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On the systematic status of the late Neogene hominoids from Yunnan Province, China

Late Miocene and Pliocene hominoids from Yunnan Province in southern China have been recovered from four sites or site complexes: Xiaolongtan, Yangyi, Shihuiba and Yuanmou. Of these, Shihuiba and Yuanmou are among the most prolific fossil hominoid sites in Eurasia, and they have yielded important evidence that is critical for documenting the evolutionary history, biogeography and paleobiology of later Neogene hominids. The aim of this paper is to clarify their taxonomy and nomenclature, and to present a preliminary synthesis of their phylogenetic relationships and biogeography. The morphological pattern and degree of variation observed in the fossil samples is consistent with there being a single, sexually dimorphic species represented at each site. Provisionally, we consider the Shihuiba, Xiaolongtan and Yuanmou samples to belong to two separate species within a single genus. The valid names for these species are *Lufengpithecus lufengensis* (from Shihuiba) and *L. keiyuanensis* (from Xiaolongtan and Yuanmou). From a phylogenetic perspective, the currently available evidence suggests that *Lufengpithecus* is either a primitive hominid that represents the sister taxon of the Ponginae+Homininae or a primitive sister taxon to the Ponginae. We tend to favor the second alternative, but acknowledge that a more comprehensive comparative analysis is needed to substantiate the phylogenetic and taxonomic affinities of *Lufengpithecus*. Importantly, the Yunnan fossil apes provide a unique temporal perspective on the evolutionary history of hominoids. Their continued occurrence during the late Miocene and Pliocene (~8–2 Ma), when hominoids became extinct throughout the rest of Eurasia, suggests that southern China (and presumably southeast Asia in general) was an important refugium for hominoids, including the ancestors of the orang-utans and gibbons. The uplift of the Tibetan plateau and its impact on regional climatic conditions may have been an important contributing factor in isolating the hominoids geographically and ecologically. We speculate that changed climatic condition in the mid-Pliocene, and possibly the arrival of *Homo* soon after, may have precipitated the regional extinction of large hominoids in southern China and in mainland southeast Asia.

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Introduction

Yunnan Province in southern China is renowned for its important paleoanthropological discoveries, especially those of Neogene hominoids and early Pleistocene *Homo erectus*. Fossil hominoids were first

discovered in Yunnan in the late 1950s, and since that time several thousand specimens have been recovered from late Miocene and Pliocene localities. These localities are unquestionably among the most prolific fossil hominoid sites in Eurasia, and have yielded evidence critical for documenting

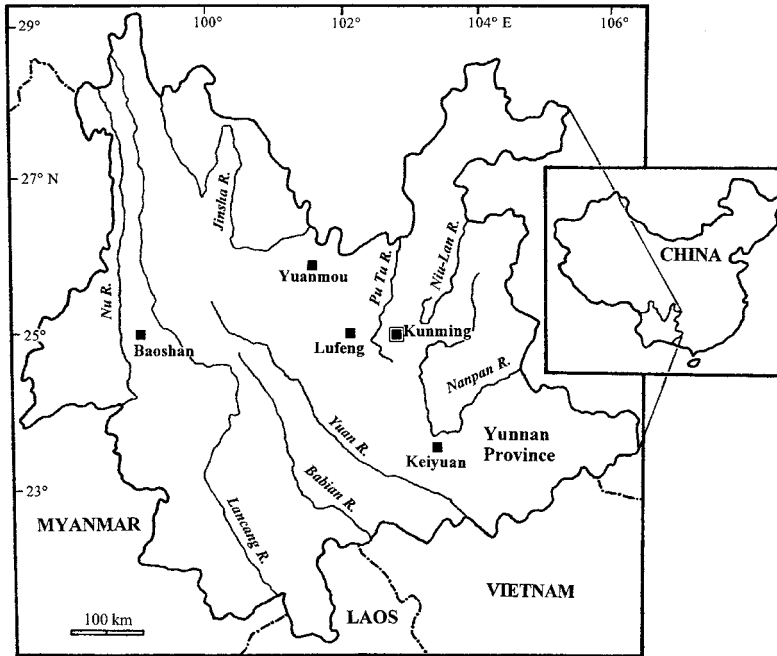


Figure 1. Map showing the location of fossil sites (solid squares) in Yunnan Province (adapted from Ho, 1988; Meng, 1997).

the evolutionary history, paleobiology, and biogeography of later Neogene Eurasian hominoids. Four sites or site complexes in Yunnan have produced fossil hominoids: (1) Xiaolongtan near the city of Keiyuan; (2) Shihuiba in Lufeng County; (3) Zhupeng, Xiaohe, and Leilao in the Yuanmou basin; and (4) Yangyi in Baoshan Prefecture (Figure 1).

The fossil hominoids from Xiaolongtan and Shihuiba have been described and discussed in some detail (Woo, 1957, 1958*a,b*; Wu *et al.*, 1983, 1984, 1985, 1986; Kelley & Pilbeam, 1986; Wu, 1987; Zhang, 1987; Schwartz, 1990, 1997), but only preliminary accounts of the material from the Yuanmou basin and Baoshan have been published to date, and few of these have appeared in English (Ho, 1988, 1990; Wu & Poirier, 1995). One of the key issues facing paleoanthropologists attempting to interpret the phylogenetic relationships of the fossil

hominoids from Yunnan is their complicated taxonomy. For example, since 1987 six different generic and seven different species names have been applied to the large hominoids from the Yuanmou basin. The main goal of this paper, therefore, is to offer a critical commentary on the taxonomy and nomenclature of the fossil hominoids from Yunnan, and hopefully to provide some clarification. Given the importance of this material for hominoid evolution, and the general lack of familiarity of the primary literature on this material outside China, we take this opportunity to offer also a brief review of the history of investigations in the region and present some new findings, especially those pertaining to the more recently described and less well-known discoveries. The information presented here is based primarily on the published literature, but it also includes preliminary observations of the original material made by the authors.

In order that the taxonomy can be appreciated in the appropriate historical context, the hominoid-bearing sites are discussed below in the sequence in which they were discovered.

Xiaolongtan, Keiyuan

The Xiaolongtan (=Hsiaolongtan) coal mine near Keiyuan is situated 210 km south of Kunming, the provincial capital (Figure 1). In 1956, geologists Wang Taimao and Ling Wenshan found five hominoid teeth (left P₄, M₂, right P₄, M₂₋₃) representing an associated lower dental series belonging to a single individual. The material was subsequently described as a new species, *Dryopithecus keiyuanensis* by Woo (1957). Later that year, researchers from the Yunnan Provincial Museum found a dental series comprising right P₃–M₃ from a second, slightly larger individual (Woo, 1958a,b), and in the early 1980s a lower molar series and a palate of a female individual with left I²–M³ and right C–M₂ were recovered from the same site (Zhang, 1987; Pan, 1994; Wu & Poirier, 1995).

The associated fauna is inferred to be slightly older than that from Lufeng (see below), and correlated with the Nagri faunas of the Siwaliks or the early Vallesian (MN 9, ~10 Ma) of Europe (Dong, 1987; Qiu & Qiu, 1995; Pickford & Liu, 2001). Paleomagnetic studies indicate a correlation of 8.30 ± 0.10 Ma (Yin, 1994), somewhat younger than that inferred from the mammalian fauna.

Following Woo (1957), most subsequent workers have tended to subdivide the hominoid material into large and small forms, and to assign these to previously recognized species of *Ramapithecus* and/or *Sivapithecus* (e.g., Simons & Pilbeam, 1965; Delson, 1977; Xu *et al.*, 1978; Szalay & Delson, 1979; Kay & Simons, 1983). However, Kelley & Pilbeam (1986) preferred to retain the material in *Dryopithecus*, based on their

observation that the dentine–enamel relationship of the Keiyuan specimens implied relatively thin molar enamel, as in the European representatives of this genus. Zhang *et al.* (1983, 1987a) recognized the material as a distinctive species of *Ramapithecus*, which they identified as *R. keiyuanensis*. However, Wu *et al.* (1989) considered that the Xiaolongtan material was most similar to that from Lufeng, and assigned it to the newly described genus *Lufengpithecus* Wu, 1987. Subsequently, Zhang *et al.* (1990) created a separate genus, *Sinopithecus*, to accommodate all of the Neogene hominoids from Yunnan, and they included the material from Xiaolongtan in the species *Sinopithecus keiyuanensis*. Zhang *et al.* (1993), following earlier workers, concluded that the hypodigm contained two species of different size, and as a consequence proposed *S. xiaolongtanensis*, presumably to accommodate material belonging to the larger-sized taxon. However, this species name was published without providing morphological characters that purportedly serve to differentiate the taxon, making it a *nomen nudum* and therefore unavailable according to the *International Code of Zoological Nomenclature* (ICZN, Article 13.1.1).¹ Most recently, Zhou (1998) recognized the Xiaolongtan material as a distinct subspecies of *S. yunnanensis* Xu & Lu, 1979, which he identified as *S. yunnanensis keiyuanensis*. Unfortunately, Zhou (1998) inappropriately applied the name *yunnanensis* Xu & Lu, 1979 in combination with a prior available species-group name, *keiyuanensis* Woo, 1957 (assuming that Zhou's variation in spelling does not constitute a different concept from that of Woo, 1957, in which case the name would represent a *nomen nudum* in the absence of a description to differentiate it as a distinct taxon). The

¹All references to the International Code of Zoological Nomenclature pertain to the Fourth edition of the Code (International Commission on Zoological Nomenclature, 1999).

valid name referring to this taxonomic concept would thus be *S. keiyuanensis keiyuanensis*.

A summary of the names applied to the fossil hominoids from Xiaolongtan is presented below:²

- Dryopithecus keiyuanensis* Woo, 1957
Dryopithecus (Sivapithecus) sivalensis—
 Simons & Pilbeam (1965)
Dryopithecus (Sivapithecus) indicus—
 Simons & Pilbeam (1965)
Ramapithecus punjabicus—Simons &
 Pilbeam (1965)
Dryopithecus cf. indicus—Delson (1977)
cf. Ramapithecus punjabicus—Delson
 (1977)
Ramapithecus punjabicus—Szalay &
 Delson (1979)
Sivapithecus indicus—Szalay & Delson
 (1979)
Sivapithecus sivalensis—Kay & Simons
 (1983)
Ramapithecus keiyuanensis—Zhang *et al.*
 (1983)
Ramapithecus (Dryopithecus) keiyua-
nensis—Zhang (1987) (invalid combi-
 nation)
Lufengpithecus keiyuanensis—Wu *et al.*
 (1989)
Sinopithecus keiyuanensis—Zhang *et al.*
 (1990)
Sinopithecus xiaolongtanensis Zhang *et al.*
 (1993) (*nomen nudum*)
Sivapithecus (D.) keiyuanensis—Pan
 (1994)
Sivapithecus yunnanensis keiyuanensis
 Zhou, 1998 (invalid combination)

²The following conventions are used in the synonymy lists presented in this paper. (1) A species name directly followed by an author's name without an intervening dash represents the original authorship of a species based on a holotype from that locality. (2) A species name separated from the author's name by a dash represents the assignment by those authors of material from that locality to a prior nomen. (3) The list includes all formal taxonomic names to which material from that locality has been referred, arranged in chronological order, and including only the earliest documented reference to that particular nomen.

Shihuiba, Lufeng

The site of Shihuiba in Lufeng County is located 90 km west of Kunming. In 1975, Wang Zhengju, a member of the Lufeng Cultural Center discovered a hominoid tooth in a lignite horizon on the southern slope of Miaoshanpo Hill. Between 1975 and 1983, the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Academia Sinica, the Yunnan Provincial Museum, and the Lufeng Cultural Center jointly conducted large-scale excavations at the site. These expeditions succeeded in recovering numerous fossil hominoid specimens, in association with a diverse mammalian fauna. The fossil-bearing sediments are ~5–6 m thick and consist of massive lignites, alternating with carbonaceous clays, silts and sands with interbedded lignites (Wu *et al.*, 1982; Qi, 1985, 1993; Wu & Xu, 1985). Currently, the hominoid collection includes five partial crania, 57 additional cranial and mandibular fragments, 29 associated upper and lower dentitions, over 600 isolated teeth, as well as several fragmentary postcranials, including a scapula, clavicle, radius, femur, metatarsal, and two phalanges (Xu *et al.*, 1978; Xu & Lu, 1979, 1980; Lu *et al.*, 1981; Wu *et al.*, 1981, 1983, 1986; Xiao, 1981; Wu, 1984; Wu & Xu, 1985; Lin *et al.*, 1987). In addition to the hominoids, the primate fauna includes the large crouzeliin plio-pithecoid, *Laccopithecus robustus*, and the sivaladapines, *Sinoadapis carnosus* and *S. shihuibaensis* (Wu & Pan, 1984, 1985; Pan & Wu, 1986).

The Lufeng fauna is inferred to be younger than that from Xiaolongtan, as indicated by the more derived proboscideans (i.e., *Zygodon lufengensis* and *Tetralophodon cf. exoletus*) (Wu & Poirier, 1995; Qiu & Qiu, 1995). The fauna correlates best with the Dhok Pathan Formation of the Siwaliks (Pilbeam *et al.*, 1996) or early Turolian (MN 11) of Europe, with an

estimated age of ~8–9 Ma (Flynn & Qi, 1982; Badgley *et al.*, 1988; Qiu & Storch, 1990; Qiu & Qiu, 1995; Pickford & Liu, 2001; Ni & Qiu, 2002). Paleomagnetic stratigraphy indicates that the hominoid-bearing lignites at Lufeng correlate to 4.0 ± 0.10 Ma (Yin, 1994), an age estimate that is clearly too young to be concordant with the fauna.

Initially, the Lufeng hominoids were assigned to two species, *R. lufengensis* Xu *et al.*, 1978 and *S. yunnanensis* Xu & Lu, 1979, that were considered to represent different-sized morphs (Xu *et al.*, 1978; Xu & Lu, 1979; Lu *et al.*, 1981; Wu *et al.*, 1981, 1982; Wu & Oxnard, 1983a,b; Wu & Xu, 1985; Lieberman *et al.*, 1985; Oxnard, 1985, 1987, 1988; Zhang *et al.*, 1993). This view has been largely abandoned, but there is still considerable disagreement about whether the sample represents two morphologically similar species that overlap in size (Martin, 1991; Cope & Lacy, 1992; Plavcan, 1993) or a single sexually dimorphic and highly variable species (Wu *et al.*, 1983, 1986; Pilbeam, 1986; Kelley & Pilbeam, 1986; Wu, 1987; Kelley & Etlar, 1989; Wood & Xu, 1991; Kelley & Xu, 1991; Kelley, 1993; Kelley & Plavcan, 1998; Liu *et al.*, 1999, 2000). The current consensus, however, is that the Lufeng material can all be attributed to a single species. Wu *et al.* (1986) combined the material previously assigned to *R. lufengensis* and *S. yunnanensis* in a single highly sexually dimorphic species, which they recognized as *S. lufengensis*. Subsequently, Wu (1987) included the species in a distinct genus, *Lufengpithecus*. Zhang *et al.* (1990) later transferred the species to a newly proposed genus, *Sinopithecus*, based on *Sin. hudianensis* as the type species (see also Zhang *et al.*, 1993). However, as noted by Gao (1998) *Sinopithecus* Zhang *et al.*, 1990 is a junior subjective synonym of *Lufengpithecus* Wu, 1987 if the genus includes the species *lufengensis* (see below for further discussion of

this point). Most recently, Zhou (1998) has suggested that all of the Neogene hominoids from Yunnan can be assigned to a single species, *Sivapithecus yunnanensis*, and that the Lufeng sample should be differentiated from those from Keiyuan and Yuanmou at the subspecific level only, thus recognizing *Sivapithecus yunnanensis lufengensis*. However, this nomenclatural combination does not take into consideration the fact that both *keiyuanensis* Woo, 1957 (see above) and *lufengensis* Xu *et al.*, 1978 have priority over *yunnanensis* Xu & Lu, 1979. Therefore, the valid name for this taxonomic concept would be *Sivapithecus keiyuanensis lufengensis*.

The various names that have been applied to the Lufeng hominoids are summarized as follows:

- Ramapithecus lufengensis* Xu *et al.*, 1978
- Sivapithecus yunnanensis* Xu & Lu, 1979
- Sivapithecus sivalensis*—Kay & Simons (1983)
- Sivapithecus indicus*—Kay & Simons (1983)
- Sivapithecus lufengensis*—Wu *et al.*, 1986
- “*Sivapithecus*” *lufengensis*—Kelley & Pilbeam (1986)
- Lufengpithecus lufengensis* (Xu *et al.*, 1978) Wu, 1987
- Sinopithecus lufengensis* (Xu *et al.*, 1978) Zhang *et al.*, 1990 (invalid combination)
- Sinopithecus yunnanensis*—Zhang *et al.* (1993)
- Sivapithecus yunnanensis lufengensis* Zhou, 1998 (invalid combination)

Yuanmou Basin

The Yuanmou Basin is located about 110 km northwest of Kunming. The basin is bordered by elevated regions of metamorphic rocks and granites of the Precambrian basement and by Jurassic to Cretaceous sediments. These rocks are overlain by a

thick series of later Tertiary and Quaternary fluvio-lacustrine deposits. The Neogene hominoid-bearing sediments (Xiaohe Formation) are mainly distributed in the northwestern part of the basin, and comprise more than 80 m of clays, silts, sands and gravels (Qian & Zhou, 1991; Qian *et al.*, 1997; Qian, 1998; Zhou, 1998). These strata are overlain by sediments of the Longchuan and Shagou Formations (Pliocene), and by sediments of the Gantang and Yuanmou Formations (Late Pliocene-Pleistocene) associated with fossil hominins (Qian & Zhou, 1991; Urabe *et al.*, 1996, 2001).

Fossil hominoids from the Xiaohe Formation have been recovered from four localities. Three of these are located in the vicinity of the villages of Zhupeng and Xiaohe, about 25 km northwest of Yuanmou, the county capital. Baozidongqing (locality #8601, 8602, 8603, 8604, 8605, 8606) is situated just to the southwest of Zhupeng village, Hudieliangzi (locality #8701, 8702, 8704) is situated to the northwest of Xiaohe, while Fangbeiliangzi (=Gaipailiangzi; locality #8703, 8801, 8802, 9001, 9002) is situated to the southwest of Xiaohe (Jiang, 1997; Jiang & Zhang, 1997). The fourth locality, Dashuqingliangzi near Leilao village is located about 8 km to the southwest of Zhupeng (Zong *et al.*, 1991; Jiang *et al.*, 1993; Jiang, 1997; Jiang & Zhang, 1997) (Figure 2).

Fossil mammals of late Pleistocene age were first discovered in the Yuanmou Basin in the late 1920s by the Central Asiatic Expedition of the American Museum of Natural History (Colbert, 1940). However, it was not until 1965, when Qian Fang and his colleagues found two upper central incisors of an early middle Pleistocene hominin, later attributed to *Homo erectus yuanmouensis* (Hu, 1973), that intensive investigations began in the region. In 1986, following a visit by Jiang Nengren from the Yunnan

Institute of Geological Sciences to the Xiaohe-Zhupeng area to the northwest of Yuanmou, local villagers made a small collection of fossils that included a hominoid tooth.

Between 1986 and 1990, the Yunnan Provincial Museum, the Chuxiong Prefecture Cultural Relics Office, and the Yuanmou Man Exhibition Hall conducted joint excavations in the Xiaohe Formation in the Zhupeng-Xiaohe area. They recovered a large collection of fossil hominoids, including a face of a juvenile individual (YV 0999), eight maxillary fragments, eleven mandibular fragments, and over 1200 isolated teeth (Ji, 1998). From 1992 to 1997, the Yuanmou Exhibition Hall collected specimens at the site of Leilao, including a relatively complete mandible and more than 300 isolated teeth. In addition to hominoids, at least two other primates are represented in the collections from the Xiaohe Formation (Yu & Jiang, 1997). One of these, just as at Lufeng, is an adapid primate belonging to *Sinoadapis*, although the material from Yuanmou differs from *S. carnosus* and *S. shihuibaensis* from Lufeng in being smaller in size and having more strongly developed cingula on the molars (Pan, 1997a; Pan & Zheng, 1998). A further species of fossil primate was initially considered to belong to *Laccopithecus* (Pan, 1994, 1997a), but specimens identified as such were later transferred to a new genus and species, *Dianopithecus progressus* (Pan, 1996, 1997b). However, as discussed below, the hypodigm on which this latter taxon is based consists of deciduous teeth of the large hominoid, and is, therefore, a junior subjective synonym of prior nomina. Nevertheless, some of the isolated teeth in the Xiaohe collections do represent a small catarrhine primate. A preliminary assessment of the material indicates that the teeth belong to a distinct genus, possibly related to the extant gibbons. If this identification is confirmed it would provide the earliest known record

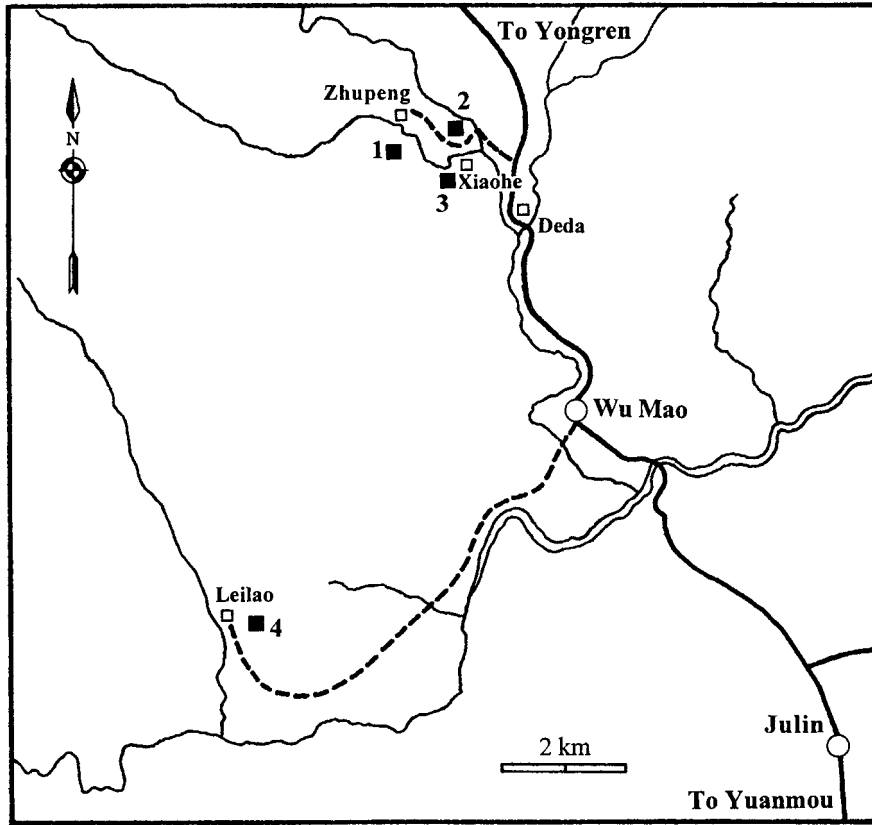


Figure 2. Map showing the location of the fossil sites in Yuanmou County, Yunnan Province (location of Yuanmou indicated in Figure 1). Fossil sites: 1, Baozidongqing; 2, Hudieliangzi; 3, Fangbeiliangzi; 4, Dashuqingliangzi. Geographical detail: towns (open circles); villages (open squares); major roads (heavy lines); minor roads (heavy broken lines); rivers (fine lines) Adapted from Jiang (1997).

of the Hylobatidae, which is otherwise known only from the Pleistocene-Recent (Gu, 1986, 1989; Pan, 1994).

The mammalian fauna from the Xiaohe Formation is generally similar to that from Lufeng, although initial comparisons suggested to some researchers a younger age for the Xiaohe fauna (Zong *et al.*, 1991; Ji & Zhang, 1997; Zong, 1996, 1997, 1998; Pan & Zheng, 1998). However, Ni & Qiu (2002), based on an analysis of the micro-mammalian assemblage from Leilao, concluded that the Xiaohe fauna is slightly older than that from Lufeng, with an estimated age of ~ 9 Ma. The fauna is certainly older than that from the overlying Shagou

Formation, which is best correlated with the early Villanyian of Europe (MN 16, ~ 3.0 – 3.4 Ma). Jiang *et al.* (1989) and Urabe *et al.* (2001) have published paleomagnetic correlations for the Shagou Formation that indicate an age of ~ 3 – 4 Ma. Qian & Zhou (1991) and Qian (1997) have reported paleomagnetic correlations for sections of the Xiaohe Formation at Baozidongqing of 3.9 – 4.9 Ma and Hudieliangzi of 4.5 – 5.2 Ma and 3.8 – 5.44 Ma (with an estimated age for the hominoid-bearing horizons of 4.75 – 0.25 Ma). Yin (1994) has published much younger dates for these sections of 2.13 ± 0.10 Ma and 2.76 ± 0.10 Ma respectively, and more recently Yin & Liang

(1998) have suggested that the hominoid-bearing horizons in the Zhupeng area correlate with dates of 7.50–6.42 Ma or 3.38–2.14 Ma. Recently published ESR dating of rhinocerotid teeth from the hominoid horizon at Baozidongqing and Hudieliangzi has provided an age of 3.25 Ma (Huang *et al.*, 2000). A combination of evidence from the mammalian fauna (Pickford & Liu, 2001; Ni & Qiu, 2002) and from the most recently published paleomagnetic correlations (Yin & Liang, 1998; Urabe *et al.*, 2001) indicates that the hominoids from Yuanmou are probably ~7–9 Ma (Yin & Liang, 1998; Ni & Qiu, 2002), and broadly contemporaneous with those from Lufeng.

Jiang *et al.* (1987) were the first to apply a new name to the Neogene hominoids from Yuanmou. They described an isolated tooth from Zhupeng as belonging to *H. habilis zhupengensis*, but unfortunately, since they did not publish any features that purportedly distinguish it from other taxa (according to ICZN Article 13.1.1), it constitutes a *nomen nudum* and is therefore unavailable. Later that same year, Zhang *et al.* (1987a,b) published *R. hudiensis*, based on a maxilla with P³–M³ (YV 0916) from Hudieliangzi (Locality 8701), and *H. orientalis*, based on a type series of isolated teeth (YV 0910–0915) from Baozidongqing (Locality 8601). Both of these names are available. In 1988, a partial cranium of a juvenile hominoid (YV 0999) was discovered at Hudieliangzi (Locality 8704) and referred to *R. hudiensis* (Zhang *et al.*, 1988). The specimen consists of much of the face and palate with dC–dP⁴+M¹ on both right and left sides (Zhang *et al.*, 1988; Ho, 1988, 1990; Wu & Poirier, 1995).

Zhang *et al.* (1990) made *Ramapithecus hudiensis* the type species of a new genus, *Sinopithecus*. Although no explicit diagnosis was presented, the description given of the key features of the juvenile partial cranium (YV 0999) complies with ICZN Article 13.1, and we therefore consider *Sinopithecus*

an available name. However, in addition to recognizing *S. hudiensis*, Zhang *et al.* (1990) also designated the Lufeng and Xiaolongtan material as *Sin. lufengensis* and *Sin. keiyuanensis* respectively. This is not appropriate given that one of the included taxa has a prior and available generic name, *Lufengpithecus* Wu, 1987. *Sinopithecus* can be used as a valid name if *hudiensis* or *hudiensis*+*keiyuanensis* is deemed a distinct genus, but, as noted by Gao (1998), *Sinopithecus* is a junior subjective synonym of *Lufengpithecus* Wu, 1987 if the genus includes all of the Neogene hominoids from Yunnan. The concept of *Sinopithecus* was further expanded upon by Zhang *et al.* (1993), who recognized that each of the samples from Keiyuan, Lufeng and Yuanmou contained two species of different size. The larger specimens from Xiaohe, for example, were referred to a new species, *Sin. xiaoheensis*. However, since no characters were presented to differentiate the new taxon it represents a *nomen nudum*.

Pan (1996) referred a collection of isolated teeth from Xiaohe region to a new genus and species of small catarrhine primate, *Dianopithecus progressus* (see also Pan, 1997b). However, Pan (1998) has modified her view, and now regards these specimens as deciduous teeth of *Lufengpithecus*. Harrison & Gu (1999:268) independently reached the same conclusion.

With further discoveries and more detailed comparisons, most subsequent workers have tended to assign the Yuanmou hominoids to the genus *Lufengpithecus* (e.g., Pan, 1994; Jiang, 1996; Zheng & Zhang, 1997; Gao, 1998; Pan & Zheng, 1998; Liu *et al.*, 2000). Zheng & Zhang (1997) have created a new species, *Lufengpithecus yuanmouensis*, based on the juvenile face (YV 0999) from Hudieliangzi. However, it is evident from the accompanying descriptive account that *L. yuanmouensis* is intended to include all of the material from the Yuanmou basin. For example, the

hypodigm explicitly includes YV 0916, the name-bearing type of *R. hudiensis* Zhang *et al.*, 1987a. Although the name remains available, as currently constituted by Zheng & Zhang (1997), the name *L. yuanmouensis* represents a junior subjective synonym of *R. hudiensis*. An alternative taxonomic scheme presented by Gao (1998) places the hominoids from Yuanmou and Xiaolongtan together in *L. keiyuanensis*.

Zhou (1998) considered that the Keiyuan, Lufeng and Yuanmou hominoids should all be included together in a single species, *S. yunnanensis*, but he differentiated the samples at the subspecies level, i.e., as *Siv. y. kaiyuanensis*, *Siv. y. lufengensis*, and *Siv. y. yuanmouensis*. As noted above, however, there are several problems with this nomenclatural scheme. First, the species name *yunnanensis* Xu & Lu, 1979 is inappropriately used in combination with the prior species group names *keiyuanensis* Woo, 1957 and *lufengensis* Xu *et al.*, 1978. Second, the name *yuanmouensis* Zheng & Zhang, 1997 is used to encompass all of the hominoids from Yuanmou, even though *hudiensis* Zhang *et al.*, 1987a, *orientalis* Zhang *et al.*, 1987b, and *progressus* Pan, 1996 are all available as prior *nomina* for this species concept.

The taxonomic names used for the Neogene hominoids from the Yuanmou Basin are summarized below:

Homo habilis zhupengensis Jiang *et al.*, 1987 (*nomen nudum*)

Ramapithecus hudiensis Zhang *et al.*, 1987a³

Homo orientalis Zhang *et al.*, 1987b

³Although the correct spelling for the species names is *hudiensis*, as established in the original publication (Zhang *et al.*, 1987a), variations in spelling have appeared in subsequent publications. These include: *hudiensis* (e.g., Pan, 1994; Wu & Poirier, 1995; Jiang, 1996; Zheng & Zhang, 1997; Harrison & Gu, 1999) and *hudiensis* (e.g., Zhou, 1998; Ji, 1998). However, these incorrect subsequent spellings do not constitute available names and do not enter into homonymy (ICZN, Article 33.3).

Sinopithecus hudiensis—Zhang *et al.* (1990)

Homo erectus zhupengensis (Jiang *et al.*, 1987)—Zong *et al.* (1991) (?*lapsus calami*)

Sinopithecus xiaoheensis—Zhang *et al.* (1993) (*nomen nudum*)

Sivapithecus sp.—Jiang *et al.* (1993)

Lufengpithecus spp.—Pan (1994)

Dianopithecus progressus Pan, 1996

Lufengpithecus yuanmouensis Zheng & Zhang, 1997

Lufengpithecus keiyuanensis—Gao, 1998

Sivapithecus yunnanensis yuanmouensis Zhou, 1998

Yangyi, Baoshan

The hominoid locality of Yangyi in Baoshan Prefecture is located ~350 km west of Kunming. The locality is situated on the eastern slopes of the Gaoligongshan mountains, between the Nu River and the Lancang River, and is the most westerly hominoid locality in Yunnan Province (Figure 1). In 1992, Xu Qinghua of IVPP discovered a left mandible fragment with C-M₃ of a female hominoid in the uppermost lignite layer of the Qingshuigou coal mine at Yangyi. The specimen has not yet been formally described, but several news articles and reviews have made reference to the discovery (Xu, 1992; Geng, 1994; Zhang, 1994). The age of the Yangyi deposits has not been reliably established. Based on the associated proboscideans, the Yangyi fauna is suggested to be younger than the Lufeng and Xiaohe faunas (Yunbo, 1975; Jiang *et al.*, 1983; Zong *et al.*, 1996). It corresponds well with other Pliocene faunas from China, including that from the Shagou Formation, Yuanmou Basin [which has an estimated age of ~3–4 Ma, based on paleomagnetic correlations (Jiang *et al.*, 1989; Urabe *et al.*, 2001)] and the Yushean aged fauna from northern China (correlated

AGE (Ma)	EUROPEAN LAND MAMMAL AGES	MN ZONE	CHINESE LAND MAMMAL AGES	KEY CHINESE HOMINOID LOCALITIES	KEY EURASIAN HOMINOID LOCALITIES		
5 10	Oldenburgian		Zhoukoudian	Liucheng, Jianshi [Gi]			
	Biharian		Nihewanian				
	Villanyian		17				
	Ruscinian	16	Yushean	Yangyi [L]			
		15					
	Turolian	14	Baodean/ Lufengian	Shihuiba [L] Yuanmou [L]			
		13					
		12					
	Vallesian	11				9	Xiaolongtan [L]
		10					
						Baccinello V2 [O] Monte Bamboli [O]	
				Baccinello V1 [O]			
				Ravin de la Potwar [S] Pluie [Gr]			
				Rudabanya [D] Can Ponsic [D] Can Llobateres [D]			

Figure 3. Chronology of late Neogene and Quaternary hominoids from key localities in China and the rest of Eurasia. The abbreviations in [] following locality names refer to hominoid taxa known from those sites: D, *Dryopithecus*; Gi, *Gigantopithecus*; Gr, *Graecopithecus* (= *Ouranopithecus*); L, *Lufengpithecus*; O, *Oreopithecus*; S, *Sivapithecus*. Sources: Andrews *et al.* (1996); Pan (1994); Flynn *et al.* (1995); Qiu & Qiu (1995); Pickford & Liu (2001); Ni & Qiu (2002).

with the Ruscinian and Villanyian in Europe, MN 14–16, 5.2–2.6 Ma) (Qiu & Qiu, 1995). If an estimated age of ~3–5 Ma is confirmed, the fossil primate from Yangyi will be, with the exception of *Gigantopithecus*⁴, the youngest known representative of an extinct hominoid genus from Eurasia (Figure 3).

Provisional synthesis

Further research on the anatomy, comparative morphology, and chronology of the Neogene fossil hominoids from Yunnan Province is needed before any definitive conclusions can be reached concerning their taxonomic and phylogenetic relationships. We also recognize that such studies are an

⁴*Langsonia liquidens* Schwartz *et al.*, 1995 from the Middle Pleistocene of Tham Khuyen Cave is almost certainly attributable to *Pongo pygmaeus weidenreichi* (see Harrison, 2000).

essential prelude to making informed assessments of their evolutionary history, paleobiology, and biogeography. With this caveat in mind, however, we offer a provisional interpretation of the material.

Taxonomy and nomenclature

A number of workers have suggested that the large sample of fossil hominoids from Lufeng is too variable to be included in a single species (Wu *et al.*, 1983; Wu & Oxnard, 1983a,b; Lieberman *et al.*, 1985; Oxnard, 1985, 1987; Martin, 1991; Cope & Lacy, 1992; Martin & Andrews, 1993; Plavcan, 1993), while others interpret the material as a highly variable and strongly sexually dimorphic species that exceeds the range of variation seen in extant hominoids (Andrews, 1983; Wu *et al.*, 1986; Wu, 1987; Kelley & Etlar, 1989; Kelley & Xu, 1991; Wood & Xu, 1991; Kelley, 1993; Kelley & Plavcan, 1998). Our own comparative

studies of the Lufeng material indicate that the variation is consistent with the sample comprising male and female morphs of a single species. Nevertheless, we acknowledge that by accepting a single species we are obliged to account for the high degree of dental variation. We offer two possible explanations.

First, we see no *a priori* justification for assuming that extinct species of hominoids would *never* have exceeded the range of variation present in extant apes (see Kelley & Xu, 1991; Kelley, 1993). Second, the degree of variation in fossil collections is subject to the confounding influences of time-averaging (see Kelley & Etlter, 1989). It is likely that remains recovered from populations that sample even a short period of geological time, such as those from Lufeng, will tend to exhibit a greater range of variation compared with modern taxa (Kelley & Etlter, 1989; Martin, 1991). The hominoids from Shihuiba derive from Beds 2 to 6, which comprise about 5–6 m of fine- to coarse-grained laminated sediments (Qi, 1993). An accurate estimation of the time elapsed for deposition of these sediments is not possible, but given what we know about sedimentation rates and compaction factors in modern-day tropical lakes (see Harrison *et al.*, 2001), and paleontological contexts with precise radiometric age determinations (such as Plio-Pleistocene localities in East Africa), we can assume that the hominoid-bearing sequence at Shihuiba represents a time-scale in the order of tens of thousands of years. Palynological evidence for a significant ecological and climatic change through the sequence (Sun & Wu, 1980; Qi, 1993) provides additional circumstantial support for a time-scale of this magnitude. Paleontologists, who largely focus on macroevolutionary problems, tend to regard such slender slices of time as inconsequential. However, microevolutionary changes can result in expanded ranges of metrical variation in hominoid species. For example,

levels of variation in the teeth of orang-utans (*Pongo pygmaeus*) increase beyond their modern limits through the inclusion of data derived from subfossil samples of *P. pygmaeus* from early Holocene (or possibly late Pleistocene) cave sites in Sumatra (Table 1). It has been shown previously that the subfossil orang-utans from Sumatra (described as *P. p. palaeosumatrensis* by Hooijer, 1948) have significantly larger teeth (about 15% larger by area on average) than their modern counterparts (Hooijer, 1948; Harrison, 2000). Although only just over half (53%) of the coefficients of variation (CV) for the dental dimensions increased with the addition of the subfossil orang-utans (since CVs tend to decrease with increasing sample size), the average CV does increase (Table 1). The Lufeng sample still shows higher CVs for most dimensions (21 out of the 32, 66%), but the average CV is only 11.3 (only 3% higher than the combined sample of modern and subfossil orang-utans). The application of randomization methods to take into account the smaller sample sizes from Lufeng may reduce even further the magnitude of this difference. In any event, adding a 10–20 ka range to the temporal dimension of orang-utan samples, a period presumably generally comparable to that represented by the hominoid-bearing deposits at Shihuiba, more closely approximates the degree of variation seen in the *L. lufengensis* sample.

This demonstrates that time-averaging of paleontological samples over relatively brief periods of geological time can impact on the degree of metrical variation, and that such influences should be taken into account when assessing ranges of variation in fossil species. It is also worth noting that the apparent diminution in dental size of orang-utans in Sumatra and Borneo during the late Quaternary is linked to ecological and climatic change associated with elevated global temperatures since the Last Glacial Maximum at 20–17 ka (Harrison, 1996,

Table 1 Comparisons of coefficients of variation (CV) in extant and subfossil orang-utans and in *Lufengpithecus**

	Extant <i>Pongo pygmaeus</i>			<i>P. pygmaeus</i> <i>palaeosumatrensis</i> (subfossil) Hooijer (1948)	Extant <i>P. pygmaeus</i> + <i>P. pygmaeus</i> <i>palaeosumatrensis</i> Hooijer (1948) Harrison (unpub.)	<i>Lufengpithecus</i> <i>lufengensis</i> Wood & Xu (1991)
	Martin & Andrews (1993)	Wood & Xu (1991)	Hooijer (1948) Harrison (unpub.)			
I ¹ M-D	8.89	11.2	10.05 (85)	9.45 (28)	10.47 (113)	7.6 (47)
I ¹ B-L	10.34	11.2	9.81	7.68	10.84	9.1 (62)
I ² M-D	8.14	11.3	8.52 (85)	9.60 (36)	10.90 (121)	10.4 (30)
I ² B-L	12.11	12.9	11.52	8.51	11.47	11.0
C M-D	16.2	16.0	18.55 (85)	21.34 (55)	20.36 (140)	17.3 (39)
C B-L	17.55	17.3	17.82	18.61	18.17	18.4 (37)
P ³ M-D	7.43	9.2	10.12 (85)	9.17 (196)	9.54 (281)	11.3 (34)
P ³ B-L	7.53	8.9	9.73	10.51	10.68	11.1 (35)
P ⁴ M-D	10.71	10.7	9.05 (85)	8.57 (273)	8.85 (358)	8.8 (38)
P ⁴ B-L	8.22	9.0	9.15	9.64	9.91	9.5
M ¹ M-D	6.83	7.1	8.68 (85)	7.32 (328)	7.71 (413)	9.0 (41)
M ¹ B-L	6.34	6.5	7.61	7.08	7.27	8.9
M ² M-D	9.22	10.2	10.81 (85)	8.42 (342)	9.72 (427)	9.9 (44)
M ² B-L	7.31	8.3	8.72	8.16	8.92	9.8
M ³ M-D	13.19	12.2	12.74 (85)	10.01 (228)	10.67 (313)	12.0 (24)
M ³ B-L	7.42	9.7	9.72	10.60	10.53	11.2
I ₁ M-D	10.36	11.7	8.45 (84)	7.77 (49)	8.87 (133)	8.1 (33)
I ₁ B-L	8.80	9.7	9.94	9.97	10.83	11.6 (34)
I ₂ M-D	10.11	12.9	7.81 (84)	8.39 (141)	8.92 (225)	8.5 (35)
I ₂ B-L	10.16	10.1	12.42	10.25	11.33	14.1
C M-D	13.86	20.2	14.97 (84)	15.44 (101)	15.84 (185)	17.5 (48)
C B-L	19.47	14.1	20.39	21.06	21.50	15.7 (47)
P ₃ M-D	12.67	10.5	12.25 (84)	11.70 (255)	12.01 (339)	15.0 (32)
P ₃ B-L	9.19	13.8	10.55	11.33	11.57	15.1 (33)
P ₄ M-D	10.65	9.3	12.25 (84)	8.86 (266)	9.98 (350)	11.7 (46)
P ₄ B-L	10.9	9.0	8.93	8.73	8.99	9.6
M ₁ M-D	5.92	6.9	7.61 (84)	6.92 (207)	7.77 (291)	9.2 (42)
M ₁ B-L	6.56	7.1	7.72	6.98	7.53	10.4 (43)
M ₂ M-D	8.22	7.9	10.21 (84)	8.06 (225)	9.85 (309)	10.2 (63)
M ₂ B-L	7.95	8.4	9.11	7.75	9.03	10.5
M ₃ M-D	9.98	9.7	11.15 (84)	9.95 (214)	10.36 (298)	9.7 (38)
M ₃ B-L	8.74	10.0	10.48	9.88	10.21	10.3 (39)

*Sample size in parentheses.

2000). Similar trends in dental reduction have been noted in other mammals in south-east Asia, and for primates at least, these data are consistent with modern ecogeographic models relating differences in ambient temperature to the effects of Bergmann's rule (Fooden & Albrecht, 1993; Harrison, 1996, 2000). It is interesting to note in this regard that the palynological data from Shihuiba indicate a climatic and ecological shift from a warm and humid tropical/subtropical forest setting to cooler decidu-

ous woodland and bushland conditions (Sun & Wu, 1980; Qi, 1993). To date, the Lufeng hominoid sample has been studied collectively, but given the indications above we advocate reanalysis of the collections to test whether sub-samples from individual beds are metrically more uniform (while accounting for the reduced sample sizes) and whether there are indications of microevolutionary changes in dental size associated with climatic variation or other ecological factors.

The collections from Xiaolongtan and Yuanmou also exhibit a morphological pattern and degree of variation that is consistent with a single sexually dimorphic species (see also Liu *et al.*, 1999, 2000). Nevertheless, the recognition of a single species of hominoid at each site still does not resolve the question of how many species in total are represented. Provisionally, we consider the Lufeng and Xiaolongtan+Yuanmou samples to belong to two species (see also Gao, 1998). The combined Xiaolongtan and Yuanmou material differs morphologically from that from Lufeng in having: upper canines higher crowned; upper and lower canines more bilaterally compressed, at least in females; small disto-buccal style present on P³, upper molars with more distinct lingual cingulum remnants; I₂ that tends to have a more convex distal margin, rather than being angular; lower canines with less well-developed lingual cingulum that does not continue around the base of the lingual pillar; P³ more bilaterally compressed, with less well-developed lingual cingulum, distinct disto-lingual bulge, and more weakly developed metaconid; mesostylid better developed on M₂ and M₃; distinctive lower molar wear pattern with earlier exposure of dentine on all cusp tips, suggestive of thinner enamel; and greater degree of molar enamel wrinkling. The Yuanmou and Xiaolongtan teeth also differ in overall size—the cheek teeth are 19% smaller in occlusal area on average than those from Shihuiba, and they have only a 62% overlap of their ranges (data from Woo, 1957, 1958a; Wood & Xu, 1991; Zhang, 1987; Liu, 2000). It is noteworthy, perhaps, that the older samples from Xiaolongtan and Yuanmou can be inferred to have a more primitive dental pattern than the younger sample from Shihuiba.

Our preliminary comparisons, and those of other recent workers, have served to highlight the close morphological and metrical

similarities between these species, and there seems to be good grounds to include them together in a single genus distinct from all other Eurasian hominoids. Given the discussion above, the valid names for these species are *L. keiyuanensis* (Woo, 1957) from Keiyuan and Yuanmou and *L. lufengensis* (Xu *et al.*, 1978) from Shihuiba, Lufeng. If the Yuanmou material later proves to be a separate species from that from Keiyuan, then the name *L. hudienensis* would be available. Similarly, if the material from Yuanmou is considered to belong to several distinct species, then the following additional *nomina* are available: *orientalis* Zhang *et al.*, 1987b from Baozidongqing; *progressus* Pan, 1996 from Fangbeiliangzi; and *yuanmouensis* Zheng & Zhang, 1997 from Hudieliangzi. Moreover, if it were found desirable to distinguish the Yuanmou sample (or Yuanmou+Keiyuan samples) at the generic level, then the genus name *Sinopithecus* Zhang *et al.*, 1990 is available.

Phylogenetic relationships

A range of opinions has been expressed about the relationships of *Lufengpithecus* (Wu *et al.*, 1983, 1986; Kelley & Pilbeam, 1986; Wu & Wang, 1987; Kelley & Etlar, 1989; Schwartz, 1990, 1997; Begun *et al.*, 1997; Harrison & Rook, 1997), and there is currently little agreement about its phylogenetic position. However, most authors acknowledge that *Lufengpithecus* largely exhibits primitive hominid⁵ features (even though there is little consensus about the inferred polarities of individual characters). Possible primitive hominid traits exhibited by *Lufengpithecus* include: temporal lines converge anteriorly to form a frontal trigon

⁵The taxonomic terminology for major extant hominoid groups (and their extinct close relatives) used here follows that of Harrison & Rook (1997): Hominoidea (hominoids)=Hylobatidae (hylobatids)+Hominidae (hominids); Hominidae=Ponginae (pongines)+Homininae (hominines); Ponginae=*Pongo* (orang-utans); Homininae=African apes+humans; Hominini (hominins)=humans.

and a low sagittal crest in males; weakly developed supraorbital torus, without a supraorbital sulcus; wide interorbital region; orbits slightly broader than high; relatively short face with anteriorly placed zygomatic root; flattened anteriorly facing and deep zygomatic bone; short nasoalveolar clivus; broad incisive fossa with stepped subnasal floor; mandibular corpus relatively deep and quite slender; well-developed inferior transverse torus of mandible with weaker superior torus; relatively narrow incisors; canines relatively large in males and strongly sexually dimorphic; canines relatively slender; P^3 with a relatively long mesial face; P_4 broader than long; lower molars with buccal cingulum vestigial to absent; M_3 subequal in occlusal area to that of M_2 (Wu *et al.*, 1986; Kelley & Etlar, 1989; Schwartz, 1990, 1997).

Superimposed on this primitive hominid cranio-dental pattern are a few specializations that can be interpreted as uniquely derived (i.e., depressed glabellar region and relatively tall and slender incisors) or possible synapomorphies linking *Lufengpithecus* to the *Sivapithecus-Pongo* clade (i.e., increased wrinkling of molar enamel, and I^2 small in relation to I^1) (Wu *et al.*, 1983, 1986; Wu, 1987; Kelley & Etlar, 1989; Schwartz, 1990, 1997). Given the currently available evidence, two interpretations seem to be the most plausible: (1) that *Lufengpithecus* is a primitive hominid that, like the Dryopithecinae, represents the sister taxon to the Ponginae+Homininae (Andrews *et al.*, 1996; Harrison & Rook, 1997; but see Begun, 1992, 1994 and Begun & Kordos, 1997 for an alternative perspective on the position of *Dryopithecus*), or (2) that *Lufengpithecus* is a primitive sister taxon to the Ponginae. Although we favor, on balance, the latter alternative, we recognize that a more comprehensive comparative analysis is needed to substantiate the phylogenetic and taxonomic affinities of *Lufengpithecus*.

Biogeography and hominoid extinctions

One of the most important implications of the fossil hominoids from Yunnan is that they provide a unique temporal perspective on the evolutionary history of hominoids. They occur during a time interval (based on the correlations discussed above) when hominids became extinct throughout much of Eurasia (Andrews *et al.*, 1996) (Figure 3). The hominid fauna that occupied Europe, southwest Asia, Indo-Pakistan and China during the middle and earliest late Miocene (~15–9 Ma) witnessed a significant decline in diversity by the close of the Vallesian (at ~9.0 Ma) (Andrews *et al.*, 1996). Apart from *Oreopithecus bambolii*, which survived to ~6–8 Ma (MN 12–13) as a specialized island endemic in the Tusco-Sardinian region of southern Europe (Rook *et al.*, 1996; Harrison & Rook, 1997), hominids had become extinct in Europe by ~8 Ma (MN 11) (Andrews *et al.*, 1996). In Indo-Pakistan, *Sivapithecus* survived until at least 7.4 Ma, and was subsequently succeeded by *Gigantopithecus giganteus*, which possibly occurred until 6.3 Ma (Johnson *et al.*, 1983; Barry, 1986; Flynn *et al.*, 1995) (see Figure 3). The discovery of abundant remains of hominids at the late Miocene localities of Shihuiba and Yuanmou (~7–9 Ma) and early Pliocene locality of Baoshan (~3–5 Ma) therefore takes on special significance.⁶ They are among the youngest known hominoid-bearing localities in Eurasia. In fact, the latter site may represent the only known hominid locality in Eurasia of early Pliocene age, broadly contemporaneous with the emergence and initial diversification of hominins in Africa.

⁶It has been suggested that the hominoid specimen from the early Pleistocene locality of Longgupo, initially attributed to early *Homo* (Huang *et al.*, 1995), might, in fact, belong to an ape, possibly related to *Lufengpithecus* (Etlar & Zhou, 1998; Wu, 2000). While we recognize that the taxonomic status of this specimen is problematic, we are not persuaded by the morphological evidence that purportedly links it to *Lufengpithecus*.

It appears that southern China (and presumably southeast Asia in general, for which we have no pertinent fossil evidence) was an important refugium for hominoids after their extinction in mainland Europe by the early Turolian (~8–9 Ma) and in South Asia by the close of the Miocene (~5–6 Ma). This primate fauna presumably also included the ancestors of extant gibbons and orang-utans, whose fossil record is first documented in the region from the early Pleistocene onwards (Hooijer, 1948, 1960; Kahlke, 1972; Aigner, 1978; Von Koenigswald, 1982; Han & Xu, 1985; Gu, 1986, 1989; Gu *et al.*, 1987; Nisbett & Ciochon, 1993; Pan, 1994; Schwartz *et al.*, 1994, 1995). An important contributing factor in the survival of hominoids in Yunnan may be related to a major phase in the uplift of the Tibetan Plateau to the west, which occurred at 8–10 Ma (Harrison *et al.*, 1992; An *et al.*, 2001; Qiang *et al.*, 2001). This isolated them regionally, and helped to maintain a more mesic, subtropical climatic system (Li, 1991; Liu *et al.*, 1997; Jablonski & Whitfort, 1999) at a time (~8 Ma) when South Asia and the East Asian interior were experiencing increased seasonality (An *et al.*, 2001). These conditions probably persisted until the end of the Pliocene, when further uplift of the Tibetan Plateau (at ~3.6–2.6 Ma) led to intensification of the winter monsoon, and coincided with the onset of a major phase of glaciation in the Northern Hemisphere (at ~2.7 Ma), resulting in more seasonal conditions regionally, at least in the northern sector of the southeast Asian province (An *et al.*, 2001; Qiang *et al.*, 2001). Further study of the hominoid faunas from Yunnan and their paleoecology is therefore critical for a better understanding of the biogeography, diversity, and evolutionary history of Asian hominoids in general.

Another important consideration, perhaps, is the impact on the primate fauna of the arrival of hominins in southern China

(and southeast Asia) during the early Pleistocene. It is possible, given the level of technological sophistication of *H. erectus*, and later-arriving *H. sapiens*, that they may have been capable of hunting large hominoids, especially in those areas predominated by seasonal subtropical woodlands where terrestriality was likely to be a significant component of the locomotor repertoire of hominoid primates (Smith & Pilbeam, 1980). Hunting by hominins may have been a contributing factor in the extirpation of orang-utans (and perhaps *Gigantopithecus*) from south China, mainland southeast Asia, and Java by the early Holocene (Harrison, 1996, 1998, 2000; Delgado & van Schaik, 2000). Relict populations of orang-utans survived to the present in the perhumid tropical forests of Borneo and Sumatra, probably because of a combination of factors: (1) these populations may have been smaller in body size and more committed to a fully arboreal habit than mainland orang-utans (Smith & Pilbeam, 1980; Harrison, 1996, 1998, 2000; but see Bacon & Long, 2001 for potentially contrary evidence); (2) current evidence suggest that modern human hunter-gatherers were unable to extensively exploit tropical forests in southeast Asia prior to the introduction of agriculture because of the limited subsistence base that these ecosystems offer to obligate hunter-gatherers (and we can assume the same ecological constraints applied to *H. erectus*) (Hutterer, 1983; Headland, 1987; Bailey *et al.*, 1989; Bailey & Headland, 1991; Endicott & Bellwood, 1991). Orang-utans were therefore able to survive in Borneo and Sumatra because of their specialized arboreality in tropical forest ecosystems and because of the low population densities of hominins on these islands (Harrison, 1996, 1998, 2000). By contrast, fast-moving arboreal hylobatids (and cercopithecids) would probably have proved beyond the hunting capabilities of Plio-Pleistocene hominins

(given that humans in Borneo could only effectively exploit small to medium-sized arboreal mammals subsequent to the introduction of projectile technology during the latest Pleistocene; see [Medway, 1959, 1977](#); [Harrison, 1996](#)). The widespread distribution of hylobatids throughout Southeast Asia was probably largely unaffected, therefore, by the arrival of *Homo*. In order to test these ideas, it will be necessary to document as fully as possible the diversity and paleobiology of the hominoid fauna from the Pliocene of Yunnan prior to the arrival of hominins, and to examine the factors that may have contributed to changes in the Pleistocene faunas resulting from ecological change, including the impact of *Homo*. Further paleontological work in Yunnan should help to clarify aspects of the evolutionary history of Asian hominoids, including their patterns of extinction.

Summary

Late Miocene and Pliocene localities in Yunnan Province, China have yielded evidence critical for documenting the evolutionary history, biogeography, and paleobiology of later Neogene hominids in Eurasia. Unfortunately, the taxonomy of these fossil apes is presently in a confused state, and one of the main goals of this paper has been to provide a clarification of their taxonomy and nomenclature. The morphology and degree of variation observed in the fossil samples is consistent with there being a single, sexually dimorphic species represented at each site. At present, we recognize the Xiaolongtan+Yuanmou and Shihuiba samples as belonging to two separate species within a single genus. The valid names for these taxa are *L. keiyuanensis* ([Woo, 1957](#)) and *L. lufengensis* ([Xu et al., 1978](#)) respectively.

A preliminary assessment of the phylogenetic relationships of *Lufengpithecus* suggests that it is either a primitive hominid

that represents the sister taxon of the Ponginae+Homininae or a primitive sister taxon to the Ponginae. Although we favor the latter alternative, we acknowledge that a more comprehensive comparative analysis is needed. An important observation is that the Yunnan fossil apes provide a unique temporal perspective on the evolutionary history of hominoids. Their continued occurrence during the late Miocene and Pliocene (~8–2 Ma), when hominoids became extinct throughout the rest of Eurasia, suggests that southern China (and presumably southeast Asia in general) was an important refugium for hominoids, including the ancestors of orang-utans and gibbons. An important contributing factor in the survival of hominoids in Yunnan may be related to uplift of the Tibetan plateau (at ~8–10 Ma) and the resulting regional climatic conditions which isolated them geographically and ecologically. The more seasonal climatic condition associated with further uplift of the Tibetan plateau and a major phase of glaciation in the Northern Hemisphere in the late Pliocene (between 3.6–2.6 Ma), and possibly the arrival of *Homo* soon after, may have precipitated the regional extinction of large hominoids in southern China and in mainland southeast Asia.

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