A new primate from the Eocene Pondaung Formation of Myanmar and the monophyly of Burmese amphipithecids

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The family Amphipithecidae is one of the two fossil primate taxa from Asia that appear to be early members of the anthropoid clade. *Ganlea megacanina*, gen. et sp. nov., is a new amphipithecoid from the late middle Eocene Pondaung Formation of central Myanmar. The holotype of *Ganlea* is distinctive in having a relatively enormous lower canine showing heavy apical wear, indicating an important functional role of the lower canine in food preparation and ingestion. A phylogenetic analysis of amphipithecoid relationships suggests that *Ganlea* is the sister taxon of *Myanmarpithecus*, a relatively small-bodied taxon that has often, but not always, been included in Amphipithecidae. *Pondaungia* is the sister taxon of the *Ganlea* + *Myanmarpithecus* clade. All three Pondaung amphipithecoid genera are monophyletic with respect to *Siamopithecus*, which is the most basal amphipithecoid currently known. The inclusion of *Myanmarpithecus* in Amphipithecidae diminishes the likelihood that amphipithecoids are specially related to adapiform primates. Extremely heavy apical wear has been documented on the lower canines of all three genera of Burmese amphipithecoids. This distinctive wear pattern suggests that Burmese amphipithecoids were an endemic radiation of hard object feeders that may have been ecological analogues of living New World pitheciin monkeys.

Keywords: Amphipithecidae; Eocene; Myanmar; anthropoid origins

1. INTRODUCTION

Since their initial description in the early twentieth century, amphipithecoid primates have figured prominently in discussions of anthropoid origins (Pilgrim 1927; Colbert 1937; Szalay 1970, 1972; Simons 1971; Ba Maw *et al.* 1979; Ciochon *et al.* 1985). Thanks to renewed field efforts in the Eocene Pondaung Formation of Myanmar, a great deal of additional amphipithecoid material has been recovered and described during the past decade (Jaeger *et al.* 1998, 2004; Chaimanee *et al.* 2000a; Gunnell *et al.* 2002; Shigehara *et al.* 2002; Marivaux *et al.* 2003; Takai & Shigehara 2004). This new-found abundance of amphipithecoid fossils has so far failed

to quell the longstanding debate regarding their phylogenetic affinities. A majority of recent workers support anthropoid affinities for amphipithecoids (Jaeger *et al.* 1998, 2004; Chaimanee *et al.* 2000a; Beard 2002, 2004; Marivaux *et al.* 2003, 2008; Beard *et al.* 2005, 2007; Bajpai *et al.* 2008; Rose *et al.* 2009). Others maintain that dental and gnathic similarities between amphipithecoids and early anthropoids merely reflect convergent adaptations to similar diets, thereby obscuring what they regard to be the adapiform affinities of the former group (Ciochon & Holroyd 1994; Ciochon & Gunnell 2002, 2004; Gunnell *et al.* 2002, 2008).

Much of the ongoing disagreement about the higher-level relationships of amphipithecoids can be attributed to the nature of their fossil record. Amphipithecoids are documented primarily on the basis of teeth and jaws from the Pondaung Formation, although the group is also known from the latest Eocene of peninsular Thailand

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and the Oligocene of central Pakistan (Chaimanee *et al.* 1997, 2000b; Marivaux *et al.* 2005). Several cranial and postcranial fossils from the Pondaung Formation have been allocated to Amphipithecidae, but none of these specimens was found in direct association with diagnostic amphipithecoid dental remains, rendering all of them controversial to a greater or lesser extent. Particularly problematic in this regard are a partial skeleton of a large-bodied primate (NMMP 20) and two cranial fragments (NMMP 19 and NMMP 27) that have been referred to the Amphipithecidae (Ciochon *et al.* 2001; Gunnell *et al.* 2002; Takai *et al.* 2003). The purported amphipithecoid affinities of the NMMP 20 partial skeleton conflict with the anatomy of an isolated primate astragalus from the Pondaung Formation, which bears diagnostic anthropoid traits (Marivaux *et al.* 2003). We regard the NMMP 20 partial skeleton as that of a large-bodied sivaladapid adapiform, rendering it irrelevant to discussions of amphipithecoid relationships (Beard *et al.* 2007; Marivaux *et al.* 2008). Similarly, the Pondaung cranial fragments do not appear to pertain to any primate and are unlikely to be mammalian (Beard *et al.* 2005).

The lower-level systematics of amphipithecoids from Myanmar is also in a state of flux. The first two genera that were proposed, *Pondaungia* and *Amphipithecus*, are now considered to be synonymous by some experts (Jaeger *et al.* 2004), a view that is endorsed here. Questions remain regarding the number of valid species of *Pondaungia*, an issue that is complicated by the possibility of a high level of sexual dimorphism in this group. More problematic is *Myanmarpithecus*, another fossil primate from the Pondaung Formation that was initially described as a probable basal anthropoid of uncertain taxonomic affinities (Takai *et al.* 2001). Subsequent authors have regarded *Myanmarpithecus* as either an omomyid (Ciochon & Gunnell 2002; Gunnell *et al.* 2008) or another member of the Amphipithecidae (Kay *et al.* 2004a,b; Marivaux *et al.* 2005). Here, we describe a new genus of Amphipithecidae from the Pondaung Formation and reassess the phylogenetic and paleobiological affinities of this group in light of this new taxon.

2. SYSTEMATIC PALAEONTOLOGY

Class Mammalia Linnaeus, 1758

Order Primates Linnaeus, 1758

Suborder Haplorhini Pocock, 1918

Infraorder Anthroidea Mivart, 1864

Family Amphipithecidae Godinot, 1994

Ganlea megacanina, gen. et sp. nov.

Holotype: NMMP 70, a right dentary preserving the crowns of C_1 and M_2 and the roots or alveoli for P_2 – M_1 (figure 1). Partial alveoli for I_{1-2} are also preserved.

Type locality: Ganle kyitchaung, GPS coordinates = 21°44'04.6" N, 94°43'25.0" E (figure 2).

Age and distribution: Late middle Eocene Pondaung Formation, Myanmar.

Hypodigm: The holotype; NMMP 69, an isolated left M_1 from Nyaungpinle (figure 3d); NMMP 71, an isolated left I_2 from Nyaungpinle (figure 3e–i); NMMP 72, an isolated right M_2 from Nyaungpinle (figure 3m–o); NMMP 73, an isolated left M_1 from Thamingyauk (figure 3j–l);

NMMP 74, a right dentary preserving P_{3-4} from Thamingyauk (figure 3a–c); NMMP 75, an isolated left M^1 or M^2 from Paukkaung kyitchaung 2 (figure 3t); and NMMP 76, an isolated left P^4 from Paukkaung kyitchaung 2 (figure 3s).

Diagnosis: Amphipithecoid primate smaller than *Pondaungia* and *Siamopithecus* but larger than *Myanmarpithecus*. Symphyseal region of dentary less vertical in orientation than in *Pondaungia* and *Siamopithecus*. C_1 , at least in male individuals, and P_2 larger relative to molar size than in other amphipithecoids. C_1 further differs from that of *Pondaungia* and *Siamopithecus* in having a small, distobuccal tubercle or heel. P_{2-4} relatively larger and less compressed mesiodistally than in *Pondaungia*. P_{3-4} with elevated and mesially oriented preprotocristid, in contrast to the condition in other amphipithecoids. P_3 further differs from that of *Myanmarpithecus* and *Pondaungia* in lacking a metaconid and having a reduced talonid heel. Lower molars differ from those of *Bugtipithecus* in lacking a prominent lingual notch at the base of the postvallid. M_{1-2} without hypoconulid, in contrast to *Siamopithecus*.

Etymology: The generic name derives from the village of Ganle, situated near the type locality. The trivial name refers to the relatively massive canine preserved in the holotype.

Description of the holotype: The dentary is robustly constructed, measuring 14.15 mm in depth and 6.75 mm in width just behind the symphysis. The symphysis is unfused, but its surface is characterized by a highly rugose pattern of alternating ridges, pits and valleys that would have interlocked with corresponding structures on the opposite side. As it is preserved, the greatest vertical height of the symphysis is 18.05 mm. It extends inferiorly and posteriorly to a point below the junction of the mesial and distal roots of P_3 . The inclination of the main axis of the symphysis in relation to a horizontal line through the toothrow is 53°. The planum alveolare slopes at roughly 21°. The pit for the genioglossus muscle is notable for its depth, and it lies above a stoutly constructed inferior transverse torus. The lateral side of the dentary bears dual mental foramina anteriorly, and a third emissary foramen below the mesial root of M_1 . The anteriormost mental foramen lies beneath the interstitial junction between C_1 and P_2 . It is significantly larger than the other mental foramen, which lies beneath the junction between P_2 and P_3 .

Based on roots and/or alveoli preserved in the holotype, the lower dental formula of *Ganlea* was 2-1-3-3. The lower incisors are documented by partial alveoli located mesial to the lower canine crown. Based on the radius of curvature of the preserved lingual parts of these alveoli, it appears that I_2 would have been slightly larger than I_1 . Both incisors were tiny (the estimated mesiodistal dimensions of the lower incisor roots are 0.85 mm for I_1 and 1.10 mm for I_2) and oriented almost vertically within the dentary. Given the narrow space available between the symphyseal surface and the lower canine crown, it is clear that the anterior lower dentition of *Ganlea megacanina* was tightly spaced. Indeed, a distinctive, vertically oriented groove on the mesial side of the canine root and the basal part of its crown is appropriate in position to have served as an embrasure for the adjacent I_2 .

The lower canine is massive (length, 5.90 mm; width, 4.30 mm), being absolutely larger in terms of both

Figure 1. *Ganlea megacanina*, gen. et sp. nov.: holotype right dentary (NMMP 70) preserving the crowns of C_1 and M_2 and the roots or alveoli for P_2 – M_1 . Partial alveoli for I_{1-2} are also preserved. The specimen is presented by 3D rendering in (a) occlusal, (b) inferior, (c) distal, (d) mesial, (e) buccal and (f) lingual views. Images (a–f) have been generated from 3D data obtained by X-ray synchrotron microtomography (SR- μ CT) on the beamline ID19 at the European Synchrotron Radiation Facility (ESRF, Grenoble, France). Images g and h are 3D rendering of NMMP 70 showing the colour-coded crowns and roots of individual teeth, which have been virtually delimited by manual segmentation. Scale bar equals 1 cm.

mesiodistal length and buccolingual width than the lower canine of NMMP 24, a dentary of *Pondaungia* that pertains to an animal that was clearly much larger than *Ganlea megacanina* (Gunnell *et al.* 2002; Jaeger *et al.*

2004). The apex of the canine crown has been worn nearly flat, making it impossible to estimate the unworn height of the canine crown. From the enamel–dentine junction on the buccal side of the canine to the wear

Figure 2. Location map for the fossiliferous localities in the Bahin (Nyaungpinle, Paukkaung Kyitchaung 2, Ganle) and Pangan (Thamingyauk) areas of central Myanmar.

facet near its apex, the crown measures 4 mm in height. The level of the enamel–dentine junction is not uniform about the circumference of the canine crown. Rather, this junction extends apically on either side of the mesial embrasure groove for I_2 noted earlier. In occlusal view the canine is roughly ovoid in outline, with a gently convex buccal surface and a nearly flat lingual surface. These surfaces are separated by the vertically oriented groove mesially and by a small heel or distension of the crown distally. The latter structure was probably characterized by a small tubercle in the unworn condition, but this cusplule (if it actually existed) has been nearly obliterated by the apical wear on the canine noted previously. Similarly obscured by apical wear, there appears to have been a distal crest that would have connected the apex of the canine crown with the distal heel or tubercle. A modest cingulid, which becomes more marked distally, adorns the lingual side of the canine crown, but no similar structure exists on the buccal side of the tooth.

P_{2-4} are documented in the holotype solely by their roots and aveoli. The crowns of P_{3-4} are preserved in a referred specimen, and these are described in the following section. We estimate that the combined mesiodistal length of P_{2-4} would have been roughly 9.25 mm. As is the case in other amphipithecids (and eosimiids), P_2 is single-rooted while P_{3-4} are double-rooted. The single root of P_2 is strongly compressed mesiodistally, so that its buccolingual width greatly exceeds its mesiodistal length. This condition also occurs in other amphipithecids, but it contrasts with the presumably more primitive condition found in eosimiids, in which the alveolus or root for P_2 is roughly circular in cross section. High-resolution synchrotron images reveal that the P_2 root in the holotype of *Ganlea* was particularly stout and asymmetrical in cross section. Although *Myanmarpithecus* and *Pondaungia* share the strong mesiodistal compression of P_2 that occurs in *Ganlea*, the latter taxon is unique among amphipithecids in having a P_2 root

that is broader buccolingually than the corresponding roots of M_{1-2} . Both P_{3-4} show the typical amphipithecoid pattern of having the mesial root located farther buccally than the distal root, a condition that also occurs in eosimiids and many other basal anthropoid taxa.

M_1 is documented in the holotype only by its roots and alveoli. Knowledge of the crown of M_1 is based on two referred specimens that are described in the following section.

M_2 (length 4.70 mm; width 4.50 mm) is a relatively quadrate, low-crowned tooth characterized by poorly defined cusps and weakly developed crests (figure 3*p–r*). The M_2 crown in the holotype is moderately worn, obscuring some details of its morphology (NMMP 72 is a relatively unworn M_2 that is described in the following section). The mesiodistally compressed trigonid shows no evidence of having a paraconid. The protoconid appears to have been slightly larger than the metaconid (at least in terms of its basal circumference), and the two cusps were partly separated by a longitudinal valley. A tiny mesial cingulid occurs in front of the metaconid. The talonid is broad, surrounded by low crests, and simple in construction. It bears a low entoconid and a much higher hypoconid. The cristid obliqua meets the postvallid very buccally, so that the hypoflexid is extremely shallow. Several minor folds of enamel run from the hypoconid and the cristid obliqua toward the central part of the talonid basin. A small interstitial wear facet on the distal side of the talonid demonstrates that M_3 was present.

Description of the referred specimens: NMMP 71 (figure 3*e–i*) is an isolated left lower incisor (apical mesiodistal length, 1.90 mm; basal labiolingual breadth, 1.85 mm) that we tentatively identify as I_2 on the basis of the mesiodistal dimension of its root (1.10 mm), which matches the size of the partial I_2 alveolus in the holotype lower jaw (see earlier mentioned). The crown is broken apically, but that which remains can be described as being spatulate in shape. In mesial or distal

Figure 3. *Ganlea megacanina*, gen. et sp. nov.: (a–c) right dentary fragment bearing P_{3-4} (NMMP 74) in (a) occlusal, (b) lingual and (c) buccal views; (d) left M_1 (NMMP 69) in occlusal view; (e–i) left lower incisor (NMMP 71) in (e) occlusal, (f) lingual, (g) labial, (h) mesial and (i) distal views; (j–l) left M_1 (NMMP 73) in (j) occlusal, (k) buccal and (l) lingual views; (m–o) right M_2 (NMMP 72) in (m) occlusal, (n) buccal and (o) lingual views; (p–r) right M_2 of the holotype (NMMP 70) in (p) occlusal, (q) buccal and (r) lingual views; (s) left P^4 (NMMP 76) in occlusal view; (t) left M^1 or M^2 (NMMP 75) in occlusal view. Scale bar equals 2 mm. The 3D renderings (d–r) have been obtained by X-ray SR- μ CT. Original art (drawings a–c, s–t) by Laurence Meslin, copyright CNRS-Meslin.

view, the crown is roughly wedge-shaped, being broader at its base than near its apex. The enamel–dentine junction is not uniformly distributed about the base of the crown. Rather, it extends farther toward the root on the labial and lingual surfaces of the crown. Distally and (especially) mesially, the enamel–dentine junction arcs toward the apex of the tooth, thereby covering less of

the root. The labial surface of the crown is gently convex, while the lingual surface is more irregular, but generally concave. The lingual surface of the crown is dominated by a central, pillar-like structure that is bounded mesially and distally by well-developed cingulids. The latter structures are connected by a more modest cingulid near the lingual base of the crown.

NMMP 74 (figure 3a–c) is a fragmentary dentary preserving the crowns of P_{3-4} , both of which are double-rooted. P_3 (length, 2.80 mm; width, 2.90 mm) is distinctive in showing strong basal distensions of enamel both buccally and lingually. The lingual base of the P_3 crown is notably more asymmetrical than its buccal counterpart, because the degree of enamel distension is far more pronounced distally than mesially on the lingual side of the tooth. Similar P_3 morphology occurs in *Myanmarpithecus* and *Pondaungia*, but *Siamopithecus* lacks the pronounced basal distension of P_3 enamel that characterizes all three Burmese amphipithecids. The trigonid of P_3 bears an elevated paraconid that is situated directly mesial to the protoconid. The latter two cusps are connected by the preprotocristid, yielding a relatively trenchant structure that approximates a blade-like morphology. The lingual side of the trigonid bears a relatively complete cingulid, but there is no development of a metaconid. The lingual cingulid is stronger distally than mesially, and it traces the general contour of the base of the crown. As such, the lingual cingulid reaches its inferiormost point near the junction of the trigonid and talonid. From there, it continues superiorly to define the lingual side of the abbreviated talonid. The talonid itself lacks a distinct basin. Rather, it forms a heel-like structure that consists of the hypoconid, the distalmost part of the lingual cingulid, and a vertically oriented crease that separates the trigonid and the talonid. A short, almost vertically oriented crest unites the hypoconid with the protoconid.

P_4 (length, 3.05 mm; width, 3.10 mm) shows greater enamel distension buccally than lingually, thereby displaying the muted exodaenodont condition that is typical of most basal anthropoids. The trigonid is more nearly molariform than that of P_3 , because the metaconid is relatively well developed. The latter cusp is situated inferiorly and distally with respect to the protoconid. A modestly developed crest runs from the apex of the protoconid to the base of the metaconid. As is the case for P_3 , the preprotocristid is somewhat elevated and it extends almost directly mesially to unite with a small paraconid. The lingual cingulid is restricted to the trigonid, where it forms a thick shelf extending distally and inferiorly from the paraconid. Because the lingual cingulid fails to unite the paraconid with the metaconid, the trigonid is open lingually. The talonid of P_4 is abbreviated, but better developed than that of P_3 . It is dominated by the hypoconid, which occurs at roughly the same height on the crown as the metaconid. Two moderately developed crests emanate from the hypoconid to line the buccal and distal margins of the talonid. The short cristid obliqua climbs the trigonid to become confluent with the base of the protoconid. The postcristid runs lingually and inferiorly from the hypoconid, connecting that cusp with a tiny entoconid. The talonid itself consists of a short, arcuate valley between the trigonid and the postcristid.

NMMP 69 (figure 3d) (length, 4.30 mm; width, 3.90 mm) and NMMP 73 (figure 3j–l) (length, 4.20 mm; width, 3.80 mm) are isolated left M_1 s referred to *Ganlea megacanina* on the basis of their appropriate size and morphology. NMMP 69 shows slightly less wear than NMMP 73, but otherwise the two specimens are remarkably similar in morphology. The trigonid

is less compressed mesiodistally than is the case for M_2 in the holotype (see earlier mentioned), being roughly triangular in occlusal outline. The protoconid and metaconid are low, rounded cusps separated by either a sinuous valley (NMMP 69) or a tiny depression (NMMP 73). In terms of basal circumference, the protoconid is appreciably larger than the metaconid, but there is no apparent difference in the height of these cusps. Weakly developed crests, including an arcuate crest defining the mesial margin of the trigonid and a transverse crest marking the distal side of the trigonid, connect the protoconid with the metaconid. There is no development of a distinct paraconid. The talonid is remarkably broad and encircled by weak crests. The hypoconid and the cristid obliqua are much taller than the entoconid and its associated crests. The cristid obliqua is relatively straight, and it joins the postvallid very buccally, resulting in an extremely shallow hypoflexid. The hypoconulid is not developed as a distinct cusp.

NMMP 72 (figure 3m–o) (length, 4.45 mm) is an isolated right M_2 from Nyaungpinle that appears to be an unerupted tooth germ. We tentatively refer this specimen to *Ganlea megacanina* here. Although the tooth is broken buccally, it appears to have been relatively narrower than M_2 in the holotype. Its unworn condition is reflected by the presence of numerous enamel crenulations.

NMMP 76 (figure 3s) (length, 2.85 mm; width, 4.65 mm) is an isolated left P^4 from Paukkaung kyitchaung 2. The crenulated crown is nearly rectangular in occlusal outline, although its lingual margin is rounded and slightly narrower than its buccal counterpart. The buccal margin of the crown is dominated by the paracone, the base of which is buccolingually compressed. Pre- and post-paracristae run mesially and distally from the apex of the paracone toward the margins of the tooth. The mesial cingulum is thick and continuous, running lingually from the terminus of the preparacrista to a point directly mesial to the protocone. The distal cingulum is similar in thickness but less distinct because it is interrupted by multiple enamel crenulations. The protocone is a low, rounded cusp situated near the mesiolingual margin of the crown. The preprotocrista is low but extensive, running buccally more or less parallel to the mesial cingulum until it reaches the base of the paracone. A short postprotocrista is confluent with the distal cingulum. The central part of the crown is covered by an irregular pattern of enamel crenulations that defies any systematic attempt at description.

The upper molar morphology of *Ganlea* is documented by NMMP 75 (figure 3t), an isolated left M^1 or M^2 (length, 4.15 mm; width, 5.25 mm). The crown is bunodont, bears crenulated enamel, and is basically tritubercular. The paracone is slightly larger than the metacone, and both buccal cusps are situated near the buccal margin of the crown, rather than being located more internally as is often the case in *Pondaungia*. Conules are not apparent. The protocone is situated mesial of the midline, such that it is closer to the paracone than the metacone. The pre- and post-protocristae are evident, but neither of these crests are well defined. The postprotocrista runs distally before turning buccally to become confluent with a lingual crest from the metacone (hypometacrista). There is no evidence of a pseudohypocone. The mesial cingulum is relatively strong and

continuous, while the distal cingulum is narrower and interrupted by numerous enamel crenulations. A tiny cusple that could be regarded as an incipient hypocone occurs near the lingual termination of the distal cingulum. Buccal and lingual cingula are either extremely weak or entirely absent.

Discussion: The adult body mass of *Ganlea megacarina* can be estimated on the basis of regressions of body mass as a function of M_1 area in living primates (Conroy 1987). Using the anthropoid regression equation provided by Conroy (1987), we derive a mean adult body mass estimate of roughly 2.4 kg. The all-primate regression equation provided by Conroy (1987) yields a slightly lower estimate of mean adult body mass of roughly 1.9 kg. Hence, *Ganlea* would have been about the same size as the New World monkey *Pithecia*.

3. PHYLOGENETIC ANALYSIS

In order to assess the impact of *Ganlea* on the evolutionary relationships of Amphipithecidae, we performed a phylogenetic analysis based on a data matrix including 39 taxa and 326 characters (see the electronic supplementary material). Twelve maximally parsimonious trees were recovered. These trees have a tree length of 1584, a consistency index of 0.3226 and a retention index of 0.5467. A strict consensus tree that summarizes the phylogenetic resolution obtained by our analysis is depicted in figure 4.

Notable results from this analysis include the novel finding that all three Burmese amphipithecids (*Pondaungia*, *Myanmarpithecus* and *Ganlea*) are monophyletic with respect to the Thai genus *Siamopithecus*. To reflect their seemingly close phylogenetic relationships, we refer all three Burmese amphipithecids to the subfamily Amphipithecinae, while *Siamopithecus* is classified here in a separate amphipithecoid subfamily, Siamopithecinae. Many previous workers have failed to recognize that *Myanmarpithecus* is an amphipithecoid (Takai et al. 2001; Ciochon & Gunnell 2002; Gunnell et al. 2002, 2008). Those who have accepted the amphipithecoid affinities of *Myanmarpithecus* have typically regarded it as lying outside a putative clade of large-bodied forms including *Pondaungia* and *Siamopithecus* (Kay et al. 2004b; Marivaux et al. 2005). All Burmese amphipithecids (or Amphipithecinae) share a distinctive, derived suite of features in the lower premolar dentition that readily distinguishes them from *Siamopithecus* and other early anthropoids. In general, the crowns of P_{2-4} show a greater degree of mesiodistal compaction in Amphipithecinae (and particularly in *Pondaungia*) than is the case in *Siamopithecus* (table 1). This mesiodistal compaction is manifest in several morphological characters. For example, the root or alveolus for P_2 in Amphipithecinae is mesiodistally compressed, such that its buccolingual breadth exceeds its length. Additionally, the bases of the crowns of P_{2-3} in Amphipithecinae are distended distolingually, often incorporating a strong lingual cingulid into this distolingual lobe. Finally, the talonids of P_{3-4} are extremely abbreviated in Amphipithecinae, such that they consist of little more than transverse furrows running lingually and inferiorly from the hypoconid. The talonid of P_4 in *Siamopithecus* is less abbreviated, so that it retains a small but distinct talonid basin.

Figure 4. Strict consensus of 12 equally most parsimonious trees of 1584 steps each (CI = 0.32; RI = 0.54). This cladogram is a simplified tree highlighting the principal dichotomies among higher taxonomic primate groups. Further information is available as electronic supplementary material.

Table 1. Quantification of the degree of lower premolar compaction among Amphipithecidae, based on the ratio of lower premolar length versus M_2 length.

Species	specimen	length, P_{2-4} (mm)	length, M_2 (mm)	ratio, $P_{2-4} : M_2$
<i>Ganlea megacarina</i>	NMMP 70	9.25	4.70	1.97
<i>Siamopithecus eocaenus</i>	TF 7624	13.67	6.75	2.02
<i>Pondaungia cotteri</i> (large)	NMMP 17	9.26	8.20	1.13
<i>Pondaungia cotteri</i> (large)	NMMP 24	8.42	7.50	1.12
<i>Pondaungia cotteri</i> (small)	NMMP 30	8.64	6.70	1.29

Recognizing the amphipithecoid affinities of *Myanmarpithecus* diminishes the possibility that amphipithecids are adapiforms rather than anthropoids. Previous workers who have argued for the adapiform affinities of amphipithecids have always maintained that *Myanmarpithecus* pertains to some other higher-level primate taxon, such as Omomyidae (Ciochon & Gunnell 2002; Gunnell et al. 2008). The dentition of *Myanmarpithecus* diverges radically from that of adapiform primates, rendering detailed comparisons virtually meaningless (Takai et al. 2001). Our phylogenetic analysis conflicts with the hypothesis that amphipithecids are related to adapiforms and places them in or near crown anthropoids instead. Indeed, all 12 of the most parsimonious trees used to generate the strict consensus tree shown in figure 4 recognize amphipithecids as being nested within crown clade anthropoids. These trees differ only in recognizing a closer relationship between amphipithecids and propithecids (as originally suggested by Jaeger et al. 1998) or a closer relationship between amphipithecids and platyrrhines. Accordingly, current evidence indicates that amphipithecids are much more advanced anthropoids than eosimiids. Additional evidence, particularly from the postcranium and skull of amphipithecids, is needed to test this hypothesis.

Table 2. Quantification of Gingerich's (1981) canine molar ratio (CMR) among Amphipithecidae and Pitheciini.

species	specimen(s)	length $\times$ width, C ₁ (mm ²)	length $\times$ width, M ₁ (mm ²)	CMR
<i>Ganlea megacanina</i>	NMMP 70, 69, 73	25.4	16.8	1.51
<i>Myanmarpithecus yarshensis</i>	NMMP 9, 37	8.1	10.5	0.77
<i>Siamopithecus eocaenus</i>	TF 7624	32.0	39.0	0.82
<i>Pondaungia cotteri</i> (large)	NMMP 24	22.4	34.4	0.65
<i>Pondaungia cotteri</i> (small)	NMMP 61, 63	13.1	26.5	0.49
<i>Nuciraptor rubricae</i>	IGM 251074	14.6	15.5	0.94
<i>Cebupithecus sarmientoi</i>	UCMP 38762	20.8	13.3	1.56
<i>Chiropotes satanas</i>	CM 51862	33.4	15.8	2.11
<i>Chiropotes satanas</i>	CM 76820	33.4	15.7	2.13

4. FEEDING ADAPTATIONS

The unique morphology of the teeth and jaws of amphipithecids has led many workers to regard them as hard object feeders that specialized on seeds and fruits with tough, resistant exteriors (Gunnell *et al.* 2002; Ciochon & Gunnell 2004; Kay *et al.* 2004a). The most detailed analysis of feeding adaptations in amphipithecids published to date is that of Kay *et al.* (2004a), who cite upper incisor morphology, molar shearing development, molar enamel thickness and mandibular morphology as evidence favoring hard object feeding for this group. Here, we explore the implications of the highly specialized lower canine morphology and lower canine wear pattern found in *Ganlea* and other amphipithecids for reconstructing their dietary habits.

The holotype of *Ganlea megacanina* is unique among Amphipithecidae in having a greatly enlarged lower canine relative to M₁, which can be quantified using Gingerich's (1981) canine molar ratio (or CMR) (table 2). We interpret this as evidence that the holotype represents a male individual. However, some of the other amphipithecoid specimens in our comparative sample, notably including the holotype of *Myanmarpithecus yarshensis* and a referred lower jaw of *Siamopithecus eocaenus*, probably also represent male individuals, yet their CMR values are much lower than that of the holotype of *Ganlea megacanina* (table 2). This suggests that the lower canine of *Ganlea megacanina* was hypertrophied beyond the level associated merely with canine dimorphism. Among living anthropoid primates, taxa that habitually use their canines to open hard objects such as highly resistant fruits have stouter canines that confer resistance to bending or breaking in both the mesiodistal and buccolingual planes (Plavcan & Ruff 2008). The hypertrophied lower canine of *Ganlea* could therefore reflect a similar functional adaptation in this amphipithecoid.

The unusual apical wear pattern that occurs on the lower canine of *Ganlea megacanina* is consistent with this view. Apical wear such as that on the lower canine of *Ganlea megacanina* can only result from repetitive contact with hard food items that abrade the tooth crown. Normal tooth-on-tooth wear facets (attrition facets) are oriented more obliquely with respect to the tooth crown (Kay & Hiiemae 1974). Modern primate seed predators such as New World monkeys of the tribe Pitheciini habitually use their upper and lower canines to open hard, tough fruits to obtain the seeds contained inside (Kinzey 1992). We interpret both the hypertrophy of the lower canine in *Ganlea megacanina* and its heavy apical wear as evidence that this taxon engaged in

pitheciin-like seed predation in which the canines were used to husk the hard exteriors of resistant fruits.

Although other amphipithecids lack the extreme canine robusticity seen in *Ganlea* (table 2), many of these taxa also show remarkably heavy apical wear on their canines, suggesting that they too engaged in pitheciin-like husking of hard fruits. For example, the holotype of *Myanmarpithecus yarshensis* (NMMP 9) shows extremely heavy apical wear on its lower canine (Takai *et al.* 2001), as does one of the few specimens of *Pondaungia* (NMMP 24) that preserves the lower canine crown intact (Gunnell *et al.* 2002; Jaeger *et al.* 2004). The heavy apical wear patterns on the lower canines of all three genera of Burmese amphipithecids suggest that the entire group was an endemic radiation of hard object feeders. Variation in canine robusticity among Burmese amphipithecids resembles that found among living pitheciins, in which *Chiropotes* and *Cacajao* show extreme canine hypertrophy while *Pithecia* has only modestly enlarged canines (Kinzey 1992). The degree of canine hypertrophy shown by *Ganlea* closely matches that which occurs in the Miocene pitheciin *Cebupithecus sarmientoi*, while less specialized amphipithecids resemble the Miocene pitheciin *Nuciraptor rubricae* in this regard (table 2). The extant pitheciin *Chiropotes satanas* shows an even greater degree of canine hypertrophy than does *Ganlea* (table 2). Although our reconstruction of dietary adaptations in amphipithecids is generally consistent with that of Kay *et al.* (2004a), consideration of the heavy apical wear on the lower canine of *Myanmarpithecus yarshensis* suggests that this taxon was also a specialized seed predator, rather than a generalized frugivore as Kay *et al.* (2004a) infer.

5. DISCUSSION

The discovery of *Ganlea* provides some welcome resolution to the ongoing debate regarding the phylogenetic position of amphipithecids with respect to other primates, while at the same time it clarifies the evolutionary relationships within this extinct group of primates. *Ganlea* can be referred with confidence to the Amphipithecidae on the basis of its dental morphology, which shares numerous features in common with *Pondaungia* and *Myanmarpithecus*. *Ganlea* has the same lower dental formula that typifies all amphipithecids (and many other basal anthropoid taxa), and its single P₂ root is strongly compressed mesiodistally (rather than being circular in cross section), as is also the case in other amphipithecids. However, its lower premolar series shows a lower degree of mesiodistal compaction

(both in terms of the crowns and the roots) than is the case in *Pondaungia*, which has severely compressed its lower premolars relative to M_2 length (table 1). In this respect, *Ganlea* resembles *Myanmarpithecus* and *Siamopithecus*, but this resemblance is probably only due to symplesiomorphy. Canine morphology suggests that *Ganlea* is the sister group of *Myanmarpithecus*, because both taxa share a distinctive distobuccal distension of the canine crown that yields a sinuous apical wear facet in older individuals. The loss of hypoconulids on M_{1-2} , the greater degree of mesiodistal compaction of the lower premolars, and the strong distolingual distension of enamel on P_{2-3} that are shared by all of the amphipithecids from Myanmar appear to be derived characters linking these taxa to the exclusion of *Siamopithecus*.

The inclusion of *Ganlea* and *Myanmarpithecus* in Amphipithecidae makes it less probable that this extinct group of primates is closely related to adapiforms, as some recent workers have suggested (Ciochon *et al.* 2001; Ciochon & Gunnell 2002, 2004; Gunnell *et al.* 2002, 2008). Even those scholars who have emphasized similarities between certain adapiforms and large amphipithecids such as *Pondaungia* admit that *Myanmarpithecus* is unlikely to be related to the former group (Ciochon & Gunnell 2002; Gunnell *et al.* 2008). In many respects *Ganlea* is metrically and morphologically intermediate between *Pondaungia* and *Myanmarpithecus*, and our phylogenetic analysis suggests that all three of these Burmese taxa are nested within Amphipithecidae. Fossils of all three genera of Burmese amphipithecids show heavy apical wear on their lower canines, suggesting that all Burmese amphipithecids used their canines to husk the hard exteriors of fruits to extract the nutritious seeds contained inside. This apparent shared dietary specialization for hard object feeding corroborates our phylogenetic analysis, suggesting that the Burmese amphipithecids radiation was ecologically analogous to the radiation of modern New World pitheciin primates. Seed predation is an uncommon dietary strategy among primates, and there is no evidence that adapiforms ever invaded this dietary niche.

In terms of both abundance and alpha-level diversity, amphipithecids are the dominant primate group in the Pondaung Formation, although both eosimiids and sivaladapids occur there in much lower numbers (Jaeger *et al.* 1999; Gebo *et al.* 2002; Takai *et al.* 2005; Beard *et al.* 2007). At first glance, the diversity and abundance of amphipithecids appear to be at odds with the specialized dietary adaptation posited for them here. However, modern pitheciins of the Amazon Basin have radiated into three genera of seed predators that utilize different parts of the floodplain and different foraging strategies to minimize interspecific competition (Ayres 1989). The amphipithecids of the Pondaung Formation inhabited a paleo-Irrawaddy fluvial system that may have resembled the modern Amazon Basin in terms of seasonal flooding and general environmental conditions (Aung Naing Soe *et al.* 2002). The degree to which sedimentary and taphonomic processes may have biased the fossil record of the Pondaung Formation can only be determined by further field investigations.

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