NEW ASSESSMENT OF *PONDAUNGIA* AND *AMPHIPITHECUS* (PRIMATES) FROM THE LATE MIDDLE EOCENE OF MYANMAR, WITH A COMMENT ON 'AMPHIPITHECIDAE'

BY

GREGG F. GUNNELL, RUSSELL L. CIOCHON, PHILIP D. GINGERICH, AND PATRICIA A. HOLROYD

Frontispiece — Lotus pond near Wetkya in Myanmar, with Pondaung Hills in the background. Photograph by RLC reproduces an image first published by Barnum Brown in 1925.

NEW ASSESSMENT OF *PONDAUNGIA* AND *AMPHIPITHECUS* (PRIMATES) FROM THE LATE MIDDLE EOCENE OF MYANMAR, WITH A COMMENT ON 'AMPHIPITHECIDAE'

BY

GREGG F. GUNNELL[1], RUSSELL L. CIOCHON[2], PHILIP D. GINGERICH[1], AND PATRICIA A. HOLROYD[3]

Abstract — Fossil primates have been known from the late middle to late Eocene Pondaung Formation of Myanmar since the description of *Pondaungia cotteri* in 1927. Three additional primate taxa, *Amphipithecus mogaungensis*, *Bahinia pondaungensis*, and *Myanmarpithecus yarshensis* have been described subsequently. *Siamopithecus* from the late Eocene of Thailand has been allied with *Pondaungia* and *Amphipithecus* in the family Amphipithecidae, and this family has been placed in Anthropoidea as a sister group to Egyptian Fayum anthropoids. A new analysis of all known larger-bodied fossil primates from Myanmar leads to the following conclusions: (1) *Pondaungia*, *Amphipithecus*, and *Siamopithecus* are notharctid adapiforms that belong in a distinct subfamily, Pondaunginae; (2) the Myanmar pondaungine taxa (Pondaungini) can be distinguished at the tribal level from *Siamopithecus* (Siamopithecini, new tribe); (3) three species of larger-bodied primates are now represented in Myanmar: *Pondaungia cotteri*, *Pondaungia savagei* new species, and *Amphipithecus mogaungensis*; (4) there is no evidence favoring inclusion of any of these taxa in Anthropoidea; (5) Amphipithecidae is a junior synonym of Pondaungidae; and (6) dental and cranial resemblances between pondaungines and anthropoids are probably functional convergences resulting from a diet consisting of hard and tough food objects utilized by these Southeast Asian primates.

INTRODUCTION

The first fossil primate named from Myanmar was *Pondaungia cotteri* Pilgrim, 1927, from a locality near Pangan (Pankan) village in the Pondaung Formation of central Myanmar (formerly Burma; Fig. 1). Ten years later Colbert (1937) described *Amphipithecus mogaungensis* from near Mogaung village in the Pondaung Formation. No other primates were reported from the Pondaung Formation over the intervening 40 years until four new specimens were discovered at Mogaung in

[1]Museum of Paleontology and Department of Geological Sciences, The University of Michigan, Ann Arbor, Michigan 48109-1079
[2]Department of Anthropology, The University of Iowa, Iowa City, Iowa 52242
[3]Museum of Paleontology, University of California, Berkeley, California 94720-4780
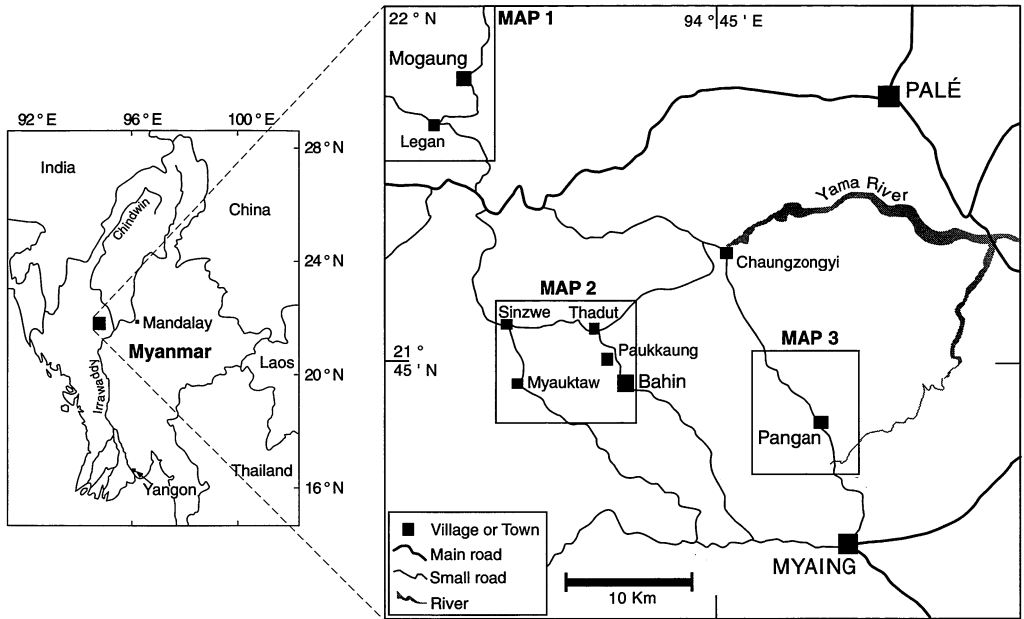
FIG. 1 — Location map of Myanmar with inset showing the major field areas where the middle and upper Eocene Pondaung Formation outcrops west of Mandalay. Maps 1, 2, and 3 within the inset here are enlarged in Figure 2 to show outcrop areas.

1978 (Ba Maw et al., 1979; Ciochon et al., 1985; Takai et al., 2000). More recently, several new primate specimens have been reported from Pangan and Mogaung, and specimens have been found at new localities near Bahin, Paukkaung, and Sinzwe (Fig. 1; Jaeger et al., 1998, 1999; Tin Thein, 1999; Aye Ko Aung, 1999a; Takai et al., 2000).

Primates known from Myanmar include at least four taxa: the original two species, plus *Bahinia pondaungensis* (Jaeger et al., 1999) and *Myanmarpithecus yarshensis* (Takai et al., 2000, 2001). New discoveries of primate remains from the Pondaung Formation are the result of a Myanmar joint government-university initiative started in 1997 by the Office of Strategic Studies, the Ministry of Defence, and by the University of Taunggyi, Dagon University, and Hlaing College. Table 1 lists all known Myanmar primate specimens, with updated and corrected specimen number and locality information. What follows is an extensive description and discussion of these important primate specimens, with a focus on the larger-bodied primates from Myanmar. The fossils described here all come from kyitchaungs—a *kyitchaung* is the local language equivalent of "outcrop," and translates approximately to "clay gullies" (*kyit* = clay, and *chaung* = gullies).

AGE OF THE PONDAUNG FORMATION

The Pondaung Formation was originally considered to be late Eocene in age (Colbert, 1938). More recently, Holroyd and Ciochon (1994) argued that most of the Pondaung Formation represents the latest middle Eocene (Bartonian) based on vertebrate faunal correlations, biostratigraphic relationships with adjacent marine units, and an updating of the middle-to-late Eocene boundary. Work on the distribution of nannoplankton species (Hla Mon, 1999), floral assemblages (Thet Wai, 1999), and fission track dating of tuffaceous sediments (Aye Ko Aung, in press; Tsubamoto, 2000) has helped refine the relative ages of Pondaung Formation fossil primate localities (Figs. 2-3). The localities near Mogaung Village (Thandaung and Lema kyitchaungs) fall in nannozones NP 15/16, which span the later Lutetian and early Bartonian (middle Eocene) while the localities

Table 1 — Catalogue of primate specimens described from the late middle Eocene of Myanmar.

| Specimen	Locality (kyitchaung)	Genus and species	Description	Type designation	Alternate number(s)
GSI D201-203	Pangan Roadcut	*Pondaungia cotteri*	L max. M^{1-2}, L dent. M_{2-3}, R dent. M_3	Holotype	
AMNH 32520	Thandaung	*Amphipithecus mogaungensis*	L dent. P_4-M_1	Holotype	
NMMP 1	Lema	*Pondaungia savagei*	R dent. M_{2-3}	Holotype	DGMU-P4, UCMP 120377
NMMP 2	Thandaung	*Amphipithecus mogaungensis*	L dent. M_{1-2}		DGMU-P1
NMMP 3	Lema	*Pondaungia savagei*	L dent. M_{2-3}		DGMU-P2
NMMP 4	Lema	*Pondaungia cotteri*	R dent. M_{1-3}	Part of holotype?	DGMU-P3
NMMP 5	Lema	*Pondaungia savagei*	R dent. M_{2-3}	Type of "*P. minuta*"	
NMMP 6	Thandaung	*Amphipithecus mogaungensis*	L dent. M_{1-2}		
NMMP 7	Yarshe	*Amphipithecus mogaungensis*	L dent. P_3-M_3, R dent. P_4-M_3		
NMMP 8	Yarshe	*Myanmarpithecus yarshensis*	R max. P^4-M^3	Holotype (part)	NMMP-KU 0001a
NMMP 9	Yarshe	*Myanmarpithecus yarshensis*	L dent. C_1-P_3	Holotype (part)	NMMP-KU 0001b
NMMP 10	Yarshe	*Myanmarpithecus yarshensis*	L dent. M_{2-3}	Holotype (part)	NMMP-KU 0001b
NMMP 11	Yarshe	*Myanmarpithecus yarshensis*	L dent. M_3		NMMP-KU 0002
NMMP 12	Taungnigyin	*Pondaungia savagei*	L max. I^1, C^1, P^3, M^2, frags. P^4, M^1, M^3		NMMP-KU 0003
NMMP 13	Yarshe	*Bahinia pondaungensis*	L dent. P_2-M_1	Holotype (part)	
NMMP 14	Yarshe	*Bahinia pondaungensis*	L max. P^2-M^2	Holotype (part)	
NMMP 15	Yarshe	*Bahinia pondaungensis*	R max. P^2-M^2	Holotype (part)	
NMMP 16	Yarshe	*Bahinia pondaungensis*	R dent. P_3-M_1	Holotype (part)	
NMMP 17	Thandaung	*Pondaungia savagei*	R dent. P_2-M_3		
NMMP 18	Paukkaung	*Amphipithecus mogaungensis*	R max. P^4-M^3		
NMMP 19	Paukkaung	?*Amphipithecus mogaungensis*	Frontal (assoc. with NMMP 18?)		
NMMP 20	Sabapondaung	*Pondaungia savagei*	Postcrania		
NMMP 21	Paukkaung	*Myanmarpithecus yarshensis*	L M_3		
NMMP 22	Lema	*Pondaungia savagei*	R P^4		
NMMP 23	Paukkaung	Eosimiid	R calcaneum		
NMMP 24	Paukkaung	*Pondaungia savagei*	R dent. C_1-M_3		
NMMP 25	Lema	*Pondaungia savagei*	L M_1		
NMMP 27	Payama	?*Amphipithecus mogaungensis*	Frontal		
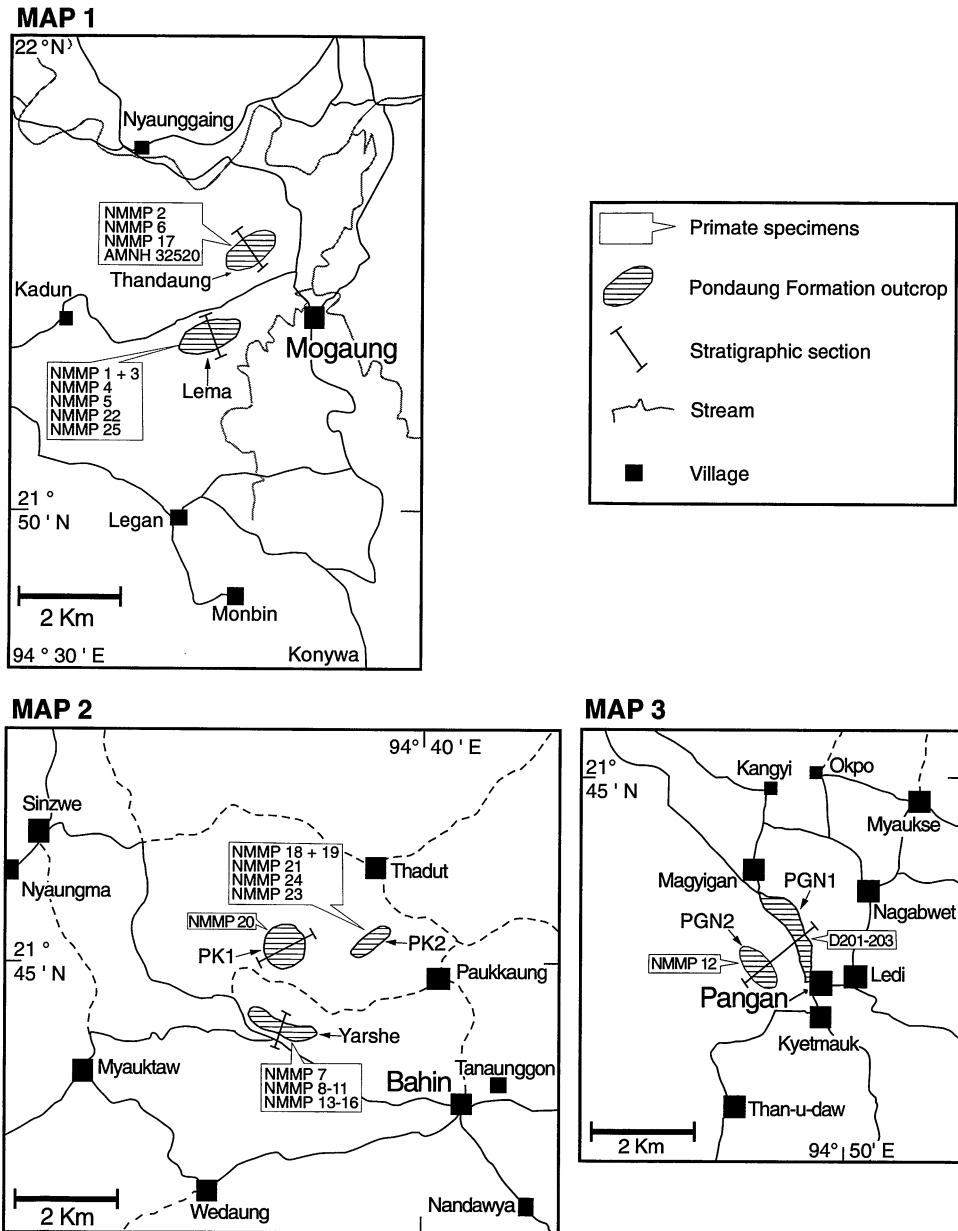
MAP 1

MAP 2

MAP 3

FIG. 2 — Enlarged maps showing the location of kyitchaungs or outcrops (hatched pattern) yielding fossil mammals in the Mogaung (Map 1), Bahin (Map 2), and Pangan (Map 3) areas. Locations of stratigraphic sections are shown as well. Primate specimens from each kyitchaung are indicated in boxes except for NMMP 27 which is from Payama kyitchaung near Sinzwe (Map 2).

near Pangan village (Roadcut or PGN1 and Taungnigyin or PGN2 kyitchaung) and near Bahin village (Fig. 4; Sabapondaung or PK1, Yarshe, Paukkaung or PK2, and Payama kyitchaungs) fall in nannozones NP 17-20, later Bartonian and Priabonian (late middle to late Eocene) based on the Berggren et al. (1995) time scale. A fission track age of 37.2 ± 1.3 Ma was obtained from zircon crystals from a tuffaceous layer approximately 2 meters above the primate-bearing horizon at Sabapondaung kyitchaung (Tsubamoto, 2000). This fission track age substantiates a latest Bartonian
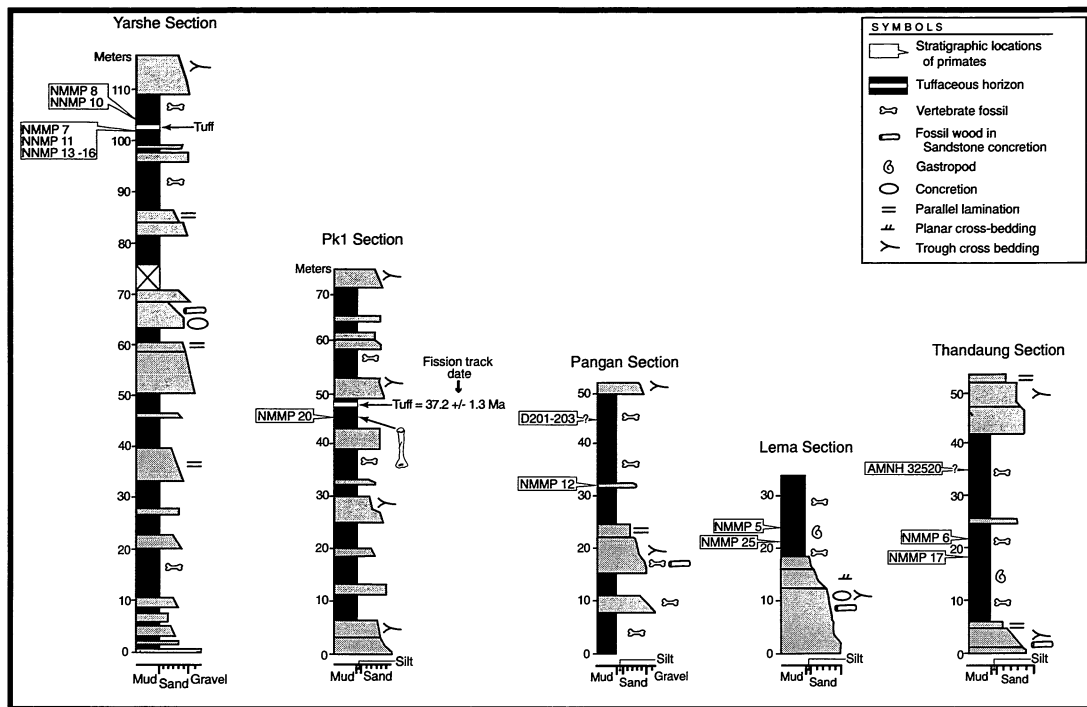
FIG. 3 — Stratigraphic sections measured at Yarshe, Sabapondaung, Pangan, Lema, and Thandaung
kyitchaungs. Note the presence of a tuffaceous layer at Yarshe and Sabapondaung. This layer has been
dated at 37.2 Ma ± 1.3 Ma by fission-track techniques. All sections are in the upper member of the
Pondaung Formation.

age for the Bahin area primate localities, as nearly all localities are stratigraphically at or below the
primate horizon at Sabapondaung kyitchaung (Aye Ko Aung, 1999b, in press; Ciochon et al.,
2001; see also Fig. 3).

INSTITUTIONAL ABBREVIATIONS

AMNH   — American Museum of Natural History, New York (U.S.A.)
GSI   — Geological Survey of India, Calcutta (India)
DGMU   — Mandalay University, Department of Geology, Mandalay (Myanmar; DGMU
              = MUGD)
NMMP   — National Museum of Myanmar Primate, Yangon (Myanmar)
NMMP-KU   — National Museum of Myanmar Primate–Kyoto University, Yangon
              (Myanmar)
UCMP   — University of California, Museum of Paleontology, Berkeley (U.S.A.)

SYSTEMATIC PALEONTOLOGY

Order PRIMATES Linnaeus, 1758
Infraorder ADAPIFORMES Szalay and Delson, 1979
Family NOTHARCTIDAE Trouessart, 1879

FIG. 4 — Photograph of Yarshe kyitchaung, which yielded a specimen of *Amphipithecus mogaungensis* and the type specimens of *Bahinia pondaungensis* and *Myanmarpithecus yarshensis* (see Table 1).

Subfamily PONDAUNGINAE Ciochon and Holroyd, 1994

Diagnosis.— Differs from Notharctinae in lacking P_1, in lacking or having very tiny paraconids on lower molars, and in having I_1 larger than I_2, less distinct cheek tooth cusps, great molar basal inflation, very deep dentaries, shortened rostra with crowding of anterior cheek teeth, and calcaneum with very deep, dorsoplantarly oriented calcaneocuboid facet.

Tribe PONDAUNGINI Ciochon and Holroyd, 1994

Emended diagnosis.— Differs from Siamopithecini in lacking lingually distended upper molars, in having a less distinct and lower postprotocingulum on upper molars, P^4 broader buccolingually and flatter with lingual shelf more extended, M_1 smaller than M_2, P_{3-4} shortened anteroposteriorly with more bucally distended surfaces and reduced relative to molars, and cheek tooth occlusal surfaces generally flatter with less topographic relief.
Included genera.— *Pondaungia* and *Amphipithecus*.

Pondaungia Pilgrim, 1927

Type species.— *Pondaungia cotteri*
Included species.— Type species and *P. savagei*, new species
Age and distribution.— Late middle to late Eocene, Pondaung Formation, Myanmar.
Emended diagnosis.— Differs from *Amphipithecus* in having relatively shorter, broader, and more bulbous lower premolars (premolars wider than long), lower molars with better definition of
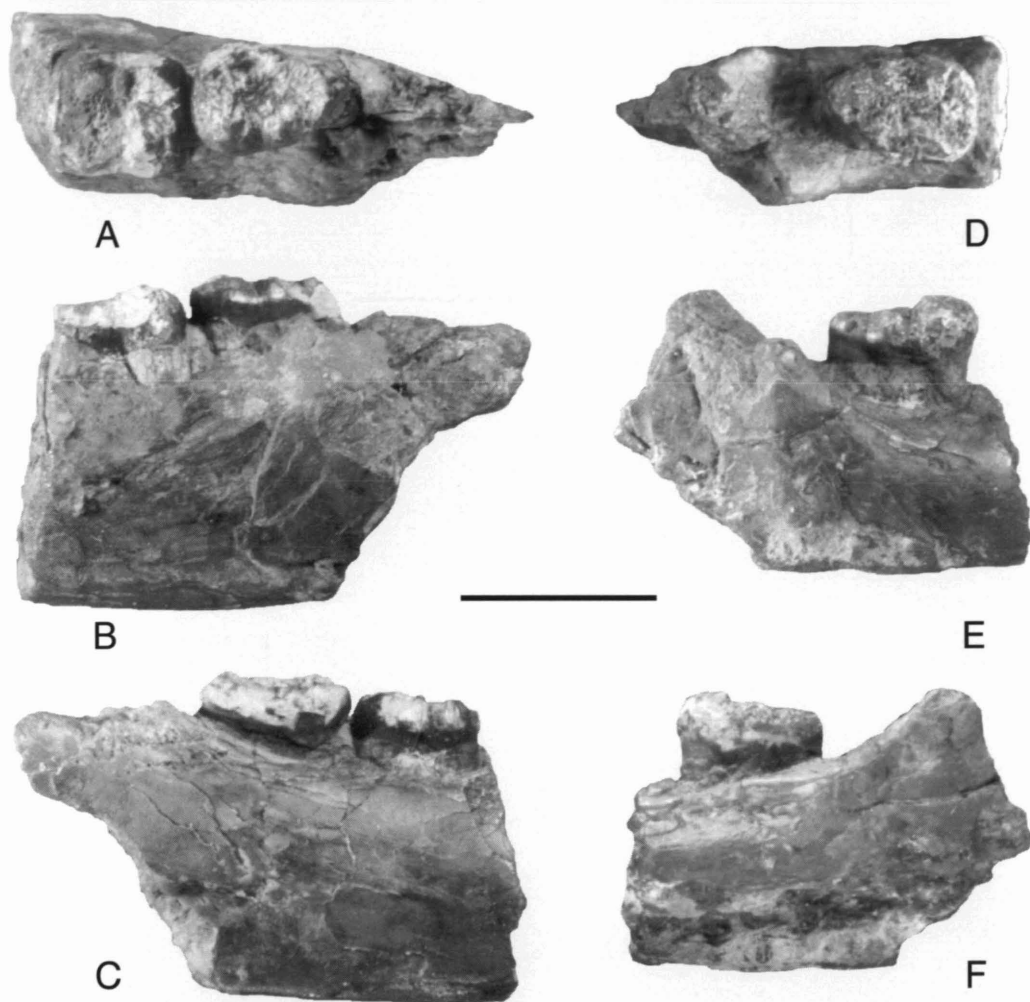
FIG. 5 — *Pondaungia cotteri.* GSI D201 (part of holotype), left dentary with broken M_2 and M_3 in occlusal (A), medial (B), and lateral (C) views. GSI D202 (part of holotype), right dentary with M_3 in occlusal (D), lateral (E), and medial (F) views. Scale bar equals one centimeter.

cusps, lower molars with heavy enamel crenulation, lower molar hypoflexids more distinct with basal shelves, and M_3 not reduced relative to M_2.

Pondaungia cotteri Pilgrim, 1927
(Figs. 5-8)

Pondaungia cotteri Pilgrim, 1927.
Pondaungia cotteri (in part), Ciochon and Holroyd, 1994; Takai et al., 2000.
Pondaungia minuta Jaeger et al., 1998; Chaimanee et al., 2000b.

Holotype.— GSI D201-203, including a left dentary M_{2-3} (GSI D201), a right dentary M_3 (GSI D202), and a left maxilla M^{1-2} (GSI D203).
Referred specimens.— Holotype and NMMP 4 (= DGMU-P3), a right dentary with M_{1-3} (Fig. 6).
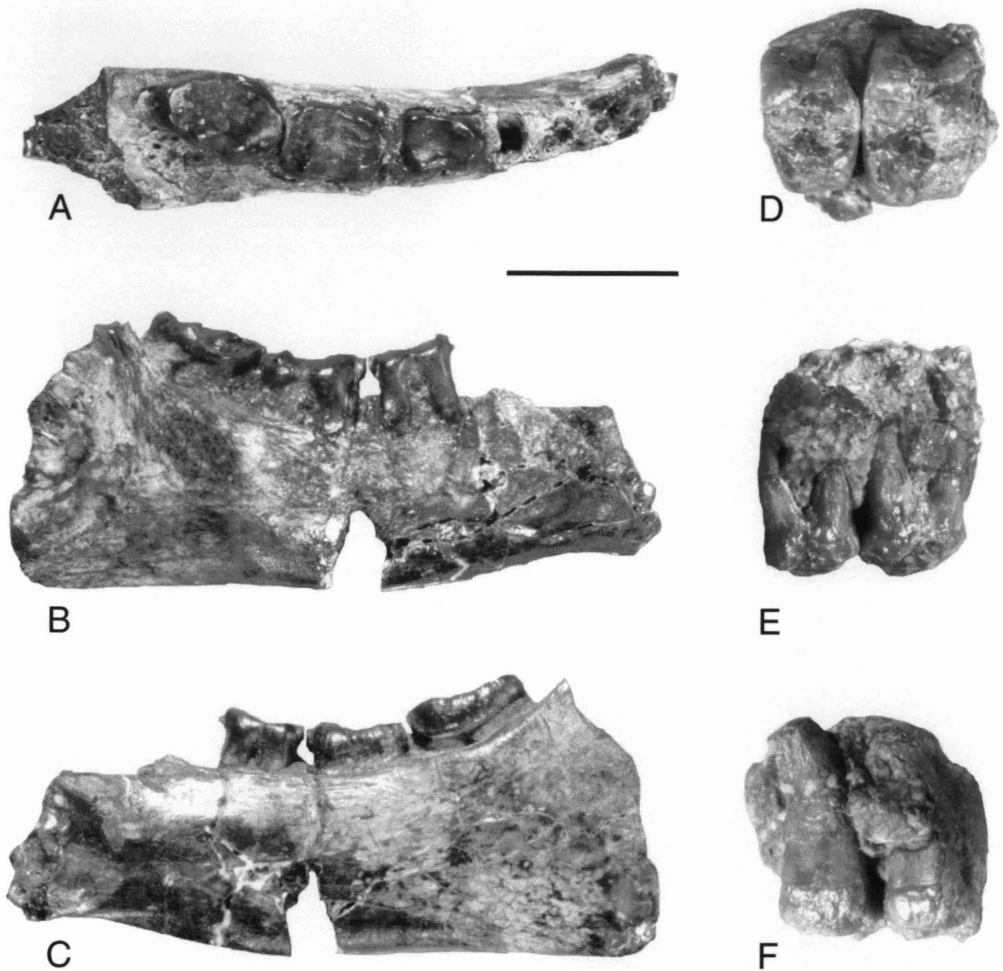
FIG. 6 — *Pondaungia cotteri*. NMMP 4, right dentary with heavily worn and eroded M_{1-3} in occlusal (A), lateral (B), and medial (C) views. This is the holotype of *Pondaungia minuta*. Enamel islands are preserved between M_1 and M_2, but virtually all other enamel has been removed by digestion (see text). GSI D203 (part of holotype), left maxilla with M^{1-2} in occlusal (D), lateral (E), and medial (F) views. Scale bar equals one centimeter.

Locality and distribution.— The holotype is from a roadcut near Pangan village, central Myanmar. Referred specimen is from Lema kyitchaung near Mogaung village, central Myanmar.

Diagnosis.— Differs from *P. savagei* in being 15% to 20% smaller in tooth dimensions, molar hypoflexids relatively deeper with little or no development of buccally extended basal shelves, lower molars relatively less basally inflated with weaker buccal cingulids, M_3 trigonids narrower than talonids, and horizontal ramus shallowing anteriorly.

Discussion.— As now understood, *Pondaungia cotteri* is the rarest larger-bodied primate known from Myanmar being represented by only two specimens. There are now ten specimens representing *Pondaungia* from the Pondaung Formation. If *P. cotteri* were simply representative of the female *Pondaungia* morph, a more even split between male and female specimens would be expected.
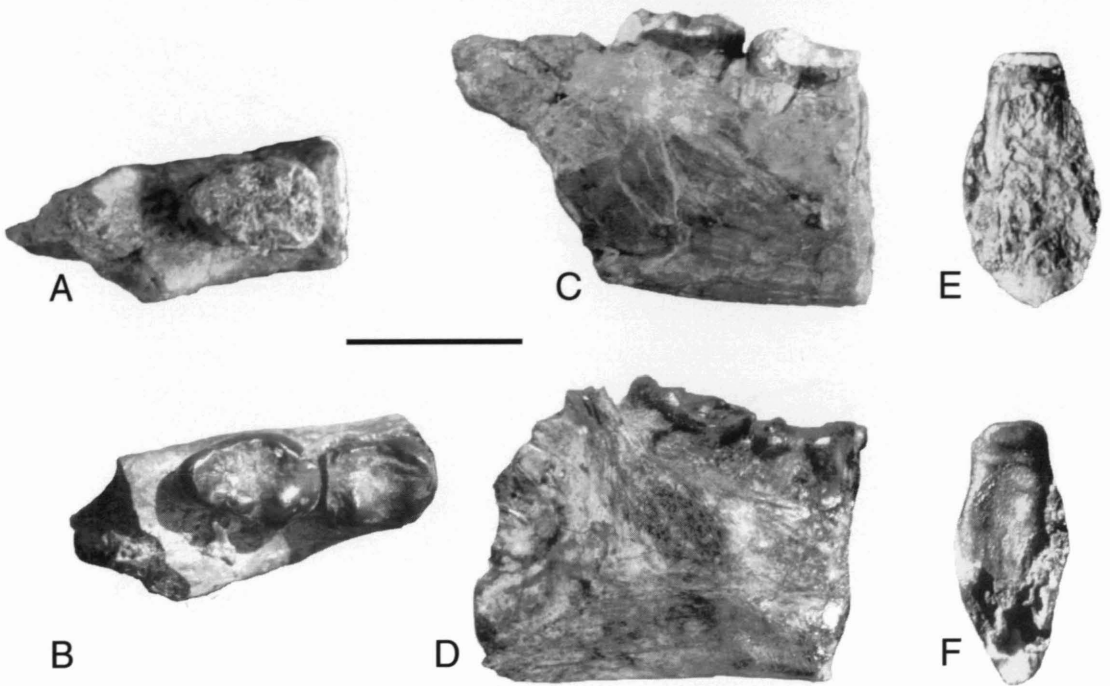
FIG. 7 — *Pondaungia cotteri*. Comparison of holotype specimens GSI D202 (A) and GSI D201 (C,E) with NMMP 4 (B,D,F) in occlusal, lateral, and anterior views. Note close similarity in tooth size, tooth morphology, and mandibular depth and width. Scale bar equals one centimeter.

Recent description of new specimens of *Pondaungia* (Jaeger et al., 1998; Takai et al., 2000) necessitates a reappraisal of the systematics of this taxon. The original description of *Pondaungia* was based on three syntypes from exposures near the village of Pangan (Fig. 2; Pilgrim, 1927). These specimens (Geological Survey of India numbers D201, D202, D203; Figs. 5-8) comprise a left maxilla with M^{1-2}, a left dentary with M_{2-3}, and a right dentary with M_3, and almost certainly representing a single individual (Pilgrim, 1927). Ciochon and Holroyd (1994) designated all three specimens as the holotype (synlectotypes) of *Pondaungia cotteri*. An additional specimen of *Pondaungia* (right dentary with M_{2-3}) was described by Ba Maw et al. (1979) and was originally published under the number UCMP 120377. This specimen was transferred to the Department of Geology, Mandalay University, as DGMU-P4, and then recataloged in the National Museum of Myanmar as NMMP 1. Ba Maw et al. (1979) noted that the newly described specimen was larger than the original type material but suggested that this might only represent sexual dimorphism.

Jaeger et al. (1998) described and figured two new specimens of *Pondaungia* (NMMP 4 and NMMP 5) and figured a third without discussion, NMMP 3 (=DGMU-P2). Jaeger et al. (1998) indicated that NMMP 4 was distinctly smaller than most other *Pondaungia* specimens and designated it as the holotype of a new species, *Pondaungia minuta*, also referring one of the original syntypes (GSI D202) of *P. cotteri* to this new species (Figs. 6-7). Takai et al. (2000) briefly described and figured another specimen of *Pondaungia* (NMMP 12 = NMMP-KU 0003), while three additional specimens (NMMP 17, NMMP-KU 0004, 0051) are mentioned but not described in their Table 1. NMMP 17, a right dentary with M_{2-3} is illustrated but not described in Aye Ko Aung (1999b).

A review of all *Pondaungia* specimens (Table 1) reveals several taxonomic problems. As Takai et al. (2000) and Chaimanee et al. (2000b) noted, the holotype of Jaeger et al.'s (1998) "*P. minuta*" (NMMP 4) is a specimen lacking enamel so that any dental measurements are misleading (Figs. 6A-
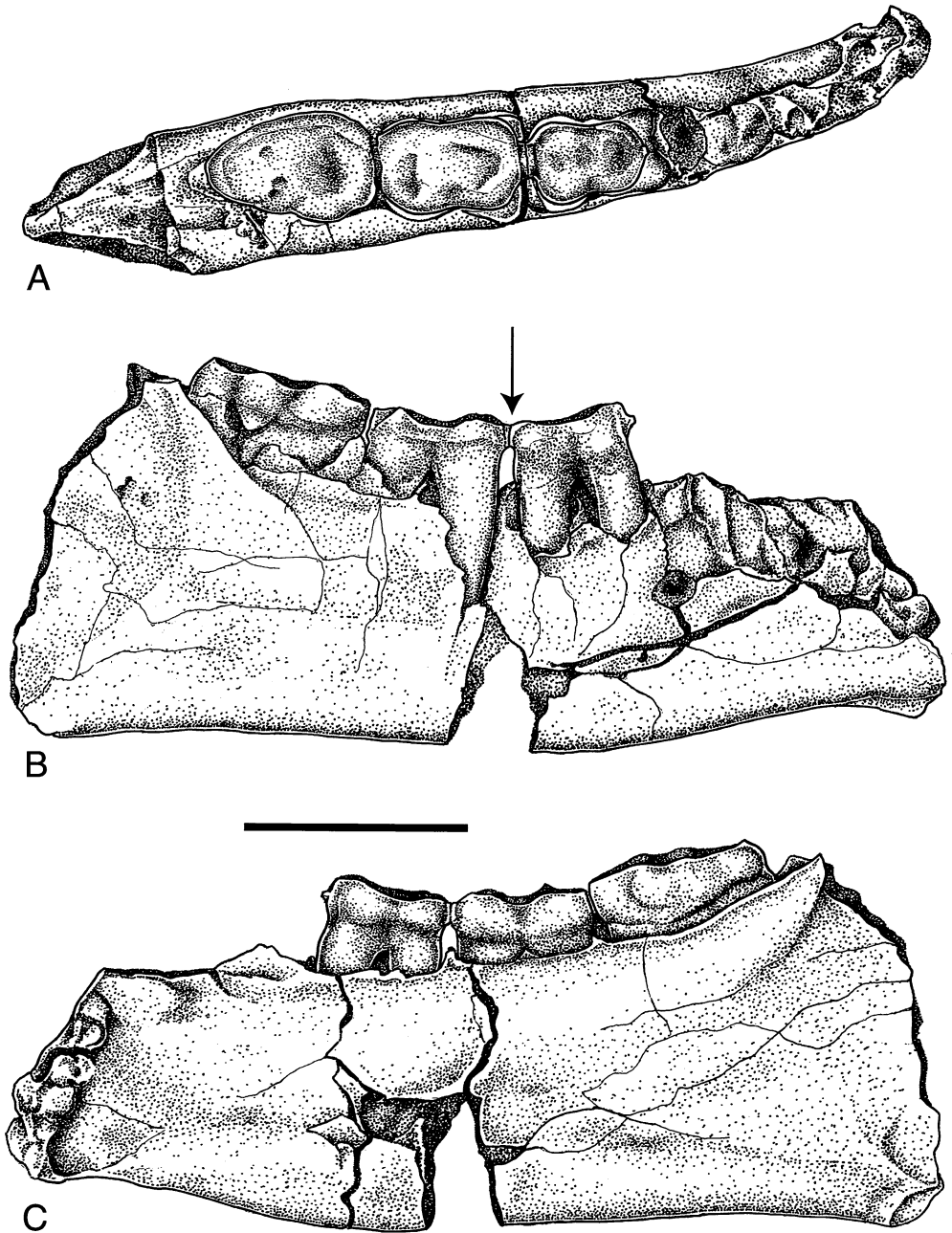
FIG. 8 — *Pondaungia cotteri*. NMMP 4, drawing of right dentary with heavily worn and eroded M_{1-3} in occlusal (A), lateral (B), and medial (C) views, for comparison with photograph in Figure 6. Arrow in B points to enamel islands preserved between M_1 and M_2.   Scale bar equals one centimeter.   Drawing by Kyaw Min.

C, 8). Takai et al. (2000) suggested that this individual represents an infant, but this seems impossible given that M_3 is fully erupted.

The more probable explanation for the condition of this specimen is that it may have been digested by a crocodilian (Fisher, 1981a,b). Close examination reveals that all of the enamel has been removed from the teeth of NMMP 4 (Fig. 8) except for small islands of enamel at interdental

boundaries (see Fisher, 1981a, Fig. 4d-f, p. 271, for an example of this type of enamel erosion in another faunal assemblage). This matches the expected pattern of tooth enamel erosion documented by experiments with modern crocodilians conducted by Fisher (1981a,b). Crocodilian predation on primates has been documented from Messel in Germany (Franzen, 1988, 1997; Franzen and Frey, 1993), and given the diversity and abundance of crocodilians in the Pondaung Formation (Hutchison and Holroyd, 1996) there is every reason to believe that similar predation may have occurred in Myanmar.

Additionally, the second specimen (GSI D202) referred to "*P. minuta*" by Jaeger et al. (1998) was claimed to be "distinctly smaller than the M_3 of other specimens of *Pondaungia*" (p. 956). Comparisons of the original *Pondaungia cotteri* type material shows the M_3 of GSI D202 to be virtually identical in size, wear pattern, and preserved morphology to the M_3 of GSI D201. Furthermore, GSI D201, D202, and D203 almost certainly represent the same individual (Pilgrim, 1927; Ciochon and Holroyd, 1994), and should certainly not be placed in different species. There is no compelling evidence to suggest that NMMP 4 differs in any way from the species represented by the holotype of *Pondaungia cotteri* (Fig. 7), thus "*P. minuta*" is considered a subjective junior synonym of the genotype species.

Takai et al. (2000) noted the presence in Myanmar of two distinct sizes of *Pondaungia* specimens. They suggested that these differences may result from sexual dimorphism. Our reanalysis reveals that the differences are sufficient to justify recognition of a new species of *Pondaungia*, described below in the context of a revised understanding of its relationships.

<div align="center">

Pondaungia savagei, new species
(Figs. 9-14)

</div>

Pondaungia cotteri (in part), Ba Maw et al., 1979; Ciochon and Holroyd, 1994; Jaeger et al., 1998; Takai et al., 2000; Chaimanee et al., 2000b.

Holotype.— NMMP 1 (=UCMP 120377 and DGMU-P4), right dentary with unworn M_{2-3}. NMMP 3 (=DGMU-P2) is a left dentary with unworn M_{2-3}. While given separate catalog numbers, these two specimens almost certainly represent the same individual (Fig. 9). In 1978, Ba Maw and Thaw Tint both took groups of students to the Mogaung area. In April, Ba Maw's team discovered NMMP 1, while in September Thaw Tint's team recovered NMMP 3. In 1979 D. E. Savage and R. L. Ciochon discovered that both Ba Maw and Thaw Tint had been led to the same locality (Thandaung kyitchaung) by local farmers from Mogaung village. When both specimens were compared it became clear that each shared the same pattern of fossilization, the same degree of wear, and the same pattern of breakage, and the same red sediment was adhering to each specimen. NMMP 1 was described by Ba Maw et al. (1979), but NMMP 3 remained unpublished until Jaeger et al. (1998) figured it without discussion.

Hypodigm.— Holotypes and NMMP 5, right dentary M_{2-3}; NMMP 12, left maxilla I^1, C^1, P^2, M^2, and parts of P^4, M^1, and M^3; NMMP 17, right dentary P_2-M_3; NMMP 20, complete left humerus, distal half of left calcaneum, and fragments of right humerus and left and right ulnae; NMMP 22, right P^4; NMMP 24, right dentary C_1-M_3; and NMMP 25, left M_1.

Locality and distribution.— The holotypes are from Lema kyitchaung near Mogaung village, west-central Myanmar. Referred specimens are from Lema kyitchaung (NMMP 5, NMMP 22, NMMP 25), Taungnigyin kyitchaung near Pangan village (NMMP 12), Thandaung kyitchaung near Mogaung village (NMMP 17), Sabapondaung kyitchaung (PK1) near Bahin village (NMMP 20), and Paukkaung kyitchaung (PK2) near Paukkaung village (NMMP 24). These kyitchaungs are all in west-central Myanmar.

Diagnosis.— Differs from *P. cotteri* in being 15% to 20% larger in tooth dimensions; molar hypoflexids shallower but with relatively larger, buccally extended basal shelves; molars more basally inflated with relatively heavier buccal cingulids; M_3 trigonids wider than talonids; and horizontal ramus does not shallow anteriorly, maintaining nearly uniform jaw depth from posterior to anterior.
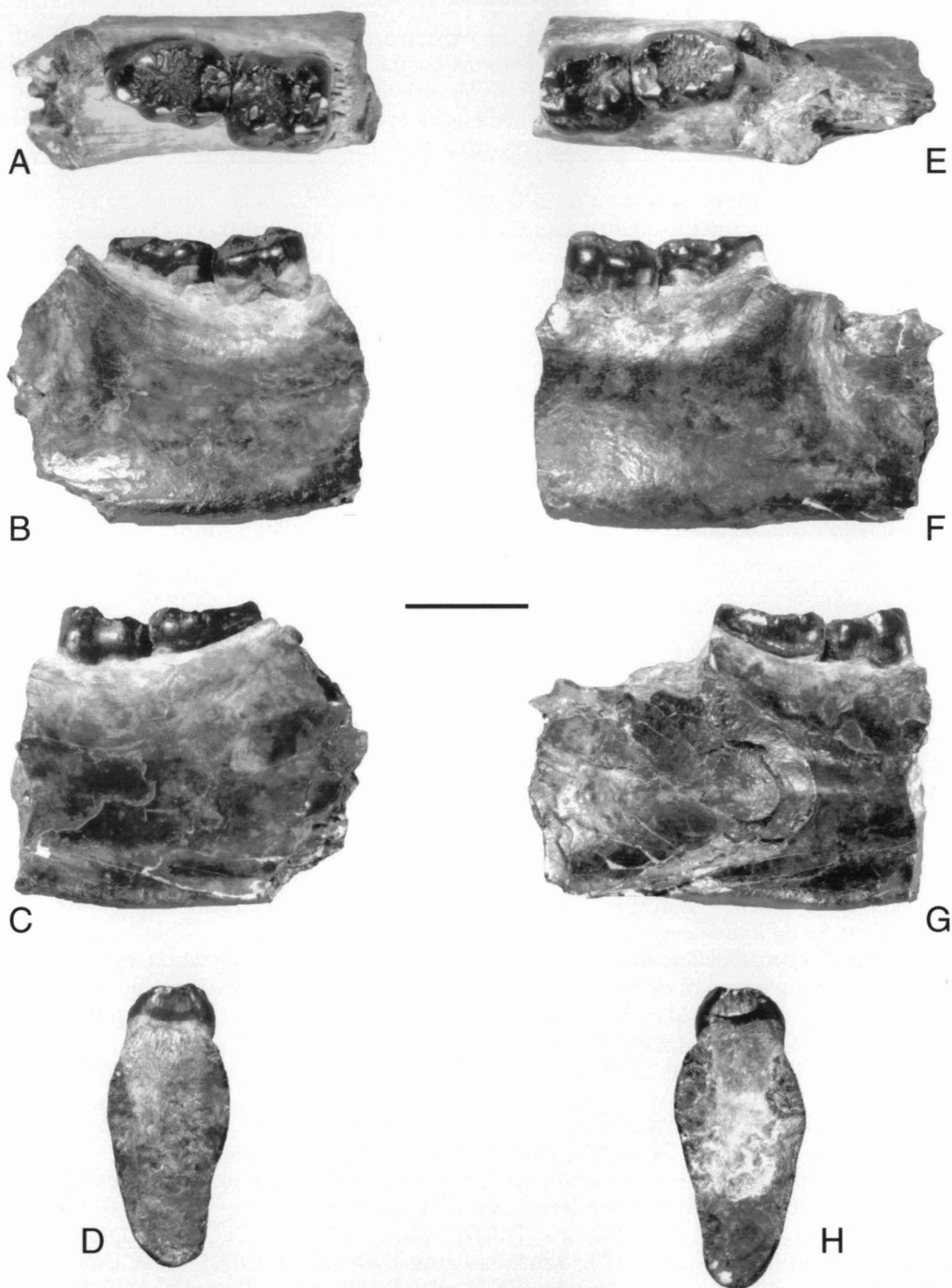
FIG. 9 — *Pondaungia savagei*, new species, NMMP 1 (holotype), right dentary with unworn M$_{2-3}$ in occlusal (A), lateral (B), medial (C), and anterior (D) views. NMMP 3 (probably part of holotype), left dentary with unworn M$_{2-3}$, in occlusal (E), lateral (F), medial (G), and anterior (H) views. Scale bar equals one centimeter.
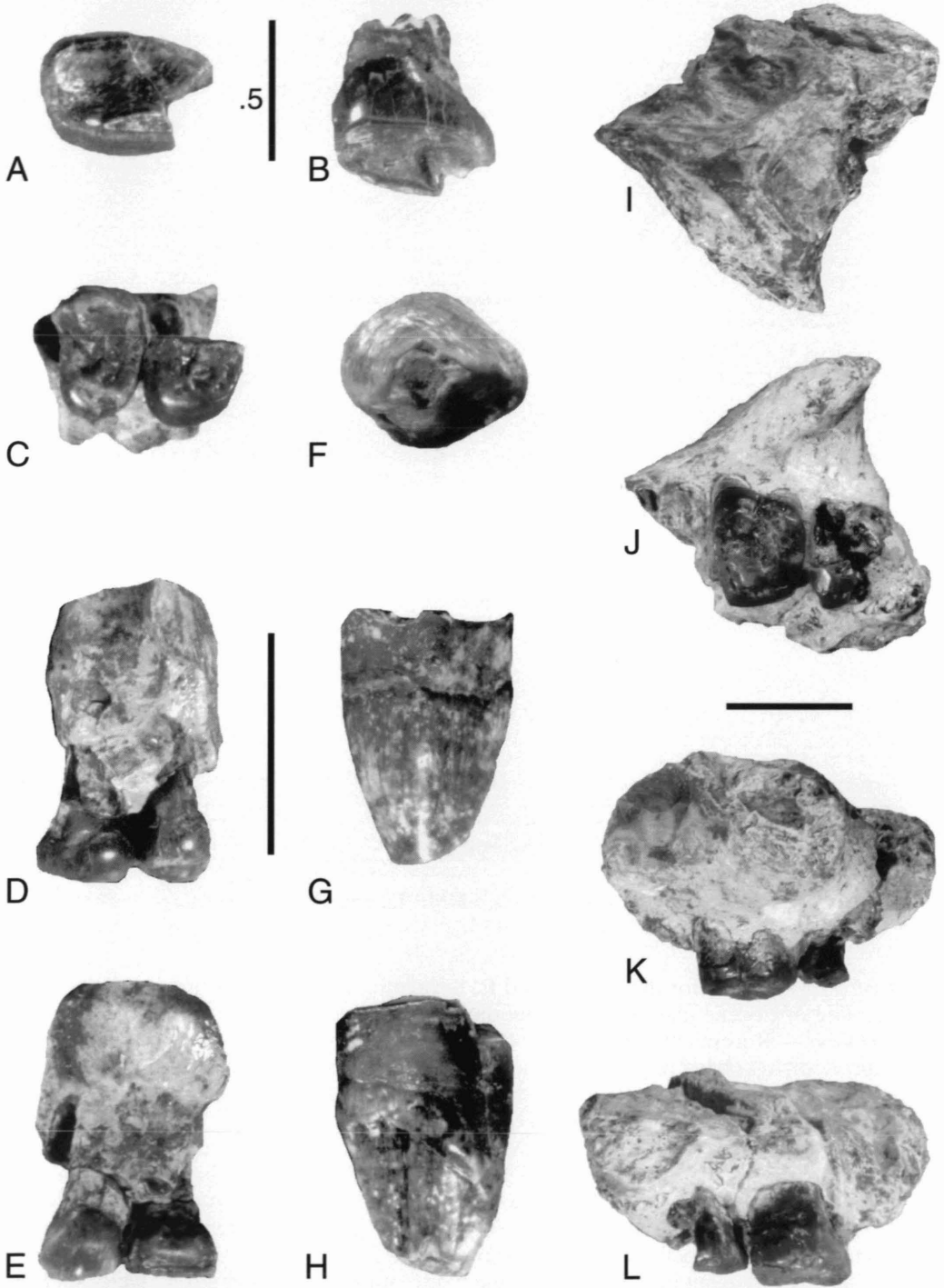
FIG. 10 — *Pondaungia savagei*, new species, NMMP 12, left I^1, C^1, left maxillary fragment with P^3 and lingual part of P^4. I^1 is shown in occlusal and lingual views (A,B); P$^{3-4}$ are shown in occlusal, medial, and lateral views (C-E); C^1 is shown in occlusal, buccal, and lingual views (F-H); maxillary fragment with M2-3 in dorsal, occlusal, buccal, and lingual views (I-L). Scale bar for A-B equals 0.5 centimeters, and those for C-H and I-L equal one centimeter, respectively.
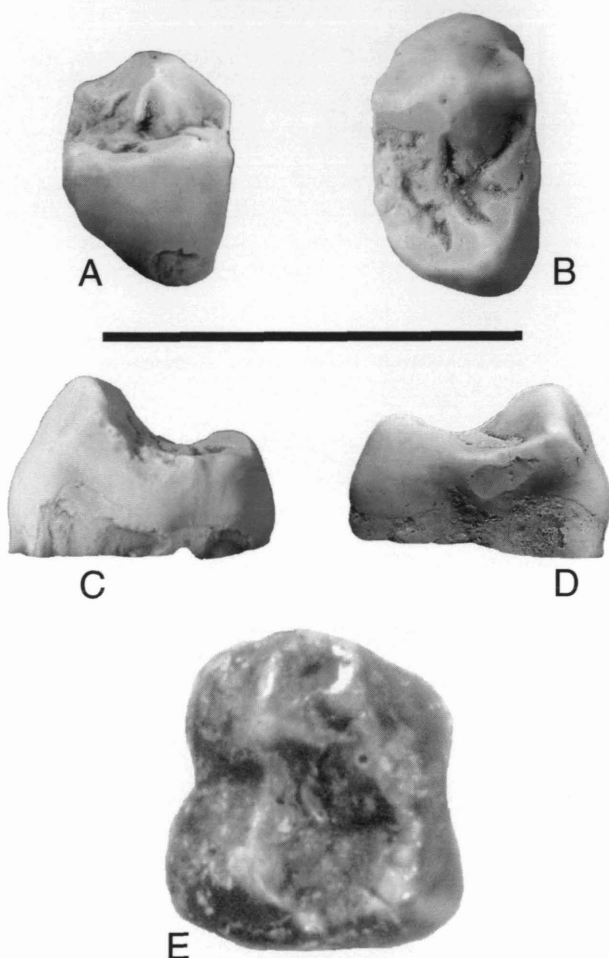
FIG. 11 — *Pondaungia savagei*, new species. A-D, NMMP 22, right P^4 in lingual (A), occlusal (B), posterior (C), and anterior (D) views. E, NMMP 25, left M$_1$ in oclusal view. Scale bar equals one centimeter.

Etymology.— Named for the late Donald E. Savage in recognition of his contributions to our understanding of Eocene mammalian evolution in southeastern Asia and China.

Description.— Recent collecting efforts combined with our redefinition of the hypodigms of *P. cotteri* and *P. savagei* have resulted in a much better understanding of the dental and mandibular morphology of the latter species. We take this opportunity to present descriptions and illustrations of all tooth positions now known to represent *P. savagei*.

Upper dentition (Figs. 10-11A-D). NMMP 12 (Takei et al., 2000, their specimen number NMMP-KU 0003) consists of portions of a left maxilla of *P. savagei* including a broken I^1, complete C^1 and P^3, the lingual halves of P^4 and M^1, a complete M^2, and a small fragment of M^3. NMMP 22 is a complete, nearly unworn P^4 of *P. savagei*. Tooth measurements of all *Pondaungia* and *Amphipithecus* specimens are listed in Tables 2 and 3.

I^1 is relatively large, but broken buccally and worn. It has a relatively strong labial shelf with a lingually spatulate, flatly worn crown. C^1 is robust with a worn tip. It has a strong labial cingulum that extends from the distobuccal corner to the labial side. The labial surface is divided by a longitudinal valley into a larger mesial and a smaller distal portion.

P^3 has a strong paracone that is inflated both buccally and lingually. The preparacrista is short but the postparacrista is relatively longer and more robust. There is no evidence for the presence

FIG. 12 — *Pondaungia savagei*, new species. NMMP 17, right dentary with P_2-M_3 in occlusal (A), lateral (B), and medial (C) views. Scale bar equals one centimeter.

of a metacone but the tooth is somewhat worn. The protocone is low and anterior and well separated from the base of the paracone. There is a faint postprotocrista that extends to the base of the paracone and divides the lingual shelf in half. A relatively stronger preprotocrista extends to the proximobuccal corner of tooth. The lingual shelf is inflated lingually and covered with rugose enamel.
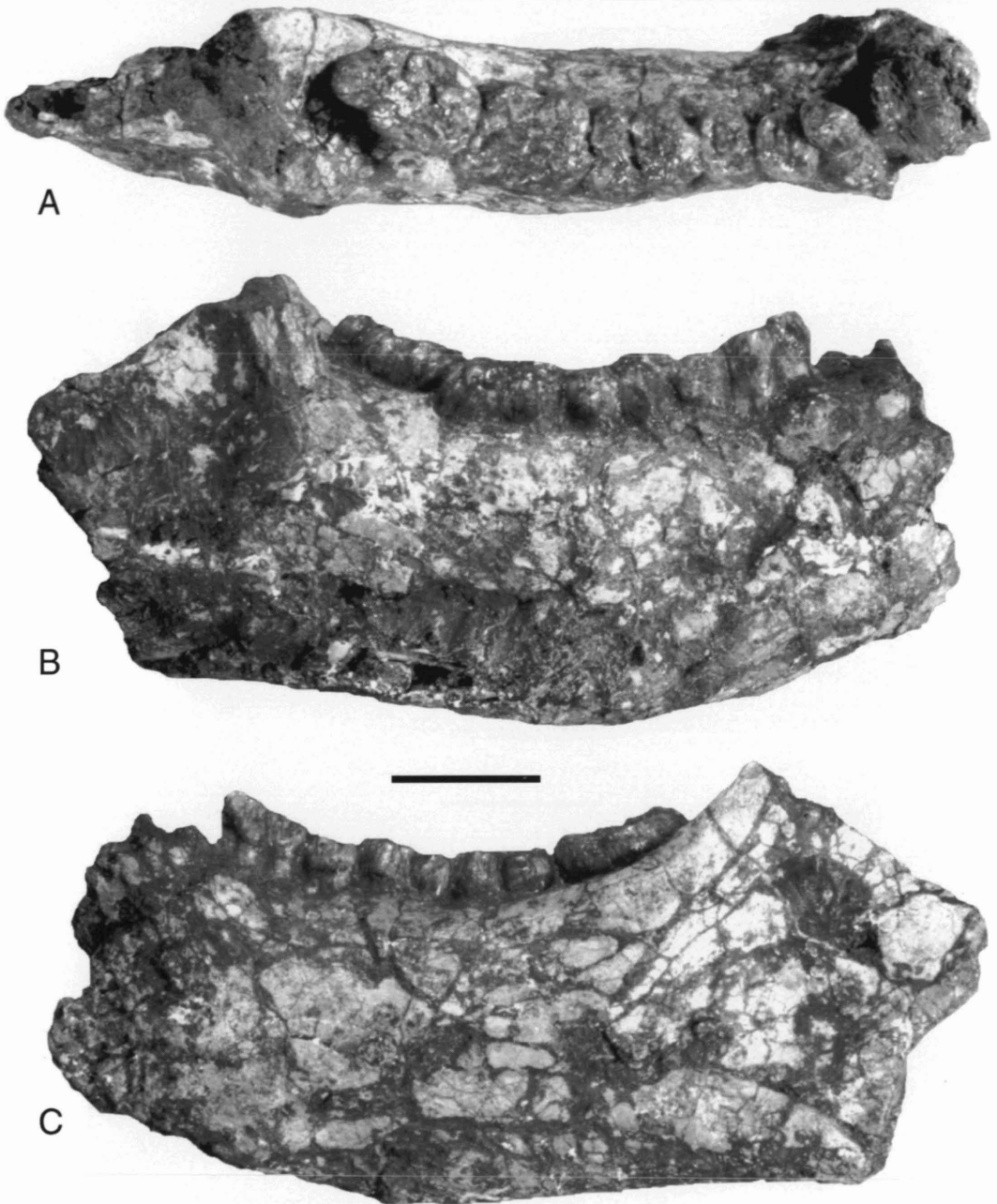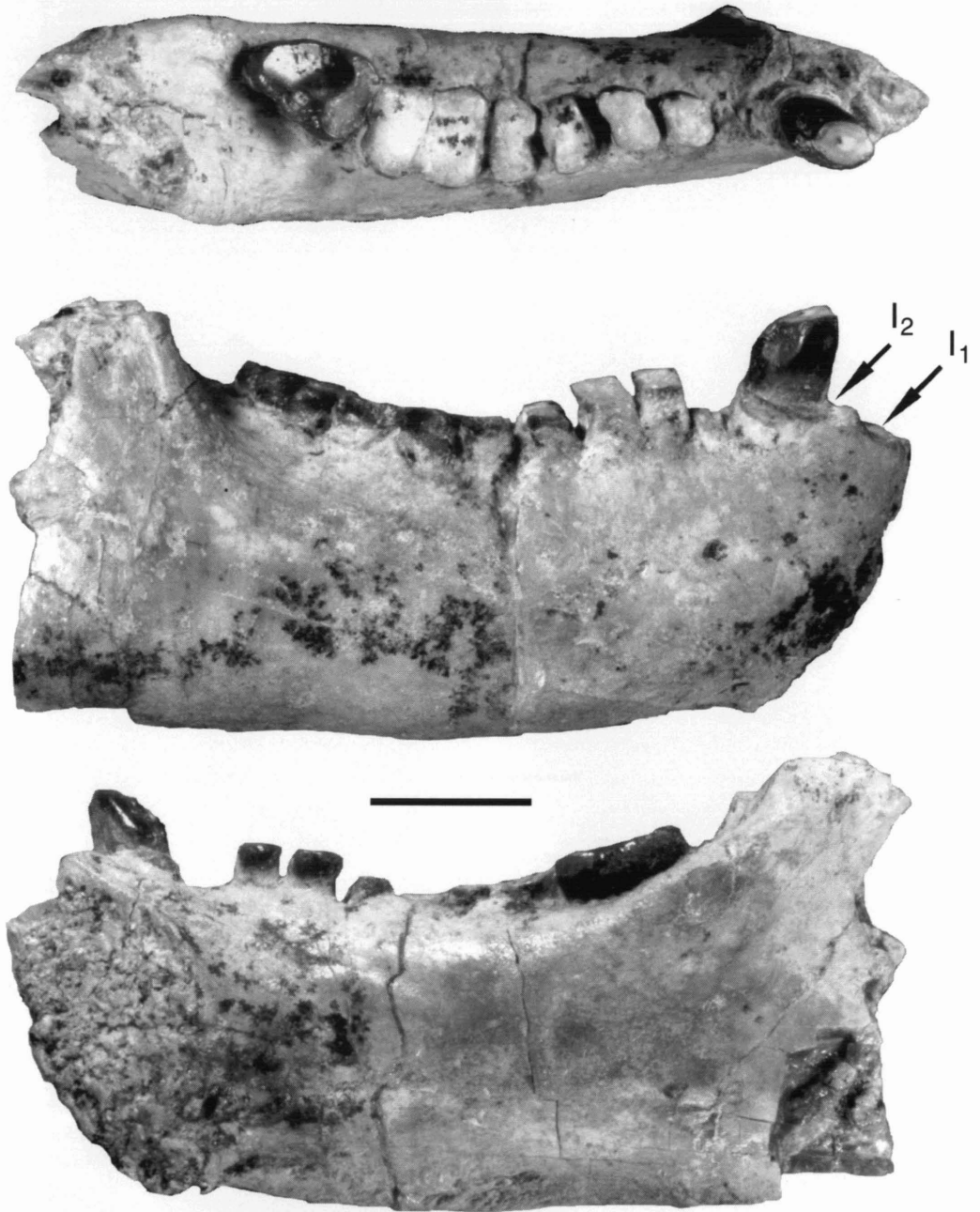
FIG. 13 — *Pondaungia savagei*, new species. NMMP 24, right dentary with C_1-M_3 in occlusal (A), lateral
(B), and medial (C) views. Arrows in B indicate alveoli for I_1 and I_2, note that I_1 alveolus is larger than that
for I_2. Scale bar equals one centimeter.

P^4 (NMMP 22, Fig. 11A-D) has a massive, centered paracone with an inflated buccal flank.
The preparacrista is robust and inflated but there is no parastylar development. The postparacrista
is also robust and inflated and terminates as a small, rounded metastyle that is incorporated into
the postparacrista. There are no cingula developed. The protocone is low, rounded, and anteriorly
placed. A relatively large paraconule is present (nearly as large as the protocone) that is appressed
to the base of the paracone and connected to the preparacrista by a small shelf. There is an

FIG. 14 — Comparative dental series of *Pondaungia* and *Amphipithecus* specimens in occlusal view. A, *P. cotteri*, NMMP 4. B, *P. savagei*, NMMP 3 (reversed). C, *P. savagei*, NMMP 17. D, *P. savagei*, NMMP 24. E, *A. mogaungensis*, NMMP 7 (left side, reversed). Scale bar equals one centimeter.
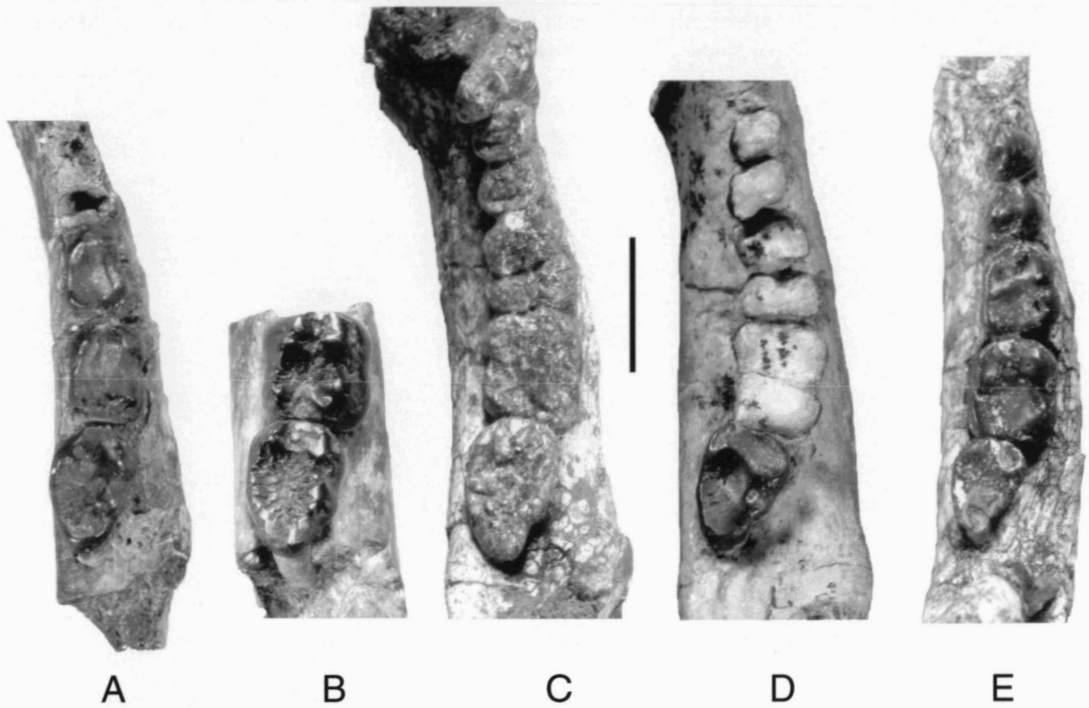
additional worn, rounded cuspule present between the paraconule and protocone. The postprotocrista is relatively strong and broad and extends to the posterior base of the paracone where it widens to form an indistinct metaconule. A small fovea is present between the para- and metaconules. A strong and very broad postprotocingulum extends from the apex of the protocone to the posterior corner of the tooth and forms a posterior shelf that has two small bunodont accessory cuspules formed along its posterior margin. Enamel crenulation is developed along the posterior edge of the postprotocrista.

Only the lingual part of M^1 is known for *P. savagei* (NMMP 12). Among the few features that can be discerned from this fragmentary tooth are the presence of a robust, low protocone and a hypocone formed from the postprotocingulum that is nearly as robust as the protocone.

M^2 has a bulbous paracone and metacone, both of which are very low and buccally inflated (the paracone more so than the metacone). The hypoflexus is very shallow being just a small notch between the paracone and metacone. A short preparacrista leads to a tiny parastylar area that joins with a robust anterior cingulum. This anterior cingulum is continuous with a weaker lingual cingulum, but no posterior or buccal cingula are present. The protocone is distinct, inflated, and marginal but less massive than the paracone or metacone. The hypocone is nearly the size of the protocone and is formed from the postprotocingulum (but closely appressed to protocone). The preprotocrista is short and does not reach the base of the paracone leaving the trigon basin open anteriorly through a narrow notch between the protocone and paracone. A strong, robust postprotocrista extends to the base of the metacone and closes the trigon basin distally. Posterior to the postprotocrista a small depression is formed between the bases of the hypocone and metacone. The enamel of the trigon basin is crenulated and rugose.

Lower dentition (Figs. 11E, 12-14). The lower dentition of *Pondaungia savagei* is represented by the two holotypes (NMMP 1 and NMMP 3) both of which preserve M_{2-3}, NMMP 5 (M_{2-3}), NMMP 17 (P_2-M_3), NMMP 24 (C_1-M_3), and NMMP 25 (M_1).

Table 2 — Measurements of upper teeth of primates described from the late middle Eocene of Myanmar. Abbreviations: *L*, mesiodistal length; *W*, buccolingual width. Measurements in mm.

		Amphipithecus mogaungensis	*Pondaungia cotteri*	*Pondaungia savagei*	
		NMMP 18	GSI D203	NMMP 12	NMMP 22
I^1	L	–	–	4.60	–
	W	–	–	5.70	–
C^1	L	–	–	7.60	–
	W	–	–	6.35	–
P^3	L	–	–	3.84	–
	W	–	–	5.51	–
P^4	L	–	–	–	3.61
	W	–	–	–	6.28
M^1	L	5.47	5.00	–	–
	W	7.09	6.28	–	–
M^2	L	5.63	5.59	6.96	–
	W	7.48	7.72	8.52	–
M^3	L	4.98	–	–	–
	W	6.73	–	–	–

Only one specimen of *P. savagei* (NMMP 17, Figs. 12, 14C) preserves any morphology of the lower premolars (Chaimanee et al., 2000b). Another specimen (NMMP 24, Fig. 13, 14D) has the premolars in place but they are completely worn flat. In general, the premolars of *P. savagei* are low, bulbous, crowded together, and wider than long.

P_2 has a large protoconid that is rounded and blunt (partially due to wear). No distinct paraconid or metaconid is present, although there is a relatively weak, short metaconid pillar developed. The tooth is basally inflated and distolingually distended with a bulging buccal surface. P_2 has no talonid or posterior shelf developed and lacks any cingulids.

P_3 is similar to P_2 in having a low, bulbous, and massive crown. It differs from P_2 in being larger in over-all dimensions, in having a stronger metaconid pillar, and in also having a postprotocristid that extends from the apex of the protoconid into a massive, broad, lingually sloping posterior shelf (posterior to the metaconid pillar). P_3 also is more distended distolingually than P_2. P_4 is a more massive version of P_3 with a relatively larger and more massive metaconid pillar and a broader postprotocristid and posterior shelf.

NMMP 25 (Fig. 11E) preserves a nearly unworn left M_1 of *P. savagei*. Other specimens preserving M_1 (NMMP 17 and NMMP 24) have this tooth nearly worn away. The M_1 protoconid is robust. There is a broad, curving, and mesially extended paracristid with a small paraconid cuspule at the mesiolingual corner of the trigonid. The paraconid and metaconid are enclosed in a continuous crest closing the lingual border of the trigonid. The metaconid is double-cusped with the posterior cuspule positioned distal to the protoconid. The trigonid fovea is separated into a larger depression mesially and a smaller depression posteriorly, which is continuous with a deep groove separating the metaconid and protoconid. The fovea also is divided by a transverse crest originating from the anterior metaconid cuspule and extending to the lingual edge of the protoconid. There is a weak mesiobuccal cingulid and stronger distobuccal cingulid that continues posteriorly

Table 3 — Measurements of lower teeth of primates described from the late middle Eocene of Myanmar. Abbreviations: *AW*, buccolingual width of trigonid; *L*, mesiodistal length; *MD*, mandibular depth below M_2; *PW*, buccolingual width of talonid; *W*, buccolingual width. Measurements in mm.

| | | *Amphipithecus mogaungensis* | | | *Pondaungia cotteri* | *Pondaungia savagei* | | | | | |
	AMNH 32520	NMMP 2	NMMP 6	NMMP 7	GSI D201-202	NMMP 1	NMMP 3	NMMP 5	NMMP 17	NMMP 24	NMMP 25
C_1 L	–	–	–	–	–	–	–	–	–	5.40	–
W	–	–	–	–	–	–	–	–	–	4.10	–
P_2 L	–	–	–	–	–	–	–	–	3.24	–	–
W	–	–	–	–	–	–	–	–	3.76	–	–
P_3 L	4.30	–	–	3.62	–	–	–	–	3.48	–	–
W	4.10	–	–	3.38	–	–	–	–	4.45	–	–
P_4 L	4.40	–	–	4.44	–	–	–	–	3.67	–	–
W	4.30	–	–	4.06	–	–	–	–	4.47	–	–
M_1 L	5.90	6.04	5.36	5.93	–	–	–	–	6.98	–	6.05
AW	3.90	4.48	3.96	4.44	–	–	–	–	4.98	–	3.61
PW	5.00	5.34	4.74	4.74	–	–	–	–	5.31	–	4.04
M_2 L	–	6.41	5.63	6.47	5.95	6.59	6.87	–	7.54	–	–
AW	–	5.39	4.74	4.78	–	4.97	4.83	–	5.13	–	–
PW	–	5.81	4.84	5.37	4.81	5.55	5.45	–	6.06	–	–
M_3 L	–	–	–	6.04	7.12	8.18	8.01	8.28	9.01	7.82	–
AW	–	–	–	4.54	4.48	5.12	5.20	–	5.34	5.73	–
PW	–	–	–	3.74	4.62	5.11	5.11	–	5.24	4.84	–
MD	17.80	–	14.34	14.53	12.40	17.74	18.53	16.95	19.81	18.60	–

to join the postcristid. The hypoconid is marginal, somewhat inflated, and enclosed in a high cristid obliqua that joins the postvallid buccal of center. There is no distinct entoconid but a tall entocristid with four accessory cuspules formed along its margin. The entocristid closes the talonid lingually (no talonid notch) but the talonid is open posteriorly as there is no hypoconulid. The trigonid is only slightly higher than the talonid and the talonid is covered with weakly crenulated enamel.

M_{2-3} are best represented in the two holotype specimens (NMMP 1 and NMMP 3), both teeth being either heavily eroded (NMMP 5 and NMMP 17) or worn nearly flat (NMMP 24) in other specimens where they are present. M_2 lacks a paraconid but has a broad and sloping paracristid that extends anteriorly. The metaconid is somewhat larger than protoconid and double-cusped. The hypoconid is very robust and low and is incorporated into a very broad, short, and inflated cristid obliqua. The entoconid is more marginal, lower, and less inflated with a lower and less broad entocristid (talonid notch still closed). There is no hypoconulid. Like M_1, the trigonid is only slightly higher than talonid and the talonid basin is covered with heavily crenulated enamel. There is a weak buccal cingulid very high on buccal flank of the tooth. Beneath the cingulid the tooth bulges buccally. The hypoflexid is distinct but shallow with an enamel ridge that extends into the hypoflexid from the base of the protoconid, placed higher than the buccal cingulid.

M_3 lacks a paraconid and has a double-cusped metaconid as in M_2. The hypoconid is large. The entoconid is absent but there is an entocristid that is continuous with the postcristid and postmetacristid, the latter of which is divided into two portions by crenulations. The entocristid is
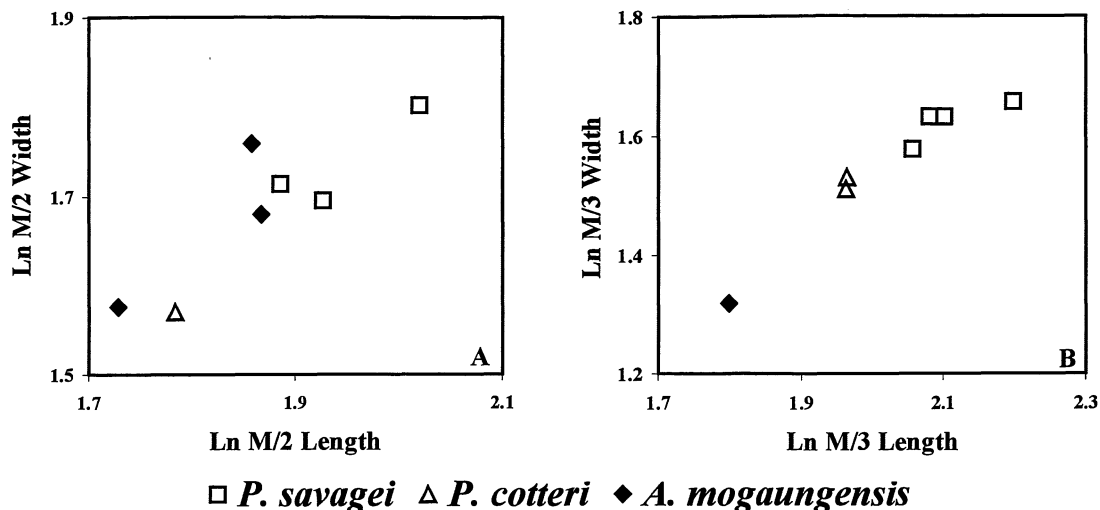
FIG. 15 — Bivariate plots of M_2 length versus width for *Pondaungia* and *Amphipithecus* (A), and M_3 length versus width for *Pondaungia* and *Amphipithecus* (B).
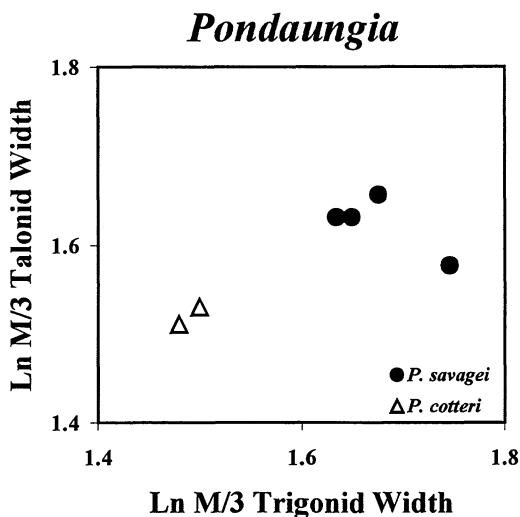

FIG. 16 — Bivariate plot of M_3 trigonid width versus M_3 talonid width in *Pondaungia*.

relatively low and has five accessory cuspules formed along its crest by crenulations. The hypoconulid also is low, single cusped, and relatively large. There is a weak, discontinuous buccal cingulum with the anterior portion being better developed than in M_2. A small enamel ridge extends from the protoconid to the base of the hypoflexid that is somewhat more distinct than in M_2 and much more buccally extended to form a small, enclosed shelf (straight on M_2 with no shelf). The talonid basin is shallow with very crenulated enamel.

Additional morphology. NMMP 17 and NMMP 24 preserve relatively complete dentaries of *P. savagei* that detail some additional dental morphology. Horizontal ramus depth remains consistent from posterior to anterior, tapering only very slightly anteriorly. The symphysis is unfused and extends back to P_3 (P_2 in NMMP 24). The mandible is thickest (buccolingually) beneath P_4-M_1. Judging by the roots, I_1 is larger than I_2 (Fig. 13C). The lower canine is relatively robust but not markedly projecting. P_2 is single-rooted while P_{3-4} are double rooted with the lingual root

being bifurcate in P_3 and both buccal and lingual roots being bifurcate in P_4. Two mental foramina are present, one beneath P_2 and a second beneath P_4.

Discussion.— Figures 15-16 summarize some aspects of tooth size between the two species of *Pondaungia*. Figure 15A,B depicts lower second and third molar size, with two distinct groupings being present in each case: a smaller group represented by *P. cotteri* and a larger group represented by *P. savagei*. Figure 16 shows the relationship between M_3 trigonid and talonid width in the two *Pondaungia* species. *P. cotteri* has M_3 trigonids that are somewhat narrower than the talonids, while *P. savagei* has M_3 trigonids that are broader than the talonids. In combination with the morphological features cited above, these differences in size also support the recognition of two distinct species of *Pondaungia*. Both species of *Pondaungia* are present throughout the Pondaung sequence, but *P. savagei* is relatively more common.

Amphipithecus Colbert, 1937

Type and only species.— *Amphipithecus mogaungensis*
Age and distribution.— Late middle to late Eocene, Pondaung Formation, Myanmar.

Emended diagnosis.— Differs from *Pondaungia* in having somewhat longer, narrower, and less bulbous lower premolars with more distinct cuspules (premolars longer than wide), lower molars with poorly defined cusps, lower molar crenulation weak or absent, lower molar hypoflexids shallow, and M^3/M_3 reduced relative to M^2/M_2.

Amphipithecus mogaungensis Colbert, 1937
(Figs. 17-23)

Amphipithecus mogaungensis, Ciochon et al., 1985; Ciochon and Holroyd, 1994; Jaeger et al., 1998; Takai et al., 2000.

Holotype.— AMNH 32520, left dentary with P_3-M_1 (Fig. 17).

Referred specimens.— Holotype and NMMP 2 (=DGMU-P1), left dentary M_{1-2}, NMMP 6, left dentary M_{1-2}, NMMP 7, left dentary P_3-M_3 and right dentary P_4-M_3, and NMMP 18, right maxilla P^4-M^3. Two isolated frontal bones (NMMP 19 and NMMP 27) may also represent *Amphipithecus mogaungensis*.

Locality and distribution.— The holotype is from Thandaung kyitchaung near Mogaung village, west-central Myanmar. Referred specimens are from Thandaung kyitchaung (NMMP 2, NMMP 6), Yarshe kyitchaung near Bahin village (NMMP 7), and Paukkaung (PK2) kyitchaung near Bahin village (NMMP 18). The two possible frontal bones of *Amphipithecus* are from Paukkaung (PK2) kyitchaung (NMMP 19) and Payama kyitchaung near Bahin village (NMMP 27).

Diagnosis.— See generic diagnosis.

Description.— The following descriptions are based on an examination of all known specimens of *Amphipithecus*.

Upper dentition (Figs. 18-19). The only known upper teeth of *Amphipithecus* are preserved in NMMP 18, a right maxilla with a fragment of P^4, a mesiolingually broken M^1, and complete M^{2-3}. Unfortunately, M^{1-2} are heavily worn so that much of the tooth morphology is gone. Little can be said of M^1. The buccal cusps of M^2 are still present and show a massive, low, rounded, and buccally distended paracone and a metacone. The metacone is slightly smaller than the paracone but otherwise also massive and buccally distended (but not quite as much as the paracone). There is no stylar shelf but M^2 has slightly rugose enamel along its buccal margin. M^{1-2} appear to have had hypocones but it is not possible to tell how they were formed because the teeth are too worn. In general the roots of all of the upper molars are somewhat distended buccally and the molar crowns appear to have been nearly flat.

M^3 is mostly unworn. It is virtually flat with only a very tiny, shallow trigon basin at the center of the tooth. The paracone is low, rounded, massive and buccally distended, while the metacone is reduced, but also massive, rounded and flat. A very weak hypoflexid is developed between the
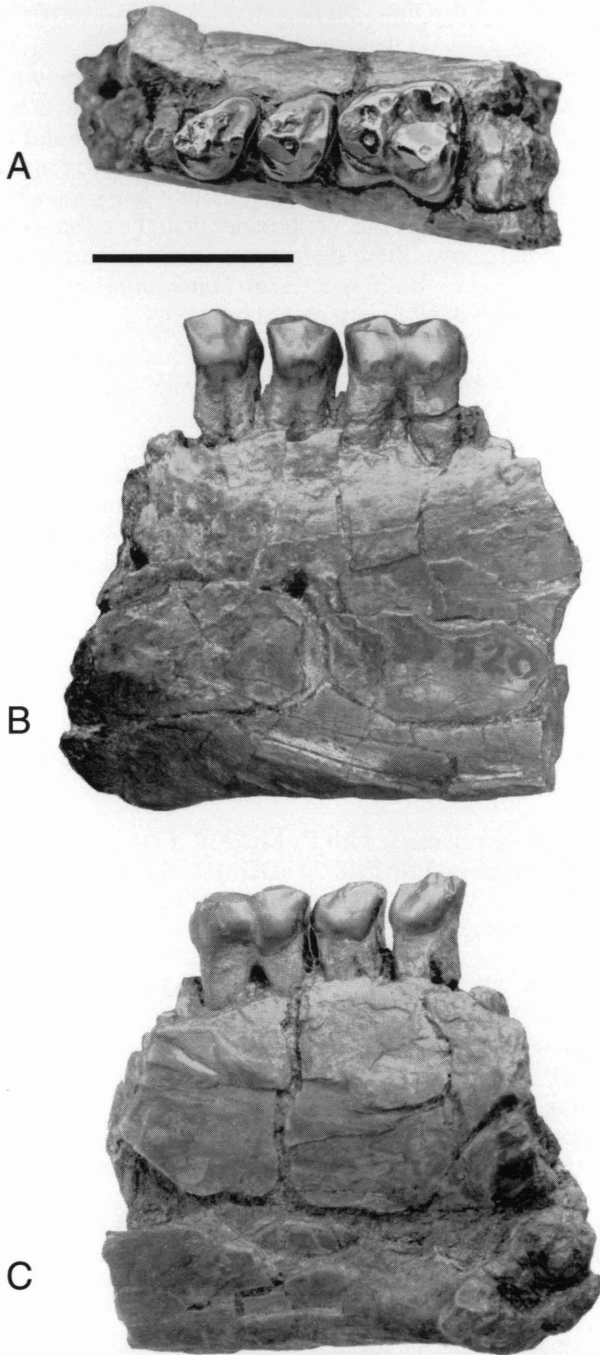
FIG. 17 — *Amphipithecus mogaungensis*, AMNH 32520 (holotype), left dentary with P_3-M_1 in occlusal (A), lateral (B), and medial (C) views. Scale bar equals one centimeter.

para- and metacones. The protocone is massive and placed slightly anterior of center. There is no discernable preprotocrista but there is a weak postprotocrista that closes the tiny trigon basin posteriorly. There is a distal, sloping shelf extending from the postprotocrista but no hypocone is present. The enamel of the trigon basin is slightly rugose. M^3 is reduced in size compared to M^2.

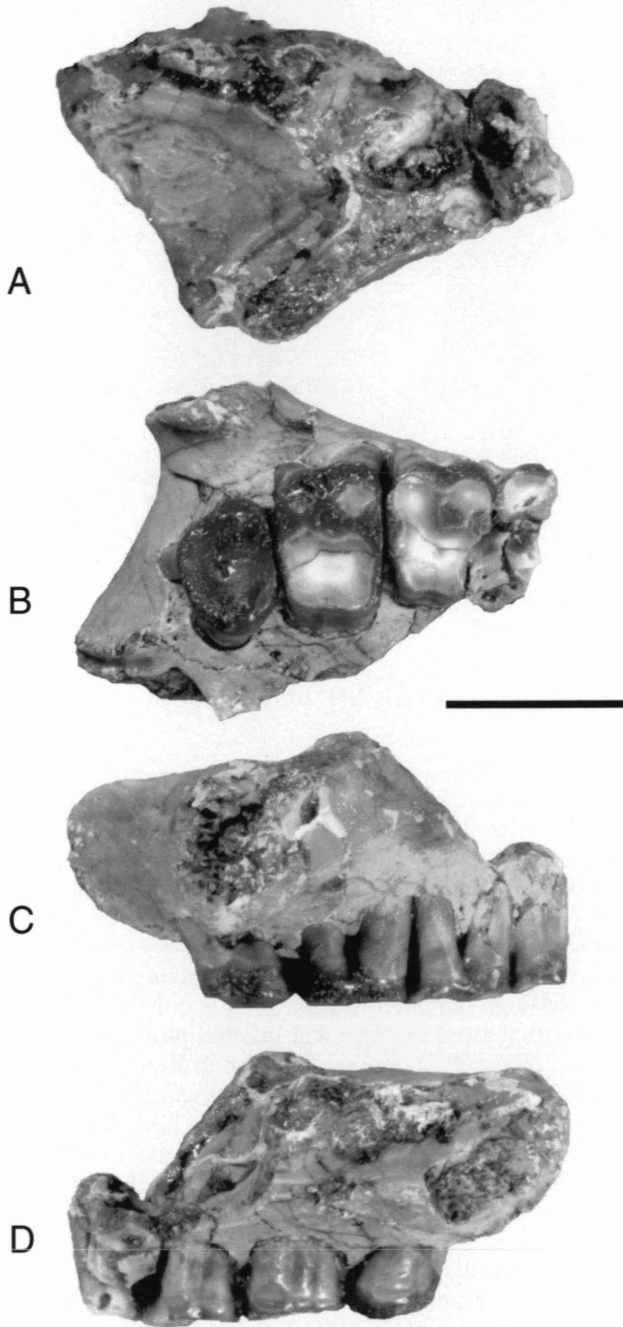FIG. 18 — *Amphipithecus mogaungensis*, NMMP 18, right maxilla with fragment of P^4, M^{1-3} in dorsal (A), occlusal (B), lateral (C), and medial (D) views. Scale bar equals one centimeter.

Lower dentition (Figs. 20-21). Four specimens of *Amphipithecus* preserve partial lower dentitions including AMNH 32250 (holotype with P_3-M_1), NMMP 2 (M_{1-2}), NMMP 6 (M_{1-2}), and NMMP 7 (P_3-M_3).
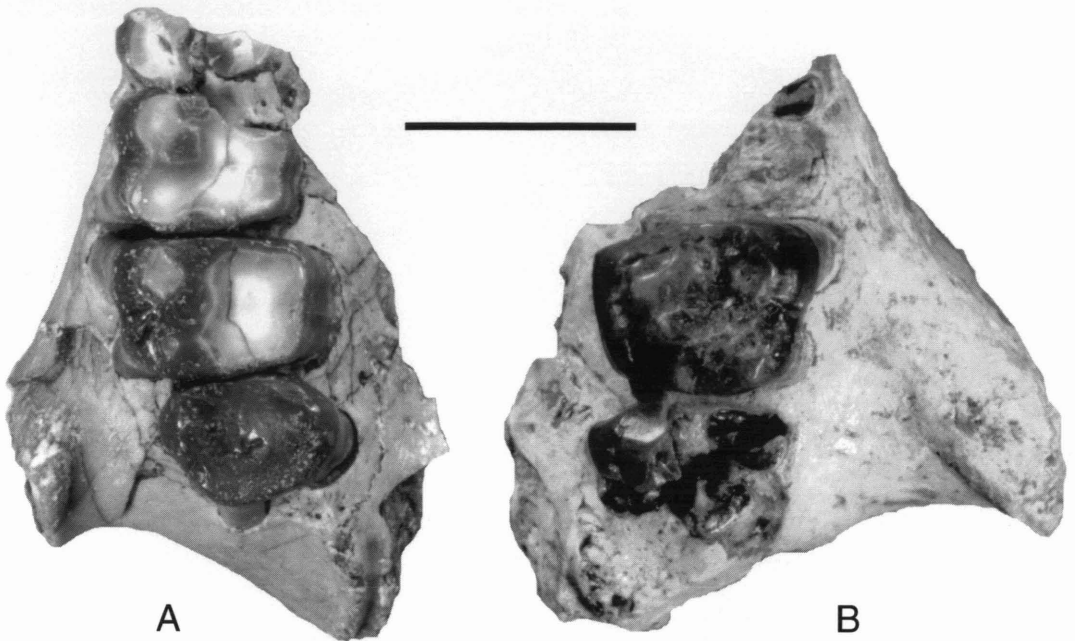
FIG. 19 — Comparison of upper dentitions of *Amphipithecus* and *Pondaungia* in occlusal view. A, *Amphipithecus*, NMMP 18. B, *Pondaungia*, NMMP 12. Scale bar equals one centimeter.

P_3 has a tall and buccally inflated protoconid. The paraconid is elevated (nearly as tall as protoconid), appressed to anterior flank of the protoconid, and extended anteriorly and excavated beneath such that it would have over-hung P_2. There is no distinct metaconid but a very broad, robust metacristid is present that extends down the lingual flank of the protoconid. A small fovea is present between the paraconid and the metacristid. P_3 is distolingually distended and has a very heavy postprotocristid (as heavy as the metacristid) that curves from the protoconid to the distolingual corner of the tooth. A relatively deep valley is present between the metacristid and postprotocristid. P_3 is buccoproximally distended as well, giving it the appearance of being somewhat skewed in the jaw, although the anterior root of P_3 is only slightly displaced buccally.

P_4 is similar to P_3 but with a more massive and inflated protoconid. The paraconid and metaconid are more distinct and relatively more massive than in P_3 with a relatively larger fovea being developed between them on the lingual flank of the protoconid. The metaconid is formed as a massive, inflated, pillar-like metacristid that is appressed to lingual side of protoconid (instead of forming a broad, less massive ridge as in P_3). The postprotocristid is stronger and relatively larger than in P_3 and curves to the distolingual border of the tooth. Because the postprotocristid is so massive it gives the appearance of being developed as a talonid shelf but there is no real talonid development.

In general, lower molars lack distinct cusps. Trigonids are only slightly more elevated than talonids and talonids are very shallow and broad with very weak or absent enamel crenulations. The tooth crowns are very basally inflated.

M_1 has a small paraconid and a massive and bulbous protoconid and metaconid. The metaconid is extended distally and placed close to the protoconid. The paraconid is equidistant and centered so that the trigonid cusps form an equilateral triangle. There is no trigonid fovea present. A very weak proximobuccal cingulid is present high on the flank of the protoconid. The hypoflexid is very shallow with no cingular or ridge development, unlike the condition in *Pondaungia*. The cristid obliqua is short and broad and the hypoconid is marginal but basally inflated. The entoconid is also marginal, smaller than the hypoconid, but still somewhat inflated. The entocristid is short, high, and broad (talonid notch closed) but not as massive as the cristid obliqua. The talonid
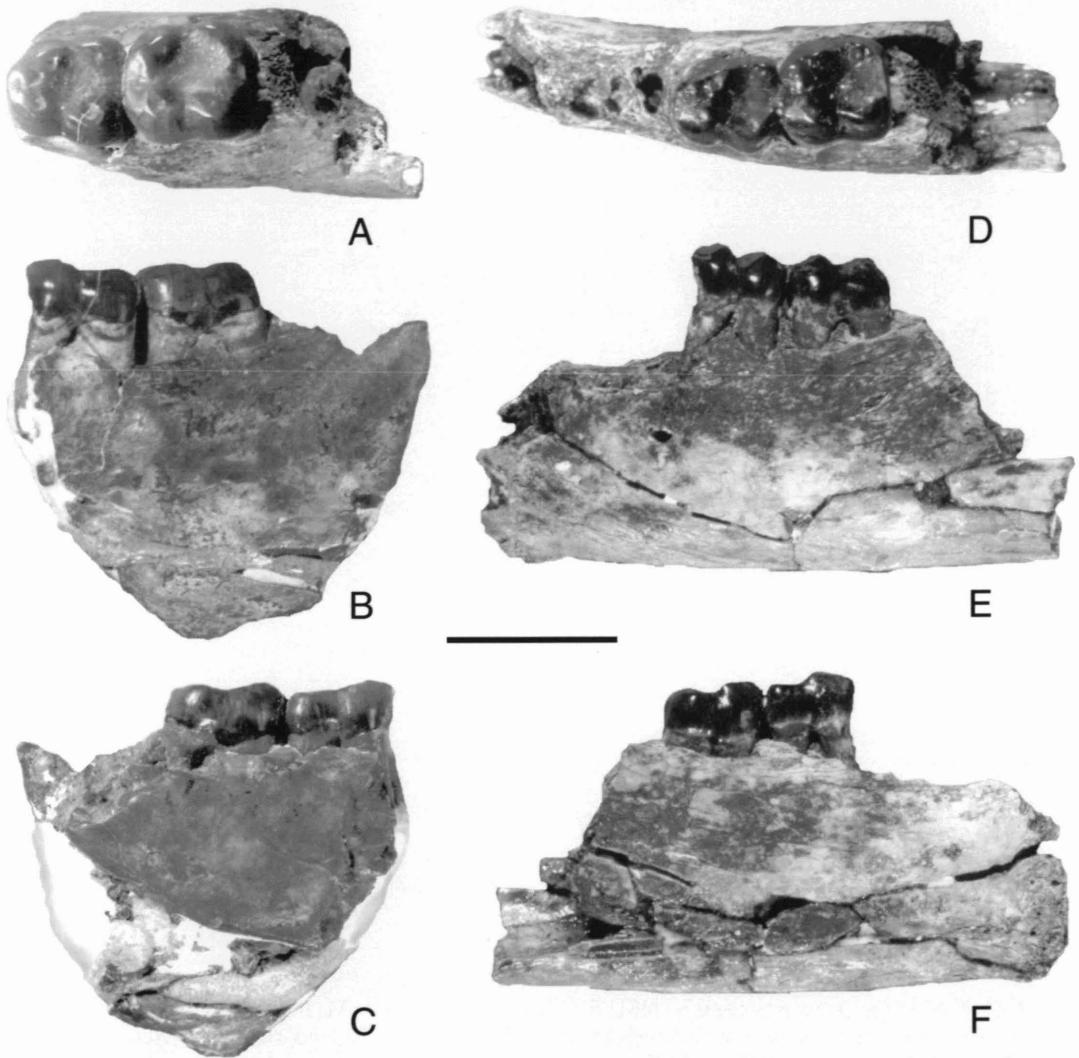
FIG. 20 — *Amphipithecus mogaungensis.* NMMP 2, left dentary with M_{1-2} in occlusal (A), lateral (B), and medial (C) views. NMMP 6, left dentary with M_{1-2} in occlusal (D), lateral (E), and medial (F) views. Scale bar equals one centimeter.

basin is relatively shallow and open distally with either a very tiny, centered hypoconulid (NMMP 6) or no hypoconulid (NMMP 2) and no enamel crenulation.

M_2 is similar to M_1 but lacks a paraconid, instead having a low, sloping paracristid enclosing a slight trigonid fovea. The protoconid is massive, low, and rounded. The metaconid is taller (as in M_1), and is also massive but somewhat more narrow buccolingually. The metaconid is double-cusped with a faint groove running down the lingual surface and a stronger groove extending down the buccal surface separating the cusplets. The talonid is as in M_1 except for some faint rugosity developed on the inner surfaces of the cristid obliqua and entocristid. There is no hypoconulid present so the talonid is open distally. M_2 has a slightly stronger proximobuccal cingulid and a slightly deeper hypoflexid than M_1.

The M_3 of *Amphipithecus* is only known from one specimen (NMMP 7). Unfortunately both the left and right M_3's in this specimen are worn and damaged, however some morphology can be discerned. M_3 lacks a paraconid. The entocristid is strong and low closing the talonid lingually
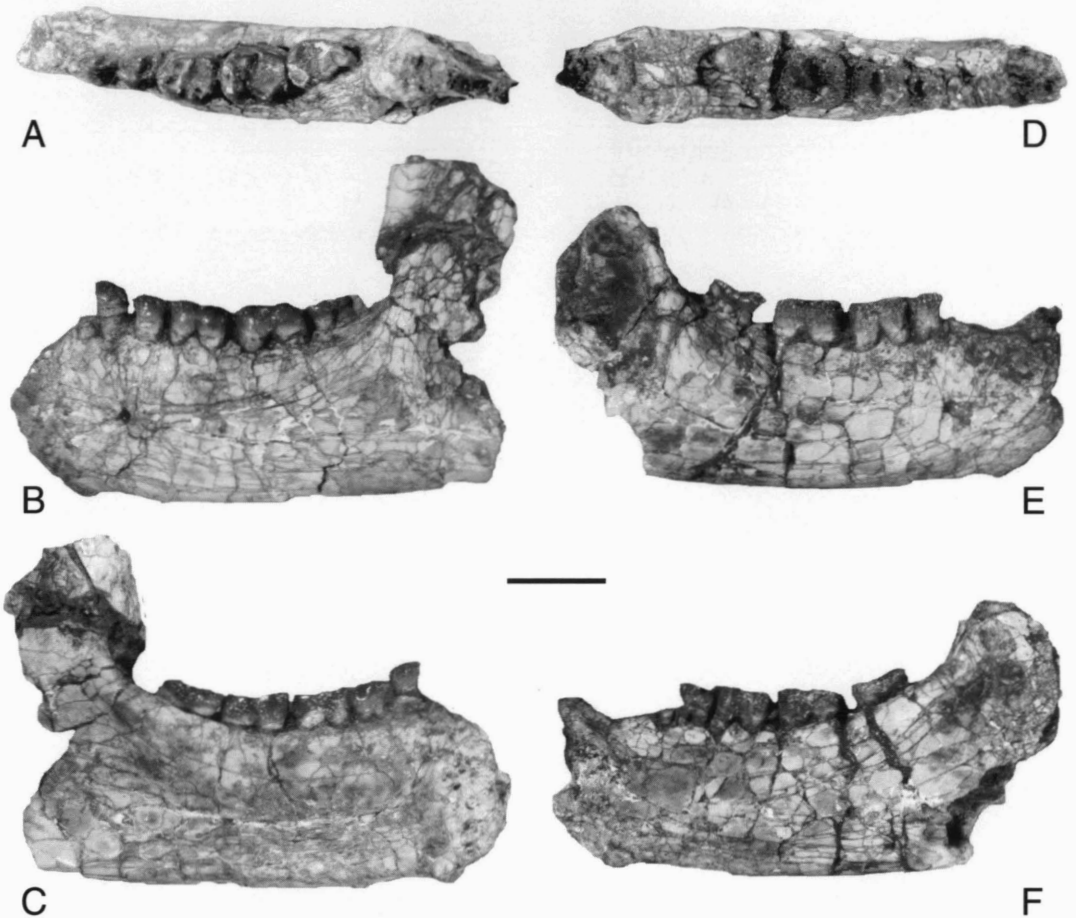
FIG. 21 — *Amphipithecus mogaungensis*. NMMP 7, left dentary with P_3-M_3 in occlusal (A), lateral (B), and medial (C) views; right dentary with P_4-M_3 in occlusal (D), lateral (E), and medial (F) views. Scale bar equals one centimeter.

(no talonid notch). The cristid obliqua is short, high, and massive. A proximobuccal cingulid is absent but the hypoflexid is somewhat more excavated than in M_{1-2} and has a small area of rugose enamel at its base. Talonid enamel is weakly crenulated as in M_2. Unlike *Pondaungia*, the M_3 of *Amphipithecus* is somewhat reduced compared to M_2.

Additional morphology. NMMP 7 preserves relatively complete dentaries of *Amphipithecus*. A lower dental formula of 2.1.3.3 can be confirmed. The canine is relatively large judging from the alveolus. P_2 is reduced and single-rooted. P_3 has a coalesced root on the buccal side but the root is bifurcate lingually while P_4 is double-rooted. The horizontal ramus has a small mental foramen beneath the posterior root of P_4 and a larger one beneath the posterior root of P_3. The symphysis was unfused and extends posteriorly to just beyond the posterior edge of the canine alveolus (Fig. 22C).

Frontals (Fig. 23). Two frontal bones (NMMP 19 and NMMP 27) potentially may represent *Amphipithecus*. NMMP 19 was found in close proximity to NMMP 18, the maxilla of *Amphipithecus* and could be associated with it. NMMP 27 was found at a different locality but matches the morphology of NMMP 19 closely.
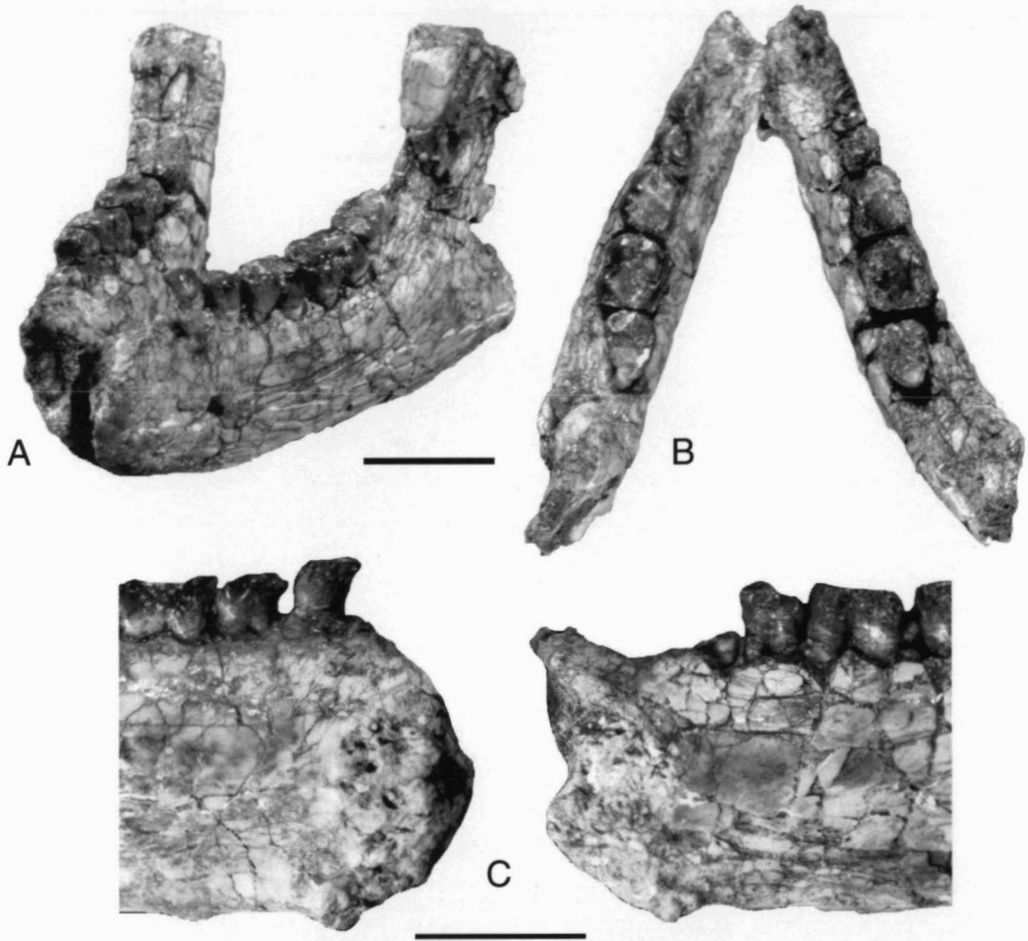
FIG. 22 — *Amphipithecus mogaungensis.* NMMP 7, left and right dentaries in left anterolateral (A) and occlusal (B) views; left and right symphyses in medial view (C). Scale bar equals one centimeter.

There is a limited amount of morphological detail preserved on these frontals. Neither frontal has a fused metopic suture and it is apparent from both specimens that whatever animals they represent, neither had postorbital closure. Postorbital constriction is relatively strong, similar to that seen in the European adapine *Adapis*, relatively stronger than in *Hesperolemur* and *Notharctus* (two North American notharctine adapiforms), and much stronger than in fossil anthropoids such as *Aegyptopithecus* or extant anthropoids like *Aotus* and *Saimiri* (Table 4). Only small portions of the superior orbital margins are preserved but it appears that the orbits were relatively anteriorly facing. Ventrally, both frontals indicate that the olfactory regions were relatively reduced. These last two features do suggest that both frontals may represent primates and could represent *Amphipithecus*.

As an interesting side note, NMMP 19 has clear evidence of a puncture wound on the dorsal surface of the frontal (Fig. 23B). The puncture mark is not inconsistent with having been produced by a crocodile tooth and adds some additional evidence in favor of at least occasional crocodile predation on Myanmar primates.
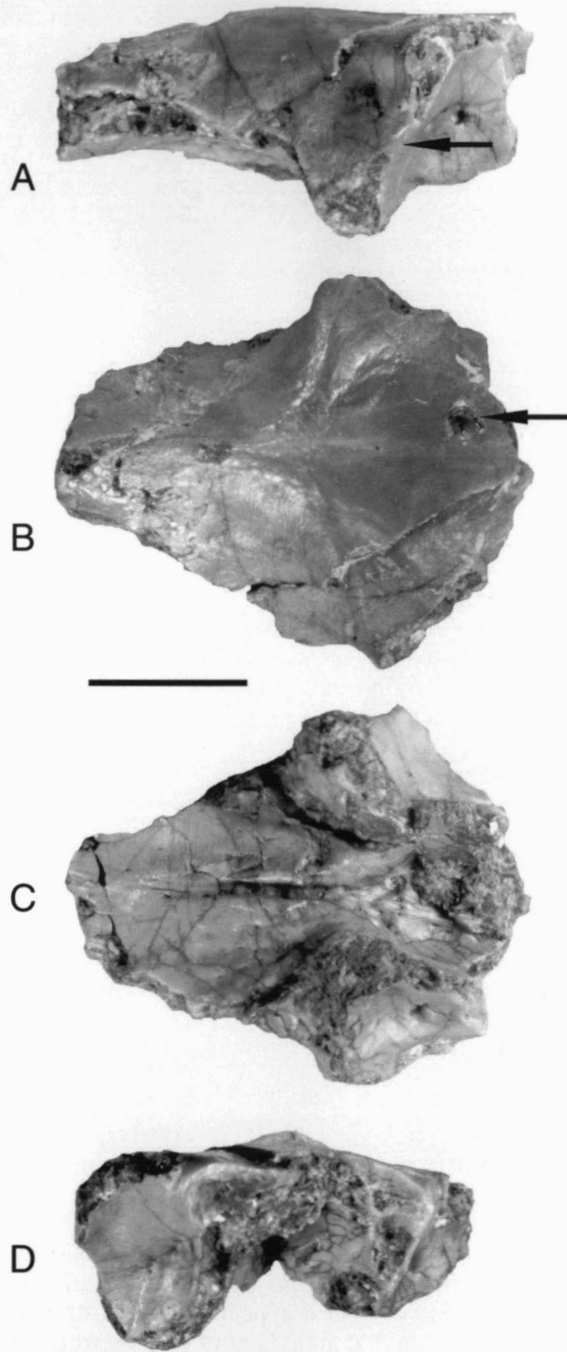
FIG. 23 — *Amphipithecus mogaungensis* (?). NMMP 19, frontal in lateral (A), dorsal (B), ventral (C), and anterior (D) views. Arrow in A points to continuous orbital margin indicating a lack of postorbital closure; arrow in B points to puncture wound. Scale bar equals one centimeter.

Table 4 — Breadth of postorbital constriction of braincase and postorbital constriction relative to M_1 length for *Amphipithecus mogaungensis* compared to that in other primate species. Measurements in mm. Note that the postorbital constriction in *Amphipithecus* is relatively narrow like that in adapoids and other prosimians, and not wide like that in *Aegyptopithecus* and other anthropoids.

Genus and species	Postorbital breadth	M_1 length	Postorbital breadth/ M_1 length
Amphipithecus mogaungensis	16.97	5.84	2.91
Adapis parisiensis	15.30	4.67	3.28
Hesperolemur actius	20.90	5.20	4.02
Smilodectes gracilis	21.22	4.72	4.50
Rooneyia viejaensis	20.59	4.56	4.52
Lemur sp.	30.82	5.99	5.15
Aegyptopithecus zeuxis	32.43	5.57	5.82
Saimiri sciurensis	29.28	3.00	9.76
Aotus trivirgatus	34.59	3.17	10.91

Tribe **Siamopithecini**, new

Diagnosis.— Differs from Pondaungini in having lingually distended upper molars, in having a more distinct and taller postprotocingulum on upper molars, P^4 buccolingually narrower with lingual shelf deeper and less extended, M_1 larger than M_2, P_{3-4} more rounded in occlusal outline, not as shortened anteroposteriorly, and much more robust relative to molars, and cheek tooth occlusal surfaces generally somewhat more complex with greater topographic relief.

Included genera.— *Siamopithecus*.

Discussion.— *Siamopithecus* remains enigmatic. In general, it resembles *Pondaungia* and *Amphipithecus* in having deep dentaries, robust but relatively short canines, generally low-crowned molars with reduced cusps, and loss of lower molar paraconids. However, in other features like the great lingual distension of the upper molars and the more robust upper and lower premolars, it appears distinctly different. We have included it in Pondaunginae pending more discoveries and further analysis.

ANTHROPOID STATUS OF PONDAUNGINAE

The taxonomic history of *Pondaungia* and *Amphipithecus* is relatively complex, in part because of the meager remains that represented these two taxa until recently. When originally described (Pilgrim, 1927), *Pondaungia* consisted of a single specimen with eroded and broken upper and lower molars. Pilgrim (1927) was uncertain of the relationships of *Pondaungia*, noting some resemblances with the North American and European notharctine *Pelycodus* (=*Cantius*) and with some fossil anthropoids. Pilgrim, citing the low, isolated molar cusps and broad basins, felt that the "nearest affinities" of *Pondaungia* were with anthropoids but that it was more primitive than the then known fossil anthropoids from the Fayum in Egypt (Pilgrim, 1927, p. 15).

Colbert (1937) described *Amphipithecus* based on a single dentary fragment containing P_3-M_1. In extensive comparisons between *Amphipithecus* and many fossil and extant primate taxa, Colbert (1937, 1938) argued that the closest affinities of *Amphipithecus* were with anthropoids, although he felt that *Amphipithecus* was more primitive than any other known form. He noted that *Amphipithecus* seemed to be quite different from *Pondaungia*, and was unable to determine what the relationships of the latter genus might be.

For the following 40 years, little of substance could be added to the discussions of Pilgrim (1927) and Colbert (1937, 1938) concerning *Pondaungia* and *Amphipithecus*. There were occa-

sional references to these two Burmese taxa (e.g. Le Gros Clark, 1959; Simons, 1963, 1965, 1971, 1972; Simons and Pilbeam, 1965; von Koenigswald, 1965; Van Valen, 1969; Szalay, 1970, 1972), but since no new material was available for study, these were limited, for the most part, to reinterpretation of their possible affinities. The situation began to change in 1978 with the discovery of new specimens of *Pondaungia* (Ba Maw et al., 1979) and *Amphipithecus* (Ciochon et al., 1985).

The new *Pondaungia* specimen (NMMP 1, originally described under the number UCMP 120377) was assigned to *P. cotteri* by Ba Maw et al. (1979) even though the authors acknowledged that it was difficult to compare the new, unworn specimen with the eroded holotype of that species. These authors argued, based on the new specimen, that *Pondaungia* (and *Amphipithecus*) were at or near the ancestry of anthropoids, while noting that it was possible that these two taxa represented adapoids or omomyids that had converged on an anthropoid-like dental morphology as suggested by Szalay (1970, 1972). Szalay and Delson (1979) in the same year suggested that *Amphipithecus* was a probable adapiform while *Pondaungia* might be a basal catarrhine.

Ciochon et al. (1985) described a new specimen of *Amphipithecus* (NMMP 2, referred to as DGMU-P1 in that paper). This specimen, along with NMMP 1 and two as yet then undescribed primate specimens (NMMP 3 and NMMP 4) were all found in 1978. Based on this new specimen, Ciochon et al. (1985) argued that *Amphipithecus* and *Pondaungia* had reached an anthropoid adaptive zone, perhaps intermediate between adapiforms and anthropoids.

After 1985, there was once again a relatively long hiatus before published reports on additional Pondaung Formation primates resumed. In 1994, Ciochon and Holroyd re-examined all of the available evidence for *Amphipithecus* and *Pondaungia* and suggested that *Pondaungia* should be recognized as a notharctine adapiform, placing it in a new tribe, Pondaungini. These authors also noted that the taxonomic position of *Amphipithecus* still remained vague. Kay and Williams (1994) in the same volume also concluded that there was not enough evidence to confidently resolve the affinities of *Amphipithecus*. Similarly, Kay and Williams (1994) noted that the taxonomic position of *Pondaungia* could not be resolved, although its most parsimonious position on their trees linked *Pondaungia* with adapiforms such as *Mahgarita* and *Cantius*.

Jaeger et al. (1998) described several specimens of *Pondaungia* and *Amphipithecus* including the two undescribed specimens found in 1978 (NMMP 3 and NMMP 4), along with three new specimens discovered by the Myanmar Pondaung Fossil Expedition Team in 1997. NMMP 3 is a left dentary of *Pondaungia* with M_{2-3} found at the same time from the same locality (Lema kyitchaung) as NMMP 1 and most likely represents the same individual as that specimen (see above). NMMP 4 is a heavily worn and eroded dentary with M_{1-3}, described as a new species of *Pondaungia* by Jaeger et al. (1998), but recognized as *P. cotteri* here. Other new specimens included a fragmentary and worn right dentition with M_{2-3} of *Pondaungia* (NMMP 5), a fragment of dentary containing an unworn M_{1-2} of *Amphipithecus* (NMMP 6), and associated left and right dentaries of *Amphipithecus* preserving left P_3-M_3 (NMMP 7) in relatively good condition and right P_4-M_3 in poor condition.

A phylogenetic analysis of all of these new specimens led Jaeger et al. (1998) to recognize a new anthropoid family, the Amphipithecidae, that included *Amphipithecus* and *Pondaungia* along with their sister taxon *Siamopithecus* from the late Eocene of Thailand (Chaimanee et al., 1997). This clade was the sister taxon to a clade consisting of the Fayum propliopithecine catarrhines *Aegyptopithecus*, *Propliopithecus*, and *Moeripithecus*, with the oligopithecines *Oligopithecus* and *Catopithecus* as the sister group to that clade. Recent papers by Tin Thein (1999), Chaimanee et al. (2000a, b), and Ducrocq (2001) have continued to support the anthropoid status of Amphipithecidae. However, Amphipithecidae is a junior synonym of Pondaungidae, raised from Pondaungini Ciochon and Holroyd (1994, p. 158).

Recent field work in the Pondaung Formation west of Mandalay has produced a number of new specimens of *Pondaungia* and *Amphipithecus*, including nearly complete lower dentitions of both taxa and the first well preserved remains of upper teeth (see above). Close examination of all specimens has led us to question the allocation of *Pondaungia* and *Amphipithecus* to Anthropoidea. Our evidence for questioning these allocations comes in three forms: a new phylogenetic analysis performed on all known specimens of Myanmar and Thailand primates; close examina-
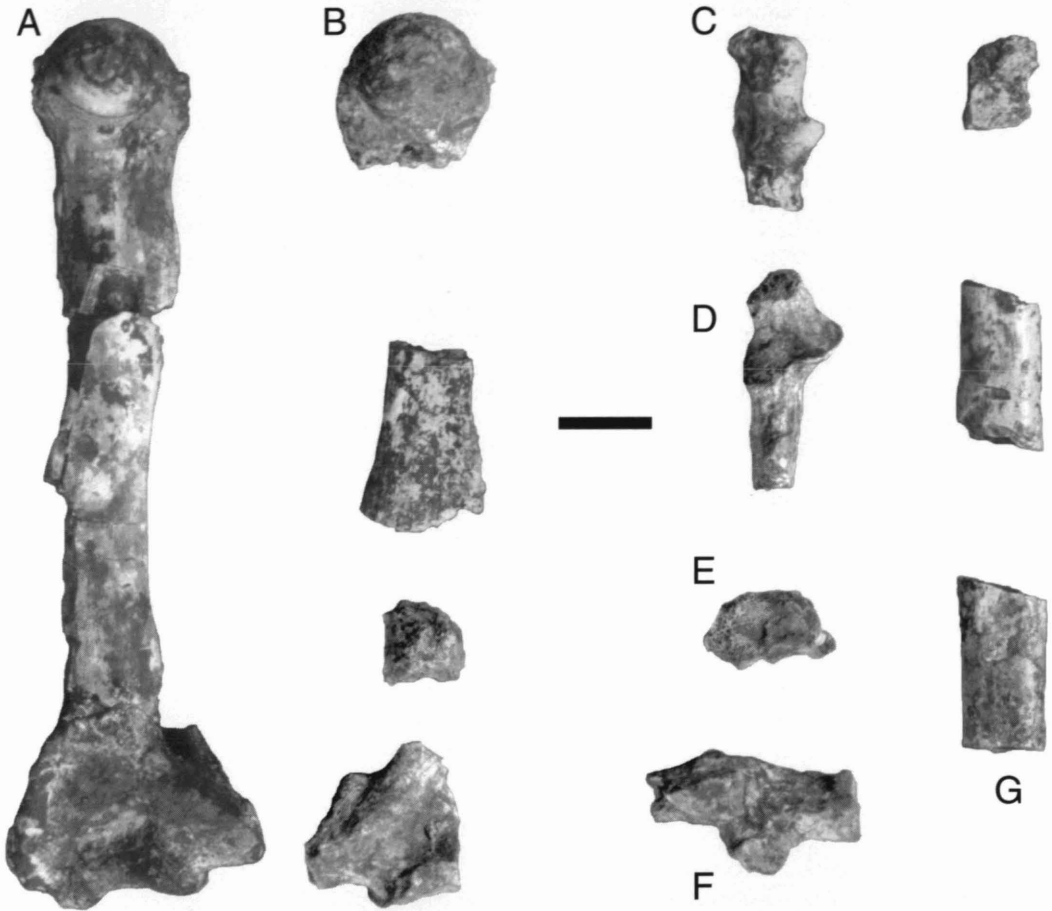
FIG. 24 — Postcrania of *Pondaungia savagei*. NMMP 20, left humerus in posterior view (A), fragmentary right humerus in posterior view (B), proximal right ulna in anterior view (C), proximal left ulna in anterior view (D), distal left calcaneum in distal (E) and dorsal (F) views, and associated long bone fragments (G). Scale bar equals one centimeter.

tion and comparison of the morphological details of dental anatomy; and new details of dental, cranial, and postcranial anatomy (Ciochon et al., 2001; Fig. 24) now available for the first time.

We performed a phylogenetic analysis based on 19 taxa and 22 dental, cranial, and postcranial characters as outlined in Tables 5 (character list) and 6 (matrix). We employed PAUP 4.1 and performed a heuristic search with 1000 replicates treating all characters as unordered and of equal weight under ACCTRAN optimization. Our resulting consensus tree is shown in Figure 25 (see figure caption for tree statistics). "Amphipithecids" are nested within a paraphyletic group consisting of the North American notharctine adapiforms *Hesperolemur*, *Notharctus*, and *Cantius*. This paraphyletic adapiform clade is the sister group to all included true anthropoids. Eosimiids (*Eosimias* and *Bahinia*) and *Afrotarsius* form a clade that is the sister group to the adapiform-anthropoid clade.

The results of our phylogenetic analysis led us to a close examination of all characters including those that have been used to unite a monophyletic Amphipithecidae with Anthropoidea (Jaeger et al., 1998; Chaimanee et al., 2000a, b). Among these characters are: (1) deep, heavy dentaries; (2) symphysis deep and heavy; (3) cheek teeth low crowned and bunodont, often with crenulations; (4) anterior dentary shortened with crowded anterior cheek teeth; (5) lower premolars short

Table 5 — Morphological characteristics of primates and their character coding used in phylogenetic analysis. Character matrix is shown in Table 6.

Number	Characteristic and coding
1.	Postorbital closure— absent (0); complete (1).
2.	Metopic suture— open (0); fused (1).
3.	Lacrimal foramen— outside orbit (0); within orbit (1).
4.	Incisors— incisiform (0); small, extremely vertical, incipiently spatulate (1); small, subvertical, spatulate (2); large, subvertical, spatulate (3).
5.	Canines— projecting, ?dimorphic (0); projecting, dimorphic (1); projecting, honing, dimorphic (2).
6.	P_2— as large as P_3 (0); smaller than P_3 (1); larger than P_3 (2); absent (3).
7.	P_4— not exodaenodont, not obliquely oriented (0); not exodaenodont, oblique (1); exodaenodont; not oblique (2); exodaenodont, oblique (3).
8.	P_3— premolariform (0); semimolariform (1); narrow, blade-like (2).
9.	P_4 metaconid— low, distolingual, not connected to protoconid (0); intermediate, lingual, not connected to protoconid (1); higher, lingual, connected to protoconid (2); higher, distolingual, not connected (3); absent (4); pillar-like (5).
10.	P_4— premolariform (0); semimolariform (1); blade-like (2).
11.	Cheek teeth— non-bunodont (0); bunodont, not cuspate (1); bunodont, cuspate (2).
12.	M_{1-2}— heterodont with paraconid (0); heterodont, paraconid reduced to absent (1); homodont without paraconid (2); homodont with paraconid (3).
13.	Lower molar paraconids— small, present on all molars (0); small, absent on M_{2-3} (1); larger, present on all molars (2); tiny to absent on all molars (3).
14.	M_{1-2} hypoconulids— centered (0); lingual or twinned (1), absent (2).
15.	Lower molar accessory cusps— absent (0); present (1).
16.	Upper molars— hypocone absent (0); small, cingular hypocone (1); larger, cingular hypocone (2); pseudohypocone (3).
17.	Upper molars— with small paraconule and metaconule (0); conules absent (1); metaconule only (2); large paraconule and metaconule (3).
18.	M_3 size— M_3 equivalent in size to M_2 (0); M_3 reduced (1).
19.	Mandibular symphysis— shallow (0); deep, unfused (1); deep, fused (2).
20.	Humeral capitulum— flattened (0); rounded (1); cylindrical (2).
21.	Humeral trochlea— medial lip only (0); medial and lateral lip (1).
22.	Humeral trochlear gutter— absent (0); present (1).

and broad, often appearing skewed; and (6) lower molars with trigonid and talonid subequal in height.

We have examined dental morphology in several taxa of Fayum anthropoids, including *Apidium, Parapithecus, Qatrania, Catopithecus, Oligopithecus, Proteopithecus, Propliopithecus,* and *Aegyptopithecus,* and have documented the following character states: (1) cheek teeth are cuspate with occlusal surfaces forming complex topographical patterns; (2) cheek tooth cusps are basally inflated, bulbous, and set internally away from tooth margins; (3) talonid basins are relatively narrow; (4) tooth rows are flat and angled posteriorly (especially in more derived forms); (5) the ascending ramus is broad where known; and (6) mandibles are relatively shallow in primitive forms while more derived forms have the anterior part of the mandible deeper than the posterior part.

In contrast to the character states shown in Fayum anthropoids, pondaungines have the following: (1) cheek teeth with weakly developed cusps and simple occlusal surfaces (except for enamel crenulation in *Pondaungia*); (2) cheek teeth have basally inflated crowns, noninflated cusps, and cusps are set at the margins of the teeth; (3) talonid basins are wide and flat; (4) cheek tooth rows are concave; (5) the ascending ramus is broad where known; (6) mandibles are equally deep throughout.

We believe that, while there is a general similarity in tooth and mandibular structure between Fayum anthropoids and Southeast Asian pondaungines, differences in detail suggest that shortened faces, crowded anterior premolars, enlarged cheek tooth crushing surfaces, and deep, heavy
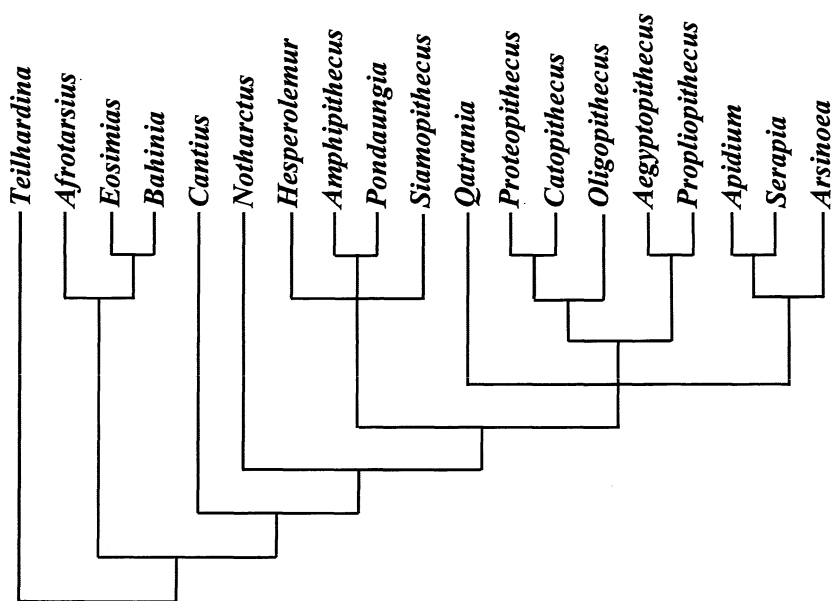
FIG. 25 — Fifty-percent-majority-rule consensus phylogenetic tree based on a branch and bound analysis of 19 taxa and 22 dental, cranial, and postcranial characters (see Tables 5 and 6). Results based on 36 equally parsimonious trees of 64 steps. CI = 0.688, RI = 0.756, HI = 0.312 (PAUP 4.1).

Table 6 — Matrix of character codings for primates used in phylogenetic analysis here. Characters listed by number are described more fully in Table 5.

Taxon	Character number																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Teilhardina	?	?	?	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	?	?	?
Arsinoea	?	?	?	2	0	0	3	0	0	1	2	0	1	1	0	?	?	1	1	?	?	?
Proteopithecus	1	1	1	2	0	2	3	0	3	1	0	1	1	1	0	1	0	1	0	2	0	0
Serapia	?	?	?	?	0	2	2	0	3	1	2	1	1	1	0	?	?	1	1	?	?	?
Qatrania	?	?	?	?	?	?	2	?	0	1	2	1	1	0	1	?	?	1	1	?	?	?
Apidium	1	1	1	3	1	2	2	1	0	1	2	2	3	0	1	2	3	1	1	2	0	0
Catopithecus	1	1	1	2	1	3	2	2	2	1	0	1	1	1	0	0	1	0	1	2	0	0
Oligopithecus	?	?	?	?	1	3	3	2	2	1	0	1	1	1	0	0	1	?	1	?	?	?
Propliopithecus	?	?	?	3	2	3	3	2	2	1	2	1	3	0	0	2	1	0	2	2	0	0
Aegyptopithecus	1	1	1	3	2	3	3	2	2	1	2	1	3	0	0	2	1	0	2	2	0	0
Eosimias	?	?	?	1	0	1	1	0	0	0	0	3	2	0	0	0	1	0	1	?	?	?
Bahinia	?	?	?	1	0	1	1	0	4	0	0	?	2	0	0	0	1	?	?	?	?	?
Afrotarsius	?	?	?	?	?	?	?	0	?	?	0	3	2	0	0	?	?	1	?	?	?	?
Siamopithecus	?	?	?	?	0	1	2	0	1	1	1	1	3	0	0	3	1	0	1	?	?	?
Pondaungia	?	?	?	2	0	1	2	0	5	1	1	1	1	2	0	3	1	0	1	1	1	1
Amphipithecus	0	0	?	?	0	?	2	0	5	1	1	1	1	2	0	3	1	1	1	?	?	?
Hesperolemur	0	0	1	?	?	?	?	?	?	?	1	?	1	?	0	3	?	0	?	?	?	?
Cantius	0	0	0	2	1	1	0	0	0	0	0	0	0	0	0	3	0	0	0	1	1	1
Notharctus	0	0	0	2	1	1	0	0	1	1	0	0	1	0	0	3	0	0	1	1	1	1

dentaries can all be explained as functional convergences in response to a diet dominated by hard objects and tough-skinned fruits (Gunnell and Ciochon, in preparation). The very heavy tooth wear exhibited by a number of pondaungine specimens (see NMMP 18 and NMMP 24 for example) attests to a diet rich in hard or tough food objects.

Additional anatomical details of pondaungine dentitions and cranial elements also argue against inclusion in Anthropoidea. As noted above, the two possible *Amphipithecus* frontal bones (NMMP 19 and NMMP 27) lack metopic suture fusion and NMMP 19 clearly lacked postorbital closure (see Fig. 23A). While the absence of these two traditional hallmarks of Anthropoidea does not preclude pondaungines from inclusion in a stem-based definition of anthropoids, it does indicate that pondaungines remained distinctly primitive in their cranial anatomy—especially for animals that have been suggested to be so derived towards anthropoids in their dental anatomy or to phylogenetically nest within them. A third character state that seems to unite known Fayum anthropoids is the presence of a lower second incisor that is as large or larger than the lower central incisor. This character state is true of all extant anthropoids as well. NMMP 24 is a specimen of *Pondaungia* that preserves the alveoli for I_{1-2}. While alveolar size can sometimes be misleading, it is clear that *Pondaungia* had a much larger I_1 alveolus than I_2 alveolus, suggesting that in this particular character state, *Pondaungia* is more like some omomyid primates rather than adapiforms or anthropoids. Given all other evidence, this trait simply may represent an autapomorphy of *Pondaungia*.

An additional piece of evidence against pondaungine anthropoid affinities comes from some recently described postcranial elements of a large-bodied primate from the Pondaung Formation (Ciochon et al., 2001). This specimen (NMMP 20) was collected in 1997 and consists of a complete left humerus, the distal half of a left calcaneum, and fragments of a right humerus and left and right ulnae (Fig. 24). It was assigned to *Pondaungia savagei* based on size and association, but could conceivably represent *Amphipithecus* as well. The complete humerus is virtually identical to that of the North American notharctine *Notharctus* in every detail (Fig. 24), while the calcaneum is a mixture of notharctine and adapine features. In no derived character state do any of these postcranial elements more closely resemble anthropoids than notharctines.

Combining our phylogenetic analysis with our re-assessment of dental, cranial, and postcranial anatomy suggests to us that *Pondaungia* and *Amphipithecus* (and by extension *Siamopithecus*) represent relatively large-bodied adapiform primates that share similar dental morphology to anthropoids because of the types of foods they chose, not because they share any recent common ancestry. There is no evidence for large-bodied anthropoids in Asia before the Miocene and we suspect that in the Eocene adapiforms filled this ecomorphospace (Gunnell and Ciochon, 2001). The presence of pondaungines and a broad radiation of sivaladapines suggests that adapiforms were the dominant large-bodied primates in Asia before hominoids and cercopithecoids arrived in the Miocene.

ACKNOWLEDGMENTS

LITERATURE CITED

AYE KO AUNG. 1999a. Additional findings of the Pondaung primates. Proceedings of the Pondaung Fossils Expedition Team, 1999: 179-193.

———. 1999b. Revision on the stratigraphy and age of the primates-bearing Pondaung Formation. Proceedings of the Pondaung Fossils Expedition Team, 1999: 131-151.

BA MAW, R. L. CIOCHON, and D. E. SAVAGE. 1979. Late Eocene of Burma yields earliest anthropoid primate, *Pondaungia cotteri* . Nature, 282: 65-67.

BERGGREN, W. A., D. V. KENT, C. C. SWISHER, and M.-P. AUBRY. 1995. A revised Cenozoic geochronology and chronostratigraphy. In W. A. Berggren, D. V. Kent, M.-P. Aubry, and J. A. Hardenbol (eds.), Geochronology, Time Scales and Global Stratigraphic Correlations: A Unified Temporal Framework for an Historical Geology, Society of Economic Paleontologists and Mineralogists, Special Volume, Tulsa, 54: 129-212.

CHAIMANEE, Y., S. KHANSUBHA, and J.-J. JAEGER. 2000. A new lower jaw of *Siamopithecus eocaenus* from the Late Eocene of Thailand. Comptes Rendus de l'Académie des Sciences, Paris, 323: 235-241.

———, V. SUTEETHORN, J.-J. JAEGER, and S. DUCROCQ. 1997. A new late Eocene anthropoid primate from Thailand. Nature, 385: 429-431.

———, T. THEIN, S. DUCROCQ, A. N. SOE, M. BENAMMI, T. TUN, T. LWIN, S. WAI, and J.-J. JAEGER. 2000. A lower jaw of *Pondaungia cotteri* from the late middle Eocene Pondaung Formation (Myanmar) confirms its anthropoid status. Proceedings of the National Academy of Sciences USA, 97: 4102-4105.

CIOCHON, R. L., P. D. GINGERICH, G. F. GUNNELL, and E. L. SIMONS. 2001. Primate postcrania from the late middle Eocene of Myanmar. Proceedings of the National Academy of Sciences USA, 98: 7672-7677.

——— and P. A. HOLROYD. 1994. The Asian origin of Anthropoidea revisited. In J. G. Fleagle and R. F. Kay (eds.), Anthropoid Origins, Plenum Press, New York, pp. 143-162.

———, D. E. SAVAGE, T. TINT, and B. MAW. 1985. Anthropoid origins in Asia? New discovery of *Amphipithecus* from the Eocene of Burma. Science, 229: 756-759.

COLBERT, E. H. 1937. A new primate from the upper Eocene Pondaung Formation of Burma. American Museum Novitates, 951: 1-18.

———. 1938. Fossil mammals from Burma in the American Museum of Natural History. Bulletin of the American Museum of Natural History, 74: 255-436.

DUCROCQ, S. 2001. Palaeogene anthropoid primates from Africa and Asia: new phylogenetical evidences. Comptes Rendus de l'Académie des Sciences, Sciences de la Terre et des Planètes, Paris, 332: 351-356.

FISHER, D. C. 1981a. Mode of preservation of the Shotgun Local Fauna (Paleocene, Wyoming) and its implication for the taphonomy of a microvertebrate concentration. Contributions from the Museum of Paleontology, University of Michigan, 25: 247-257.

———. 1981b. Taphonomic interpretations of enamel-less teeth in the Shotgun Local Fauna (Paleocene, Wyoming). Contributions from the Museum of Paleontology, University of Michigan, 25: 259-275.

FRANZEN, J. L. 1988. Ein weiterer Primatenfund aus der Grube Messel bei Darmstadt. Courier Forschungsinstitut Senckenberg, 107: 275-289.

———. 1997. Ein Koprolith als Leckerbissen: der siebte Primatenfund aus Messel. Natur und Museum, Frankfurt, 126: 262-266.

——— and E. FREY. 1993. Europolemur completed. Kaupia, 3: 113-130.

GUNNELL, G. F. and R. L. CIOCHON. 2001. Anthropoid ecomorphs and convergence: are there any higher primates from the Eocene of Asia? (abstract). Journal of Vertebrate Paleontology, Supplement to Number 3, 21: 57A.

HLA MON. 1999. Nannopaleontological analysis of the rock samples collected by the Pondaung fossils expedition team. Proceedings of the Pondaung Fossils Expedition Team, 1999: 94-104.

HOLROYD, P. A. and R. L. CIOCHON. 1994. Relative ages of Eocene primate-bearing deposits of Asia. In J. G. Fleagle and R. F. Kay (eds.), Anthropoid Origins, Plenum Press, New York, pp. 123-141.

HUTCHISON, J. H. and P. A. HOLROYD. 1996. Preliminary report on the lower vertebrate fauna of the late middle Eocene Pondaung sandstones (abstract). Journal of Vertebrate Paleontology, Supplement to Number 3, 16: 43A.

JAEGER, J.-J., AUNG NIANG SOE, AYE KO AUNG, M. BENAMMI, Y. CHAIMANEE, R.-M. DUCROCQ, THAN TUN, TIN THEIN, and S. DUCROCQ. 1998. New Myanmar middle Eocene anthropoids: an Asian origin for catarrhines? Comptes Rendus de l'Académie des Sciences, Sciences de la Vie, Paris, 321: 953-959.

————, TIN THEIN, M. BENAMMI, Y. CHAIMANEE, AUNG NIANG SOE, THIT LWIN, THAN TUN, SAN WAI, and S. DUCROCQ. 1999. A new primate from the middle Eocene of Myanmar and the Asian early origin of anthropoids. Science, 286: 528-530.

KAY, R. F. and B. A. WILLIAMS. 1994. Dental evidence for anthropoid origins. In J. G. Fleagle and R. F. Kay (eds.), Anthropoid Origins, Plenum Press, New York, pp. 361-445.

KOENIGSWALD, G. H. R. V. 1965. Critical observations upon the so-called higher primates from the upper Eocene of Burma. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B, 68: 165-167.

LE GROS CLARK, W. E. 1959. The Antecedents of Man. An Introduction to the Evolution of the Primates. Quadrangle Books, Chicago, 394 pp.

PILGRIM, G. E. 1927. A *Sivapithecus* palate and other primate fossils from India. Palaeontologia Indica, New Series, 14: 1-26.

SIMONS, E. L. 1963. A critical reappraisal of Tertiary primates. In J. Buettner-Janusch (ed.), Evolutionary and Genetic Biology of Primates, Volume 1, Academic Press, New York, pp. 65-129.

————. 1965. New fossil apes from Egypt and the initial differentiation of Hominoidea. Nature, 205: 135-139.

————. 1971. Relationships of *Amphipithecus* and *Oligopithecus*. Nature, 232: 489-491.

————. 1972. Primate Evolution: An Introduction to Man's Place in Nature. The Macmillan Company, New York, 322 pp.

———— and D. R. PILBEAM. 1965. Preliminary revision of the Dryopithicinae (Pongidae, Anthropoidea). Folia Primatologica, 3: 81-152.

SZALAY, F. S. 1970. Late Eocene *Amphipithecus* and the origins of catarrhine primates. Nature, 227: 355-357.

————. 1972. *Amphipithecus* revisited. Nature, 236: 5343.

———— and E. DELSON. 1979. Evolutionary History of the Primates. Academic Press, New York, 580 pp.

TAKAI, M., N. SHIGEHARA, AYE KO AUNG, SOE THURA TUN, AUNG NAING SOE, T. TSUBAMOTO, and TIN THEIN. 2001. A new anthropoid from the latest middle Eocene of Pondaung, central Myanmar. Journal of Human Evolution, 40: 393-409.

————, ————, T. TSUBAMOTO, N. EGI, AYE KO AUNG, TIN THEIN, AUNG NAING SOE, and SOE THURA TUN. 2000. The latest middle Eocene primate fauna in Pondaung area, Myanmar. Asian Paleoprimatology, Kyoto, 1: 7-28.

THET WAI. 1999. Palynological analysis of the rock samples collected by the Pondaung fossils expedition team. Proceedings of the Pondaung Fossils Expedition Team, 1999: 112-121.

TIN THEIN. 1999. The primates of Pondaung: probably the earliest anthropoid primates. Proceedings of the Pondaung Fossils Expedition Team, 1999: 35-58.

TSUBAMOTO, T. 2000. The Pondaung mammal fauna: an analysis of terrestrial mammal fauna in the latest middle Eocene of central Myanmar (southeast Asia). Ph.D. dissertation, Kyoto University, Kyoto,

VAN VALEN, L. M. 1969. A classification of the primates. American Journal of Physical Anthropology, 30: 295-296.