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Late Eocene sivaladapid primate from Guangxi Zhuang Autonomous Region, People's Republic of China

A new genus and species of Sivaladapidae is described from the late Eocene Gongkang Formation, Yongle Basin, western Guangxi Zhuang Autonomous Region, southern China. *Guangxilemur tongi*, new genus and species, shows a combination of traits that occur separately in earlier and more primitive Asian adapiforms (*Hoanghoni* and *Rencunius*) and in Miocene sivaladapines (*Sivaladapis* and *Sinoadapis*). Phylogenetic analysis of dental characters suggests that *Guangxilemur* is closely related to the Miocene sivaladapine clade. Miocene sivaladapines were the latest surviving members of a broad radiation of Eocene adapiforms in Asia that included *Hoanghoni*, *Rencunius*, and *Wailekia* in addition to *Guangxilemur*. European *Periconodon* may also be specially related to this primarily Asian clade, but current anatomical data are insufficient to test this possibility adequately. Sivaladapine adapiforms and tarsiid tarsiiforms maintained relictual distributions in southern and/or southeastern Asia far beyond the extirpation of their closest relatives on other Holarctic continents near the Eocene–Oligocene boundary. This temporal persistence was mediated by Asian paleogeography, which allowed virtually continuous access to tropical refugia during a middle Cenozoic interval of climatic deterioration that coincided with the extinction of adapiforms and tarsiiforms in Europe and North America.

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Introduction

Sivaladapid primates are distinctive elements of middle–late Miocene faunas from the Indian subcontinent and Yunnan Province, China (Gingerich & Sahni, 1979, 1984; Wu & Pan, 1985; Pan, 1988). Although the first fragmentary fossils of these animals were misinterpreted as pertaining to procyonid carnivores and lorised primates (Pilgrim, 1932; Lewis, 1933; Tattersall, 1968), discovery of more nearly complete specimens allowed Gingerich & Sahni (1979, 1984) to demonstrate the adapiform affinities of these taxa. As

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recognized by Gingerich & Sahni (1979, 1984) and subsequent authors, the persistence of sivaladapids into the late Miocene of southern Asia begs the question of how this Neogene adapiform clade relates to the much broader Paleogene radiation of these animals. However, the great stratigraphic disparity between middle–late Miocene sivaladapids and all other known adapiforms, which are virtually restricted to the Eocene (e.g. Szalay & Delson, 1979; Gheerbrant *et al.*, 1993; Simons *et al.*, 1995; Simons, 1997), has hampered attempts to place sivaladapids within an explicit phylogenetic context.

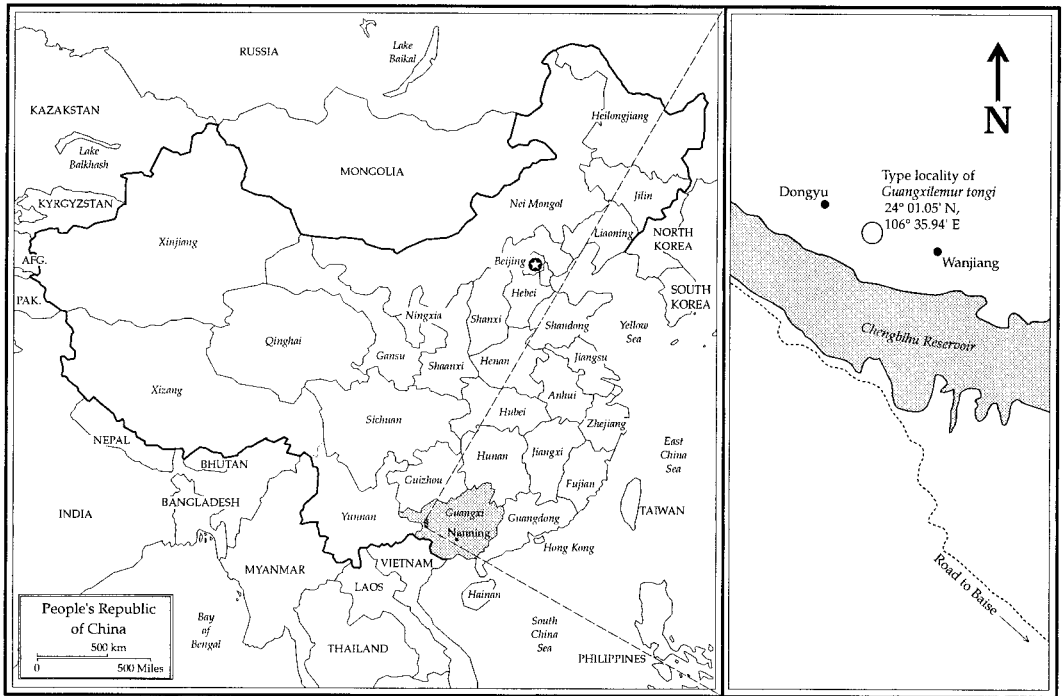


Figure 1. Map showing location of field area and type locality for *Guangxilemur tongi*.

During a joint Institute of Vertebrate Paleontology & Paleoanthropology (IVPP)-Carnegie Museum of Natural History field expedition in February and March 1995, we prospected fossiliferous outcrops of the late Eocene Gongkang Formation along the shores of Chengbihu Reservoir in the Yongle Basin, western Guangxi Zhuang Autonomous Region, China (Figure 1). Among the fossil vertebrates recovered during the course of that field work are two teeth of a sivaladapid primate, probably pertaining to the same individual. These specimens are the first fossil primates to be reported from Guangxi Zhuang Autonomous Region. In addition, they form the basis for a new genus and species of Sivaladapidae, which is described below. In light of this new taxon, we also propose a new hypothesis regarding the content and phylogeny of Sivaladapidae.

Systematic paleontology

Order Primates Linnaeus, 1758
 Suborder Strepsirhini Geoffroy, 1812
 Infraorder Adapiformes Szalay & Delson, 1979
 Family Sivaladapidae Thomas & Verma, 1979

Guangxilemur, new genus

Type species. Guangxilemur tongi, new species.

Diagnosis. Larger than *Hoanghoni*, *Rencunius*, and *Wailekia*. M^2 differs from those of *Hoanghoni* and *Rencunius* in showing greater development of external shearing crests, stronger parastyle and mesostyle, and weaker conules. M^2 differs from those of *Sivaladapis* and *Sinoadapis* in possessing

large pericone and hypocone on lingual cingulum.

Guangxilemur tongi, new species

Holotype. IVPP V11652, a left M² [Figure 2(a)]. IVPP V11653, a right C¹ [Figure 2(b)–(c)], probably pertains to the same individual (see below). Both specimens were collected by Guo Jianwei on 1 March 1995.

Type locality. Outcrop of Gongkang Formation on the north shore of Chengbiyu Reservoir, west of Wanjiang village (Figure 1). Exact coordinates of the type locality are as follows: 24°01.05'North, 106°35.94'East.

Known distribution. Late Eocene of Guangxi Zhuang Autonomous Region, China. The associated mammalian fauna from the Gongkang Formation was reviewed by Russell & Zhai (1987), who were unable to decide whether the fauna should be considered late Eocene or early Oligocene in age. However, since Russell & Zhai's (1987) survey, the position of the Eocene–Oligocene boundary with respect to Asian mammal faunas has shifted, such that many faunas formerly considered as late Eocene are now late middle Eocene, and those formerly considered as early Oligocene are now late Eocene (e.g., Berggren & Prothero, 1992; Ducrocq, 1993; Holroyd & Ciochon, 1994; Emry *et al.*, 1998).

Anthracotheriid artiodactyls are well represented in late middle Eocene and younger mammal faunas in Asia and are widely regarded to be useful for purposes of biostratigraphy (e.g., Holroyd & Ciochon, 1994; Ducrocq, 1994, 1997; Ducrocq *et al.*, 1997). Anthracotheres from the Gongkang Formation, originally reported by Tang (1978), have recently been described as "almost identical" to a species of *Anthracotherium* from the Krabi fauna of southern Thailand, also of late Eocene age (Ducrocq *et al.*, 1997). Anthracotheres from the Heti

Formation, Yuanqu Basin, Shanxi and Henan Provinces, China, are decidedly more primitive than those of either the Krabi fauna of southern Thailand or the Gongkang Formation. Indeed, all available biostratigraphic evidence suggests that the Heti Formation faunas are late middle Eocene, while those from Krabi and the Gongkang Formation are younger (Russell & Zhai, 1987; Holroyd & Ciochon, 1994; Ducrocq *et al.*, 1997). As such, *Guangxilemur* from the Gongkang Formation is significantly younger than either *Hoanghoni* or *Rencunius* from the Heti Formation, but is probably similar in age to *Wailekia* from southern Thailand.

Diagnosis. As for the genus (currently monotypic).

Etymology. For our friend and colleague Tong Yongsheng, in recognition of his many contributions to knowledge of Paleogene mammals in China and his field work in the Baise and Yongle basins of Guangxi.

Description. The holotype is a left upper molar that we identify as M² on the basis of comparisons with maxillary fragments of *Sivaladapis* and *Sinoadapis* that bear serially associated upper molars. The crown measures 6.6 mm (mesiodistal length) by 9.1 mm (buccolingual breadth). Buccal and lingual cingula are prominently developed and virtually continuous around the entire periphery of the crown. Lingually, the cingulum bears both a pericone and a hypocone. In terms of volume, the latter cusp is the larger, but both are highly conspicuous. A weak crest connects the hypocone with a series of at least three small cusps that lie buccal to the hypocone, on a cingular shelf below the level of the post-protocrista. The protocone is canted mesially, as is frequently the case in primates, so that its apex lies nearer to the paracone than the metacone. Pre- and

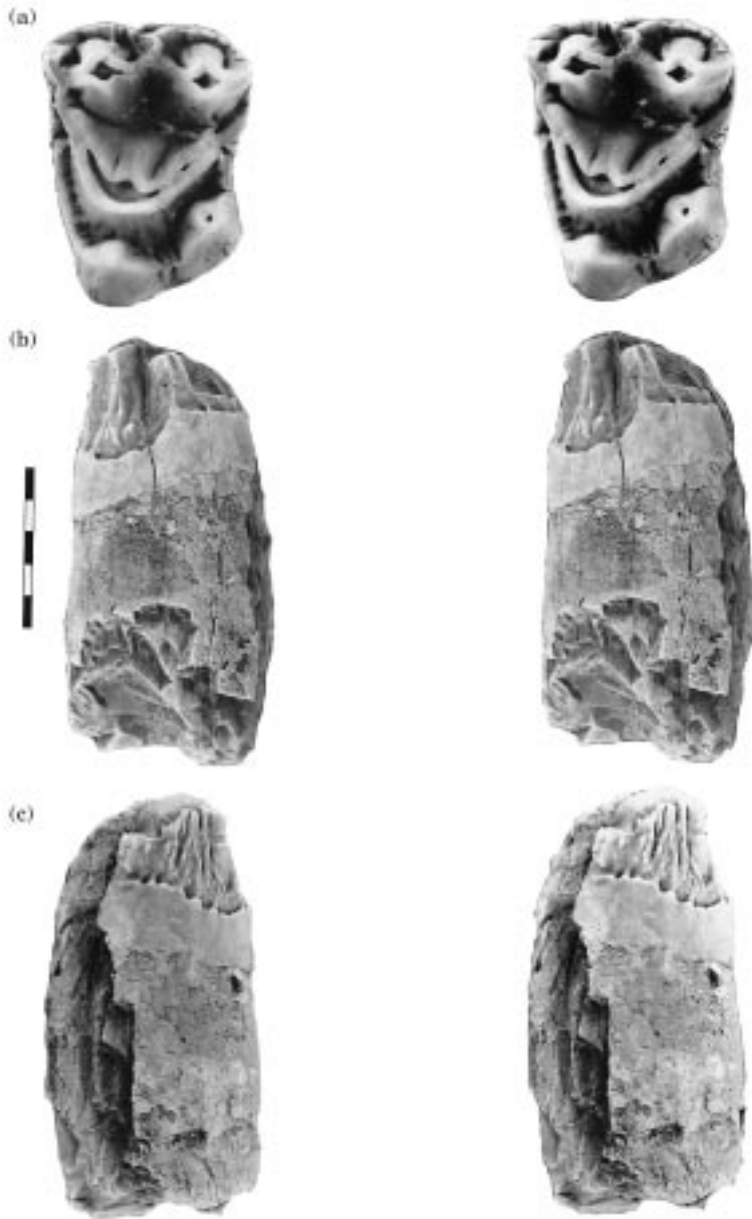


Figure 2. *Guangxilemur tongi*, n. gen. et sp.: (a) IVPP V11652, holotype left M^2 , occlusal view; (b–c) IVPP V11653, fragmentary right C^1 , probably associated with holotype, in lingual (b) and labial (c) views. All views are stereopairs. Scale = 5 mm.

postprotocristae emanate mesiobuccally and distobuccally from the protocone to form the lingual margin of the trigon basin. If they were ever present as discrete structures, the

conules have been rendered indistinguishable by wear, which is only moderate. Mesiobuccally, the preprotocrista joins the preparacrista just lingual to the parastyle.

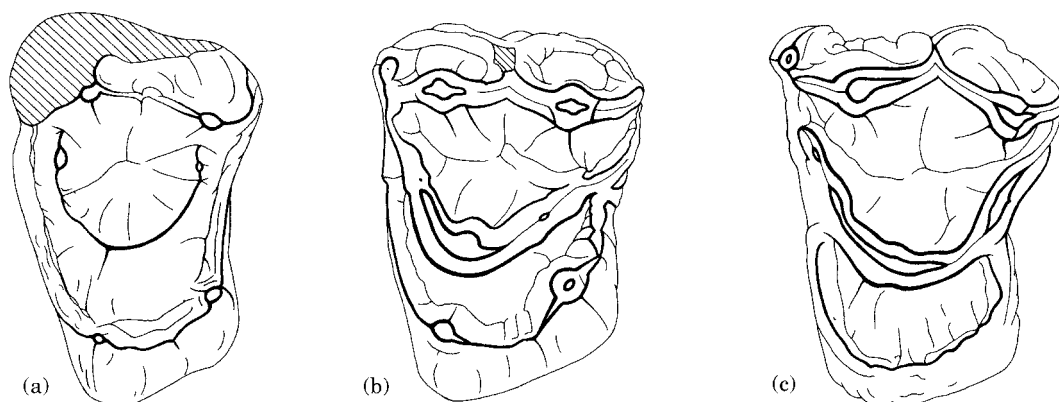


Figure 3. Comparative schematic drawings of M^2 in selected sivaladapid primates (not to scale): (a) *Hoanghoniush stehlini*; (b) *Guangxilemur tongi*; (c) *Sivaladapis nagrii*. Note the presence of pericone and hypocone in *Hoanghoniush* and *Guangxilemur*, and the increased development of external shearing crests with parastyle and mesostyle in *Guangxilemur* and *Sivaladapis*. See text for discussion of these and other characters and their possible phylogenetic significance.

The postprotocrista merges with the postcingulum distolingual to the metacone. Buccal shearing crests are well-developed, connecting the parastyle with the paracone, mesostyle and metacone. Taken as a whole, these buccal shearing crests form a buccolingually flattened, W-shaped structure.

A fragmentary canine that is appropriate in terms of size and morphology to belong to the same individual as the holotype upper molar was found near the latter specimen. If, as seems likely, this specimen also pertains to the holotype of *Guangxilemur tongi*, it can be identified as a fragmentary right C^1 on the basis of comparisons with upper and lower canines of *Sinoadapis*. At its base the crown measures 6.35 mm (mesiodistal length; minimum estimate) by 4.8 mm (labiolingual breadth). In cross-section the crown is oval in shape. The mesial part of the crown and root, as well as the apex of the crown, have been abraded away. From that which remains of the crown, only a few anatomical features can be discerned. A weak cingulum is continuous about the remaining base of the crown, and a vertical groove is situated distolingually. A distal

crest bears a well-defined wear facet that must have formed by contact with the anteriormost lower premolar (presumably P_2). The enamel is crenulated.

Comparisons. Although *Guangxilemur* is represented by extremely fragmentary remains, it shows a combination of characters that is otherwise unknown among adapiforms (Figure 3). Key among these features are the well-developed pericone and hypocone on the lingual cingulum. Only a few Eocene adapiform taxa are known to have possessed both pericone and hypocone. These taxa include *Periconodon* from the middle Eocene of France and Switzerland (e.g., Stehlin, 1916; Szalay & Delson, 1979; Godinot, 1988) and *Hoanghoniush* and *Rencunius* from the late middle Eocene Heti Formation, Yuanqu Basin of central China (Zdansky, 1930; Szalay & Delson, 1979; Gingerich *et al.*, 1994). *Guangxilemur* resembles the Chinese Eocene forms more closely than it does *Periconodon* in having a continuous lingual cingulum between the pericone and hypocone. Like *Hoanghoniush*, but in contrast to *Periconodon* and *Rencunius*, the upper molar of *Guangxilemur* is significantly longer

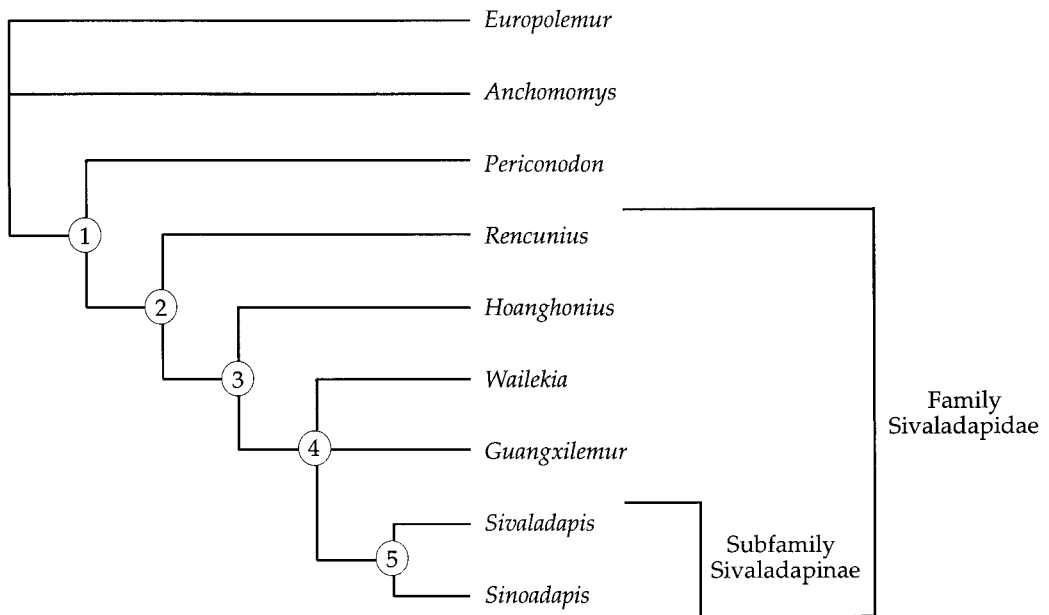


Figure 4. Strict consensus of three most parsimonious trees yielded by branch-and-bound search in PAUP 3.1.1 (Swofford, 1993) of dental characters (see Tables 1–2). Trees were rooted by designating a hypothetical ancestor (in which all characters were scored as “0”) as the outgroup to all adapiform taxa. Tree length=15; consistency index=0.867.

Using the ACCTRAN character state optimization algorithm in PAUP, character transformations supporting each node are as follows (see Table 1 for description of character states): Node 1, Character 7 (0→1); Node 2 (Sivaladapidae), Character 1 (0→1), Character 2 (0→1), Character 8 (0→1); Node 3, Character 5 (0→1), Character 9 (0→1); Node 4, Character 3 (0→1), Character 10 (0→1), Character 11 (0→1), Character 12 (0→1), Character 13 (0→1); Node 5 (Sivaladapinae), Character 4 (0→1), Character 6 (1→0), Character 7 (1→0).

buccolingually than mesiodistally (i.e., it is more transverse). Hence, of the Eocene adapiform taxa with which it can be compared, *Guangxilemur* is most similar to *Hoanghoniuss*.

The poorly known primate *Wailekia orientalis* from the late Eocene of southern Thailand (Ducrocq *et al.*, 1995) is very similar to *Hoanghoniuss stehlini* in size and comparable aspects of its anatomy, but the upper dentition of *Wailekia* remains unknown. Similarly, the lower dentition of *Guangxilemur* has yet to be recovered, so that homologous parts of *Guangxilemur* and *Wailekia* cannot be compared at the present time. Although *Wailekia* and *Guangxilemur* are similar in age, they clearly represent different taxa, if only on the basis of the

much larger size of *Guangxilemur*. Given the close similarity in lower molar morphology between *Wailekia* and *Hoanghoniuss*, it seems reasonable to predict that the unknown upper molar morphology of *Wailekia* will prove to differ in only minor details from that of *Hoanghoniuss* once upper dentitions of the former genus are recovered. As noted in the diagnosis of *Guangxilemur* above, morphological differences between the upper molars of *Guangxilemur* and *Hoanghoniuss* are sufficient to separate these forms at the generic level (Figure 3).

Guangxilemur differs from *Hoanghoniuss*, *Rencunius*, and *Periconodon* in showing greater development of external shearing crests and associated styler structures on M^2 . A strong parastyle and mesostyle adorn

Table 1 Character descriptions for phylogenetic analysis (see Figure 4)

1. Lower molar hypoconulids weak to absent (0), or strong (1).
2. Lower molar hypoconulids central in position (0), or twinned with entoconids (1).
3. Lower molars without strong lingual notch between entoconid and postvallid (0), strong lingual notch present (1).
4. Lower molar crown height moderate (0), or high-crowned (1).
5. Upper and lower fourth premolars premolariform (0), or molariform (1).
6. M¹⁻² without hypocone (0), with hypocone (1).
7. M¹⁻² without pericone (0), with pericone (1).
8. Lingual cingulum on upper molars weak and incomplete (0), strong and continuous (1).
9. M¹⁻² transverse breadth not appreciably greater than mesiodistal length (0), M¹⁻² markedly transverse (1).
10. M¹⁻² with distinct molar conules (0), conules indistinct or absent (1).
11. M¹⁻² without strong parastyle (0), with strong parastyle (1).
12. M¹⁻² without strong mesostyle (0), with strong mesostyle (1).
13. M¹⁻² external shearing crests mesiodistally straight (0), or moderately W-shaped (1).

Table 2 Taxon-character matrix used in parsimony analysis (see Table 1, Figure 4)

Ancestor	00000	00000	000
<i>Europolemur</i>	00000	10000	000
<i>Anchomomys</i>	00000	10000	000
<i>Periconodon</i>	00000	11000	000
<i>Rencunius</i>	11000	11100	000
<i>Hoanghoni</i>	1100?	11110	000
<i>Wailekia</i>	1110?	?????	???
<i>Guangxilemur</i>	?????	11111	111
<i>Sivaladapis</i>	11111	00111	111
<i>Sinoadapis</i>	11111	00111	111

the external margin of the upper molar of *Guangxilemur*, while these structures are lacking in upper molars of *Hoanghoni*, *Rencunius* and *Periconodon*. *Guangxilemur* also lacks the distinct molar conules found in *Hoanghoni*, *Rencunius* and *Periconodon*. In all of these features of upper molar anatomy, *Guangxilemur* approximates conditions in the Miocene sivaladapids *Sivaladapis* and *Sinoadapis* (Figure 4). Miocene sivaladapids differ from *Guangxilemur* primarily in showing even greater development of external shearing crests on the upper molars and in lacking the strong pericone and hypocone found in *Guangxilemur* and the other Eocene adapiforms noted above. However, it may be significant that, even though Miocene sivaladapids lack strong development of the pericone and hypocone, they retain well-developed (and usually

complete) lingual cingula on their upper molars. Indeed, some specimens of *Sinoadapis* [e.g., IVPP PA903; see Pan, 1988: Figure 4(b)] show distinct swellings of enamel on the lingual cingula of upper molars in precisely the areas occupied by the pericone and hypocone in *Guangxilemur*. These structures in *Sinoadapis* may represent vestiges of the pericone and hypocone found in *Guangxilemur*, *Hoanghoni* and the other Eocene adapiforms discussed above. If so, Miocene sivaladapids evolved from ancestors that possessed prominent pericones and hypocones on their upper molars. This subject was discussed more fully by Thomas & Verma (1979), who cautiously favored the view that Miocene sivaladapids secondarily lost pericones and hypocones on their upper molars. The new morphological evidence provided by *Sinoadapis* and *Guangxilemur* strongly corroborates the latter hypothesis.

Discussion

Recent students of fossil primates have been unanimous in supporting the adapiform affinities of Miocene sivaladapids, despite the fact that no one has attempted to place the Miocene taxa within an explicit phylogenetic framework. Indeed, several workers (Gingerich *et al.*, 1994; Ducrocq *et al.*,

1995) have noted dental resemblances between Miocene sivaladapids and the Asian Eocene adapiforms *Rencunius*, *Hoanghoni*, and *Wailekia*, but the potential phylogenetic signal underlying these shared anatomical traits has been downplayed or dismissed by previous scholars. The discovery of *Guangxilemur* allows us to reassess the possible phylogenetic ties between Miocene sivaladapids and these earlier and more primitive Asian adapiforms.

Guangxilemur possesses a unique combination of characters, certain of which occur in middle-late Eocene *Hoanghoni* and its close relatives, and others of which are found in middle-late Miocene sivaladapines. For example, the pericone and hypocone on the M² of *Guangxilemur* are shared with *Hoanghoni*, *Rencunius*, and *Periconodon* among Eocene adapiforms. However, *Guangxilemur* is more derived than any of these Eocene adapiforms in possessing stronger and somewhat W-shaped external shearing crests with a distinct parastyle and mesostyle on its upper molar. These latter features are shared with Miocene *Sivaladapis* and *Sinoadapis* (upper molars remain undescribed for *Indraloris*). Hence, what little is known regarding the anatomy of *Guangxilemur* suggests an intermediate phylogenetic position for this taxon between *Hoanghoni* and its Eocene relatives on the one hand and the Miocene sivaladapines on the other (Figure 4). Parenthetically, we note that *Rencunius*, *Hoanghoni*, and *Wailekia* all appear to be specially related to the Miocene radiation of sivaladapines (Figure 4). The subfamily Hoanghoniinae, proposed by Gingerich *et al.* (1994) for *Hoanghoni*, *Rencunius*, and possibly *Wailekia*, appears to be a paraphyletic assemblage of basal sivaladapids rather than a monophyletic group of Asian Eocene adapiforms. As such, none of these taxa is likely to be closely related to basal anthropoid or simiiform primates, notwithstanding repeated suggestions to the

contrary (Gingerich, 1977; Rasmussen & Simons, 1988; Rasmussen, 1994; Gingerich *et al.*, 1994; Ducrocq *et al.*, 1995).

If our phylogenetic reconstruction is correct, Miocene sivaladapines can be interpreted as descendants of a much earlier radiation of Eocene adapiforms that was largely, or even wholly, endemic to Asia. This radiation included *Rencunius* and *Hoanghoni* from the late middle Eocene of central China (Henan and Shanxi provinces), *Guangxilemur* from the late Eocene of southern China (Guangxi Zhuang Autonomous Region), and *Wailekia* from the late Eocene of southern Thailand. *Periconodon* from the middle Eocene of France and Switzerland may be more distantly related to Sivaladipidae (Figure 4), but this possibility requires further morphological support than current data allow.

The persistence of sivaladapine adapiforms well into the Neogene in southern and southeastern Asia may be attributable to the more-or-less continuous access to the tropics afforded by Asia throughout the Cenozoic. Access to tropical refugia presumably allowed sivaladapines to weather middle Cenozoic climatic deterioration by contracting their formerly broad geographic range toward lower latitudes. Eocene adapiforms on Europe and North America lacked similar access to tropical refugia, and adapiforms were extirpated on both of these continents by the end of the Eocene. Beard (1998) recently proposed a similar paleobiogeographic hypothesis to account for the persistence of Asian tarsiids to the Recent, in contrast to the late Eocene demise of omomyid and microchoerid tarsiiforms on other Holarctic continents. Anachronistically late occurrences of Asian sivaladapines and tarsiids therefore appear to represent the sort of "repeating pattern in nature" (cf. Grande, 1994) that is frequently sought, but rarely attained, by organismal biologists.

Based on the greater development of external shearing crests in Miocene sivaladapines compared with all of their known Eocene relatives, the evolution of dental characters among sivaladapids may have reflected increasingly efficient exploitation of a folivorous niche. If so, their eventual extinction may have resulted from taxonomic displacement by immigrating colobine monkeys, as [Gingerich & Sahni \(1979, 1984\)](#) suggested.

Summary

Guangxilemur tongi is a new genus and species of sivaladapid adapiforms from the late Eocene Gongkang Formation, Yongle Basin, Guangxi Zhuang Autonomous Region, southern China. It possesses a unique combination of dental characters, some of which are found in earlier Eocene adapiforms from Asia (*Hoanghonius* and *Rencunius*) and others of which are restricted to Miocene sivaladapines of southern and southeastern Asia. This morphological evidence suggests that *Guangxilemur* is phylogenetically intermediate between *Hoanghonius* and its close relatives on the one hand, and Miocene sivaladapines on the other. This is the first phylogenetically explicit hypothesis regarding the relationships of the youngest adapiforms currently documented in the fossil record.

Like tarsiids, sivaladapine adapiforms were able to persist far beyond the extinction of their closest relatives on other continents, presumably because of the continuous access to tropical refugia that was permitted by Cenozoic Asian paleogeography. In contrast to the highly autapomorphous tarsiids, however, sivaladapines appear to have occupied an ecologically generalized niche that was predicated upon folivory. The immigration of colobine monkeys into Asia from Africa during the late Miocene remains a

viable explanation for the extinction of sivaladapine adapiforms.

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