News and Views	A first metatarsal of <i>Hoanghonius stehlini</i> from the Late Middle Eocene of Shanxi Province, China
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On 13 May 1996, a joint field party from the Institute of Vertebrate Paleontology and Paleoanthropology (Chinese Academy of Sciences, Beijing) and the Carnegie Museum of Natural History discovered the first metatarsal of a primate at Locality 1 (also known as the "River Section") in the late middle Eocene Zhaili Member of the Heti Formation, Yuangu Basin, southern Shanxi Province, China. Historically, this site was the first locality in China to yield Eocene vertebrate fossils (Zdansky, 1930). Only two species of primates are represented at Locality 1 on the basis of an abundant sample of fossil teeth and jaws. The larger of these, Hoanghonius stehlini, is estimated to weigh 700 g (Fleagle, 1999) and is several times larger than the smaller primate, Eosimias centennicus, weighing between 91-179 g (Beard et al., 1996). The first metatarsal recovered from Locality 1 is similar in size to that of Hapalemur griseus (670-748 g, Smith & Jungers, 1997), and is attributed to Hoanghonius stehlini, the larger of the two primate species known from the site.

To date, little has been published regarding the anatomy of Hoanghonius stehlini. Although a great deal of dental and gnathic material for this species has been collected recently (Beard, 1998), the entire published hypodigm for Hoanghonius stehlini is currently restricted to a single mandibular fragment bearing M_{2-3} (the holotype) and a single, fragmentary upper molar (Zdansky, 1930; Gingerich, 1977; Szalay & Delson, 1979). This has led to conflicting interpretations of the phylogenetic position of Hoanghonius. For example, a number of workers have interpreted Hoanghonius as a transitional form linking anthropoids with adapiforms (Gingerich, 1977; Rasmussen & Simons, 1988; Gingerich et al., 1994; Rasmussen, 1994), while others have advocated omomyid affinities for this taxon (Szalay & Delson, 1979). More recently, Hoanghonius has been cited as a basal member of the Sivaladapidae (Qi & Beard, 1998), a distinctive clade of Asian adapiforms that persisted into the late Miocene. Given the diverse phylogenetic reconstructions proposed for *Hoanghonius* on the basis





Figure 1. V 11845, a left first metatarsal of *Hoanghonius*. Top: dorsal and plantar view; bottom right: proximal view; bottom left: medial and lateral view. Scale=5 mm.



Figure 2. Measurements for a first metatarsal. See Table 1.

of limited knowledge of its dentition, the discovery of even a single postcranial element provides welcome additional information. The first metatarsal described here is not inconsistent with the allocation of *Hoanghonius* to Adapiformes, and also provides the first evidence of sivaladapid postcranial anatomy.

V 11845 is a left first metatarsal which preserves the proximal joint surface, but not the distal end (Figure 1). The length of the preserved piece is 16.3 mm. The morphology resembles that of adapiform primates (Cantius, Notharctus, Adapis, and Leptadapis were examined) more than omomyid primates (Hemiacodon and Shoshonius). Morphological differences between the first metatarsals of omomyids and adapiforms can be quantified using several indices (Figure 2; Table 1). In adaptforms, the peroneal tubercle is broad (index A/B), short (index C/D), robust, and mountain-like in appearance, while in omomyids the tubercle is a thin, tall projection. Hoanghonius resembles adapiforms except that the tubercle is taller (index C/D) and extends further away from the joint surface than in all adapiform species, except Cantius. However, the tubercle is not nearly as tall as in omomyids, nor does it display the tall (index H/G), squared appearance as seen in lateral view. Like adapiforms, the peroneal tubercle of Hoanghonius lacks the oblique facet along the tubercle joint surface that characterizes

most specimens of *Hemiacodon* and *Shosho-nius* (Dagosto *et al.*, 1999).

The joint surface is saddle-shaped (Figure 3) as in other prosimian primates (Szalay & Dagosto, 1988). Its width relative to length (index D–C/B) is most similar to *Adapis* and *Leptadapis* rather than the narrower facet characteristic of omomyids and *Cantius*, or the much wider joint surface of *Notharctus* (Szalay & Dagosto, 1988).

Although there is a strong contrast in first metatarsal morphology between adapiform (and living tooth-combed lemurs) and omomyid primates, other haplorhine primates do not easily fit into these morphologies. A first metatarsal attributed to "probably Necrolemur" by Szalay & Dagosto (1988:18), is like that of adapiforms, having a relatively broad (A/B, Table 1) and somewhat shortened (C/D) peroneal tubercle. Tarsius also has a narrow and short peroneal tubercle. We regard the relatively short and broad peroneal tubercle of adapiforms, ?Necrolemur, and Tarsius as the primitive primate condition, whereas the very tall and narrow condition found only in omomyids is likely to be derived. The first metatarsal of Hoanghonius most closely resembles adapiform primates, especially Cantius, and shares no special similarity to omomyids. However, given that this condition is probably primitive for primates, the phylogenetic implications of this resemblance are equivocal. The most that can be said is that the

	Hoanghonius	Cantius	Notharctus	A dap is	Leptadapis	Hemiacodon	Shoshonius	Necrolenur	Tarsius syrichta (n=6)
	2.16 5.20	3.38 7.38	3·36 7·73	2·50 5.47	4.57	1.18 4.16	0-86 2-50	1.60 3.60	1.02 2.72
	3.25	4.72	4.05	2.50	5.10	4.26	2.03	2.50	- 1-2 1-44
	6.37	8.56	9-81	5.75	11.79	6.28	3.30	4.55	2.85
			22.49	15.88	32.62	14.40		13.00	10.75
			24.40	17.05	35.62	16.25		14.80	12.18
	3.30	5.61	5.34	2.99	5.80	4.59	2.36	2.72	1.20
	2.85	4.61	4.37	2.22	4.89	4.50	2.23	2.60	1.37
в	41.5	45.8	43.5	45.7	43.8	28.4	33·2	44.4	37.0
D	51.0	55.1	41.3	43·3	43·3	67.8	61.8	54.9	51.0
ĽL.			92.2	93.1	91.6	88.6		87.8	88.0
Ċ	86.4	82.2	81.9	74·2	84.0	0.86	94.5	95.5	87.0
C/B	0.09	52.0	75.0	59.0	58.0	49.0	49.0	56.9	51.0
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D. L. GEBO ET AL.



Figure 3. Proximal joint surfaces of first metatarsals. Left: *Hoanghonius*, V 11845; middle: *Cantius*, USGS 25030; and right: *Necrolemur*, unnumbered. Plantar surface is above.

anatomy of the first metatarsal of Hoanghonius is fully consistent with adapiform affinities for this taxon (Gingerich, 1977; Gingerich et al., 1994; Rasmussen & Simons, 1988; Beard, 1998), but is contrary to what we would have predicted if Hoanghonius were an omomyid. Similarly, despite suggestions that link Hoanghonius to anthropoids, V 11845 exhibits none of the unique characteristics of an anthropoid first metatarsal (Szalay & Dagosto, 1988), nor is it intermediate in its morphology. Significantly, the large sample of dental specimens of Hoanghonius stehlini recently collected from the type locality strongly corroborates the view that Hoanghonius is an adapiform. Such a phylogenetic reconstruction is also compatible with anatomical evidence from closely allied taxa, such as Guangxilemur and Wailekia (Qi & Beard, 1998).

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References

- Beard, K. C. (1998). Unmasking an Eocene primate enigma: the true identity of *Hoanghonius stehlini*. Am. J. phys. Anthrop. 26 (Suppl.), 69.
- Beard, K. C., Tong, Y., Dawson, M. R., Wang, J. & Huang, X. (1996). Earliest complete dentition of an anthropoid primate from the late middle Eocene of Shanxi Province, China. *Science* 272, 82–85.
- Dagosto, M., Gebo, D. L. & Beard, K. C. (1999). Revision of the Wind River Faunas, early Eocene of central Wyoming. Part 14. Postcranium of Shoshonius cooperi (Mammalia: Primates). Ann. Carnegie Mus. 68, 175–211.
- Fleagle, J. G. (1999). *Primate Adaptation and Evolution*. New York: Academic Press.
- Gingerich, P. D. (1977). Radiation of Eocene Adapidae in Europe. *Géobios, Mem. Spec.* 1, 165–182.
- Gingerich, P. D., Holroyd, P. A. & Ciochon, R. L. (1994). *Rencunius zhoui*, new primate from the late middle Eocene of Henan, China, and a comparison with some early Anthropoidea. In (J. G. Fleagle & R. F. Kay, Eds) *Anthropoid Origins*, pp. 163–177. New York: Plenum Press.
- Qi, T. & Beard, K. C. (1998). Late Eocene sivaladapid primate from Guangxi Zhuang Autonomous Region, People's Republic of China. *J. hum. Evol.* 35, 211– 220.
- Rasmussen, D. T. (1994). The different meanings of a tarsioid-anthropoid clade and a new model of anthropoid origin. In (J. G. Fleagle & R. F. Kay, Eds)

Anthropoid Origins, pp. 335–360. New York: Plenum Press.

- Rasmussen, D. T. & Simons, E. L. (1988). New specimens of *Oligopithecus savagei*, early Oligocene primate from the Fayum, Egypt. *Folia Primatol.* 51, 182–208.
- Smith, R. J. & Jungers, W. L. (1997). Body mass in comparative primatology. J. hum. Evol. 32, 523–559.
- Szalay, F. S. & Delson, E. (1979). Evolutionary History of the Primates. New York: Academic Press.
- Szalay, F. S. & Dagosto, M. (1988). Evolution of hallucial grasping in the primates. *J. hum. Evol.* 17, 1–34.
- Zdansky, O. (1930). Die alttertiären Saugetiere Chinas nebst stratigraphischen Bemerkungen. *Palaeontol. Sinica* 6(2), 1–87.