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Additional materials of *Myanmarpithecus yarshensis* (Amphipithecidae, Primates) from the middle Eocene Pondaung Formation

Abstract *Myanmarpithecus yarshensis* is an amphipithecid primate from the middle Eocene Pondaung Formation in Myanmar. It was previously known based on maxillary fragments with P^4–M^3 and mandibular fragments with C–P_3 and M_{2-3}. This study reports new materials for the genus, including a humeral head fragment, a lingual fragment of the right M^2, a lingual fragment of the right M^3, and a left I^1. These new materials were collected from approximately the same point, and likely belonged to the same individual. The upper molar morphology and size of the new materials show similarity to those of the type specimen, indicating that the new materials can be assigned to *M. yarshensis*. The humeral head is the first postcranial element that is associated with dental materials for amphipithecids. The morphological similarity between the previously reported larger humerus and this specimen confirms the assignment of the former specimen to Amphipithecidae and suggests common locomotor adaptations in the family. The upper central incisor is large relative to the molar fragments, but is within the variation among extant platyrrhines. The tooth is spatulate-shaped and high crowned, and lacks the mesial process, indicating similarity to I^1 of haplorhines and clear differences from that of adapoids. It has been suggested that amphipithecids, including *Myanmarpithecus*, have affinities with notharctine adapoids, but the morphology of I^1 does not support the notharctine hypothesis of the Amphipithecidae.

Keywords Amphipithecidae · *Myanmarpithecus* · Phylogenetic status

Abbreviations AMNH: American Museum of Natural History · NMMP: National Museum of Myanmar, Primates · NMMP-KU: National Museum of Myanmar in Paleontology—Kyoto University (indicating that the fossil specimens stored in NMM has been serially cataloged by Kyoto University, Japan) · PA: Province Anhui, China · UCMP: University of California Museum of Paleontology

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Introduction

The late middle Eocene Pondaung Formation in Myanmar has yielded several primate genera (Ciochon and Gunnell 2002a, b; Egi et al. 2004a; Takai and Shigehara 2004). Among the Pondaung primates, *Amphipithecus mogaungensis*, *Pondaungia cotteri*, *P. savagei*, and *Myanmarpithecus yarshensis* belong to the family Amphipithecidae and are endemic to the Pondaung fauna (Pilgrim 1927; Colbert 1937; Takai et al. 2001; Ciochon and Gunnell 2002a, b; Gunnell et al. 2002; Kay et al. 2004b). *Myanmarpithecus* is the most recently established genus among the three. The first description of it was published in 2001 based on right maxillary fragments with P^4–M^3 and left mandibular fragments preserving C–P_3 and M_{2-3} (Takai et al. 2001). An additional material, an isolated left M_3, has been reported by Ciochon and Gunnell (2002b). In this short paper, we report several fossil materials likely of *Myanmarpithecus* that were collected during the 2003 field season, and infer additional morphological

information to discuss the phylogenetic status of Amphipithecidae.

The new materials include a humeral head fragment (NMMP-KU 1740 = NMMP 49), a lingual fragment of the right M^2 (NMMP-KU 1764 = NMMP 50), and a lingual fragment of the right M^3 (NMMP-KU 1868 = NMMP 51). Additionally, an upper incisor (NMMP-KU 1878 = NMMP 53) possibly belongs to the same individual. The humeral head and the M^2 fragment were found during surface collecting. The M^3 fragment and the upper incisor were collected from screen-washed soils from the site. All four specimens were obtained from nearly the same point, and it is thus reasonable to consider that they belonged to the same individual.

Among the four elements included in the new materials, upper molars are already known in the type specimens (NMMP-KU 0001a, 001b = NMMP 8, 9, 10). We considered the similarity of the upper molar morphology between the new materials and the type to be close enough to assign the new materials to the genus *Myanmarpithecus*. Also, the size of the molar fragments in the new materials is similar to that in the type specimens, suggesting that the new materials likely belonged to an individual of the same species, *M. yarshensis*.

Geological settings

The Pondaung Formation distributes in central Myanmar. Primate and other mammalian fossils have been found from the lower half of "the Upper Member" of the formation (Aye Ko Aung 1999, 2004; Aung Naing Soe et al. 2002). Numerous mammalian fossil localities are known for this level of the Pondaung Formation. The fossil localities are divided into three areas according to geographic distributions (Pondaung Fossil Expedition Team 1997; Aye Ko Aung 1999, 2004; Tsubamoto 2001; Egi et al. 2004a). The type and new materials of *Myanmarpithecus* were found from the locality assemblage near Bahin and Paukkaung villages.

The new materials (NMMP-KU 1740, 1764, 1868, 1878 = NMMP 49, 50, 51, 53) were collected from the Pk12 locality (GPS 21°44.94′N, 94°39.23′E; Fig. 1). This locality is located about 2 km northeast of the Bh1 locality where the type specimen (NMMP-KU 0001a, 001b = NMMP 8, 9, 10) and the second specimen (NMMP-KU 0002 = NMMP 11) were found. The third specimen (NMMP 21) of *Myanmarpithecus*, an isolated M_3, was found in the Pk2 locality (Gunnell et al. 2002). Pk12 is located about 0.6 km south of Pk2. The geological age of the Pondaung Formation was estimated as 37.2 ± 1.3 Ma based on the fission-track method applied on the tuffaceous sediment from the Pk1 locality (Tsubamoto et al. 2002). Pk12 is located about 2 km east and slightly south of Pk1. Four nearby localities, Pk1, 5, 2, and 3, have yielded primate fossils, and these localities can be connected to the same stratigraphic horizon (Maung Maung et al. 2005; Soe

Thura Tun 2005). Although the presence of thrust makes it difficult to connect the two exposures, Soe Thura Tun (2005) suggested that Bh1 is in the same shale block as Pk1, 5, 2, and 3 among sandstone–shale alternation sequences. According to the aerial photograph and stratigraphic interpretation by Soe Thura Tun (2005), the location of Pk12 is included in a shale block stratigraphically above the sandstone covering the shale of the other localities. This implies that the *Myanmarpithecus* materials from Pk12 are slightly younger than the other primate fossils from the Bahin area.

Results: descriptions of new materials

Upper molar fragments

NMMP-KU 1764 is the lingual part of a right M^2 (Fig. 2). As in the M^2 of the type specimen, the basal face of the protocone bulges lingually. In overall size, NMMP-KU 1764 is likely to be slightly smaller than M^2 of the type specimen, although the exact mesiodistal length is not known. NMMP-KU 1764 is lightly worn compared to the condition in the type specimen, and several additional morphologies can be observed on M^2. The hypocone is developed on the distolingual cingulum, which is separated from the protocone by a shallow but distinct groove. There is a small worn conule at the distolingual base of the protocone. As in the type specimen, a ledge-like mesial cingulum is present in this specimen, which is seen in the upper molars of *Pondaungia*, another amphipithecid from the Pondaung Formation. The lingual cones, conule, and mesial cingulum are moderately worn, producing the wear facets 5, 6, 7, 8, 9, and 10 of Kay (1977). The wear facets 7 and
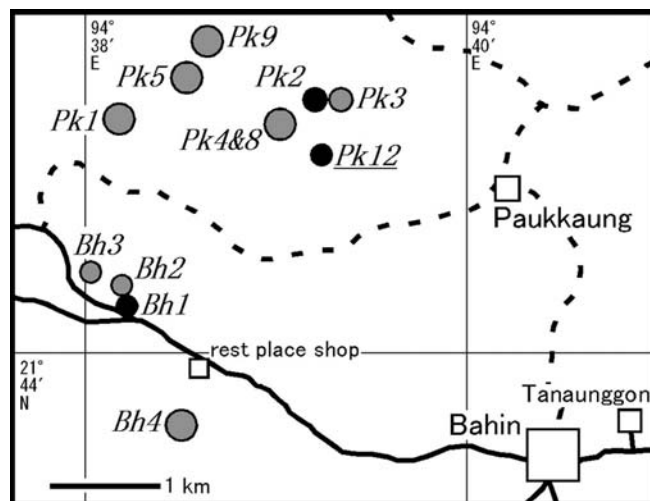

Fig. 1 Map of the fossil localities near Bahin and Paukkaung villages. *Circles* indicate fossil localities. *Myanmarpithecus* specimens were collected from the localities indicated in *black circles*. The locality numbers indicated in *italics* are cataloged by Kyoto University. *Squares* are villages or house assemblages

8 are almost continuous to each other. Unfortunately, the break of the trigon basin makes it impossible to confirm the presence/absence of the wear facet x, which is thought to be a critical feature of the anthropoid primates (Kay 1977).

NMMP-KU 1868 (Fig. 3) is a lingual fragment of P³, P⁴, or M³, because it is much shorter than NMMP-KU 1764 in mesiodistal length. The lingual face of the protocone protrudes mesiolingually rather than lingually. Both the mesial and distal faces of the protocone are

moderately worn, and the presence of the hypocone is not confirmed. Compared with the type specimen (Fig. 4), the configuration of the protocone of NMMP-KU 1868 is more similar to that of M³ than to P⁴. In addition, the pattern of the dentine exposure at the distal face of the protocone suggests a complicated structure at the distolingual part of the tooth, as seen in M³ of the type specimen. Based on these two features, we consider NMMP-KU 1868 to be M³ rather than an upper premolar.
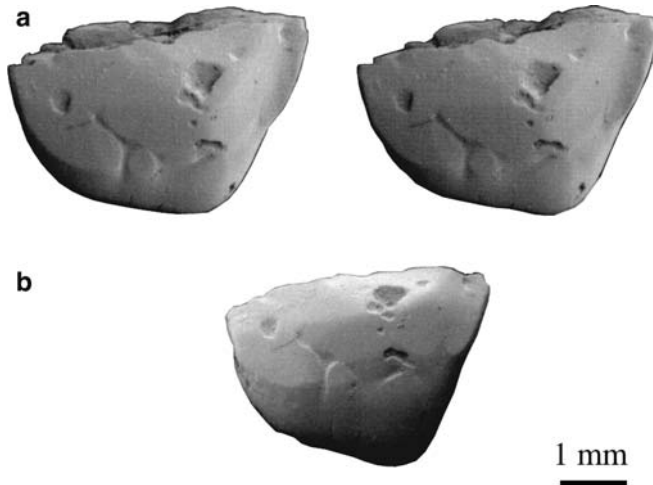

Fig. 2 SEM (scanning electronic micrograph) photos of the new upper molar specimen of *Myanmarpithecus*. The lingual part of right M², NMMP-KU 1764 in occlusal (**a**, stereo pair) and lingual (**b**) views. *Scale bar* = 1 mm
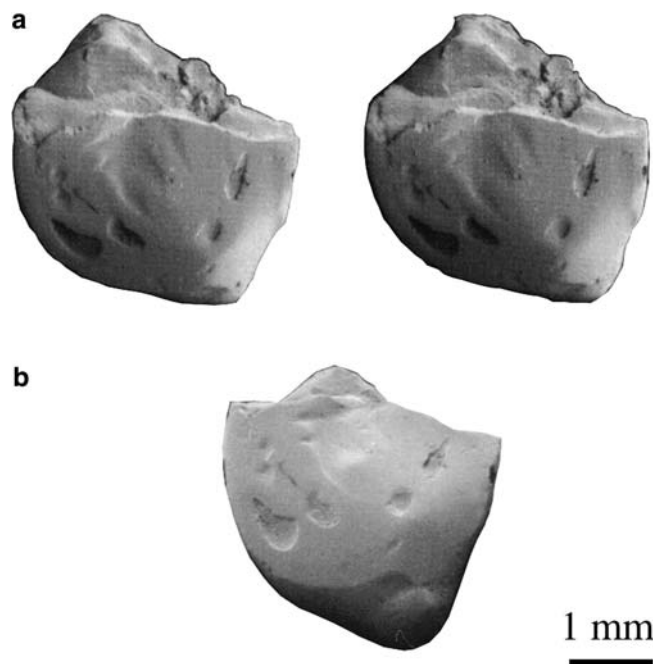
Fig. 3 SEM photos of the new upper molar specimen of *Myanmarpithecus*. The lingual part of right M³, NMMP-KU 1868 in occlusal (**a**, stereo pair) and lingual (**b**) views. *Scale bar* = 1 mm
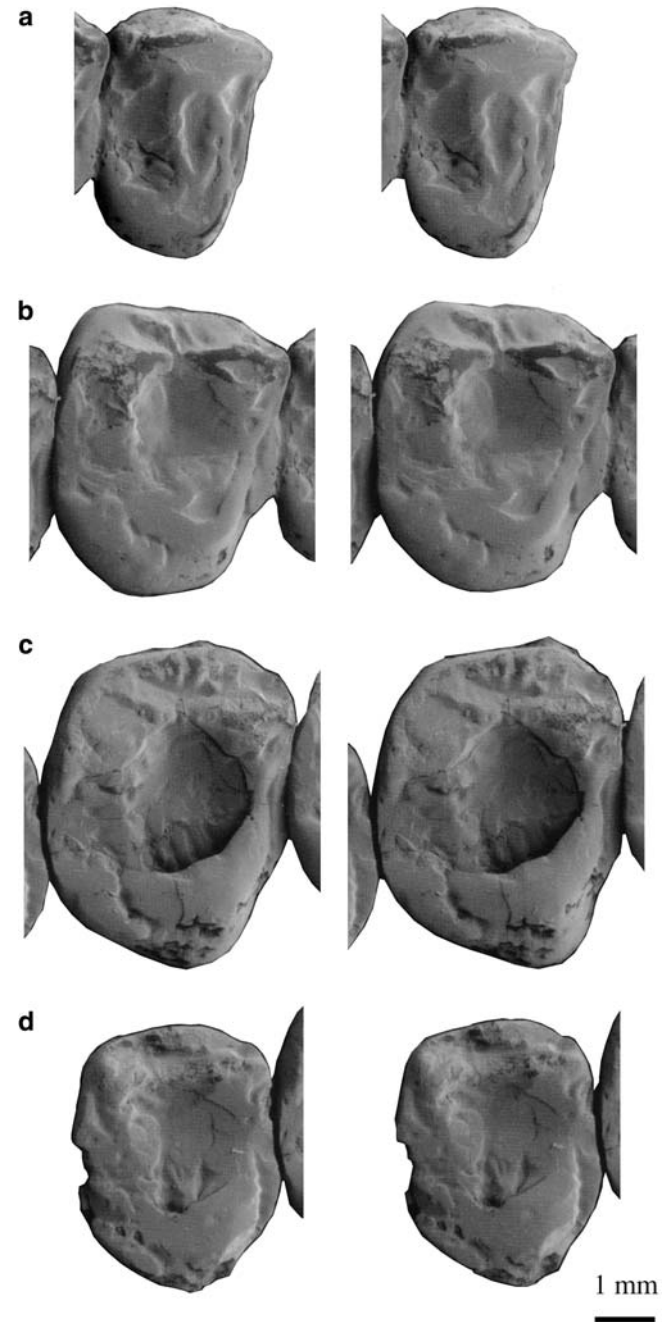
Fig. 4 SEM photos of the type specimen (NMMP-KU_0001a = NMMP 8) of *Myanmarpithecus*: right P⁴ (**a**), M¹ (**b**), M² (**c**), and M³ (**d**) in occlusal views (all stereo pairs). *Scale bar* = 1 mm
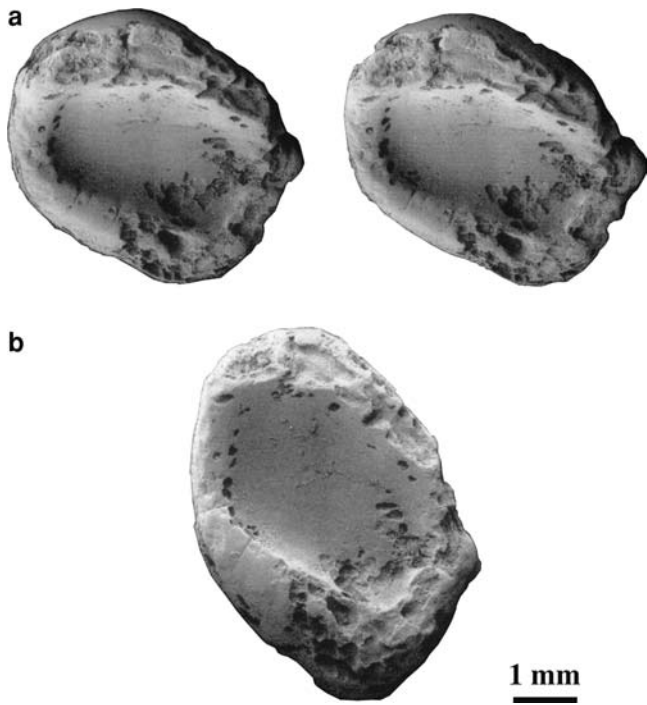
Fig. 5 SEM photos of left I[1], NMMP-KU 1878. Occlusal (**a**, stereo pair) and lingual (**b**) views. *Scale bar* = 1 mm

Upper incisor

NMMP-KU 1878 is a left upper central incisor (Fig. 5). The tooth is mesiodistally long rather than buccolingually wide (mesiodistal length, 4.23 mm; buccolingual width, 3.49 mm). The tooth crown is not symmetrical. There is no strong mesial process or angulation as seen in most adapoids (Rosenberger and Szalay 1980). Though the apical margin is moderately worn and the tooth crown is broken around the enamel/dentine boundary, the tooth crown appears relatively high (crown height > 4.19 mm). The form of the incisor is a spatulate-type. The lingual face is slightly concave and rimmed with a well-developed, continuous lingual cingulum, showing a spoon-like morphology. There is neither a lingual pillar nor a conule.

The proportion of the mesiodistal length relative to the buccolingual width of the upper central incisor has been suggested to be a feature that can separate strepsirrhines and haplorrhines (Rosenberger 1979; Rosenberger and Szalay 1980). A bivariate plot of these two measurements among small to medium size primates are shown in Fig. 6. The data for Paleogene fossil primates are from the literature cited in Table 1. Measurements for *Neosaimiri* from the middle Miocene of Colombia (Table 2) is from Takai (1994). For extant genera, the measurements were taken using digital calipers, and the statistics are shown in Table 2. The proportion of the mesiodistal length relative to the buccolingual width of the upper central incisor is almost constant among anthropoids. Omomyoids are similar to the anthropoids in this tooth morphology, ensuring that an upper central incisor with subequal mesiodistal and buccolingual dimensions is a haplorhine characteristic (Rosenberger 1979; Rosenberger and Szalay 1980). In contrast, fossil strepsirrhines (= adapoids) are characterized by a relatively low-crowned and mesiodistally large I[1], and
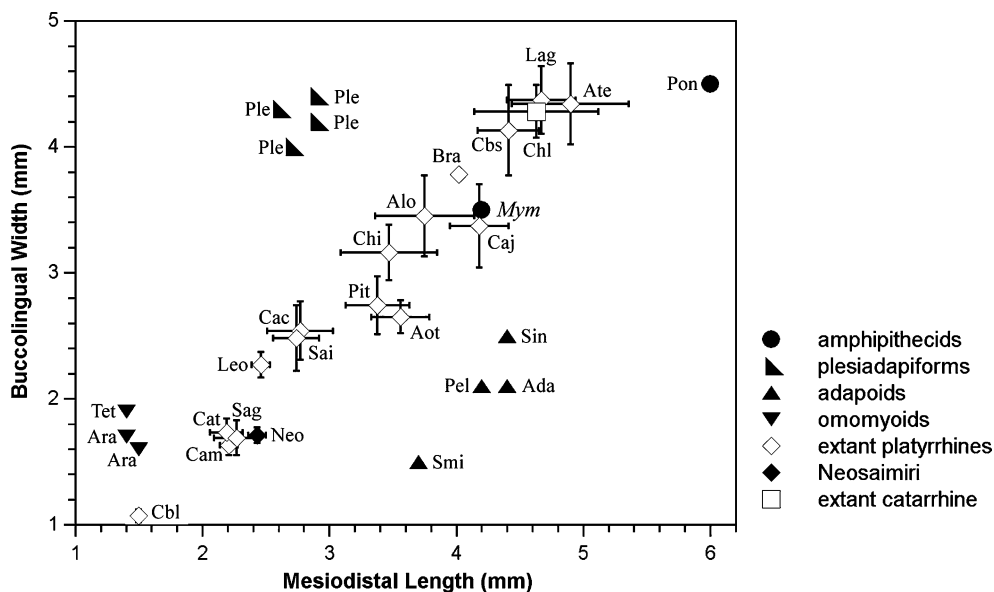
Fig. 6 Bivariate plots of mesiodistal length versus buccolingual width of the upper central incisors of some extinct and extant primates. *Open symbols*, extant genera; *filled symbols*, extinct genera. The whisks around the symbols indicate one standard deviation of the measurements within each genus. Taxonomic abbreviations: Ada, *Adapis*; Alo, *Alouatta*; Aot, *Aotus*; Ara, *Arapaphovius*; Ate, *Ateles*; Bra, *Brachyteles*; Caj, *Cacajao*; Cac, *Callicebus*; Cam, *Callimico*; Cat, *Callithrix*; Cbl, *Cebuella*; Cbs, *Cebus*; Chi, *Chiropotes*; Chl, *Chlorocebus*; Lag, *Lagothrix*; Leo, *Leontopithecus*; Mym, *Myanmarpithecus*; Neo, *Neosaimiri*; Pel, *Pelycodus*; Pit, *Pithecia*; Ple, *Plesiadapis*; Pon, *Pondaungia*; Sag, *Saginus*; Sai, *Saimiri*; Sin, *Sinoadapis*; Smi, *Smilodectes*; Tet, *Tetonius*. See Tables 1 and 2 for sources

Table 1 Measurements (mm) of upper central incisors of several Paleogene fossil taxa

Species	Specimen no.	MD	BL	Reference
Plesiadapis gidleyi	AMNH 17171	2.9	4.4	Rosenberger (1979)
Plesiadapis gidleyi	AMNH 17200	2.9	4.2	Rosenberger (1979)
Plesiadapis gidleyi	AMNH 17404	2.6	4.3	Rosenberger (1979)
Plesiadapis gidleyi	Unnumbered	2.7	4.0	Rosenberger (1979)
Adapis parisiensis	M7	4.4	2.1	Rosenberger (1979)
Pleycodus jarrovii	AMNH 14656	4.2	2.1	Rosenberger (1979)
Smilodectes mcgrewi	AMNH 55157	3.7	1.5	Gingerich (1979)
Sinoadapis shihuibaensis	PA 964	4.4	2.5	Pan and Wu (1986)
Tetonius humunculus	AMNH 88887	1.4	1.9	Rosenberger (1979)
Arapahovius gazini	UCMP V 74022[a]	1.5	1.6	Rosenberger (1979)
Arapahovius gazini	UCMP V 74022[a]	1.4	1.7	Rosenberger (1979)
Pondaungia savagei	NMMP-KU 0003	ca. 6.0	4.5	Shigehara et al. (2002)
Myanmarpithecus yarshensis	NMMP-KU 1878	4.2	3.5	This study

MD mesiodistal length, *BL* buccolingual width
[a] Locality numbers are indicated (see Rosenberger 1979, for further information)

plesiadapiforms are characterized by a relatively high-crowned and narrow I^1. When NMMP-KU 1878 is compared with the other fossil and living primates, it falls in the range of living platyrrhines, and thereby in the range of the haplorhine. The comparison of the tooth proportion indicates that NMMP-KU 1878 is clearly different from adapoid-like incisors.

Humeral head

NMMP-KU 1740 is a fragment of the left humerus (Fig. 7). The part proximal to the humeral neck was collected. The specimen is poorly preserved. The crushed part on the anterior surface formed the anteroposteriorly compressed humeral neck, the anterior edge of the lesser tuberosity is pushed into the humeral head, and the inferior rotation of the anterior edge of the greater tuberosity left a crack between the tuberosity and the head articular surface. The articular surface of the head is eroded, especially at the lateral and inferior parts.

The morphology of the humeral head articular surfaces and tuberosities can be observed despite the distortions. The measurements for NMMP-KU 1740 are listed in Table 3. The humeral head articular surface is very spherical. The mediolateral arc length is nearly equal to the proximodistal arc length. The articular surface extends anteriorly, so the head orients

Table 2 Statistics of the measurements of upper central incisors of all extant platyrrhine genera, one fossil platyrrhine genera (*Neosaimiri*), and one catarrhine species (*Chlorocebus aethiops*)

Genus	Mesiodistal length (MD)					Buccolingual width (BL)				
	Mean	SD	*N*	Min	Max	Mean	SD	*N*	Min	Max
Platyrrhini										
Alouatta	3.75	0.39	49	2.98	4.93	3.45	0.32	49	2.80	4.20
Aotus	3.56	0.23	45	3.01	4.05	2.65	0.13	45	2.28	2.91
Ateles	4.90	0.46	36	4.25	5.68	4.34	0.32	39	3.59	5.10
Brachyteles	4.02	–	1	4.02	4.02	3.78	–	1	3.78	3.78
Cacajao	4.18	0.23	15	3.81	4.64	3.37	0.33	15	2.79	3.98
Callicebus	2.77	0.26	42	2.31	3.46	2.54	0.23	42	2.06	3.09
Callimico	2.21	0.07	7	2.11	2.30	1.63	0.08	7	1.53	1.73
Callithrix	2.19	0.13	14	1.94	2.44	1.73	0.11	14	1.54	1.87
Cebuella	1.50	0.03	4	1.47	1.54	1.07	0.05	4	1.01	1.12
Cebus	4.41	0.24	31	4.00	5.16	4.13	0.36	31	3.56	5.10
Chiropotes	3.47	0.38	9	3.00	4.04	3.16	0.22	9	2.73	3.44
Lagothrix	4.67	0.27	33	4.15	5.47	4.37	0.27	34	3.85	4.85
Leontopithecus	2.46	0.07	7	2.37	2.57	2.27	0.10	7	2.15	2.47
Neosaimiri	2.43	0.07	8	2.32	2.56	1.71	0.06	8	1.60	1.76
Pithecia	3.38	0.25	10	3.15	3.92	2.74	0.23	10	2.53	3.17
Saguinus	2.27	0.18	28	1.99	2.62	1.69	0.14	28	1.45	2.01
Saimiri	2.74	0.18	27	2.40	3.11	2.48	0.26	27	2.08	2.89
Catarrhini										
Chlorocebus	4.63	0.49	34	3.4	5.49	4.28	0.21	34	3.79	4.93

SD standard deviation, *N* number of specimens, *Min* minimum value, *Max* maximum value. Measurements for all extant species except *Brachyteles* were taken from both sexes. The data for all extant taxa except *Brachyteles*, *Cebuella*, and *Callimico* were based on multiple species. Dental data of the extant primates were obtained from the specimens housed at the American Museum of Natural History (New York), Field Museum of Natural History (Chicago), and Kyoto University Primate Research Institute (Inuyama)
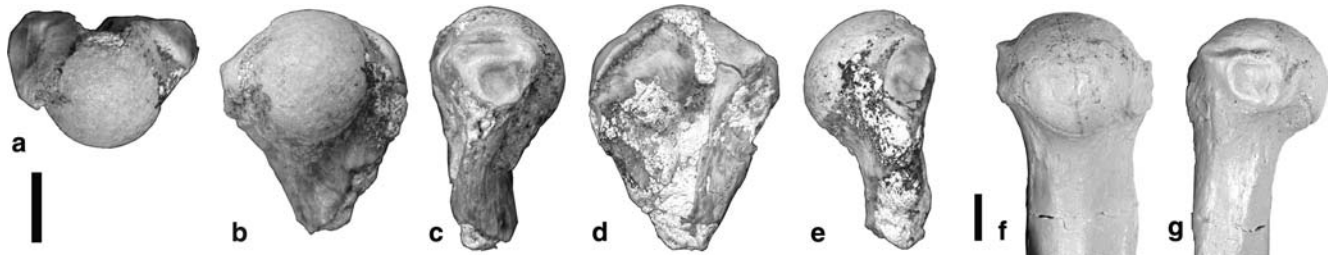
Fig. 7 Photographs of humeral head fragment, NMMP-KU 1740 (= NMMP 49), in superior (**a**), posterior (**b**), lateral (**c**), anterior (**d**), and medial (**e**) views. Proximal part of the previously known amphipithecid humerus, NMMP 20, is shown in posterior (**f**) and lateral (**g**) views. *Scale bar* = 5 mm

Table 3 Measurements (mm) of the proximal humerus. NMMP-KU 1740 (= NMMP 49) is the new material of *Myanmarpithecus* from Pk12, and NMMP 20 is an amphipithecid described by Ciochon et al. (2001)

	NMMP-KU 1740	NMMP 20
Mediolateral width of articular surface	ca. 8.9	13.1
Proximodistal length of articular surface	9.5	14.6
Articular surface depth	4.4	7.4
Bituberosity width	ca. 12.8	17.1
Greater tuberosity length	6.7	10.5
Lesser tuberosity length	6.9	9.4

superoposteriorly rather than posteriorly. The articular surface is large relative to the tuberosity, and the articular surface protrudes above the tuberosities. The lesser tuberosity is smaller than the greater tuberosity in posterior view, but the width of the lesser tuberosity is subequal to that of the greater tuberosity. The lesser tuberosity located more inferiorly than the greater tuberosity. The position of the medial edge of the greater tuberosity indicates that the deltopectoral crest runs posteriorly on the mid-line of the shaft. Overall, these features in NMMP-KU 1740 are very similar to the previously known humerus that was assigned to amphipithecids (NMMP 20).

Discussion

The four elements described here were collected from nearly the same point, which is the primary reason why we considered them to belong to an individual of *M. yarshensis*. As mentioned above, M^2 (NMMP-KU 1764) from the materials from Pk12 is slightly smaller than that of the type individual. For the humeral head fragment from Pk12, the body mass was estimated based on the relationship of the humeral head articular surface area and body mass derived from monkeys and prosimians (Egi et al. 2004a). The value was 1.14 kg with a 95% confidence interval from 1.07 to 1.23, which was slightly smaller than 1.8 kg, the estimated body mass of the type individual based on the M_2 crown area (Egi et al. 2004b). It seems reasonable

to consider that the humeral fragment and the molar fragments belonged to the same individual of *Myanmarpithecus*.

For amphipithecids, humeral materials from one individual were previously reported (Ciochon et al. 2001). This specimen, NMMP 20, is suggested to belong most likely to *A. mogaungensis* or *P. cotteri* mainly based on its size (Egi et al. 2004a). The humeral head structure in NMMP-KU 1740 is very similar to those in NMMP 20. The main difference between NMMP-KU 1740 and NMMP 20 is the size. The linear measurements of the humeral head of NMMP-KU 1740 are about 60–75% of those of the humeral head of NMMP 20. Morphologically, the humeral head articular surface of NMMP-KU 1740 is slightly flatter in the medial view than those of NMMP 20. The discovery of the humeral fragment associated with the dental materials in *Myanmarpithecus* and its morphological similarity to NMMP 20 confirms that NMMP 20, which lacks associated dental materials, truly belonged to an amphipithecid primate.

Recently published papers on the classification of amphipithecids place *Myanmarpithecus* in the family (e.g., Ciochon and Gunnell 2002a, b; Gunnell et al. 2002; Kay et al. 2004b), although the genus was first described without settlement of its family status (Takai et al. 2001). The resemblance in the humeral head structure between the *Myanmarpithecus* specimen (NMMP-KU 1740) and the *Pondaungia* or *Amphipithecus* specimen (NMMP 20) supports the close relationship between *Myanmarpithecus* and other amphipithecids from the Pondaung fauna. Because of the morphological similarity in the two humeral specimens, the reconstruction of locomotion based on NMMP 20 (Kay et al. 2004a) is also applicable for NMMP-KU 1740. The spherical shape of the humeral head articular surface, the low position of the tuberosities, and the superoposteriorly oriented humeral head indicate that the shoulder joint had a wide range of motion, especially during protraction in *Myanmarpithecus*. The shoulder joint structure suggests that the slow climbing movement is a common type of locomotion in amphipithecids.

The dimensions of the I^1 (NMMP-KU 1878) are close to that of *Cacajao* (Fig. 6). The body mass of *Cacajao* ranges from 2.7 to 3.5 kg (Fleagle 1999), so I^1 from Pk12 may be considered to be too large relative to the molar and humeral head fragments. However, this propor-

tionately large upper central incisor seems to be an acceptable phenomenon within primates based on the fact that *Aotus*, of which the body mass is from 0.7 to 1.2 kg (Fleagle 1999), has an upper central incisor approximately nearly as large as *Pithecia* and *Chiropotes*, of which the body mass ranges from 1.6 to 3.0 kg and from 2.5 to 3.2 kg (Fleagle 1999), respectively. In addition, the body mass estimates derived from the molar crown areas based on the anthropoid sample ranged from 1.8 kg of the M^1 based result to 3.2 kg of the M_3 based result (Egi et al. 2004b); thus, a degree of relative size difference between I^1 and the upper molar fragments can exist within a dental row. We consider the four materials from Pk12 to belong to the same individual, and the relative sizes to indicate the possession of a relatively large upper central incisor by *Myanmarpithecus*.

Concerning the phyletic position of amphipithecids, including *Myanmarpithecus*, several researchers insist that the notharctine adapoid hypothesis is correct (e.g., Ciochon and Holroyd 1994; Gunnell et al. 2002; Ciochon and Gunnell 2004; Kay et al. 2004b). As mentioned in the description, however, the overall shape of the upper central incisor is more similar to that of anthropoids than to adapoids. As Rosenberger (1979) and Rosenberger and Szalay (1980) have demonstrated, fossil strepsirrhines have relatively low-crowned upper incisors with a strong medial process or angulation of the I^1. In contrast, haplorhines have a more spatulate, high-crowned I^1 without an extreme mesial process, as seen in NMMP-KU 1878.

As an alternate hypothesis for the phyletic position of amphipithecids, several researchers placed the family in primitive anthropoids (Ducrocq et al. 1995; Chaimanee et al. 1997, 2000; Kay et al. 1997, 2004b; Ducrocq 2001; Gunnell and Miller 2001; Beard 2002; Shigehara et al. 2002; Marivaux et al. 2003, 2005). Kay and Williams (1994) have discussed the morphotype of the ancestral anthropoid by using the cladistic analysis of many fossil and living primate characters. Their conclusion is that the basic structure of the upper central incisor of the ancestral anthropoids is relatively high-crowned, spatulate rather than conical, buccolingually compressed, and that the lingual fovea is simple and the lingual cingulum moderate and continuous without a basal lingual cusp. All of these morphologies are true for NMMP-KU 1878, indicating the anthropoid affinity for this tooth. If NMMP-KU 1878 is found to be the remains of *Myanmarpithecus*, it strongly disputes the hypothesis of adapoid affinities not only for *Myanmarpithecus* but also for amphipithecids.

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