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Phalangeal morphology of Shanghuang fossil primates

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ABSTRACT

Here, we describe hundreds of isolated phalanges attributed to middle Eocene fossil primates from the Shanghuang fissure-fillings from southern Jiangsu Province, China. Extending knowledge based on previous descriptions of postcranial material from Shanghuang, this sample of primate finger and toe bones includes proximal phalanges, middle phalanges, and over three hundred nail-bearing distal phalanges. Most of the isolated proximal and middle phalanges fall within the range of small-bodied individuals, suggesting an allocation to the smaller haplorhine primates identified at Shanghuang, including eosimiids. In contrast to the proximal and middle phalanges from Shanghuang, there are a variety of shapes, sizes, and possible taxonomic allocations for the distal phalanges. Two distal phalangeal morphologies are numerically predominant at Shanghuang. The sample of larger bodied specimens is best allocated to the medium-sized adapiform *Adapoides* while the smaller ones are allocated to eosimiids on the basis of the commonality of dental and tarsal remains of these taxa at Shanghuang. The digit morphology of *Adapoides* is similar morphologically to that of notharctines and cercamoniines, while eosimiid digit morphology is unlike living anthropoids. Other primate distal phalangeal morphologies at Shanghuang include grooming "claws" as well as specimens attributable to tarsiids, tarsiiforms, the genus *Macrotarsius*, and a variety of adapiforms. One group of distal phalanges at Shanghuang is morphologically indistinguishable from those of living anthropoids. All of the phalanges suggest long fingers and toes for the fossil primates of Shanghaung, and their digit morphology implies arboreality with well-developed digital flexion and strong, grasping hands and feet.

1. Introduction

The ancient fossil primate community from the Shanghuang fissure-fillings in China is unique in a variety of ways. Foremost among these is its remarkable diversity: at least 18 species (both named and unnamed) are known on the basis of morphology (Beard et al., 1994; Gebo et al., 2001, 2012). This is followed closely by the highly unusual size distribution of Shanghuang primates (15–1000 g), many species of which are mouse lemur-sized or smaller, including the smallest primates ever recovered (Gebo et al., 2000, 2012). Although Shanghuang has yielded conventional Eocene primate taxa such as the Omomyidae and Adapoidea, this site also contains the oldest known members of Tarsiidae and Anthropoidea, as well as several new taxa that are not yet recorded elsewhere (Beard et al., 1994; Gebo et al., 2001, 2012). Last, Shanghuang is located in Asia, a continent which is frequently cited as the most likely locus of primate and anthropoid origins (Szalay and Li, 1986; Beard et al., 1994, 1996; Beard, 1998, 2006, 2008, 2016; Ni et al., 2004, 2005), in contrast to the better-documented and contemporaneous primate faunas known from the Eocene of North America and Europe.

The fossils from the Shanghuang fissure-fillings in China have been recovered by screen washing the karstic infillings (fissures A–E) exposed at a commercial quarry for cement production. On the basis of biostratigraphic correlation with the Irdinmanhan and early Sharamurunian Land Mammal Ages of Asia, this fauna is considered to be middle Eocene in age (~45 Ma; Beard et al., 1994). Although screen washing has produced a large number of fossils, the majority are isolated and broken elements, making the process of taxonomic allocation difficult.

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In terms of the sheer number of specimens, the teeth of adapiforms and eosimiids far exceed those of other Shanghuang primate taxa, named or unnamed. The distal phalanges of Shanghuang primates, which now number in the hundreds, demonstrate a similar pattern of relative abundance (see below). The entire Shanghuang postcranial sample is skewed toward small primates weighing less than 150 g, with most Shanghuang fossil haplorhines overlapping the size range of the smallest living primates such as *Microcebus* spp., *Tarsius pumilus*, and *Galagoides demidovii* (Musser and Dagosto, 1987; Rasoloarison et al., 2000; Dagosto et al., 2003; Gould and Sauther, 2007; Gursky, 2007; Nekaris and Bearder, 2007). The Shanghuang adapiforms are larger, but even these taxa are small compared to their close relatives on other continents, which have been estimated to weigh in excess of 1 kg. *Adapoides troglodytes*, the only named adapiform from Shanghuang, is the smallest adapiform currently known from that fauna, ranging in body size between 200 and 400 g (Gebo et al., 2012). Other adapiform dental specimens from Shanghuang suggest that at least two additional adapiform taxa are present, both of which are larger than *A. troglodytes* (Coster et al., 2012). The largest fossil primate identified at Shanghuang is *Macrotarsius macrorhysis* (800–1000 g [Beard et al., 1994; MacPhee et al., 1995]), but this taxon is quite rare in terms of dental evidence. Beard et al. (1994) named four fossil primates from the Shanghuang fissure-fillings: the adapiform *A. troglodytes*, the tarsiid *Tarsius eocaenus*, the omomyid *M. macrorhysis*, and the basal anthropoid *Eosimias sinensis*. Subsequent analyses of primate postcranial elements from Shanghuang support the notion of additional primate diversity at this site (Gebo et al., 2000, 2001, 2008, 2012).

Here we describe, compare, and interpret the sample of 453 isolated primate phalanges recovered from screen-washed sediment derived from the Shanghuang fissure-fillings (Table 1). This sample of primate finger and toe bones includes 32 proximal phalanges and 80 middle phalanges. Whether the middle phalanges pertain to the hand or foot cannot be established with confidence. Given the ease in identifying the flattened distal phalanges of nail-bearing primates (see Fig. 1), the current sample of 341 primate distal phalanges vastly outnumbers the combined sample of proximal and middle phalanges from Shanghuang.

Table 1
Total number and type of Shanghuang phalanges.

Types	*n*
Proximal Phalanges	32
Middle Phalanges	80
Proximal and Middle Phalanx TOTAL	**112**
First Digit Distal Phalanges	
Eosimiid hallux	31
Tarsiiform hallux	10
Unknown hallux – haplorhine	1
Adapiform hallux	5
TOTAL	**47**
Eosimiid pollex	11
Tarsiiform pollex	2
Tarsiid pollex	1
Unknown pollex – haplorhine	2
Adapiform pollex	4
TOTAL	**20**
First Digits TOTAL	**67**
Second Digit Grooming "Claws"	**25**
Lateral Digit Distal Phalanges	
Eosimiid lateral digits	163
Advanced anthropoid lateral digits	3
Tarsiiform lateral digits	7
Tarsiid lateral digits	6
Macrotarsius lateral digits	3
Unknown lateral specimens – haplorhines	1
Haplorhine Lateral Digits TOTAL	**183**
Adapiform Morphology A	55
Adapiform Morphology B	4
Adapiform Morphology C	3
Adapiform Morphology D	2
Unknown lateral specimens – adapiforms	2
Adapiform lateral digits TOTAL	**66**
GRAND TOTAL – Lateral Digits (2–5)	**274**
GRAND TOTAL – All Distal Phalanges	**341**
GRAND TOTAL – All Shanghuang Phalanges	**453**

2. Material, methods and results

As is true for all isolated skeletal elements, and especially for less thoroughly studied bones such as phalanges, making the correct taxonomic allocation to that of a primate is first and foremost as unassociated paleontological postcranial collections normally contain many primate-sized bones, often belonging to rodents or other small mammals. Figure 2 illustrates the proximal and middle phalangeal anatomy of two mammals, a bat (*Pteropus*) and a rodent (*Sciurus*), relative to that of a primate (*Propithecus*). Primate phalanges are distinctive from those of other mammals in several key aspects of their anatomy. For example, bat phalanges have spool-shaped heads and slender shafts. Rodents, like *Sciurus*, possess proximal joint notches, middle phalanges with dorsally oriented heads, and proximal phalanges with large flexor tubercles. In contrast, primate proximal and middle phalanges possess wedge-shaped shafts with smooth joint surfaces. For the distal phalanges, the process of identification is easier given the flattened nail to claw or hoof distinctions between primates and other mammals. After the Shanghuang mammal phalanges were sorted, only those that could be correctly identified and attributed to primate morphologies were counted, resulting in 453 primate phalangeal elements.

In terms of size, these phalanges can be segregated into smaller and larger size bins, a pattern that conforms to our previous studies of Shanghuang postcranial elements (Gebo et al., 2001, 2012). As in previous analyses, the larger specimens generally appear to belong to adapiforms, while the smaller phalanges can be allocated to several haplorhine clades, the most common of which are eosimiids. Relative to the entire sample of distal phalanges, the most common specimens are allocated to the small eosimiids (163 lateral digit distal phalanges, 31 hallucal distal phalanges, and 11 pollical distal phalanges; total = 205; 205/341 = 60%; Table 1) on the basis of commonality and shape (Gebo et al., 2015a). Lateral digit distal phalanges of eosimiids represent 89% of the haplorhine sample (163/183, Table 1), making non-eosimiid haplorhines quite rare in their frequency of occurrence (tarsiiforms, 3.8%; tarsiids, 3.2%; *Macrotarsius*, 1.6%; advanced anthropoids, 1.6%; and unknown haplorhines, 0.5%). Overall, small haplorhine distal phalanges represent over two-thirds of the total sample of distal phalanges (241/341 = 71%; Table 1).

For the Shanghuang adapiforms, lateral digit distal phalanges can be segregated into one common shape and a series of rarer varieties. The most common morph, which we designate as Adapiform Morphology A, is represented by 55 specimens (83% of lateral digit adapiform specimens; Table 1). These specimens are hypothesized to pertain to *A. troglodytes* on the basis of dental and tarsal commonality at Shanghuang. Adapiform Morphologies B, C, and D are much scarcer morphs represented by four, three, and two specimens, respectively (Table 1). We have identified two unknown adapiform distal phalanges in this sample as well. Adapiform distal phalangeal specimens represent 24% of all lateral digit specimens