

A lower jaw of *Pondaungia cotteri* from the Late Middle Eocene Pondaung Formation (Myanmar) confirms its anthropoid status

Yaowalak Chaimanee*, Tin Thein†, Stéphane Ducrocq‡, Aung Naing Soe§, Mouloud Benammi‡, Than Tun¶, Thit Lwin§, San Wai¶, and Jean-Jacques Jaeger*||

*Department of Mineral Resources, Geological Survey Division, Paleontological Section, Rama VI Road, Bangkok 10400, Thailand; †Institut des Science de l'Évolution, Université Montpellier-II, Centre National de la Recherche Scientifique, 064, 34095 Montpellier Cedex 5, France; ‡Department of Geology, University of Patheingyi, Patheingyi, Myanmar; §Geology Department, University of Yangon, Yangon, Myanmar; and ¶Office of Strategic Studies, Ministry of Defense, Yangon, Myanmar

Communicated by F. Clark Howell, University of California, Berkeley, CA, January 20, 2000 (received for review June 1, 1999)

Pondaungia cotteri is the largest primate known from the Late Middle Eocene Pondaung Formation, Myanmar. Its taxonomic status has been the subject of much debate because of the fragmentary nature of its remains. Initially described as an anthropoid, some authors recently have associated it with adapid primates. These debates have been fueled not only by the incompleteness of the fossils attributed to *Pondaungia* but also by the reticence of many authors to regard Asia as an important evolutionary theater for Eocene anthropoids. During the November 1998 Myanmar-French Pondaung Expedition, a right lower jaw was discovered that yields the most nearly complete dentition of *Pondaungia cotteri* ever found: it shows the complete horizontal ramus, alveoli for the second incisor and canine, three premolars, and three molars. The symphysis showed all characteristics of anthropoids but was unfused. The canine root is large, the first premolar is absent, and the second premolar is single-rooted, reduced, and oblique in the tooth row, as in anthropoids. The premolars show a reduced mesio-distal length compared with the tooth row, and their morphology is very similar to that of *Amphipithecus mogaungensis*. Therefore, the two Pondaung taxa appear to be closely related to each other, with *Siamopithecus* as their sister taxon.

The first specimens of *Pondaungia cotteri* were discovered in 1914 by Cotter near Pangan village in Myaing Township, Pakokku District of central Myanmar and were first described by Pilgrim in 1927 (1). They consist of a fragment of left lower jaw with M/2–M/3 [holotype, Geological Survey of India (GSI) D201], a left maxilla fragment with M/1–M/2 (GSI D203), and a fragment of right lower jaw with M/3 (GSI D202). Later, a right lower jaw fragment with M/2–M/3 [University of California Museum of Paleontology 120377 = National Museum of Myanmar (Primate) (NMMP) 1] was discovered near Mogaung Village (2). Two additional specimens of *P. cotteri* subsequently were discovered near Mogaung Village: a fragment of left lower jaw with M/2–M/3 (NMMP 3) and a right lower jaw fragment with very worn M/2–M/3 (NMMP 5) (3). NMMP 3 and NMMP 5 are identical, originate from the same site, and probably belonged to the same individual. Nevertheless, no anterior dentition previously has been found that could substantiate the phylogenetic status of this taxon. The nearly complete right lower jaw (NMMP 17) was recovered from Thandaung locality, 1.5 miles northwest of Mogaung Village. We describe it here, especially its premolars and symphysis, and confirm the anthropoid affinities of this genus.

Systematics

Order Primates Linnaeus, 1758; Suborder Anthroidea Mivart, 1864; Family Amphipithecidae, Jaeger *et al.*, 1998; *Pondaungia cotteri* Pilgrim 1927.

NMMP 17 (Fig. 1) is a right lower jaw with complete horizontal ramus and the beginning of the vertical ramus, bearing alveoli for the second incisor and canine, three complete premolars, and three molars. The second and third molars are similar to *P. cotteri* (NMMP 1, 3, and 5) in morphology and size (2, 3); therefore, NMMP 17 is referred to as that species.

The jaw is massive with an extremely robust horizontal ramus, a deep mandibular corpus, and a thick superior mandibular torus. In lateral view, the horizontal branch displays a gently convex lower border that is parallel to the occlusal surface. The concave occlusal surface indicates a convex upper tooth row. The depth of the horizontal branch shows nearly the same value under P/4 as under M/3 (Table 1). The small mental foramen opens at the level between P/2 and P/3, midway between the alveolar margin and ventral side of the jaw. The masseteric fossa is deep and limited by strong superior and inferior masseteric ridges. The superior masseteric ridge is nearly vertical to the base of the jaw (70°). A retromolar space is developed, which is rather wide labio-lingually and extended labially.

The symphysis is large and was unfused. It is rather vertical with a planum alveolare sloping with an angle of about 60° until the level of P/4. The superior torus is extremely developed and strong, whereas the genioglossal notch is extremely deep and narrow. The inferior torus is also strong but less so than the superior torus. On the inferior side of the horizontal ramus, there is strong development of the digastric notches just behind the symphysis. These characters, with the exception of the unfused symphysis, are usually found among more derived Anthroidea.

In occlusal view, the dental arcade shows a strong parabolic shape. Three premolars are present that show a morphology similar to those of *Amphipithecus*. The total mesio-distal length of the three premolars comprises only 30% of the premolar–molar length. Molar crowns are low and massive.

I/2. The anterior portion of the mandible is broken. The only available evidence is the distal part of I/2 alveolus, which shows that it had a wide, vertical root with a transverse diameter of 4.3 mm at its upper observable limit.

Canine. The canine crown is broken away. From its outline in the jaw, it appears to have been large and oval in cross-section. Its long axis is oriented obliquely to the tooth row.

Abbreviations: GSI, Geological Survey of India; NMMP, National Museum of Myanmar (Primate).

||To whom reprint requests should be addressed. E-mail: jaeger@isem.univ-montp2.fr.

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

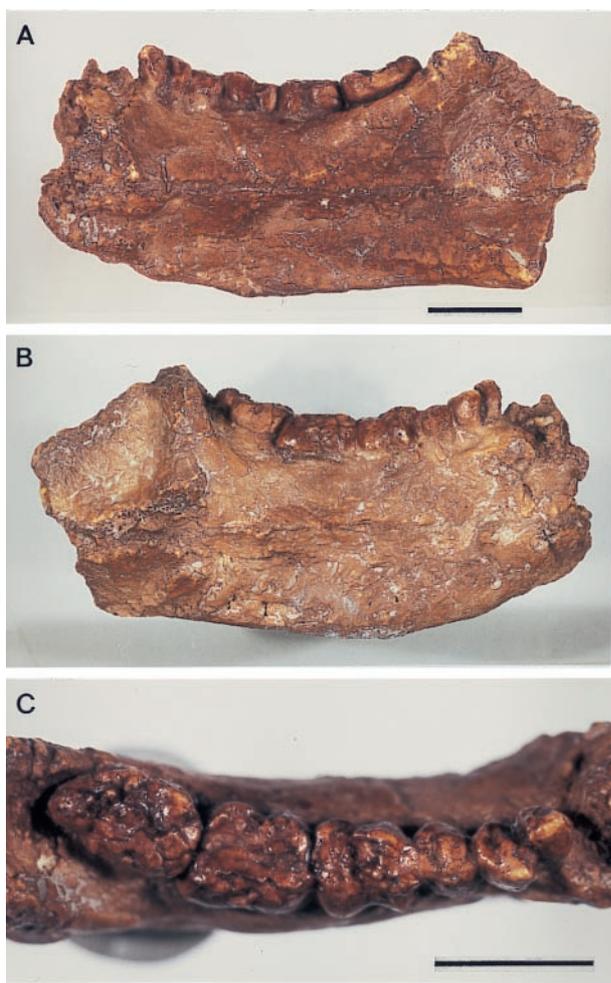


Fig. 1. Lingual (A), labial (B), and occlusal view (C) of *P. cotteri* (NMMP 17). (Scale bar, 1 cm.)

Premolars. P/1 is absent. The morphology of the three premolars is quite distinctive. They are mesio-distally short, labio-lingually wide, and obliquely oriented with respect to the tooth row. This extends the disto-lingual portion of each tooth lingually. Their crowns are as high as those of the molars. Paraconids are absent. Their trigonids are shorter and reduced mesio-distally when compared with those of *Amphipithecus*.

P/2 is the smallest of the premolars with only one root, which is strongly elongated obliquely, as is the crown. In occlusal view, P/2 shows an oval outline, with a steep labial wall. A high and dominant protoconid and a very short but elevated preprotocristid constitute its summit. There is neither a lingual nor a labial

cingulid. The tooth is slightly exodaenodont (swelling of the crown basis), as all premolars and molars. The protoconid is connected by a small disto-lingual crest to the hypoconid, which is small and low. The lingual slope of the protoconid runs gently toward the base of the crown. There is no metaconid.

P/3 is distinctly larger than P/2 with a large and high protoconid. It has an oval outline in occlusal view and is strongly oblique, with the mesio-labial part of the crown extended labially. There is neither a labial nor a lingual cingulid. The metaconid is low and located lingual to the protoconid. A shallow protocristid connects these two cusps. The preprotocristid is extremely short and mesially directed. A distal crest connects the protoconid to the hypoconid. The hypoconid is low and situated at the distal end of the crown, halfway along the crest from the protoconid. This crest is weaker than the protocristid, limits the distal part of the talonid basin, and is gently curved, running down the disto-lingual base of the crown where it becomes nearly transversely oriented. The talonid basin is narrow and situated between this crest and the protocristid. Its labial side is high and its disto-lingual extremity is largely open. P/3 has two labial and one lingual root. The antero-labial is extended mesio-labially and the lingual one is extended disto-lingually.

P/4 is larger than P/3 but also mesio-distally shorter than wide. Its outline is also broadly oval with a long axis oriented obliquely relative to the tooth row. The metaconid is nearly as large and as elevated as the protoconid. Both cusps are connected by a short and broad protocristid. The preprotocristid is very short and mesially oriented. The trigonid basin is not developed and there is no paraconid. The talonid is mesio-distally short and labio-lingually wide. The hypoconid is stronger than that of P/3 and linked to a small entoconid that develops at the lingual end of the crest issued from the hypoconid. The talonid basin is open lingually. There is neither a labial nor a lingual cingulid, and the roots are oriented obliquely as are those of P/3.

Molars. There are three molars, of which the second is the largest. They show a waisted outline as in other *Amphipithecidae* and some African *Parapithecidae*. The trigonid and talonid have nearly equal heights.

M/1 has a strongly waisted outline between trigonid and talonid. The trigonid is longer mesio-distally than the talonid. It shows two main cusps, protoconid and metaconid, with the metaconid being displaced more distally. There is a strongly developed spur-like structure that is worn obliquely on the anterior part of the occlusal surface and that slopes down toward P/4. It consists of the preprotocristid and the anterior cusp of the duplicated metaconid. There is a strongly developed entocristid. The entoconid is more distal than the hypoconid. No distinct hypoconulid can be observed on M/1.

M/2 has a rectangular outline. The trigonid shows about the same mesio-distal length as the talonid. The protoconid is rather large and connected to the metaconid. The entoconid is slightly more distal than the hypoconid and weaker than on M/1.

M/3 is rather large with a long talonid basin. Its convex lingual wall is rather characteristic. The entoconid is reduced. The hypoconulid is rather large.

Both M/2 and M/3 show weakly crenulated enamel on their occlusal surfaces and shallow and discontinuous labial cingulids. Metaconid duplication cannot be observed on M/2 and M/3. Observable characters are similar to those of the other fossils attributed to this species.

Comparisons

This lower jaw of *P. cotteri* shows all of the anthropoid characters already specified in the diagnosis of the family *Amphipithecidae* (also including *Amphipithecus* and *Siamopithecus*), as proposed by Jaeger *et al.* (3). For instance, the occurrence of only three premolars that are oriented obliquely, with a single-rooted P/2, a strong lingual metaconid on P/3 and P/4, a labially salient

Table 1. Dental measurements (mm) of *Pondaungia cotteri* (NMMP 17)

	Length	Width
P/2	3.03	3.79
P/3	3.28	4.50
P/4	3.36	4.71
M/1	6.73	5.44 (trigonid) 5.80 (talonid)
M/2	7.65	6.42 (trigonid) 6.50 (talonid)
M/3	8.83	5.89 (trigonid) 5.50 (talonid)

Length of M/1–M/3, 21.72; Length of P/2–M/3, 30.86. Depth of mandible under P/4, 18.20. Depth of mandible under M/3, 19.92.

mesio-labial root of P/3 and P/4, and exodaenodonta are typical anthropoid characters, as indicated by Beard *et al.* (4, 5). Additional anthropoid characters of *Pondaungia* have been indicated previously (3, 6). Therefore, the discovery of the premolars and symphysis of this genus fully corroborates its anthropoid status. The symphyses of the three Southeast Asian taxa are unfused but share a similar anthropoid structure (7). The strong similarity in the premolar structure between *Pondaungia* and *Amphipithecus* is rather unexpected. It suggests close phylogenetic relationships between these two taxa, closer than that between *Pondaungia* and *Siamopithecus*, as previously indicated on the basis of the strong resemblance between the M/3 of these two last forms (6). Another peculiar character is the strong parabolic shape of the dental arcade. This shape also is found in the two other genera of Amphipithecidae but is less developed than in *Pondaungia*. Also, the strong concavity of the tooth row in lateral view is an additional character shared by Amphipithecidae. The adaptive meaning of these two characters is unclear but may be related to the great robusticity of the masticatory structures and the shortening of the jaws.

***P. cotteri* and *Amphipithecus mogaungensis*.** *P. cotteri* seems to have been larger than *Amphipithecus*. The expected body weight, extrapolated from M/1 dimensions, is about 8,500 g (8) to 9,000 g (9) for *P. cotteri*, according to the correlation used, and 7,600 g for *Amphipithecus* (NMMP 7) (9). The horizontal ramus in *Amphipithecus* is smaller and lower than that of *Pondaungia*. Both taxa show parabolic tooth rows and reduced premolar lengths compared with molar length. However, degree of premolar reduction is stronger in *Pondaungia* than in *Amphipithecus*. Premolar preprotocristid length is more reduced in *Pondaungia* than in *Amphipithecus*. The main differences between these two taxa concern the size, occlusal molar structure, and dimension of M/3. *Amphipithecus* has a rather reduced M/3, but this tooth is enlarged in *Pondaungia*. They also share the distal position of the entoconid on M/1 relative to the hypoconid, but the entoconid is less reduced on *Pondaungia* than on *Amphipithecus*. M/1 of *Pondaungia* has a relatively longer trigonid than in *Amphipithecus*. The M/1–M/2 hypoconulids of *Pondaungia* are double but not clearly differentiated. This cusp is absent in *Amphipithecus*. *P. cotteri* (NMMP 1, 3, and 5) shows a duplicated metaconid, but this character cannot be observed on M/2 and M/3 of the lower jaw because of its poor preservation.

***P. cotteri* and *Siamopithecus eoceanus*.** These two taxa show nearly the same size of mandible and molars (6, 7). They therefore had a similar body weight, about 8,000–9,000 g (8, 9). They also share a deep mandibular ramus, but their premolars are different in structure. Those of *Siamopithecus* show a more primitive structure, being larger, more extended mesio-distally, and with a stronger protoconid on P/3–P/4. The molar proportions of these two taxa are also different. M/1 of *Pondaungia* is smaller than M/2 and M/3, unlike *Siamopithecus* in which M/1 is larger than M/2. The proportions of talonid and trigonid length are also different. *Siamopithecus* has a higher trigonid than talonid by comparison with *Pondaungia* and *Amphipithecus*. The hypoconulid on M/1 and M/2 of *Siamopithecus* is strong and double (7). The entoconid of *Siamopithecus* is not as distal as on the Burmese taxa. *Siamopithecus* has no duplicated metaconid. The structure of M/3 is similar in both taxa, with the same convex lingual outline of the crown and a reduced entoconid, but this tooth is more enlarged in *Pondaungia* than in *Siamopithecus*.

Phylogenetic Relationships

The phylogenetic status of *Pondaungia* has long been debated, its affinities having been thought to lie with anthropoids (1–4, 6, 10, 11), adapids (12), and even condylarths (13). Recently, the discovery of *Siamopithecus* (6, 7) and the recovery of remains of *Amphipithecus* and *Pondaungia* allowed a reassessment of these

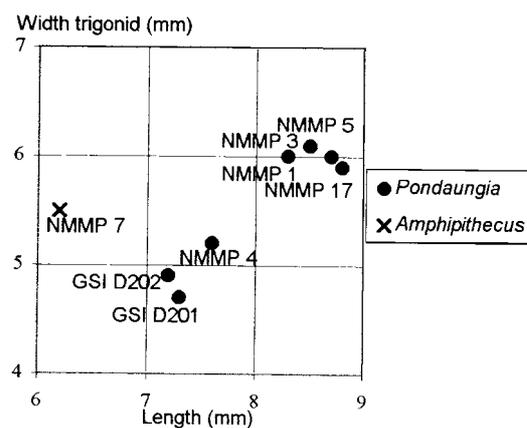


Fig. 2. Size distribution of M/3 of Pondaung Amphipithecidae.

three Southeast Asian fossils that led to the erection of the anthropoid family Amphipithecidae (3). Also, the main notharctine characters of *Pondaungia* proposed by Ciochon and Holroyd (12) have been refuted, so that *Pondaungia* can be affiliated with other two Asian genera among the Amphipithecidae. Subsequently, the discovery that some *Amphipithecus* have a duplicated metaconid (NMMP 6) and others crenulated enamel (left M/3 of NMMP 7), characters previously restricted to *Pondaungia*, indicates close affinities between these two Burmese taxa. New discoveries have therefore strongly increased the resemblance between these taxa. They share similar jaw, symphysis, premolar and molar structure, strong variability concerning the occurrence of crenulated enamel and some striking characters, like the duplicated metaconid. Remaining differences include the proportion of M/3 and overall size. However, size differences could be related to sexual dimorphism and M/3 size to strong variation and sexual dimorphism. Nevertheless, the size distribution of Pondaung M/3 (Fig. 2) indicates the occurrence of three groups that may correspond to male and female *Pondaungia*, and to a single *Amphipithecus* specimen (NMMP 7), which lies outside the *Pondaungia* range. Following this interpretation, the holotype of *Pondaungia* (GSI D201) and even *Pondaungia minuta* (GSI D202 and NMMP 4) would correspond to females of *P. cotteri*. We therefore consider that, pending the recovery of additional fossils, these two genera may in fact represent two closely related species or even the same species with very high variability and strong sexual dimorphism. *Siamopithecus*, with its more primitive premolars and its higher molar trigonids, but which also bears many anthropoid characters, is the sister group of the Burmese forms.

In conclusion, the recent discovery of the complete lower jaw of *Siamopithecus* (7) and the jaw of *Pondaungia* described here confirm the anthropoid affinities of these fossils that belong to the Amphipithecidae and allow us to reinterpret their phylogenetic relationships. As these Burmese anthropoids are among the oldest known, being of Late Middle Eocene age (14), they may have played an important role in the early evolution of this group. More complete specimens are nevertheless necessary to establish more precisely the relationships of these Asian anthropoids with respect to their African vicariants.

We thank B. Marandat and M. Pons for preparing fossils, making casts, and providing photos. This work was supported by the Fyssen Foundation, the Centre National de la Recherche Scientifique program “Paléoenvironnements et Evolution de l’Homme,” the Office of Strategic Studies (Myanmar), and the Department of Mineral Resources (Bangkok). This is Institut des Sciences de l’Evolution de Montpellier publication 99-125.

1. Pilgrim, G. E. (1927) *Mem. Geol. Surv. India (Paleontol. Indica)* **14**, 1–26.
2. Ba Maw, Ciochon, R. L. & Savage, D. E. (1979) *Nature (London)* **282**, 65–67.
3. Jaeger, J.-J., Aung Naing Soe, Aye Ko Aung, Benammi, M., Chaimanee, Y., Than Tun, Tin Thien & Ducrocq, S. (1998) *C. R. Acad. Sci. (Paris)* **321**, 953–959.
4. Beard, K. C., Qi, T., Dawson, M. R., Wang, B. & Li, C. (1994) *Nature (London)* **368**, 604–609.
5. Beard, K. C., Tong, Y., Dawson, M. R., Wang, J. & Huang, X. (1996) *Science* **272**, 82–85.
6. Chaimanee, Y., Jaeger, J.-J., Suteethorn, V. & Ducrocq, S. (1997) *Nature (London)* **385**, 429–431.
7. Chaimanee, Y., Khansubha, S. & Jaeger, J.-J. (2000) *C. R. Acad. Sci. (Paris)* **323**, 1–7.
8. Legendre, S. (1989) *Münchn. Geowiss. Abh.* **16**, 1–110.
9. Gingerich, P. D., Smith, B. H. & Rosenberg, K. (1980) *Am. J. Phys. Anthropol.* **52**, 231–232.
10. Simons, E. L. (1972) *Primate Evolution: An Introduction to Man's Place in Nature* (Macmillan, New York).
11. Szalay, F. S. & Delson, E. (1979) *Evolutionary History of the Primates* (Academic, New York).
12. Ciochon, R. L. & Holroyd, P. A. (1994) in *Anthropoid Origins*, eds Fleagle, J. G. & Kay, R. F. (Plenum, New York), pp. 143–162.
13. von Koenigswald, G. H. R. (1965) *Proc. K. Ned. Akad. Wet. B* **68**, 165–167.
14. Holroyd, P. A. & Ciochon, R. L. (1994) in *Anthropoid Origins*, eds Fleagle, J. G. & Kay, R. F. (Plenum, New York), pp. 123–141.