Basin is also called the Shuitangba hominoid after the name of the fossil

locality Shuitangba within the basin (Chang et al., 2015). Because of its important evolutionary significance as the youngest known hominoid in Southeast Asia, the Shuitangba hominoid has attracted close attention in recent years concerning its possible habitat (Chang et al., 2015; Zhang et al., 2016). Multiple studies including palynology (Chang et al., 2015) and clay mineralogy (Zhang et al., 2016) indicated a mildly warm and humid environment in the late Miocene Zhaotong Basin. Furthermore, the palynological analysis suggested a mixed forest dominated by broad-leaved trees and shrubs (Chang et al., 2015). The deduced mildly warm and humid mixed forest vegetation would have provided a suitable habitat for the Shuitangba hominoid. This explains the existence of the Shuitangba hominoid in the late Miocene Zhaotong Basin. Recently, hundreds of carpological remains (fruits and seeds) were discovered from the same sedimentary layer that yielded the hominoid fossil at Shuitangba (Huang et al., 2015; Zhu et al., 2016). These carpological remains may allow us to re-consider the botanical richness and ecosystem complexity in the late Miocene Zhaotong Basin, because most of the newly recognized plant taxa are not represented in the previous pollen record, e.g., *Euryale* (Huang et al., 2015) and *Zanthoxylum* (Zhu et al., 2016).

The environment has dramatically influenced early hominoids (Elton, 2008; Wood and Harrison, 2011; Potts, 2013; Maslin et al., 2014), but environment alone cannot fully explain their survival or extinction. Other determinant factors such as natural food resources are also closely associated with their occurrence (Deane et al., 2013; Bigga et al., 2015). Within our fossil collection are some edible and nutritious fruits

and seeds, e.g., hickory nut (*Carya*), hazel nut (*Corylus*), gorgon fruit (*Euryale*) and water chestnut (*Trapa*). These fruits and seeds could have been exploited by the Shuitangba hominoid, and thus may further explain its existence in the late Miocene Zhaotong Basin.

In the present study, the newly recovered carpological remains from the hominoid-bearing layer at Shuitangba were used in combination with the previous pollen record to depict the habitat of the Shuitangba hominoid, and assess plant food resources possibly utilized by the hominoid.

2. Materials and method

2.1. Geological setting and age determination

Our work focuses on the carpological remains which came from Shuitangba Village in the Zhaotong Basin (Fig. 1). The Zhaotong Basin, covering an area of ~230 km², is one of the fault-related basins of the Xianshuihe-Xiaojiang fault zone and one of the major fault zones within the fold belts in Southwest China (Wang et al., 1998). The basin is filled with late Miocene to Pliocene lacustrine or swampy clays, silts, lignites and peaty clays (Ji et al., 2013; Chang et al., 2015). Outcropping in an open-pit lignite mine at the Shuitangba Village is the section named Shuitangba (27°19'44" N, 103°44'15" E; 1918 m a.s.l.; Fig. 1). The Shuitangba section measures ~16 m in thickness, consisting of seven sedimentary layers (Table 1; Chang et al., 2015). Our fossil fruits and seeds were unearthed from the black peaty clay layer of the section, which also yielded the Shuitangba hominoid cranium (*Lufengpithecus* cf. *lufengensis*), other mammalian fossils and abundant pollen grains.

Lignites and peaty clays are extensively distributed in Southwest China (Li et al., 2013). They are commonly late Neogene in age (Zhu et al., 2008; Biasatti et al., 2012; Li et al., 2013). The recovered mammalian fauna from the black peaty clay layer of the Shuitangba section belongs to the East Asian Baoden Stage/Age (Ji et al., 2013; Jablonski et al., 2014), a standard terrestrial biochron for the late Miocene bracketed by dates in the time span of 7.2–5.3 Ma (Qiu et al., 2013). Several rodent genera within the fauna such as *Sinocastor* (a beaver), *Kowalskia* (a hamster), *Alilepus* (a leporid) and *Pliopetaurista* (a flying squirrel) are typical taxa of the period from late Miocene to early Pliocene (Ji et al., 2013; Jablonski et al., 2014). High-resolution magnetostratigraphy further constrained the time range of the Shuitangba section to 6.7–6.0 Ma, while the black peaty clay layer was estimated as ~6.2 Ma (Chang et al., 2015) according to the Astronomically Tuned Neogene Time Scale (Hilgen et al., 2012). Based on all the above evidence, the black peaty clay layer of the Shuitangba section is unambiguously late Miocene in age.

Fig. 1, Table 1 here

2.2 Fossil collection and examinations

Fossil fruits and seeds were collected during three field trips in 2013–2014. Fossil compressions such as the infructescences of *Alnus* were collected directly from the black peaty clay layer of the Shuitangba section, whereas structurally preserved fossils were obtained after a series of treatments. Firstly, fresh clays were exposed and sampled from the black peaty clay layer. They were then treated using running water and a set of sieves following the method described in Huang et al. (2012). Air dried,

the unfiltered materials were examined with the unaided eye, and fossil fruits and seeds were singled out using a stainless tweezer. A total of more than 600 fossil fruits and seeds were isolated, among which seeds of *Euryale* and *Zanthoxylum* were described previously (Huang et al., 2015; Zhu et al., 2016). The remaining fossils are considered in the present contribution. They were first cleaned in an ultrasonic bath (KO-50M) at a frequency of 50 KHz for 20–30 seconds to remove clay particles adhering to the fossil surface. Air dried, the fossils were digitally imaged under a camera (Zeiss AxioCam HRc) mounted on a binocular microscope (Zeiss Ste REO Discovery V20). The diminutive fossils, i.e., seeds of *Aldrovanda* and *Cucubalus*, were further viewed under a scanning electron microscope (SEM, Zeiss EVO LS10) to observe surface sculptures which could help to achieve a more accurate identification. All studied fossil specimens are housed at the Key Laboratory for Plant Biodiversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences.

2.3. Palaeoclimate reconstruction

Plant fossils are a valuable proxy for quantitative palaeoclimate reconstructions using appropriate approaches. The Coexistence Approach (CoA), initiated by Mosbrugger and Utescher (1997), is one of the invaluable tools widely used in climate reconstructions for the Neogene of the Northern Hemisphere (e.g., Mosbrugger et al., 2005; Xu et al., 2008; Jacques et al., 2011; Liu et al., 2011; Sun et al., 2011; Utescher et al., 2011; Li et al., 2015). It is based on the assumption that the fossil taxa had similar climate requirements to those of their nearest living relatives (NLRs;

Mosbrugger and Utescher, 1997). Climate intervals in which the maximum number of NLRs of a given fossil assemblage can coexist are considered to reflect the past climate regime (Mosbrugger and Utescher, 1997; Utescher et al., 2014). This method functions with all types of fossils provided that their taxonomic identities can be determined reliably (Mosbrugger and Utescher, 1997; Utescher et al., 2014). Although the reliability and resolution of the CoA have been questioned in recent years (Grimm and Denk, 2012; Grimm and Potts, 2016), for non-leaf fossils it appears to be the only quantitative approach that can be relied upon. As the Shuitangba fossils are non-leaf organs, we chose the CoA to quantitatively reconstruct the palaeoclimate. The formerly reported pollen data were also included since the pollen fossils originated from the same sedimentary layer and thus must be contemporaneous with our fruit and seed fossils. To avoid possible errors caused by fossil identification at the species level, the palaeoclimate was calculated based on climate requirements of NLRs at the generic or family level which were freely accessed at the Palaeoflora website updated in 2015 (<http://www.palaeoflora.de>; Utescher and Mosbrugger, 2015). Six temperature and precipitation related parameters were calculated, i.e., mean annual temperature (MAT), mean temperature of the coldest month (CMMT), mean temperature of the warmest month (WMMT), mean annual precipitation (MAP), mean monthly precipitation of the three wettest months (MP-Wet), and mean monthly precipitation of the three driest months (MP-Dry). The climate conditions in the late Miocene Zhaotong Basin were then interpreted based on the calculated climate parameters. The modern climate of the Zhaotong Basin was based on records at meteorological

stations (Yunnan Meteorological Bureau, 1984).

3. Results

3.1. Systematics of the carpological remains

Most of our carpological remains were identified, leaving only a few specimens undetermined. Twelve plant taxa were newly identified from these carpological remains (Fig. 2; Fig. 3; Fig. 4). Together with the two taxa formerly published (*Euryale* and *Zanthoxylum*), there are totally 14 taxa belonging to 14 genera in 11 families. Seven taxa are determined at the species level, while the other seven taxa are left at the generic level due to lacking specific diagnostic features. Detailed information about the carpological taxa is given in Table 2. It is noteworthy that these plant taxa exhibit various growth forms, e.g., trees and shrubs (*Alnus*, *Carya*, *Corylus*, *Ligustrum*, *Staphylea* and *Zanthoxylum*), lianas (*Ampelopsis* and *Cayratia*), herbs (*Chenopodium* and *Cucubalus*), and aquatics (*Aldrovanda*, *Euryale*, *Nymphaea* and *Trapa*). It is obvious that *Euryale* accounts for the majority in terms of specimen number followed by *Trapa*, while most other taxa such as *Alnus*, *Carya* and *Corylus* are represented by only a few fossil specimens. This may be the result of a taphonomic bias since *Euryale* and *Trapa* grow as floating aquatics in a lake and thus their fruits or seeds had a better chance of being buried, whereas diaspores of the terrestrial plants first had to undergo transportation before deposition in a lacustrine environment.

Fig. 2, Fig. 3, Fig. 4, Table 2 here

3.2. Reconstructed palaeoclimate

As aforementioned, the palaeoclimate here was reconstructed by integrating both our carpological remains and the previous pollen record. In the plant list, 19 fossil taxa of fruits, seeds and pollen contributed to the palaeoclimate reconstruction by the CoA (Table 3). Based on climate intervals required by their NLRs, six climate parameters were calculated. The climate requirements of all these 19 taxa fall within the reconstructed climate intervals; in other words, no outlier was observed. The reconstructed results together with modern climate values of the Zhaotong Basin are given in Table 5. As shown, estimates of the three temperature related parameters, i.e., MAT, CMMT and WMMT are 11.3–17.6 °C, 0.1–7.1 °C and 21.9–27.5 °C, respectively, compared to 11.6 °C, 2.2 °C and 19.6 °C today; those of the three precipitation related parameters, i.e., MAP, MP-Wet and MP-Dry are 1042–1547 mm, 141–212 mm and 8–55 mm, respectively, compared to 796 mm, 135 mm and 7 mm at present.

Table 3 here

4. Discussion

4.1. New floristic information from carpological remains

Preserved with the present carpological remains in the black peaty clay layer of the Shuitangba section are abundant pollen grains (Chang et al., 2015). Most pollen taxa represent trees and shrubs, such as the coniferous *Pinus* and *Tsuga* and broad-leaved *Alnus*, *Carpinus*, *Castanea/Castanopsis* *Quercus* and *Ulmus*, with *Quercus* being the dominant element (Table 4). Other growth forms such as herbs and aquatic plants are rare, represented only by grasses (Poaceae) and an aquatic (*Trapa*).

According to a comparison with the previous pollen record (Table 4), we found that our carpological remains contain ten components that have not been reflected in the pollen, i.e., *Aldrovanda*, *Ampelopsis*, *Cayratia*, *Chenopodium*, *Cucubalus*, *Euryale*, *Ligustrum*, *Nymphaea*, *Staphylea* and *Zanthoxylum*. Although the majority of these carpological remains represent trees and shrubs, other growth forms are well-represented, including a few lianas (*Ampelopsis* and *Cayratia*) and herbs (*Chenopodium* and *Cucubalus*), and several aquatic taxa (*Aldrovanda*, *Euryale*, *Nymphaea* and *Trapa*). The lianas and herbs are new growth forms in the fossil flora. In addition, *Ligustrum*, *Staphylea* and *Zanthoxylum* are new members of broad-leaved trees and shrubs not observed in the previous pollen record. All these newly recognized plant taxa underscore the diversity of the late Miocene vegetation in the Zhaotong Basin.

Table 4 here

4.2. Ecosystem of the Shuitangba hominoid

Based on the carpological and palynological records, it is clear that there were two types of plant ecosystems in the late Miocene Zhaotong Basin: an aquatic ecosystem and a terrestrial ecosystem. In the aquatic ecosystem, *Euryale* was predominant followed by *Trapa*, as revealed by the numbers of their fossil specimens. Other aquatic plants such as *Aldrovanda* and *Nymphaea* were present as subordinate components. The previous study on vertebrate fossils indicated that various waders (Ardeidae, Charadriidae, Gruidae, Scolopacidae and Threskiornithidae) and natatores (Anatidae, Gaviidae, Pelecanidae, Phalacrocoracidae and Podicipedidae) concurrently

lived in the aquatic ecosystem of the Zhaotong Basin (Jablonski et al., 2014). Our recovered aquatic plants further enrich the aquatic ecosystem from a botanical standpoint. In the terrestrial ecosystem, most of the plants were broad-leaved trees and shrubs (Fig. 5). Moreover, *Quercus* in the Fagaceae occurred as the dominant tree as demonstrated by its higher percentage of pollen grains (Chang et al., 2015). Because a few conifers (*Pinus* and *Tsuga*) coexisted with the broad-leaved trees and shrubs (Chang et al., 2015), a mixed forest dominated by broad-leaved plants can be deduced, as was also hypothesized on the basis of pollen fossils alone (Chang et al., 2015). This kind of mixed forest was also observed from other contemporary floras nearby in Southwest China, e.g., the Xianfeng flora to the southwest of the Zhaotong Basin (Xing et al., 2010, 2012, 2013). Besides standing woody plants that chiefly built up the forest, there were other plants with different growth forms that contributed to the terrestrial ecosystem. For example, a few lianas (*Ampelopsis* and *Cayratia*) likely occurred on forest margins; some herbs (*Chenopodium* and *Cucubalus*) and grass (Poaceae) probably grew in open areas as they prefer open environments (Collins and Pickett, 1987, 1988). Based on the coexistence of trees, shrubs, lianas, herbs and grasses that occupied different ecological niches, the terrestrial plant ecosystem in the late Miocene Zhaotong Basin was presumably highly stratified. This was possibly the general habitat in which the Shuitangba hominoid once lived.

4.3. Climate for the Shuitangba hominoid

In the present section, we discuss the palaeoclimate backdrop for the Shuitangba hominoid in a quantitative way and focus mainly on the seasonality of temperature

and precipitation, which was not apparent in previous palynological (Chang et al., 2015) and mineralogical studies (Zhang et al., 2016). The reconstructed MAT (11.3–17.6 °C) would seem to suggest a moderately warm climate, probably slightly warmer than today (11.6 °C) though minor overlap exists. The estimated WMMT (21.9–27.5 °C) was much higher than the CMMT (0.1–7.1 °C), indicating a strong temperature seasonality with warm summers and cool winters. The reconstructed MAP (1042–1547 mm) would imply humid conditions, in line with conclusions based on palynology (Chang et al., 2015) and clay mineralogy (Zhang et al., 2016). A marked contrast existed between precipitations of the three wettest (141–212 mm per month) and three driest (8–59 mm per month) months. This precipitation seasonality characterizes the Asian monsoon climate which started in the late Oligocene (Sun and Wang, 2005) or early Miocene (Guo et al., 2008). The late Miocene Asian monsoon in the Zhaotong Basin was inferred formerly by a clay mineralogical study (Zhang et al., 2016), and our results verified it from a quantitative perspective. Being a monsoonal region, Southwest China has the wet season in summers and the dry season in winters (Wang, 2006), which was also the case since the late Oligocene or early Miocene. Based on the above discussions, the Shuitangba hominoid most likely lived in a mildly warm and humid climate under the control of the Asian monsoon, with warm and wet summers but cool and dry winters.

Table 5 here

4.4. Potential plant food resources for the hominoid

Natural food resources played an important role in the life of the early hominoids

(Deane et al., 2013; Bigga et al., 2015). Being an important plant food resource, fruits and seeds can tell us something about the possible diet of the hominoids. The present carpological remains include some edible fruits and seeds, i.e., hickory nut (*Carya*), hazel nut (*Corylus*), gorgon fruit (*Euryale*) and water chestnut (*Trapa*). The nuts contain a fatty and proteinaceous kernel, while the aquatic fruits contain a starchy seed. Owing to their high nutritional value, these reproductive organs are among the popular plant foods for human beings today. Moreover, these fossil fruits and seeds had a considerable size though they are still small compared to their modern relatives (e.g., Huang et al., 2014, 2015). For example, our fossil hickory nuts are approximately 11×10 mm in size (Fig. 3), and our fossil water chestnuts are up to 20 mm in height (Fig. 4). However, this still suggests a fairly good volume of nutritious food. There are also some pollen taxa such as *Carpinus* (Chang et al., 2015) whose nuts are edible. All these plants might have served as natural food resources that could have been exploited by the Shuitangba hominoid during the late Miocene. It is worth mentioning that the harder fruits such as the hickory nut and hazel nut could benefit the hominoid as a seasonal fallback during a period of fruit shortage, e.g., in the cool and dry winter.

5. Conclusions

Based on the combination of carpological and palynological results, it is possible to reveal the full potential of the habitat for the Shuitangba hominoid in the late Miocene Zhaotong Basin, Southwest China. The Shuitangba hominoid probably lived in a mixed forest dominated by broad-leaved trees and shrubs and associated by lianas

and herbs, in the vicinity of a lake with various floating aquatics. The hominoid had a mildly warm and humid environment under the influence of the Asian monsoon, with warm and wet summers but cool and dry winters. Edible and nutritious fruits and seeds of some plants, e.g., *Corylus*, *Carya*, *Euryale* and *Trapa*, in the ecosystem were possibly exploited by the Shuitangba hominoid. The diverse habitat, mild climate and various plant food resources might together have induced the Shuitangba hominoid to exist in the late Miocene Zhaotong Basin.

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Table 1. Lithological facies of the late Miocene Shuitangba section in the Zhaotong Basin after Chang et al. (2015).

Table 2. The identified carpological remains, their specimen numbers and growth forms.

Table 3. Climate requirements of nearest living relatives (NLRs) of 19 fossil taxa (fruits, seeds and pollen) from the late Miocene Zhaotong Basin. Those of the remaining few fossil taxa are unavailable at the Palaeoflora website.

Table 4. Floristic comparison between the present carpological remains and previous pollen record.

Table 5. The reconstructed palaeoclimate using the CoA and modern climate parameters in the Zhaotong Basin.

Fig. 1. Locality of the fossil site, and the late Miocene Shuitangba section that yielded the hominoid cranium, and fossil fruits and seeds. a. Geographical location of Southwest China, and sites (Yuanmou, Lufeng and Zhaotong) where late Miocene hominoid fossils were found; b. Location of the Shuitangba Village in the Zhaotong Basin; c. The lignite mine and the late Miocene Shuitangba section that yielded the Shuitangba hominoid, other mammalian fossils and plant remains (fruits, seeds and pollen); d. Cranium of the Shuitangba hominoid.

Fig. 2. Compressed infructescences of *Alnus* from the late Miocene Zhaotong Basin, showing the cross (images a, b) and longitudinal (image c) sections. Scale bars = 5 mm.

Fig. 3. Fruits and seeds of terrestrial plant taxa from the late Miocene Zhaotong Basin.

a, b. Seeds of *Cucubalus prebaccifer* Huang, Liu et Zhou; c. Seed of *Chenopodium album* L.; d. Hazel nut (*Corylus* sp.); e–h. Hickory nuts (*Carya* sp.); i, j. Seed of *Staphylea forrestii* Balf.f., showing the general and apical views, respectively; k, l. Seed of *Cayratia* sp., showing the ventral and dorsal faces, respectively; m, n. Seed of *Ampelopsis* sp., showing the ventral and dorsal faces, respectively; o. Drupe of *Ligustrum* sp.; p. Seed of *Zanthoxylum trachyspermum* H. Zhu et Z.K. Zhou formerly described (Zhu et al., 2016); q–t. Other unidentified fossil remains.

Fig. 4. Fruits and seeds of aquatic plants from the late Miocene Zhaotong Basin. a–d. Seeds of *Aldrovanda vesiculosa* L., showing general views and magnified surface, respectively; e, f. Seed of *Euryale yunnanensis* Y. Huang & Z. Zhou formerly described (Huang et al., 2015); g, h. Seed of *Nymphaea* sp., showing the general view and enlarged surface, respectively; i–k. Fruits of *Trapa* cf. *bispinosa* Roxb.

Fig. 5. Five types of plant taxa from the late Miocene Zhaotong Basin, and their taxon numbers and percentages.

Taxon number/percentage
dominant element

Table 1. Lithological facies of the late Miocene Shuitangba section in the Zhaotong

Basin after Chang et al. (2015).

Bed number	Lithology	Depth interval
Overlying strata: cultivated soil		
1	Grey or yellowish-grey clays	0–2.7 m
2	Grey clayey silts	2.7–5.4 m
3	Gravels	5.4–5.9 m
4	Clayey silts containing a large number of fossil shellfish	5.9–6.4 m
5	Middle lignite layer	6.4–7.6 m
6	Black peaty clay containing animal and plant fossils	7.6–12.3 m
7	Lower lignite layer	12.3–16 m
Underlying strata: lignite		

Table 2. Climate requirements of nearest living relatives (NLRs) of 19 fossil taxa (fruits, seeds and pollen) from the late Miocene Zhaotong Basin. Those of the remaining few fossil taxa are unavailable at the Palaeoflora website.

NLRs of the fossil taxa	Fossil type	MAT min (°C)	MAT max (°C)	CMMT min (°C)	CMMT max (°C)	WMMT min (°C)	WMMT max (°C)	MAP min (mm)	MAP max (mm)	MP-Wet min (mm)	MP-Wet max (mm)	MP-Dry min (mm)	MP-Dry max (mm)
<i>Aldrovanda</i>	Seed												
<i>Alnus</i>	Fruit, pollen	−13.3	27.4	−40.9	25.6	12	38.6	41	2559	8	353	0	135
<i>Ampelopsis</i>	Seed	9.3	23.9	−2.8	19.4	21.6	29.7	169	1547	27	212	2	83
<i>Carpinus</i>	Pollen	0	25.8	−22.7	21.1	16.8	28.7	164	2648	20	350	2	55
<i>Carya</i>	Fruit, pollen	4.4	26.6	−11.5	22.2	19.3	30.6	373	1724	68	434	8	93
<i>Castanea/Castanopsis</i>	Pollen	8.7	27.9	−3.9	27	12.7	32.5	397	3151	68	610	0	165
<i>Cayratia</i>	Seed	11.3	27.7	0.1	27	21.9	32.2	1042	3151	141	389	1	165
<i>Chenopodium</i>	Seed												
<i>Corylus</i>	Fruit, pollen	−4.9	24	−32.4	16.7	12.9	29.4	389	1682	45	343	3	73
<i>Cucubalus</i>	Seed												
Ericaceae	Pollen												
<i>Euryale</i>	Seed												
<i>Ilex</i>	Pollen	−0.4	27.7	−12.9	27	10.4	33.6	641	3151	98	389	2	165
<i>Ligustrum</i>	Fruit	0	27.7	−22.7	27	14.8	29.3	422	3151	58	389	7	165
<i>Nymphaea</i>	Seed	−3.4	26.9	−25.8	24.8	12.8	33.6	287	2399	56	467	0	108
Oleaceae	Pollen	−1.1	27.7	−25.8	27	19.6	33.1	37	3155	8	389	0	165
<i>Pinus</i>	Pollen	−9.2	25.5	−36.8	21.4	7.1	32.9	180	1741	28	293	0	94
Poaceae	Pollen												
<i>Quercus</i>	Pollen	−1.4	27	−25.1	25.9	8.4	28.3	201	3905	33	610	0	180
<i>Staphylea</i>	Seed	4.4	17.6	−11.5	7.1	16.4	27.5	224	1958	43	294	0	70
<i>Trapa</i>	Fruit, pollen	−1.1	27.7	−25.8	27	19.6	28.3	177	3151	27	389	2	165
<i>Tsuga</i>	Pollen	−1.8	21.9	−15.6	15.6	11	29.5	285	2648	48	350	0	108
<i>Ulmus</i>	Pollen	−4.9	26.6	−25.8	26.1	16	29.4	201	3285	33	569	0	75
<i>Zanthoxylum</i>	Seed	3.4	27.8	−12.9	26.4	18.9	28.9	735	1882	83	366	5	59

Table 3. List of fossil taxa represented by both pollen and carpological remains, and their growth form, habitat and potential as natural food resource for the hominoid.

Fossil taxa	Carpological remains and their specimen number	Pollen fossil and its percentage	Growth form	Habitat	Potential as natural food resource
<i>Aldrovanda</i>	5	Unrepresented	Floating aquatic to shrub	Lacustrine	Unknown
<i>Euryale</i>	>500	Unrepresented	Floating aquatic	Lacustrine	Yes
<i>Nymphaea</i>	2	Unrepresented	Floating aquatic	Lacustrine	Unknown
<i>Trapa</i>	38	0.9%	Floating aquatic	Lacustrine	Yes
<i>Alnus</i>	4	7.4%	Broad-leaved tree	Terrestrial	Unknown
<i>Ampelopsis</i>	1	Unrepresented	Liana	Terrestrial	Unknown
<i>Carpinus</i>	Unrepresented	1.4%	Broad-leaved tree to shrub	Terrestrial	Unknown
<i>Carya</i>	5	4.1%	Broad-leaved tree	Terrestrial	Yes
<i>Castanea/Castanopsis</i>	Unrepresented	2.0%	Broad-leaved tree	Terrestrial	Yes
<i>Cayratia</i>	1	Unrepresented	Liana	Terrestrial	Unknown
<i>Chenopodium</i>	3	Unrepresented	Herb	Terrestrial	Unknown
<i>Corylus</i>	1	1.7%	Broad-leaved tree to shrub	Terrestrial	Yes
<i>Cucubalus</i>	3	Unrepresented	Herb	Terrestrial	Unknown
Ericaceae	Unrepresented	1.1%	Broad-leaved tree to shrub	Terrestrial	Unknown
<i>Ilex</i>	Unrepresented	1.7%	Broad-leaved tree to shrub	Terrestrial	Unknown
<i>Ligustrum</i>	1	Unrepresented	Broad-leaved tree to shrub	Terrestrial	Unknown
Oleaceae	1	0.8%	Broad-leaved tree to shrub	Terrestrial	Unknown
<i>Pinus</i>	Unrepresented	4.5%	Conifer	Terrestrial	Unknown
Poaceae	Unrepresented	9.8%	Grass	Terrestrial	Unknown
<i>Quercus</i>	Unrepresented	46.8%	Broad-leaved tree to shrub	Terrestrial	Unknown
<i>Staphylea</i>	1	Unrepresented	Broad-leaved tree to shrub	Terrestrial	Unknown
<i>Tsuga</i>	Unrepresented	5.6%	Conifer	Terrestrial	Unknown
<i>Ulmus</i>	Unrepresented	1.6%	Broad-leaved tree	Terrestrial	Unknown
<i>Zanthoxylum</i>	27	Unrepresented	Broad-leaved tree to shrub	Terrestrial	Unknown

Table 4. The reconstructed palaeoclimate using the CoA and its comparison to modern climate in the Zhaotong Basin.

Age	Proxy	MAT (°C)	CMMT (°C)	WMMT (°C)	MAP (mm)	MP-Wet (mm)	MP-Dry (mm)
Late Miocene	Plant fossils (fruits, seeds and pollen)	11.3–17.6	0.1–7.1	21.9–27.5	1042–1547	141–212	8–55
Modern	Meteorological stations	11.6	2.2	19.6	796	135	7

Table 5. The reconstructed palaeoclimate using the CoA and modern climate parameters in the Zhaotong Basin.

Age	Proxy			MAT (°C)	CMMT (°C)	WMMT (°C)	MAP (mm)	MP-Wet (mm)	MP-Dry (mm)
Late Miocene	Plant fossils	(fruits,		11.3–17.6	0.1–7.1	21.9–27.5	1042–1547	141–212	8–55
		seeds and pollen)							
Modern	Meteorological stations			11.6	2.2	19.6	796	135	7