

PRIMATE HUMERAL REMAINS FROM THE MIDDLE EOCENE OF CHINA

DANIEL L. GEBO

Research Associate, Section of Vertebrate Paleontology; Department of Anthropology, Northern Illinois University, DeKalb, IL 60115
(dgebo@niu.edu)

MARIAN DAGOSTO

Research Associate, Section of Vertebrate Paleontology; Department of Cell and Molecular Biology, Northwestern University Medical School, Chicago, IL 60611 (m-dagosto@northwestern.edu)

K. CHRISTOPHER BEARD

Section of Vertebrate Paleontology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, PA 15213 (beardc@carnegiemnh.org)

XIJUN NI

Research Associate, Section of Vertebrate Paleontology; Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P.O. Box 643, Beijing, China 100044 (nixijun@iupp.ac.cn)

TAO QI

Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P.O. Box 643, Beijing, China 100044

ABSTRACT

Two distal humeral fragments are described from the middle Eocene Shanghuang fissures (southern Jiangsu Province, China). These specimens provide the first evidence of forelimb morphology among Shanghuang primates. One specimen belongs to an adapiform strepsirhine primate that is morphologically similar to European adapines, while the other pertains to a small haplorhine primate having numerous features in common with North American omomyids. Both fossils exhibit classic primate elbow adaptations that are functionally related to arboreality and climbing.

INTRODUCTION

This contribution on Chinese fossil primates is written to honor the career of Dr. Mary Dawson, a longtime collaborator with the Institute of Vertebrate Paleontology and Paleoanthropology (Beijing, China). Mary's long list of distinguished publications reveal her remarkable career in mammalian paleontology and we are happy to contribute to this volume in her honor. Our best wishes go out to her.

Over the last several years, the continued washing, sorting, and identification of fossils from the Shanghuang fissures in southern Jiangsu Province, China, has produced additional postcranial elements, including two primate humeral fragments from Shanghuang fissure D that we describe below. These specimens are middle Eocene in age (~45 Ma) and provide the first evidence of forelimb morphology among Shanghuang primates. The Shanghuang humeral fragments represent two different lineages, one from each of the two primate suborders, Strepsirhini and Haplorhini. Both specimens show classic primate elbow features for forearm rotation and mobility related to arboreality and climbing (see Szalay and Dagosto 1980). Their discovery permits us to consider the contribution of forelimb anatomy to our understanding of primate diversity and evolution at Shanghuang and for Asian Eocene primates in general.

Institutional abbreviations are as follows: **AMNH**, American Museum of Natural History; **CM**, Carnegie Museum of Natural History; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology (Chinese Academy of Sciences, Beijing, China); **NIU**, Department of Anthropology, Northern Illinois University; **NMMP**, fossil primate collection, National Museum of Myanmar (Yangon, Myan-

mar); **UCMP**, University of California Museum of Paleontology.

DESCRIPTION

The IVPP V13021 humeral fragment is broken proximally and is eroded in several regions distally (Fig. 1). Its trochlea is poorly preserved. The specimen measures 17.85 mm in absolute length and 8.75 mm in its distal epicondylar width (Table 1). Its width dimensions are similar to *Galago senegalensis* (193–210 g; Bearder 1986), *Cheirogaleus major* (235–470 g; Wright and Martin 1995), *Loris tardigradus* (227–355 g; Bearder 1986), and *Callithrix argentata* (320–357 g; Ford 1994). Our size comparisons suggest that the IVPP V13021 humerus from Shanghuang belongs to a primate that weighed between 200 and 300 g. Although the IVPP V13021 distal humerus is morphologically similar to those of *Adapis parisiensis* (see below), it differs in being much smaller (Table 1). *Adapis parisiensis* is estimated to weigh 1300 g (Fleagle 1999). Based on frequency of dental remains, the most common adapiform at Shanghuang is *Adapoides troglodytes* (Beard et al. 1994). We estimated the body mass of *Adapoides troglodytes* on the basis of its lower first molar dimensions (length, 2.98 mm; width, 2.13 mm) using regression equations provided by Conroy (1987). Conroy's (1987) prosimian regression yielded a mean body mass estimate of 285 g for *Adapoides troglodytes*, while his all-primate regression produced a mean body mass estimate of 343 g. Given the apparent correspondence in both size and morphology, we regard IVPP V13021 as pertaining to *Adapoides troglodytes* here.

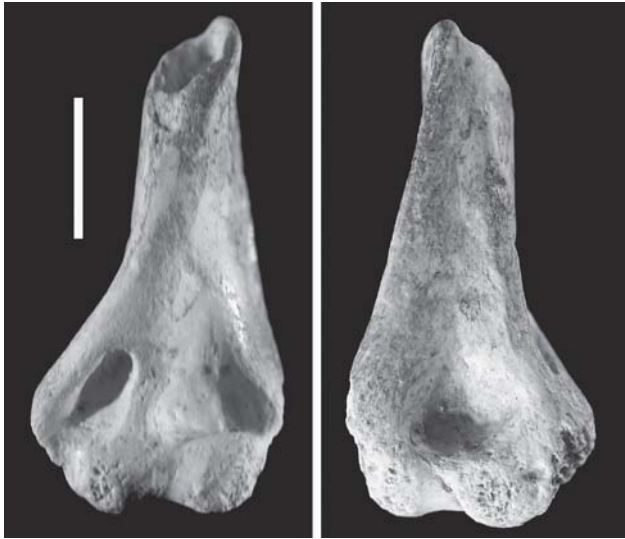


Fig. 1.—Anterior and posterior views of IVPP V13021. Scale bar = 5 mm.

The IVPP V13021 humerus is narrow distally with a small brachial flange. Both of these features are similar to conditions in European *Adapis* and extant lorisine primates and distinguish them from more typical euprimates. The capitulum and trochlea in IVPP V13021 are compressed together with a greatly reduced or absent zona conoidea (Fig. 2). This elbow articular morphology is also found in *Adapis* and lorisine primates (Szalay and Dagosto 1980). The radial fossa is very large and deep in IVPP V13021 (relatively deeper than in *Adapis* and lorises). The entepicondylar foramen is relatively distal in position in IVPP V13021. In contrast, this foramen lies above the level of the radial fossa

in *Adapis* and lorises. Table 2 lists several humeral ratio comparisons between IVPP V13021 and *Adapis*.

The reduced distal width, reduced brachial flange, and compressed articular region in IVPP V13021 are all elbow features that are morphologically and functionally similar to *Adapis* and lorises. Lorises have greatly expanded their capitulum relative to their trochlea (Fig. 3; Szalay and Dagosto 1980). These features have been interpreted as indicating a reduction in ulnar stabilization of the forearm in lorises (Szalay and Dagosto 1980). In contrast, IVPP V13021 has trochlear width and height measures (estimated) that exceed similar measures for the capitulum. This suggests that the elbow joint is not as specialized in IVPP V13021 as it is in lorises. In this regard *Adapis* shares capitular and trochlear elbow features with IVPP V13021 that are lacking in lorises. The numerous similarities in limb morphology shared between *Adapis* and lorises have suggested lorisine-like locomotor capabilities in these fossil primates (Dagosto 1983), although some workers have suggested a more monkey-like movement pattern for *Adapis* (Godinot and Jouffroy 1984; Godinot 1991). We also interpret the IVPP V13021 distal humerus as being lorise-like rather than monkey-like in terms of elbow function and adaptive abilities. The IVPP V13021 humerus from Shanghuang is clearly that of an arboreal quadrupedal primate with good climbing capabilities. Like extant lorises, it probably did not leap frequently, although additional evidence from the hindlimb will be necessary to corroborate this inference. *Adapis* has also been interpreted as an infrequent leaper.

The IVPP V13022 humeral fragment preserves approximately the distal one-third of its original length (Fig. 4). It has a notch removed from the brachial flange and a depressed circular fracture in the center of the anterior surface.

TABLE 1. Humeral measurements (mm) for IVPP V13021. * = estimated value.

| | V13021 | <i>Galago senegalensis</i> n = 8 | <i>Cheirogaleus major</i> n = 2 | <i>Adapis parisiensis</i> n = 4 |
|-----------------------------------|--------|-------------------------------------|------------------------------------|------------------------------------|
| Distal width | 8.75 | 8.82 | 10.67 | 18.26 |
| Total length | — | 31.45 | 35.87 | — |
| Capitulum width | 2.91 | 2.33 | 2.8 | 5.43 |
| Capitulum height | 2.87 | 2.37 | 3.02 | 5.7 |
| Capitular tail length | — | 0.88 | 1.09 | 1.62 |
| Zona conoidea width | — | 0.79 | 1.0 | — |
| Anterior trochlear width | 3.51 | 2.53 | 4.05 | 6.69 |
| Anterior trochlear height—lateral | 2.48* | 2.16 | 2.83 | 4.05 |
| Anterior trochlear height—medial | 3.5* | 2.68 | 3.06 | 5.31 |
| Articular width | 6.42 | 5.51 | 7.87 | 13.8 |
| Posterior trochlear width | 3.5 | 3.4 | 4.33 | 7.8 |
| Posterior trochlear height | 3.14 | 1.93 | 2.79 | 3.68 |
| Trochlear depth | 2.89 | 2.06 | 2.7 | 4.51 |
| Capitular depth | 2.78 | 2.62 | 3.21 | 7.02 |
| Length of brachial flange | 13.84 | 13.78 | 13.67 | 27.96 |
| Midshaft m-l width | 3.44 | 2.68 | 3.15 | 5.74 |
| Midshaft a-p width | 3.5 | 2.80 | 3.06 | 6.14 |
| Medial epicondyle length | 2.23 | 2.58 | 1.63 | 4.36 |



Fig. 2.—Anterior view of distal joint surfaces in IVPP V13021 (left) and *Adapis parisiensis* (right, reversed; AMNH 10018).

The edge of the medial epicondyle is also broken. These breakage patterns are similar to those described for bones of small mammals that have been preyed upon by birds (Andrews 1990), and one might therefore infer that IVPP V13022 was preyed upon by a nocturnal owl or a diurnal raptor. IVPP V13022 is notably small, with a distal width (Table 3) between that of *Microcebus berthae* (mean body mass = 30.6 g; range = 24.5–38 g) and *Microcebus myoxinus* (mean body mass = 49 g; range = 36.5–64 g) (Rasoalison et al. 2000). We suggest that the IVPP V13022 humeral fragment belonged to a primate weighing between 30 and 50 g. Although IVPP V13022 is morphologically similar to humeri of omomyid primates, an allocation to Omomyidae is problematic because omomyid primates of the appropriate size have never been found at Shanghaung (Beard et al. 1994). Measurements for this specimen are provided in Table 3. Ratio values for IVPP V13022 and *Shoshonius* are provided in Table 2.

The IVPP V13022 humerus has a downward or obliquely angled trochlea like that of haplorhine primates (Szalay and Dagosto 1980). It has a wide zona conoidea separating the capitulum from the trochlea. The capitulum is round and oblong in shape, closely resembling that of omomyid primates. The capitulum is not as round as that of tarsiers or *Shoshonius*. The capitulum has a tail, and the capitular tail length to capitulum width ratio (48%) is relatively long but similar to that of many prosimian primates, including *Microchoerus* (47%) and *Tarsius* (44–50%) (Gebo et al. 1994). The posterodistal humerus bears an epi-

trochlear fossa like that observed in *Tetonius* (Fig. 5), *Microchoerus*, and Fayum and extant anthropoids (Conroy 1976; Fleagle and Simons 1982; Ford 1988; Dagosto 1990; Gebo et al. 1994), while tarsiers lack this feature (Dagosto et al. 1999). Distally, the IVPP V13022 humerus has a smaller and more distally located entepicondylar foramen relative to that of *Tarsius* or omomyids such as *Shoshonius* (Dagosto et al. 1999). The medial epicondyle projects medially, like that of an omomyid, but is not as wide as those of *Tarsius* and microchoerids. The brachial flange, from which the brachialis and brachioradialis muscles arise, is large and similar in shape to those of omomyids and some microchoerids. The olecranon fossa is shallow, as is the case in omomyids. There are no special morphological resemblances to the elbow regions of crown-group anthropoids, either fossil taxa from the Fayum or extant platyrrhine monkeys.

At Shanghuang, there are four different haplorhine taxa occupying the 30–50 g size range (Gebo et al. 2001). Thus, size cannot help us allocate this small humeral specimen to a particular taxon of small haplorhine primates at Shanghuang. The IVPP V13022 humerus is morphologically more similar to omomyid primates than it is to tarsiers or crown-group anthropoids. In fact, the only feature it shares with crown-group anthropoids is the epitrochlear fossa, and this feature co-occurs in omomyids and microchoerids. It seems that the best taxonomic allocation for the IVPP V13022 humerus is with either: (1) the omomyid-like primates at Shanghuang (Morphology 1 in Gebo et al. 2001); or (2) a basal anthropoid taxon such as Eosimiidae, in which case IVPP V13022 would illustrate a very primitive elbow morphology for basal anthropoids. Although the morphological evidence is strongest for the first possibility, option two remains an alternative possibility.

DISCUSSION

The two new humeral specimens from Shanghuang illustrate different primate elbow morphologies already documented among Eocene adapines and omomyids. The IVPP V13021 humerus is similar to that of *Adapis* in its reduced distal width, reduced brachial flange, and compressed articular region. It differs from *Adapis* in its smaller size, its

TABLE 2. Ratio values for Shanghuang humeri.

| Ratios | V13021 | <i>Adapis</i> | V13022 | <i>Shoshonius</i> |
|--|--------|---------------|--------|-------------------|
| Capitulum width/trochlear width | 0.83 | 0.81 | 0.84 | 0.69 |
| Capitulum width/capitulum height | 1.01 | 0.95 | 1.05 | 0.81 |
| Capitular tail length/capitulum width | — | 0.30 | 0.48 | 0.38 |
| Lateral trochlear height/medial trochlear height | 0.71 | 0.76 | 0.50 | 0.83 |
| Trochlear width/articular width | 0.55 | 0.48 | 0.38 | 0.47 |
| Trochlear height/articular width | 0.55 | 0.38 | 0.30 | 0.39 |
| Articular width/distal width | 0.73 | 0.76 | 0.73 | 0.70 |
| Medial epicondylar width/distal width | 0.25 | 0.24 | 0.22 | 0.35 |
| Brachial flange length/distal width | 1.58 | 1.53 | 1.06 | 1.63 |
| m-l shaft width/a-p shaft width | 0.98 | 0.93 | 0.96 | 1.02 |



Fig. 3.—Left distal humerus of a lorisine (*Nycticebus coucang*, NIU 99-4-1). Note the enlarged capitulum.

deeper radial fossa, and in the position of the entepicondylar foramen. The IVPP V13022 humerus is most similar to those of North American omomyids such as *Tetonius*, although its entepicondylar foramen is located more distally. It is less similar to humeri of *Tarsius*, *Shoshonius*, and European microchoerids. Although both Shanghuang humeral specimens exhibit differences from Eocene primate humeri that were previously known, they are well within the morphological range of adapine and omomyid humeral morphs. The only Eocene primate elbow morphology currently missing from the Shaunguang site is that of a notharctine or cercamoniine primate. Although the “notharctine” morphological condition is not yet documented from the Shanghuang fissures, poorly known sivaladapids like *Hoanghoni* might be predicted to possess such a morphology, given their notharctine-like first metatarsal (Gebo et al. 1999). Elsewhere in Asia, this “notharctine” elbow morphology has been documented from the Eocene of Myanmar (Pondaung Formation), in the form of a humerus included in a partial skeleton (NMMP 20; Fig. 5) that has often been attributed to the amphipithecoid *Pondaungia* (Ciochon et al. 2001) and later to *Pondaungia savagei* (Gunnell et al. 2002; Ciochon and Gunnell 2002). For an alternative taxonomic allocation for NMMP 20, see Beard et al. (2007) and Marivaux et al. (in press).

The NMMP 20 humerus is large (Fig. 6), and its allocation to *Pondaungia savagei* rests solely on the basis of its size, given that the NMMP 20 partial skeleton was not found in association with diagnostic dental remains. Ciochon et al. (2001) estimated that the NMMP 20 humerus pertains to a species having a body mass of 5 to 6 kg, based on humeral length and its diameter at midshaft. We estimate that NMMP 20 belongs to a primate that would have weighed between 3.2 and 9.6 kg, using both humeral and calcaneal dimensions as size estimators. Our mean body mass estimate for NMMP 20 is 5.9 kg. Body mass estimates for species of *Pondaungia* using dental measurements range from 4 to 9 kg according to Ciochon et al. (2001). Egi et al. (2004) provided similar estimates for *Pondaungia savagei* ranging from 8.4 to 9.5 kg, with a mean estimated

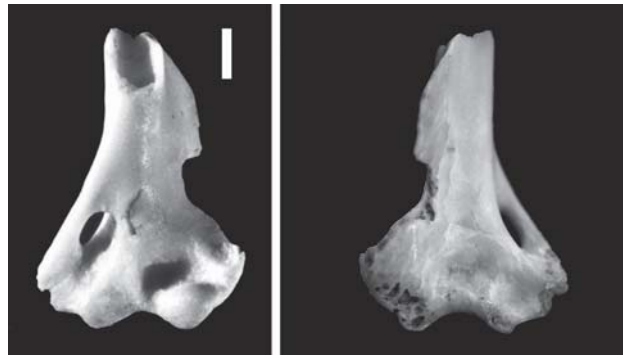


Fig. 4.—Anterior and posterior views of IVPP V13022. Scale bar = 1 mm.

body mass of 8.8 kg. Jaeger et al. (2004) revised the species-level systematics of the larger-bodied amphipithecids from the Pondaung Formation, recognizing only *Pondaungia cotteri* as a valid species exhibiting a high degree of sexual dimorphism [with an estimated body mass ranging from 5.5 to 10 kg, using the anthropoid regression equation in Conroy (1987)]. Jaeger et al. (2004) regard the holotypes of *Amphipithecus mogaungensis* and *Pondaungia savagei* as male individuals of the sexually dimorphic species *Pondaungia cotteri*. The NMMP 20 humerus fits within the lower end of the range of estimated body mass for this revised taxon, *Pondaungia cotteri*.

Ciochon and his collaborators have repeatedly argued that the notharctine-like humerus included in the NMMP 20 partial skeleton indicates that *Pondaungia* and its close relatives are adapiforms rather than anthropoids (Ciochon et al. 2001; Gunnell et al. 2002; Ciochon and Gunnell 2002, 2004). This result agrees with some phylogenetic analyses of amphipithecoid dentitions (Ciochon and Holroyd 1994; Gunnell et al. 2002). In contrast, most workers have argued that the dental evidence for Amphipithecidae provides compelling data in support of their anthropoid affinities (Pilgrim 1927; Colbert 1937; Simons 1971; Ba Maw et al. 1979; Ciochon et al. 1985; Godinot 1994; Chaimanee et al. 2000; Jaeger et al. 1998, 2004; Beard 2002; Marivaux et al. 2005). The apparently conflicting phylogenetic signal yielded by the NMMP 20 humerus on the one hand (which suggests adapiform affinities) and the amphipithecoid dentition on the other (which most workers acknowledge supports anthropoid affinities) is problematic, because it is highly unlikely that ancestral anthropoids would possess notharctine-like elbows given the similarities among anthropoids, tarsiers, and omomyids in elbow morphology (Szalay and Dagosto 1980). We are left with several unsatisfying possibilities. These include the following: (1) the dental evidence suggesting that amphipithecids are anthropoids is misleading, and amphipithecids are indeed adapiform primates (Ciochon et al. 2001; Gunnell et al. 2002; Ciochon and Gunnell 2002, 2004); (2) the postcranial evidence suggesting that amphipithecids are adapiforms is misleading, indicating a high and previously unsuspected level of homoplasy in the appendicular anatomy of early anthropoids; or (3) NMMP 20, which was not associated

TABLE 3. Humeral measurements (mm) for IVPP V13022.

| | V13022 | <i>Microcebus myoxinius</i> n = 7 | <i>Microcebus berthae</i> n = 1 | <i>Shoshonius cooperi</i> CM 69755 |
|-----------------------------------|--------|--------------------------------------|------------------------------------|---------------------------------------|
| Distal width | 4.5 | 4.97 | 4.18 | 6.12 |
| Total length | — | 20.93 | 18.37 | 24.87 |
| Capitulum width | 1.05 | 1.22 | 1.09 | 1.4 |
| Capitulum height | 1.0 | 1.44 | 1.25 | 1.72 |
| Capitular tail length | 0.5 | 0.11 | 0.15 | 0.53 |
| Zona conoidea width | 0.5 | 0.48 | 0.4 | 0.33 |
| Anterior trochlear width | 1.25 | 1.69 | 1.46 | 2.03 |
| Anterior trochlear height—lateral | 0.5 | 1.27 | 1.16 | 1.39 |
| Anterior trochlear height—medial | 1.0 | 1.58 | 1.37 | 1.68 |
| Articular width | 3.3 | 3.5 | 3.1 | 4.29 |
| Posterior trochlear width | 1.2 | 2.33 | 1.6 | 3.26 |
| Posterior trochlear height | 0.5 | 1.42 | 0.9 | 1.34 |
| Trochlear depth | 1.1 | 1.2 | 1.31 | 1.44 |
| Capitular depth | 1.75 | 1.71 | 1.44 | 1.94 |
| Length of brachial flange | 4.75 | 7.0 | 6.54 | 10.0 |
| Midshaft m-l width | 1.25 | 1.57 | 1.31 | 1.98 |
| Midshaft a-p width | 1.3 | 1.69 | 1.44 | 1.94 |
| Medial epicondyle length | 1.0 | 1.04 | 0.8 | 2.15 |

with amphipithecoid dental remains in the field, has been misallocated to the Amphipithecidae (Beard et al. 2007; Marivaux et al. in press). Option 3 decouples the NMMP 20 partial skeleton from the Amphipithecidae, leaving no reason to doubt the anthropoid phylogenetic signal provided by amphipithecoid teeth and jaws.

Overall, the Eocene record of primate humeri from Asia is exceedingly similar to the North American and European records. The IVPP V13021 elbow is *Adapis*-like, and it probably pertains to *Adapoides*. *Adapoides* is older and dentally more primitive than the adapines found in Europe (Beard et al. 1994). The dental and elbow evidence from Shanghaung supports the hypothesis of an early Asian migration to Europe for adapine primates (Beard et al. 1994). However, given the differences in humeral morphology between *Adapis* and *Leptadapis* in Europe (Dagosto 1983), the similarities in elbow morphology shared by IVPP

V13021 and *Adapis* but not *Leptadapis* suggest multiple dispersal events of adapines from Asia to Europe or a case of convergent evolution. Although Asian adapines remain poorly documented postcranially, what is known shows them to be rather distinctive relative to notharctine or ceramoniine adapiform primates.

The IVPP V13022 elbow is very similar to those of omomyid primates from North America. Unfortunately, there are several small primate taxa of this size at Shanghaung, rendering any taxonomic allocation problematic. The IVPP V13022 humerus does not share any distinctive features with tarsiers, nor does it look like the humerus of crown-group anthropoids. It matches best with our “Morphology 1” designation for the tarsal elements (Gebo et al. 2001). Unfortunately, the taxonomic affinities of the Shanghaung primates having “Morphology 1” tarsals remain obscure at present. Clearly, a reassessment of the diverse range of primate dental remains found at Shanghaung is warranted to



Fig. 5.—Posterior views of IVPP V13022 (left) and *Tetonius* (right; UCMP 134843). Note the presence of an epitrochlear fossa on both specimens (arrows).

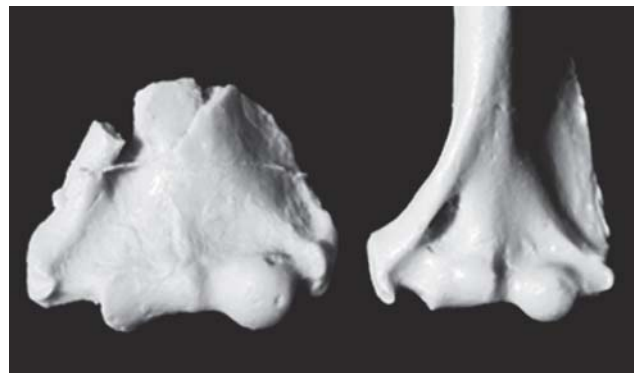


Fig. 6.—Distal humerus from Pondaung (NMMP 20; left) and *Notharctus tenebrosus* (AMNH 127167; right).

clarify the likely identity of this unnamed group of primates.

ACKNOWLEDGMENTS

Our research has been supported by U.S. National Science Foundation grant BCS 0309800 and Chinese National Science Foundation grant NSFC 40672009.

LITERATURE CITED

- ANDREWS, P. 1990. *Owls, Caves and Fossils*. University of Chicago Press, Chicago.
- BA MAW, R.L. CIOCHON, AND D.E. SAVAGE. 1979. Late Eocene of Burma yields earliest anthropoid primate, *Pondaungia cotteri*. *Nature*, 282: 65–67.
- BEARD, K.C. 2002. Basal Anthropoids. Pp. 133–149, in *The Primate Fossil Record* (W. C. Hartwig, ed.). Cambridge University Press, Cambridge.
- BEARD, K.C., L. MARIVAUX, SOE THURA TUN, AUNG NAING SOE, Y. CHAIMANEE, WANNA HTOON, B. MARANDAT, HTUN HTUN AUNG, AND J.-J. JAEGER. 2007. New sivaladapid primates from the Eocene Pondaung Formation of Myanmar and the anthropoid status of Amphipithecidae. *Bulletin of Carnegie Museum of Natural History*.
- BEARD, K.C., T. QI, M.R. DAWSON, B. WANG, AND C. LI. 1994. A diverse new primate fauna from middle Eocene fissure-fillings in southeastern China. *Nature*, 368:604–609.
- BEARDER, S.K. 1986. Lorises, bushbabies, and tarsiers: Diverse societies in solitary foragers. Pp. 11–24, in *Primate Societies* (B.B. Smuts, D.L. Cheney, R.M. Seyfarth, and R.W. Wrangham, eds.). University of Chicago Press, Chicago.
- CHAIMANEE, Y., TIN THEIN, S. DUCROCQ, AUNG NAING SOE, M. BENAMMI, THAN TUN, THIT LWIN, SAN WAI, AND J.-J. JAEGER. 2000. A lower jaw of *Pondaungia cotteri* from the late middle Eocene Pondaung Formation (Myanmar) confirms its anthropoid status. *Proceedings of the National Academy of Sciences*, 97:4102–4105.
- CIOCHON, R.L., AND G.F. GUNNELL. 2002. Chronology of primate discoveries in Myanmar: Influences on the anthropoid origins debate. *Yearbook of Physical Anthropology*, 45:2–35.
- . 2004. Eocene large-bodied primates of Myanmar and Thailand: Morphological considerations and phylogenetic affinities. Pp. 249–282, in *Anthropoid Origins: New Visions* (C.F. Ross and R.F. Kay, eds.). Kluwer Academic/Plenum Publishers, New York.
- CIOCHON, R.L., AND P.A. HOLROYD. 1994. The Asian origin of Anthropoidea revisited. Pp. 143–162, in *Anthropoid Origins* (J.G. Fleagle and R.F. Kay, eds.). Plenum Press, New York.
- CIOCHON, R.L., P.D. GINGERICH, G.F. GUNNELL, AND E.L. SIMONS. 2001. Primate postcrania from the late middle Eocene of Myanmar. *Proceedings of the National Academy of Sciences*, 98:7672–7677.
- CIOCHON, R.L., D.E. SAVAGE, THAW TINT, AND BA MAW. 1985. Anthropoid origins in Asia? New discovery of *Amphipithecus* from the Eocene of Burma. *Science*, 229:756–759.
- COLBERT, E.H. 1937. A new primate from the upper Eocene Pondaung Formation of Burma. *American Museum Novitates*, 951:1–18.
- CONROY, G.C. 1976. Primate postcranial remains from the Oligocene of Egypt. *Contributions to Primatology*, 8:1–134.
- . 1987. Problems of body-weight estimation in fossil primates. *International Journal of Primatology*, 8:115–137.
- DAGOSTO, M. 1983. Postcranium of *Adapis parisiensis* and *Leptadapis magnus* (Adapiformes, Primates). *Folia Primatologica*, 41:49–101.
- . 1990. Models for the origin of the anthropoid postcranium. *Journal of Human Evolution*, 19:121–140.
- DAGOSTO, M., D.L. GEBO, AND K.C. BEARD. 1999. Revision of the Wind River Faunas, early Eocene of central Wyoming. Part 14. Postcranium of *Shoshonius cooperi* (Mammalia: Primates). *Annals of Carnegie Museum*, 68:175–211.
- EGI, N., M. TAKAI, N. SHIGEHARA, AND T. TSUBAMOTO. 2004. Body mass estimates for Eocene eosimiid and amphipithecid primates using primate and anthropoid scaling models. *International Journal of Primatology*, 25:211–236.
- FLEAGLE, J.G. 1999. *Primate Adaptation and Evolution*. Academic Press, New York.
- FLEAGLE, J.G., AND E.L. SIMONS. 1982. The humerus of *Aegyptopithecus zeuxis*, a primitive anthropoid. *American Journal of Physical Anthropology*, 59:175–193.
- FORD, S.M. 1988. Postcranial adaptations of the earliest platyrrhine. *Journal of Human Evolution*, 17:155–192.
- . 1994. Evolution of sexual dimorphism in body weight in platyrrhines. *American Journal of Primatology*, 34:221–244.
- GEBO, D.L., M. DAGOSTO, K.C. BEARD, AND T. QI. 2001. Middle Eocene primate tarsals from China: Implications for haplorhine evolution. *American Journal of Physical Anthropology*, 116:83–117.
- GEBO, D.L., M. DAGOSTO, K.C. BEARD, AND J. WANG. 1999. A first metatarsal of *Hoanghoni stehlini* from the late middle Eocene of Shanxi Province, China. *Journal of Human Evolution*, 37:801–806.
- GEBO, D.L., E.L. SIMONS, D.T. RASMUSSEN, AND M. DAGOSTO. 1994. Eocene anthropoid postcrania from the Fayum, Egypt. Pp. 203–233, in *Anthropoid Origins* (J.G. Fleagle and R.F. Kay, eds.). Plenum Press, New York.
- GODINOT, M. 1991. Toward the locomotion of two contemporaneous *Adapis* species. *Zeitschrift für Morphologie und Anthropologie*, 78: 387–405.
- . 1994. Early North African primates and their significance for the origin of Simiiformes (= Anthropoidea). Pp. 235–296, in *Anthropoid Origins* (J.G. Fleagle and R.F. Kay, eds.). Plenum Press, New York.
- GODINOT, M., AND F.K. JOUFFROY. 1984. La main d'*Adapis* (Primates, Adapidae). Pp. 221–242, in *Actes du Symposium Paléontologique G. Cuvier* (J.M. Mazin and E. Salmon, eds.). Montbéliard, France.
- GUNNELL, G.F., R.L. CIOCHON, P.D. GINGERICH, AND P.A. HOLROYD. 2002. New assessment of *Pondaungia* and *Amphipithecus* (Primates) from the late middle Eocene of Myanmar, with a comment on 'Amphipithecidae.' *Contributions from the Museum of Paleontology, University of Michigan*, 30:337–372.
- JAEGER, J.-J., AUNG NAING SOE, AYE KO AUNG, M. BENAMMI, Y. CHAIMANEE, R.-M. DUCROCQ, THAN TUN, TIN THEIN, AND S. DUCROCQ. 1998. New Myanmar middle Eocene anthropoids. An Asian origin for catarrhines? *Comptes Rendus de l'Académie des Sciences, Paris (Sciences de la vie)*, 321:953–959.
- JAEGER, J.-J., Y. CHAIMANEE, P. TAFFOREAU, S. DUCROCQ, AUNG NAING SOE, L. MARIVAUX, J. SUDRE, SOE THURA TUN, WANNA HTOON, AND B. MARANDAT. 2004. Systematics and paleobiology of the anthropoid primate *Pondaungia* from the late middle Eocene of Myanmar. *Comptes Rendus Palevol*, 3:243–255.
- MARIVAUX, L., P.-O. ANTOINE, S.R.H. BAQRI, M. BENAMMI, Y. CHAIMANEE, J.-Y. CROCHET, D. DE FRANCHESI, N. IQBAL, J.-J. JAEGER, G. METAIS, G. ROOHI, J.-L. WELCOMME. 2005. Anthropoid primates from the Oligocene of Pakistan (Bugti Hills): Data on early anthropoid evolution and biogeography. *Proceedings of the National Academy of Sciences*, 102:8436–8441.
- MARIVAUX, L., K.C. BEARD, Y. CHAIMANEE, J.-J. JAEGER, B. MARANDAT, AUNG NAING SOE, SOE THURA TUN, HTUN HTUN AUNG, AND WANNA HTOON. In press. Anatomy of the bony pelvis of a relatively large-bodied strepsirrhine primate from the middle Eocene Pondaung Formation (central Myanmar). *Journal of Human Evolution*.
- PILGRIM, G.E. 1927. A *Sivapithecus* palate and other primate fossils from India. *Memoirs of the Geological Survey of India*, 14:1–26.
- RASOLOARISON, R.M., S.M. GOODMAN, AND J.U. GANZHORN. 2000. Taxonomic revision of mouse lemurs (*Microcebus*) in the western portions of Madagascar. *International Journal of Primatology*, 21:963–1019.
- SIMONS, E.L. 1971. Relationships of *Amphipithecus* and *Oligopithecus*. *Nature*, 232:489–491.
- SZALAY, F.S., AND M. DAGOSTO. 1980. Locomotor adaptations as reflected on the humerus of Paleogene primates. *Folia Primatologica*, 34:1–45.
- WRIGHT, P.C., AND L.B. MARTIN. 1995. Predation, pollination, and torpor in two nocturnal prosimians: *Cheirogaleus major* and *Microcebus rufus* in the rain forest of Madagascar. Pp. 45–60, in *Creatures of the Dark: The Nocturnal Prosimians* (L. Alterman, D.A. Doyle, and K. Izard, eds.). Plenum Press, New York.