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PAPERS IN HONOR OF MARY R. DAWSON**

*Edited by*

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Cover illustration: Artist's depiction of the living Laotian rodent *Laonastes aenigmamus* standing upon lacustrine strata containing a well-preserved skeleton of the early Miocene rodent *Diatomys shantungensis*. Mary Dawson and her colleagues were the first to recognize that *Laonastes* is a surviving member of the otherwise extinct rodent clade Diatomyidae (see contribution by Flynn in this volume). Original art of Mark A. Klingler.

Frontispiece: Portrait of Mary R. Dawson painted by Gina Scanlon.

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# NEW SIVALADAPID PRIMATES FROM THE EOCENE PONDAUNG FORMATION OF MYANMAR AND THE ANTHROPOID STATUS OF AMPHIPITHECIDAE

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## ABSTRACT

Fossil primates from the late middle Eocene Pondaung Formation of Myanmar have figured prominently in recent efforts to reconstruct the early evolutionary history of anthropoids. The anthropoid affinities of Amphipithecidae, the most abundant fossil primates currently known from the Pondaung Formation, have proven to be particularly controversial. Here we describe **two new genera and species**, *Paukkaungia parva* and *Kyitchaungia takaii*, of sivaladapid primates from the Pondaung Formation. Tarsal elements that are appropriate in size and morphology to belong to *Kyitchaungia takaii* are also described. These are the first undoubted adapiforms—and the first fossil primates other than anthropoids—to be reported from the Eocene of Myanmar. The discovery of sivaladapids in the Pondaung Formation enhances the taxonomic and paleoecological diversity of the late middle Eocene primate fauna of Myanmar. In this respect, the fossil primate community from the Pondaung Formation appears to have resembled roughly contemporaneous assemblages from China, Thailand, and Pakistan. The newly discovered sivaladapid tarsal elements help to resolve conflicting interpretations regarding the taxonomic allocation of large-bodied primate postcranial elements from the Pondaung Formation. The NMMP 20 partial skeleton from the Pondaung Formation, which has often been regarded as that of an amphipithecid, is more plausibly interpreted as pertaining to a third Pondaung sivaladapid. Recognizing the sivaladapid affinities of the NMMP 20 partial skeleton solidifies the anthropoid status of amphipithecids, further constraining temporal, phylogenetic, and biogeographic hypotheses regarding anthropoid origins.

## INTRODUCTION

The late middle Eocene Pondaung Formation of Myanmar has long been renowned for yielding fossils of two clades of stem anthropoids, Amphipithecidae and Eosimiidae (Pilgrim 1927; Colbert 1937; Ba Maw et al. 1979; Ciochon et al. 1985; Jaeger et al. 1998, 1999, 2004; Chaimanee et al. 2000; Takai et al. 2001, 2005; Shigehara et al. 2002; Gebo et al. 2002; Takai and Shigehara 2004; Egi et al. 2006). Despite the diversity and abundance of basal anthropoids from

the Pondaung Formation, other primate taxa have yet to be described from this rock unit. The apparent absence of adapiforms, omomyids, and tarsiids in the Pondaung Formation has long been enigmatic, because slightly older and younger fossil localities in China, Thailand, and Pakistan have yielded reasonably abundant examples of these primates alongside amphipithecids and/or eosimiids (Beard et al. 1994, 1996; Ducrocq et al. 1995, 2006; Chaimanee et al.

1997; Beard 1998; Marivaux et al. 2002, 2005; Beard and Wang 2004).

The absence of undoubted adapiform primates in the Pondaung primate fauna has also contributed to ongoing debates over the phylogenetic affinities of the Amphipithecidae. Amphipithecids have been widely regarded as anthropoids since their initial description in the early Twentieth Century (Pilgrim 1927; Colbert 1937; Simons 1971; Ba Maw et al. 1979; Ciochon et al. 1985; Jaeger et al. 1998, 2004; Chaimanee et al. 2000; Beard 2002; Marivaux et al. 2003, 2005). As is the case for many fossil taxa that are documented by fragmentary anatomical remains, amphipithecid relationships remain controversial, and some workers consider these primates as specialized adapiforms rather than anthropoids (Ciochon and Holroyd 1994; Ciochon and Gunnell 2002; Gunnell et al. 2002). Perhaps the most compelling line of evidence that amphipithecids might be related to adapiforms comes from the partial skeleton of a large-bodied primate from the Pondaung Formation, which shares numerous postcranial characters with North American notharctid adapiforms (Ciochon et al. 2001). Although this partial skeleton (NMMP 20; fossil primate collection, National Museum of Myanmar, Yangon, Myanmar) was not associated with diagnostic craniodental remains, many workers have assumed that it pertains to an amphipithecid, partly because undoubted adapiforms have never been reported from the Pondaung Formation. However, allocation of the NMMP 20 partial skeleton to the Amphipithecidae introduces significant character conflict for this taxon, resulting in unstable phylogenetic reconstructions for amphipithecids among primates (Kay et al. 2004a). Complicating matters even further, an isolated primate talus from the Pondaung Formation showing derived anthropoid features has also been regarded as pertaining to an amphipithecid (Marivaux et al. 2003).

Here, we document the presence of undoubted adapiforms in the Pondaung Formation for the first time. At least two adapiform taxa, both of which are sivaladapids, can be recognized at present. Sivaladapids have previously been reported from middle Eocene to late Miocene sites in China, India, Pakistan, and Thailand (Qi and Beard 1998; Marivaux et al. 2002). The group is well known for including the youngest members of the expansive adapiform radiation, which is otherwise confined to the Paleogene (Gingerich and Sahni 1979, 1984; Thomas and Verma 1979). Fragmentary early discoveries of Miocene sivaladapids were frequently misidentified or misinterpreted as pertaining to either carnivores or lorises (Pilgrim 1932; Lewis 1933; Tattersall 1968). Likewise, fragmentary specimens of Eocene sivaladapids have often been misinterpreted as anthropoids (Gingerich 1977; Rasmussen and Simons 1988; Gingerich et al. 1994; Ducrocq et al. 1995). The phylogenetic affinities of Eocene sivaladapids were clarified with the recent description of *Guangxilemur*, a temporally and morphologically intermediate form that links primitive Eocene taxa (*Rencunius* and *Hoanghoni*) with the more "classical" Miocene forms (Qi and Beard 1998; Marivaux et al. 2002).

SYSTEMATIC PALEONTOLOGY  
Class Mammalia Linnaeus, 1758  
Order Primates Linnaeus, 1758  
Suborder Strepsirhini Geoffroy, 1812  
Infraorder Adapiformes Hoffstetter, 1977  
Family Sivaladapidae Thomas and Verma, 1979

*Paukkaungia parva*, gen. et sp. nov.

**Holotype.**—NMMP 55, an isolated right  $M_1$ .

**Type locality.**—Nyaungpinle locality (21°45'03.6" North, 94°37'20.8" East), Myanmar (Fig. 1).

**Age and distribution.**—Late middle Eocene Pondaung Formation, Myanmar.

**Hypodigm.**—The holotype; NMMP 54, an isolated left  $P_3$  from Paukkaung Kyitchaung Locality 2; NMMP 56, an isolated left  $P_4$  from Nyaungpinle locality; and NMMP 57, an isolated right  $M_2$  from Paukkaung Kyitchaung Locality 2.

**Diagnosis.**—Smallest known member of the Sivaladapidae. Lower molar talonids differ from those of other sivaladapids in having weakly differentiated entoconid and hypoconulid strongly separated from hypoconid by deep notch in postcrisid.  $P_4$  significantly taller and mesiodistally longer than  $P_3$ , in contrast to other sivaladapids.  $P_4$  further differs from that of *Sivaladapis* and *Sinoadapis* in being premolariform, lacking development of paraconid and metaconid on trigonid and molariform talonid.  $P_4$  further differs from that of *Hoanghoni* and *Rencunius* in lacking a cuspidate metaconid, having a relatively elevated preprotocristid that descends the mesial face of the trigonid less steeply, and having a relatively broader talonid.  $P_{3-4}$  differ from those of other sivaladapids in having mesiodistally compressed crowns with roots that may have been partially fused. Lower molars, particularly  $M_1$ , differ from those of *Wailekia*, *Guangxilemur*, *Sivaladapis*, *Indraloris*, and *Sinoadapis* in having trigonids that are much less compressed mesiodistally.

**Etymology.**—The generic name derives from the village of Paukkaung, which is near both of the localities that have yielded the available hypodigm. The trivial name derives from Latin *parva* (feminine), meaning small.

**Description.**—NMMP 54 (length, 2.53 mm; width, 1.52 mm) is an isolated left lower premolar that we interpret as  $P_3$  (Fig. 2A–C). The tooth is relatively low-crowned, and it bears an elongated trigonid and an abbreviated talonid. The buccal surface of the crown is evenly convex, because there is no development of a hypoflexid separating the trigonid from the talonid. In contrast, the lingual side of the trigonid is invaginated. The protoconid is the only distinct trigonid cusp. From its apex a well-developed preprotocristid forms an elevated mesial crest that arcs slightly lingually near its terminus. Two distal crests from the protoconid descend the postvallid, defining its buccal and lingual margins. The short talonid heel lacks a distinct cristid obliqua. Its most salient feature is an arcuate postcrisid that bears a tiny, incipient hypoconid near its buccal margin.

NMMP 56 (length, 3.54 mm; width, 2.20 mm) is an isolated left lower premolar, interpreted here as  $P_4$  (Fig. 2D–F). The crown as a whole is buccolingually narrow and elongated mesiodistally. Judging from its shape and the location of its dual roots, the crown would not have been obliquely oriented in the tooththrow, in contrast to the condition that typifies Amphipithecidae and Eosimiidae. However, the broken cross-sections of the mesial and distal roots

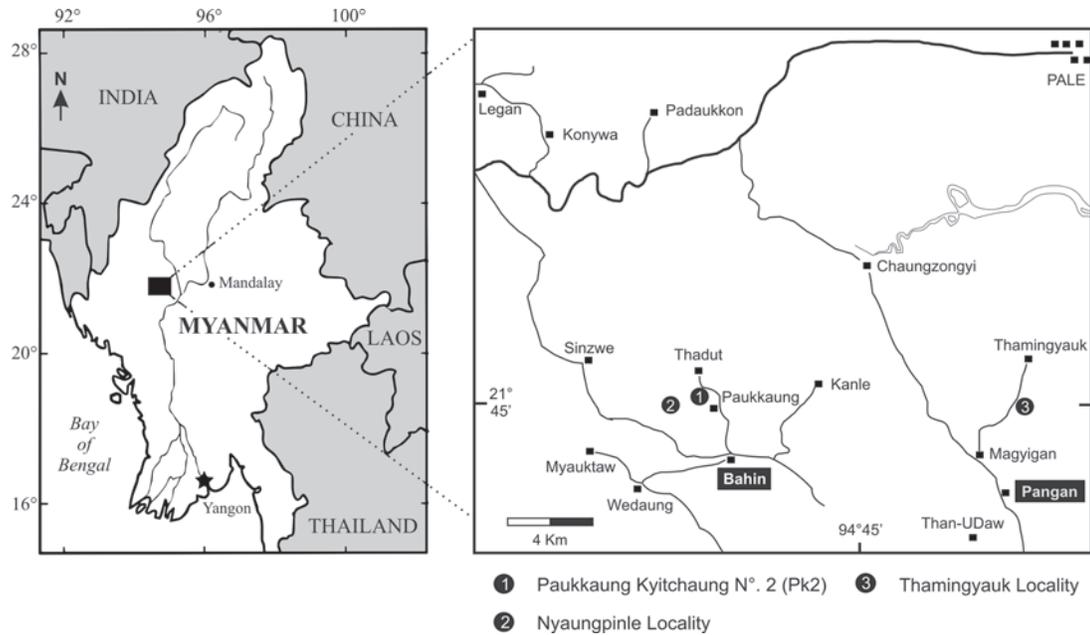


Fig. 1.—Map showing location of Pondaung Formation fossil sites yielding specimens described in this paper.

partly coalesce near their junction with the base of the crown, suggesting that the undamaged roots may have been partially fused along much or all of their length during life. The trigonid is dominated by the centrally placed protoconid, from which four distinct crests emanate. The mesial crest or preprotocristid is relatively straight but elongated. Its termination corresponds to a short mesial protuberance of enamel on the trigonid. In contrast to the condition in Miocene sivaladapids, the mesial part of the preprotocristid on  $P_4$  is only modestly deflected lingually, and it fails to form an arcuate paracristid. Rather, it deviates slightly lingually near its mesial terminus before becoming confluent with a short lingual cingulid. Neither a paraconid nor a metaconid is present. Two prominent crests, which originate at or near the apex of the protoconid, define the lingual and buccal margins of the postvallid. A third crest, which is confluent with the short cristid obliqua, occurs near the midline of the postvallid. The talonid of  $P_4$  is mesiodistally short and relatively simple in morphology. Two small cusps occur along the crest that defines the distal margin of the talonid. The more buccal of these, interpreted as the hypoconid, is continuous with the cristid obliqua. The tiny lingual cusp is appropriate in position to be regarded as an incipient entoconid. A small but well-defined talonid basin is fully enclosed by the lingual postvallid crest, the postcristid, and the cristid obliqua. A buccal continuation of the postcristid defines the distobuccal margin of the talonid. The hypoflexid is relatively deep because of the central point of termination of the cristid obliqua on the postvallid.

NMMP 55 (length, 3.59 mm; width, 2.45 mm), a right lower molar, has been designated as the holotype for the species (Fig. 2G–J). It is interpreted as  $M_1$  rather than  $M_2$  because it bears a relatively prominent paraconid and the

trigonid remains open lingually. The crown as a whole is relatively long and narrow, although the talonid basin is remarkably broad. The highest and most voluminous cusp on the trigonid is the protoconid. It is connected to the paraconid by an arcuate paracristid. The metaconid is located slightly distal to the level of the protoconid, rather than being directly lingual to it. The trigonid as a whole is less compressed mesiodistally than is the case in Miocene sivaladapids ( $M_1$  is not known with certainty in either *Wailekia* or *Guangxilemur*, but isolated lower molars of these taxa are more similar to Miocene sivaladapids than they are to *Paukkaungia* in their degree of trigonid compression). The protocristid is not elevated to form a continuous transverse crest, in contrast to the condition in Miocene sivaladapids. Rather, the buccal and lingual portions of the protocristid meet to form a relatively deep notch near the midline of the postvallid. A buccal cingulid is well developed and continuous from the mesial end of the crown to a point just distal to the hypoflexid. There is no buccal cingulid on the talonid portion of the crown. The talonid is notable for its great breadth and depth. In part, the breadth of the talonid is due to the very buccal position of the cristid obliqua, which arcs buccally from the hypoconid before turning lingually to join the postvallid inferior to the protoconid. This pattern results in an exceptionally shallow hypoflexid. Two tiny supernumerary cusps occur near the hypoconid. The more mesial of these is the larger. It occurs on the cristid obliqua, in a location appropriate for the cusp to be designated as a centroconid. The smaller cusps occur on the poorly defined postcristid, immediately adjacent to the hypoconid. Perhaps the most distinctive aspect of the talonid is the deep notch that bifurcates the postcristid. This notch is located slightly buccal to the midline, so that it lies closer to

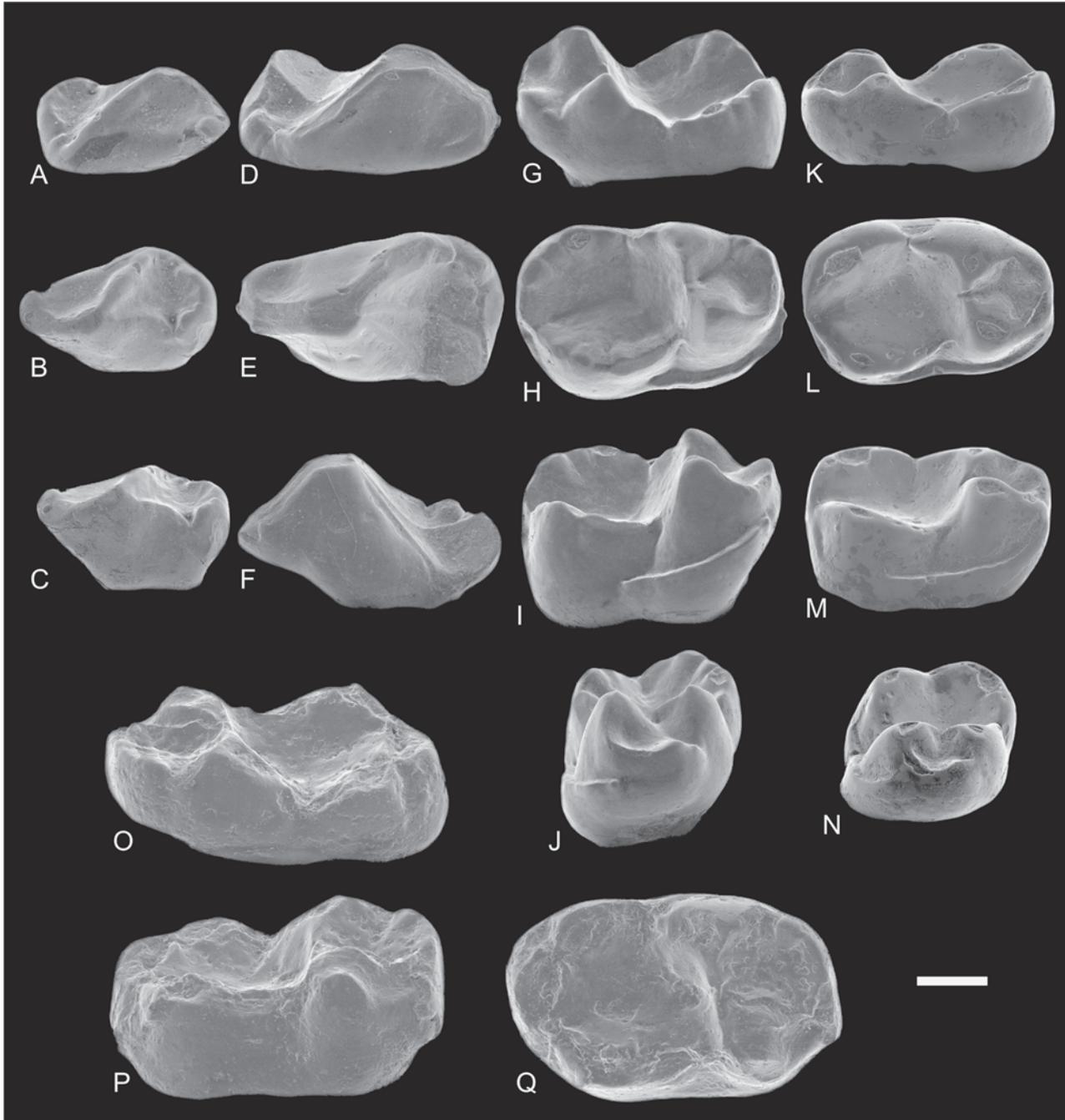


Fig. 2.—Isolated teeth of the sivaladapid primates *Paukkaungia parva* (A–N) and *Kyitchaungia takaii* (O–Q) from the Eocene Pondaung Formation of Myanmar. (A–C) Left  $P_3$  of *Paukkaungia parva*, NMMP 54, in lingual (A), occlusal (B), and buccal (C) views. (D–F) Left  $P_4$  of *Paukkaungia parva*, NMMP 56, in lingual (D), occlusal (E), and buccal (F) views. (G–J) Holotype right  $M_1$  of *Paukkaungia parva*, NMMP 55, in lingual (G), occlusal (H), buccal (I), and mesial (J) views. (K–N) Right  $M_2$  of *Paukkaungia parva*, NMMP 57, in lingual (K), occlusal (L), buccal (M), and mesial (N) views. (O–Q) Holotype right  $M_2$  of *Kyitchaungia takaii*, NMMP 28, in lingual (O), buccal (P), and occlusal (Q) views. Scale bar equals 1 mm.

the hypoconid than the hypoconulid and entoconid. The lingual margin of the talonid is defined by an elevated series of short crests and four small, poorly differentiated cusps. The distalmost of these four lingual cusps, which is located next to the talonid notch, is interpreted as the hypoconulid. Al-

though it lies on the lingual side of the talonid notch, as is typical for sivaladapids, the hypoconulid is not so clearly “twinned” with the entoconid as it is in other members of this group. However, this lack of twinning between the hypoconulid and entoconid is more apparent than real, being

obscured by two tiny supernumerary cusps that occur on either side of the entoconid. Nevertheless, an important feature that distinguishes the lower molars of *Paukkaungia* from those of other sivaladapids is the absence of highly individualized entoconid and hypoconulid cusps. Perhaps the closest approximation to the condition found in *Paukkaungia* occurs in *Indraloris*, in which the entoconid and hypoconulid on the lower molars are nearly fused to form a relatively continuous pair of cusps adjacent to the talonid notch.

NMMP 57 (length, 3.31; width, 2.41 mm) is interpreted as a right  $M_2$  on the basis of its distinctive trigonid construction (Fig. 2K–N). In contrast to the holotype  $M_1$ , NMMP 57 has a trigonid that is closed lingually, because of a crest that links the metaconid directly with the paraconid. The metaconid also appears to be situated directly lingual to the protoconid, rather than being located significantly distal to it as is often the case on  $M_1$  in adapiform primates. Many other aspects of crown morphology mirror conditions found in the holotype  $M_1$ . Significant points of resemblance include the relatively well-developed buccal cingulid (which is more extensive distally than is the case in the holotype), the very buccal position of the arcuate cristid obliqua, and the deep talonid notch that bifurcates the postcristid. Minor damage to the distolingual part of the crown precludes any attempt to identify the poorly differentiated cusps and cuspsules that likely occurred there.

**Discussion.**—All of the specimens of *Paukkaungia parva* that are currently known consist of isolated teeth that were recovered by screenwashing at two localities (Nyaungpinle and Paukkaung Kyitchaung Locality 2) in the upper part of the Pondaung Formation. Although these localities cannot be correlated directly with each other because of intervening covered terrain, they appear to be approximately the same age on the basis of their very similar mammalian faunas. Indeed, all of the primate-bearing fossil localities described to date from the Pondaung Formation seem to be closely correlative on the basis of physical stratigraphy, paleomagnetic stratigraphy, mammalian biostratigraphy, and a fission-track date of  $37.2 \pm 1.3$  Ma (Aung Naing Soe et al. 2002; Benammi et al. 2002; Tsubamoto et al. 2002; Maung Maung et al. 2005). Screenwashing at Nyaungpinle and Paukkaung Kyitchaung Locality 2 has yielded a reasonably diverse mammalian microfauna (including the eosimiid primate *Bahinia pondaungensis*, the anomaluroid rodent *Pondaungimys anomaluopsis*, and a number of undescribed bats and insectivores). *Paukkaungia parva* and *Bahinia pondaungensis*, which co-occur at these localities, are the only primates currently known from the Pondaung Formation having a reconstructed body mass of roughly 500–600 g (see below; Egi et al. 2004a). Despite their similar size, the lower dentition of *Bahinia* is well documented and easily distinguished from that of *Paukkaungia* (Jaeger et al. 1999). Accordingly, we are confident that the isolated lower premolars and molars allocated here to *Paukkaungia parva* pertain to the same species.

Most of the Eocene adapiforms that have been described

from Asia to date are sivaladapids. A notable exception is *Adapoides troglodytes* from the middle Eocene Shanghuang fissure-fillings of Jiangsu Province, China (Beard et al. 1994). *Adapoides* documents the presence of adapids in eastern Asia, a group that is otherwise recorded from various localities in western Europe. Two additional adapiform taxa, *Panobius afridi* and *Marcgodinotius indicus*, have been described from significantly older Eocene strata in Pakistan and India (Russell and Gingerich 1987; Bajpai et al. 2005). The molar morphology of both *Panobius* and *Marcgodinotius* is much more primitive than that of *Paukkaungia* or other Eocene sivaladapids described to date. The affinities of these Eocene adapiforms from the Indian subcontinent will remain enigmatic until more nearly complete specimens are recovered.

### *Kyitchaungia takaii*, gen. et sp. nov.

**Holotype.**—NMMP 28 (also referred to as NMMP-KU 0626; length, 4.39 mm; width, >2.90 mm), an isolated right lower molar, interpreted as  $M_2$  (Fig. 2O–Q).

**Type locality.**—Paukkaung Kyitchaung Locality 2 (21°45'15.8" North, 94°39'13.5" East), Myanmar (Fig. 1).

**Age and distribution.**—Late middle Eocene Pondaung Formation, Myanmar.

**Hypodigm.**—The holotype (only known specimen).

**Diagnosis.**— $M_2$  differs from those of *Rencunius*, *Hoanghoni*, *Wailekia*, *Guangxilemur*, *Indraloris*, *Sivaladapis*, and *Sinoadapis* in having lower and less cuspidate entoconid and hypoconulid, less angular hypoconid, and cristid obliqua more buccal in position.  $M_2$  differs from that of *Paukkaungia* in being larger, with entoconid and hypoconulid more salient and less integrated into system of cusps and crests along distolingual margin of crown.

**Etymology.**—The generic name derives from *kyitchaung* (Burmese, gully or topographic depression). The trivial name recognizes the contributions of Dr. Masanaru Takai, who organized field parties in the Pondaung Formation that led to the recovery of the holotype.

**Description.**—The enamel on the buccal side of NMMP 28 is broken away, precluding any accurate measurement of tooth width. Likewise, we cannot know whether or not a buccal cingulid was present, although we suspect this to have been the case. We identify the tooth as an isolated right  $M_2$  on the basis of its lingually closed trigonid, although the recovery of more nearly complete specimens is necessary to confirm this allocation. The tooth is most notable in having a very buccal cristid obliqua that projects almost directly mesially (rather than mesiolingually) from the hypoconid, a deep talonid notch between the hypoconid and hypoconulid, and a “twinned” hypoconulid and entoconid on the distolingual side of the talonid. Compared to the condition in *Paukkaungia*, the hypoconulid and entoconid on  $M_2$  are larger and more clearly delineated in *Kyitchaungia*.

**Discussion.**—The holotype was illustrated and briefly described by Takai and Shigehara (2004), who referred to the specimen simply as the “Paukkaung molar.” Takai and Shigehara (2004) noted several similarities between NMMP 28 and the lower molars of various fossil primates

and other mammals, particularly miacid carnivores. Although they recognized a number of features that are shared by NMMP 28 and sivaladapids such as *Wailekia*, Takai and Shigehara (2004) tentatively concluded that the “Paukkaung molar” pertains to an unnamed anthropoid.

Given that fragmentary sivaladapid fossils have previously been confused with carnivores (Pilgrim 1932; Gingerich and Sahni 1979, 1984), it is understandable that Takai and Shigehara (2004) noted similarities between NMMP 28 and the  $M_2$  of miacids. With the exception of *Vulpavus*, miacids differ conspicuously from NMMP 28 in having an  $M_2$  talonid that is narrower than the trigonid. All miacids differ from NMMP 28 in having stronger, more individualized trigonid cusps on  $M_2$ ; a much larger paraconid on  $M_2$  that is segregated from the metaconid by a deep notch (so that the trigonid of  $M_2$  is open lingually); and poorly developed entoconid and hypoconulid cusps that are never twinned and not strongly delineated from adjacent parts of the talonid. These important differences preclude further speculation that NMMP 28 pertains to a carnivoran.

As is true for other Eocene sivaladapids, the lower molar morphology of *Kyitthaungia* also shares many features in common with oligopithecoid anthropoids (Takai and Shigehara 2004). These include a reduced paraconid, an  $M_2$  trigonid that is closed lingually, and a lingually shifted hypo-

conulid that is “twinned” with the entoconid. However, these same molar features also occur in Eocene sivaladapids, and *Kyitthaungia* resembles the latter primates (and particularly *Paukkaungia*) in additional ways that distinguish sivaladapids from oligopithecids. These features include a relatively longer and narrower  $M_2$  crown; a cristid obliqua on  $M_2$  that is very buccal in position, resulting in a shallow hypoflexid; and greater separation between the paraconid and metaconid on  $M_2$  than occurs in oligopithecids. The close similarities in molar morphology shared by *Paukkaungia* and NMMP 28 give us confidence that the “Paukkaung molar” documents a distinctive new member of the Sivaladapidae.

#### Small Adapiform Tarsal Bones From The Pondaung Formation

Three tarsal bones pertaining to a small adapiform have been recovered from the Pondaung Formation at the Thamingyauk Locality (21°45'28.7" North, 94°50'18.3" East; Fig. 1). A nearly complete left calcaneus, NMMP 58, was recovered in 2003 (Fig. 3A–E). Two other specimens, a relatively complete right talus lacking its head (Fig. 3I–M) and the proximal part of a right calcaneus including the tuber and the area surrounding the posterior calcaneal facet

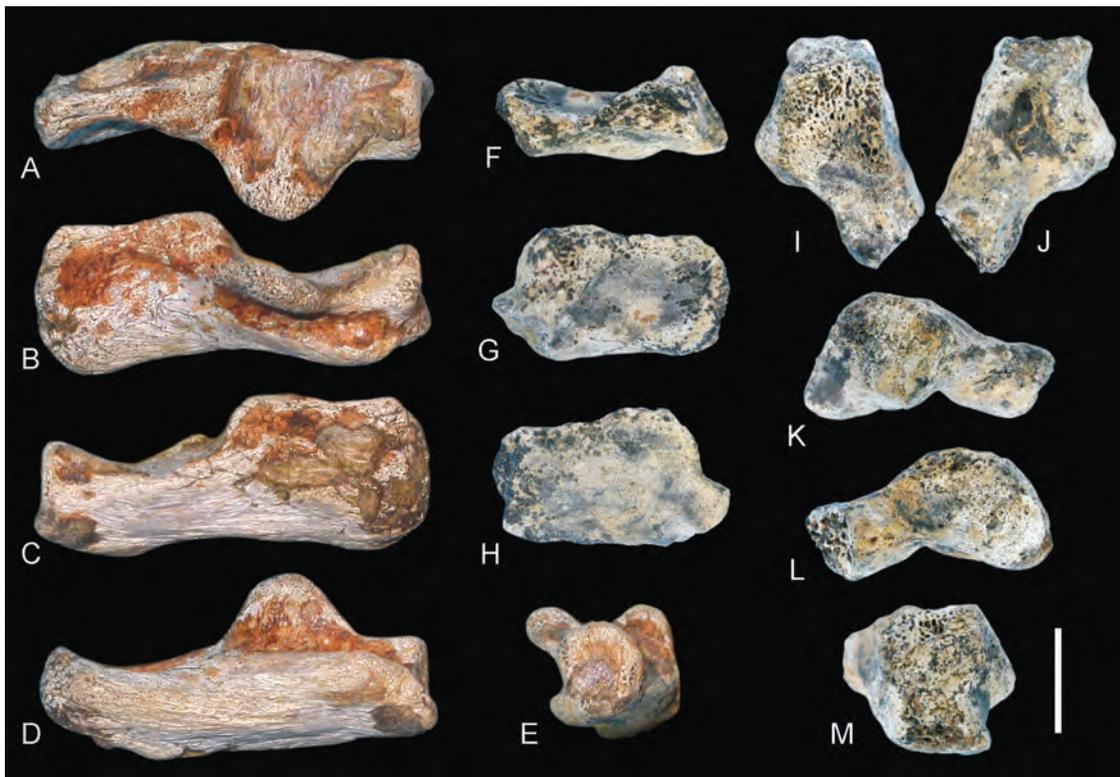


Fig. 3.—Adapiform tarsal bones from the Thamingyauk Locality, Pondaung Formation. (A–E) Relatively complete left calcaneus, NMMP 58, in dorsal (A), medial (B), lateral (C), plantar (D), and distal (E) views. (F–H) Proximal fragment of right calcaneus, NMMP 59, in dorsal (F), medial (G), and lateral (H) views. (I–M) Right talus lacking only the head, NMMP 59, in dorsal (I), plantar (J), lateral (K), medial (L), and posterior (M) views. Scale bar equals 5 mm.

(Fig. 3F–H), were collected at the same locality in December 2005. The latter two specimens were the only fossils recovered from a small bag of screenwashed concentrate, and we regard them as pertaining to the same individual (NMMP 59). All three specimens are thought to belong to the same species on the basis of the close similarity in size and morphology of the two calcaneal specimens.

The NMMP 59 talus can be confidently identified as that of a small adapiform on the basis of its laterally sloping fibular facet (Gebo 1988; Dagosto 1988). In general, the NMMP 59 talus resembles the tali of small notharctids such as *Cantius mckennai* and *Cantius ralstoni* in terms of its overall proportions and major features (Gebo et al. 1991). In contrast, talar features that are characteristic of small adapids such as *Adapis parisiensis* do not occur in the Pondaung talus (Dagosto 1983). For example, despite its absence of a head, we estimate that the talus as a whole was relatively long and narrow like that of a notharctid, rather than being shorter and wider like that of an adapid. The body of the talus is relatively tall as it is in small notharctids, but in contrast to the condition in small adapids. The trochlea is not deeply grooved, nor does the medial trochlear rim deviate strongly medially as it approaches the neck. The talar neck and head deviate only modestly (roughly 26°) from the longitudinal axis of the trochlea, again as in notharctids and in contrast to adapids. The medial facet for the tibial malleolus is large, extending to the plantar margin of the bone. The posterior trochlear shelf is damaged, but it appears to have been relatively large. Nothing can be surmised regarding the position of the groove for the flexor hallucis longus muscle on the posterior trochlear shelf. Following Dagosto and Terranova (1992), measurements for the NMMP 59 talus are as follows: minimum talar length (the head is missing), 12.07 mm; trochlear length (A3), 7.22 mm; midtrochlear width (A4), 5.01 mm; talar width (A2), 7.4 mm; medial talar body height (A7), 6.15 mm.

The calcaneal morphology of the small Pondaung adapiform is documented by NMMP 58, which is relatively complete, and the calcaneal fragment included in NMMP 59. In terms of their overall proportions, these specimens generally resemble the calcanei of small notharctids, and differ appreciably from those of adapids. They also share important similarities with the distal calcaneus included in the much larger NMMP 20 partial skeleton from the Pondaung Formation (Ciochon et al. 2001). We estimate that the distal segment of the NMMP 58 calcaneus measures 48% of the total length of the bone, making the distal calcaneus slightly longer than in a sample of small notharctid calcanei (Gebo et al. 1991). This relatively high degree of distal calcaneal elongation contrasts sharply with the condition in adapids, in which the distal part of the calcaneus is markedly foreshortened (Dagosto 1983). Due to its fragmentary condition, one cannot accurately estimate the degree of distal calcaneal elongation that would have characterized NMMP 20 (Ciochon et al. 2001). However, NMMP 20 certainly would have resembled NMMP 58 and notharctid calcanei in lacking the extreme calcaneal foreshortening that characterizes adapids. The posterior calca-

neal facet in NMMP 58 is relatively broad with respect to its length (pcfw/pcfl ratio = 64), being more similar to adapids and NMMP 20 than to notharctids in this respect. Its plantar border is well delineated. The medial side of the calcaneal tuber, just plantar to the posterior calcaneal facet, is notably invaginated. The peroneal tubercle is relatively proximal in position, being located plantolateral to the posterior calcaneal facet, as is the case in NMMP 20 and adapids. The calcaneocuboid facet possesses a relatively circular distal outline and a deep cuboid pivot that is offset toward the plantomedial side of the facet. This unusual condition, which also occurs in NMMP 20, distinguishes both Pondaung calcanei from those of notharctids (in which the cuboid pivot is plantar in position). Following Dagosto and Terranova (1992), measurements for NMMP 58 are as follows: calcaneal length (C1), 19.15 mm; distal calcaneal length, 9.2 mm; posterior calcaneal facet length (C3), 5.7 mm; posterior calcaneal facet width (C4), 3.64 mm; calcaneal tuber length (C7), 4.25 mm; calcaneal width (C2), 8.7 mm; calcaneocuboid facet width (C6), 5.07 mm; calcaneocuboid facet height (C5), 4.93 mm. A few of these dimensions can also be measured in NMMP 59, as follows: C3, 5.9 mm; C4, 3.62 mm; C7, 4.94 mm.

## DISCUSSION

*Paukkaungia* and *Kyitchaungia* can confidently be identified as sivaladapid primates on the basis of diagnostic aspects of their lower dentition. The most important features that unite the new Pondaung primates with other sivaladapids relate to the unique construction of their lower molar talonids. As is the case in all sivaladapids, the lower molar hypoconulids in *Paukkaungia* and *Kyitchaungia* are shifted to the lingual side of the crown, where they are closely aligned or “twinning” with their respective entoconids. Furthermore, the lower molar posteristids are deeply notched buccal to the hypoconulid, as is the case in other middle Eocene sivaladapids (*Hoanghoni* and *Rencunius*) and, to a lesser extent, in Miocene *Sivaladapis*. In contrast to the condition in primitive adapiforms such as *Cantius*, the postvallid of P<sub>4</sub> in *Paukkaungia* resembles that of *Hoanghoni* and *Guangxilemur* in bearing three vertical crests (a buccal crest, a lingual crest, and a central crest that is continuous with the cristid obliqua). While these dental characters document the sivaladapid affinities of *Paukkaungia* and *Kyitchaungia*, additional and more nearly complete specimens of both taxa will be required to reconstruct their relationships within the family.

The dentition of *Paukkaungia parva* deviates from the typical sivaladapid pattern in two important ways. The premolar series appears to have been reduced, as evidenced by the small size of P<sub>3</sub> and the partial coalescence of the roots of P<sub>3-4</sub> near their junction with their respective crowns. This trend toward premolar compaction in *Paukkaungia* contrasts with the tendency toward elongation and molarization of P<sub>4</sub> that occurs in most other sivaladapids. The second significant difference between the dentition of *Paukkaungia* and other sivaladapids relates to lower molar

bunodonty. The lower molars of *Paukkaungia* are characterized by relatively low cusp relief and poor development of molar shearing crests, exemplified by integration of the hypoconulid and entoconid into a single, poorly differentiated complex of cusps and crests on the distolingual side of each molar. Estimates of body mass in *Paukkaungia parva*, based on regressions of  $M_1$  area against body mass in different taxonomic assemblages of living primates (Conroy 1987), range from 480 to 610 g. This places *Paukkaungia* at—or even slightly below—“Kay’s threshold” of 500 g body mass, below which primates cannot be obligate folivores due to fundamental metabolic constraints (Kay and Covert 1984). Accordingly, *Paukkaungia* was apparently specialized for a diet consisting of fruits and other soft objects, in contrast to the predilection toward folivory that typified most or even all other sivaladapids. Based on Conroy’s (1987) regression equations, *Kyitchaungia takaii* was larger (880 g–1.2 kg), and this species possessed cheek teeth that were less bunodont than those of *Paukkaungia parva*. Its diet may have been more folivorous as a result.

The small adapiform tarsal bones from the Pondaung Formation yield estimates of body mass ranging from 685 g to 2.15 kg, depending upon which tarsal metric is used (Dagosto and Terranova 1992). Accordingly, these tarsals are appropriate in size to pertain to *Kyitchaungia takaii*. Functionally, they document a primate having a relatively generalized locomotor regime. The relatively tall talar body, low talar neck angle, and relatively elongated distal segment of the calcaneus all suggest that this taxon engaged in leaping as well as quadrupedalism and climbing (Gebo 1988). Although the NMMP 20 partial skeleton from the Pondaung Formation has been interpreted as belonging to a slow, deliberate climber (Kay et al. 2004b), its distal calcaneus lacks the extreme foreshortening that characterizes slow-climbing primates. Indeed, the functional attributes of the calcanei of the small Pondaung sivaladapid and NMMP 20 (the only element that is shared in common) appear to have been quite similar. Relatively minor proportional differences in distal calcaneal elongation could easily be attributed to the allometric effects of divergent body mass. A similar pattern characterizes North American notharctids, in which small-bodied species have calcanei bearing relatively longer distal segments than their larger-bodied relatives (Gebo et al. 1991).

An important paradox regarding the large-bodied primate fauna from the Pondaung Formation relates to the NMMP 20 partial skeleton, which has often been assumed to belong to some large-bodied amphipithecoid (Ciochon et al. 2001; Ciochon and Gunnell 2002; Gunnell et al. 2002; Takai and Shigehara 2004; Kay et al. 2004b; Egi et al. 2004b, 2006). This partial skeleton resembles adapiforms in several important ways, and its calcaneus shares numerous features in common with NMMP 58 and NMMP 59, which we refer to the sivaladapid *Kyitchaungia takaii*. Working under the assumption that NMMP 20 pertains to some unknown amphipithecoid, its adapiform postcranial characters have led several authors to question the anthropoid affinities of amphipithecoids (Ciochon et al. 2001; Cio-

chon and Gunnell 2002; Gunnell et al. 2002). However, a relatively large primate talus from the Pondaung Formation is notable for showing anthropoid rather than adapiform affinities (Marivaux et al. 2003), a morphological pattern that agrees with the anthropoid-like dentition of amphipithecoids. If we assume that the unknown talus of NMMP 20 would also have resembled that of *Kyitchaungia takaii*, it becomes obvious that two higher-level taxa of large-bodied primates are represented by tarsal remains from the Pondaung Formation. Only one of these taxa can correspond to the Amphipithecidae. A plausible solution is that NMMP 20 is exactly what it appears to be—a large-bodied adapiform, perhaps a large-bodied sivaladapid related to *Guangxilemur tongi*. Future fieldwork in the Pondaung Formation will be required to test this hypothesis and to obtain a more nearly complete picture of the diverse primate fauna of this Eocene rock unit.

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