



Human Palaeontology and Prehistory

Systematics and paleobiology of the anthropoid primate
Pondaungia from the late Middle Eocene of Myanmar

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Abstract

Several newly recovered specimens documenting the Eocene Myanmar (South East Asia) anthropoid taxa *Pondaungia* and *Amphipithecus* modify the classical understanding of the taxonomy of these two primates, which have in fact no substantial morphological differences. Using tooth wear stages and the elevation of the horizontal branch of the mandible below the foramen mentale, we show a continuous variation, here attributed to individual aging. In addition, a strong size dimorphism is demonstrated, which is attributed to sexual dimorphism. In this context, *Amphipithecus mogaungensis* holotype is interpreted as a male of *Pondaungia cotteri*, which is recognized as the only large-bodied anthropoid of the Pondaung Formation. Growth arrest lines (LAGs) have been observed in several sections of lower jaws attributed to that species. These LAGs are here interpreted as regular increments, which formed in response to seasonal variability in the environment. They likely correspond to annual cycles, and the minimum longevity of the individuals can thus be roughly estimated. Several features indicate that *P. cotteri* may have been adapted to hard food diet and to survive in a strong seasonal climate with annual food shortage periods.

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Résumé

Systematique et paléobiologie du primate anthropoïde *Pondaungia* de l'Éocène moyen supérieur du Myanmar. Plusieurs nouveaux spécimens documentant les anthropoïdes du Myanmar (Asie du Sud-Est) *Pondaungia* et *Amphipithecus* modifient sensiblement l'interprétation taxonomique classique de ces deux taxons, qui ne présentent pas de différences

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morphologiques. En utilisant le degré d'usure des dents et la hauteur de la mandibule sous le foramen mentale, nous montrons une variabilité continue attribuée à des différences d'âge entre les individus. De plus, un fort dimorphisme sexuel est mis en évidence. Nous interprétons donc l'holotype de *Amphipithecus mogaungensis* comme un mâle de *Pondaungia cotteri*, ici reconnu comme la seule espèce d'anthropoïde de grande taille de la formation de Pondaung. Des lignes d'arrêt de croissance ont été observées sur plusieurs sections de mandibules attribuées à cette espèce. Elles pourraient correspondre à des cycles annuels, en réponse à des variations saisonnières de l'environnement. Nous disposerions ainsi d'un outil permettant d'estimer approximativement la longévité minimale des individus. Plusieurs caractères semblent indiquer que *P. cotteri* était adapté à une nourriture dure et à la survie sous un climat à saisons très marquées, ainsi qu'à des périodes prolongées de sous-alimentation.

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Les dernières campagnes de terrain effectuées par la *Myanmar-French Pondaung Primates Expedition* dans le Centre-Ouest du Myanmar en novembre 2001 et 2002 ont permis de récolter plusieurs nouveaux spécimens dentaires référés ici aux Amphipithecidae [12,14,15].

La faune de primates de la formation de Pondaung comprend trois formes de petite taille : cf. *Eosimias*, *Bahinia pondaungensis* Jaeger et al. 1999 et *Myanmarpithecus yarshensis* Takai et al. 2001, et deux formes de grande taille : *Amphipithecus* et *Pondaungia*. La présente étude concerne seulement ces deux derniers genres, représentés par quatre espèces distinctes : *Pondaungia cotteri* Pilgrim 1927, *Amphipithecus mogaungensis* Colbert 1937, *Pondaungia minuta* Jaeger et al. 1998 [5,15,25] et *Pondaungia savagei* Gunnel et al. 2002.

Les nouveaux spécimens étudiés dans cet article apportent des informations inédites sur la variabilité dimensionnelle et morphologique de *Amphipithecus* et de *Pondaungia*, et permettent de tirer de nouvelles inférences en ce qui concerne la taxonomie, la paléobiologie et les adaptations de ces primates anthropoïdes d'Asie du Sud-Est. Du point de vue taxonomique, le nouveau matériel témoigne de manière significative de la très forte ressemblance morphologique entre les dents homologues des deux taxons. De plus, plusieurs caractères, qui avaient été considérés comme diagnostiques, sont maintenant observés chez les deux genres. C'est par exemple le cas des crénulations de l'émail, ou du métaconide dédoublé,

caractères diagnostiques de *Pondaungia* que l'on retrouve également sur le nouveau matériel antérieurement attribué à *Amphipithecus*. La M/3, plus réduite chez *Amphipithecus*, était aussi considérée comme un caractère séparant les deux genres [28]. Le calcul des ratios de surface réelle de M/3–M/2 (Tableau 2) montre, toutefois, que chez tous les spécimens attribués à *Amphipithecus* et *Pondaungia*, la M/3 est plus petite que la M/2, avec des valeurs recouvrantes entre les deux taxons. Il en est de même pour la hauteur de la mandibule sous M/2 (Tableau 3). En fait, la plupart des caractères mentionnés par les auteurs précédents rentrent maintenant dans la variabilité du nouveau jeu de données. Sur la base de ces nombreuses similarités et des données morphométriques recouvrantes, il apparaît désormais impossible de reconnaître deux genres distincts, comme l'avaient déjà suggéré Chaimanee et al. [5]. En suivant ces conclusions et conformément au principe d'antériorité, nous interprétons donc ici *Amphipithecus mogaungensis* comme le synonyme junior de *Pondaungia cotteri*, ici reconnu comme le seul anthropoïde de grande taille de la formation de Pondaung.

Notre nouvelle interprétation amène par conséquent à une réévaluation taxonomique :

- genre : *Pondaungia* Pilgrim, 1927
- espèce type : *Pondaungia cotteri* Pilgrim, 1927
- holotype : GSI D201–203.
- localité type : affleurement près du village de Pangan, Myanmar central
- âge et distribution : Éocène moyen supérieur, formation de Pondaung, Myanmar.

Dans le but d'expliquer la grande variabilité montrée par cette espèce, nous avons testé l'hypothèse de l'existence d'un éventuel dimorphisme sexuel entre les deux formes et ce, par la méthode des moyennes (méthode utilisée pour estimer le dimorphisme sexuel au sein d'un assemblage non sexué [22]). Nous avons considéré comme hypothèse de travail que les individus possédant les dents les plus grandes étaient les mâles et ceux présentant des dents plus petites étaient les femelles. Le degré de dimorphisme sexuel a été calculé en comparant les masses corporelles estimées pour chaque individu à partir de l'aire de la première molaire inférieure (longueur \times largeur). Le poids de chaque individu a ainsi été calculé en utilisant trois équations différentes de régressions multiples, celle de Gingerich et al. [11] pour les primates et celles de Conroy [7] pour tous primates et pour les anthropoïdes (Tableau 1). En utilisant la méthode des moyennes, nous avons obtenu les valeurs suivantes : 1,39 (Conroy, anthropoïdes), 1,46 (Conroy, tous primates) et 1,42 (Gingerich). De telles valeurs correspondent à la plupart de celles observées chez des anthropoïdes actuels, marqués d'un fort dimorphisme sexuel [18,22].

Dans le but d'estimer l'âge individuel correspondant aux différents spécimens, nous avons pris en compte la hauteur du corpus mandibulaire au-dessous et au-dessus du foramen mentale, ainsi que l'usure des dents estimée à partir du nombre de puits de dentine (Fig. 3). Nous avons pu observer que la hauteur du corpus était relativement constante au-dessus du foramen mentale et que les différences de hauteur concernaient essentiellement la partie inférieure du corpus. L'examen de celle-ci a permis d'observer des lignes d'arrêt de croissance (LAC) séparant des couches osseuses concentriques, d'épaisseurs inégales. Ces LAC [3] correspondent à des interruptions temporaires dans la croissance osseuse et permettent d'estimer approximativement la longévité minimale des individus. Par exemple, sur NMMP 24 (spécimen de grande taille probablement adulte, au vu de l'usure marquée des dents), le décompte des LAC indiquerait un âge minimum de 10 ans. Une telle estimation correspond à celles observées chez des primates actuels de taille similaire [24]. Ces LAC pourraient correspondre à des cycles annuels, en réponse à des variations saisonnières de l'environnement [19]. En effet, des données sédimentologiques obtenues dans la formation de Pondaung, telles que les fentes de dessiccation ou

concrétions carbonatées d'origine pédogénétique, indiquent aussi une saisonnalité marquée [1]. Plusieurs caractères tels que le complexe formé par la canine et les incisives, la symphyse verticale (Fig. 2), le corps mandibulaire élevé et massif, le raccourcissement de la rangée dentaire et l'épaisseur de l'émail des dents, suggèrent que *P. cotteri* avait probablement un bol alimentaire composé principalement de substances relativement dures, telles que noix et/ou graines.

1. Introduction

Last field campaigns achieved by the joint Myanmar-French Pondaung Primates Expedition (central Myanmar, in January and November 2001, then November 2002–2003) have resulted in the recovery of several new specimens of Primates here referred to the Amphipithecidae [12,14,15]. These additional specimens provide substantial information concerning the paleobiology, variation in size and morphology, which allow us to draw new inferences concerning the taxonomy, the life history and adaptations of that group of anthropoid primates from Southeast Asia.

The following new material, which completes the formerly described specimens [5,15,25] includes: NMMP 24, right lower jaw from PK2 (discovered by B. Marandat); NMMP 25, left M/1 from LK (discovered by Y. Chaimanee); NMMP 33, fragment of right M/1 from PK 2 (discovered by B. M.); NMMP 34, fragmentary mandible with root of P/4 and complete M/1 from LK (Y. C.); NMMP 35, left M1/ from LK (discovered by Soe Thura Tun); NMMP 38, left lower jaw fragment with M/1-M/2 from SP (discovered by a villager). All of these specimens were discovered by the Myanmar French Pondaung Primate Expedition. We include also in that study NMMP 22: a right P4/ from LK discovered by the Myanmar Expedition of 1997.

Abbreviations used: PK2, Paukkaung Kyitchaung 2; LK, Lema Kyitchaung; SP, Saba Pondaung; NMMP, National Museum of Myanmar, Primates.

2. Systematics

Order Primates Linnaeus, 1758; suborder Anthropoidea Mivart 1864; family Amphipithecidae Godinot 1994; *Pondaungia cotteri* Pilgrim 1927.

The primate fauna of the Pondaung Formation includes five distinct taxa, among which three small-bodied forms: cf. *Eosimias*, *Bahinia pondaungensis* Jaeger et al. 1999, and *Myanmarpithecus yarshensis* Takai et al. 2001, and two large-bodied forms, *Amphipithecus* and *Pondaungia*. This study concerns only the two large-bodied forms (*Pondaungia* and *Amphipithecus*), which are presently represented by four species: *Pondaungia cotteri* Pilgrim 1927, *Amphipithecus mogaungensis* Colbert 1937, *Pondaungia minuta* Jaeger et al. 1998, and *Pondaungia savagei* Gunnell et al. 2002. A large additional number of fossils documenting these two genera has been collected since the development of systematic paleontological surveys of the Pondaung Formation, which deeply modifies and highlights the systematic status of these primates.

For many years, according to the original diagnosis, the main differences between these two genera concerned the smaller size of teeth, the smoother enamel of *Amphipithecus* versus strong enamel crenulation in *Pondaungia*, and the reduced M/3 length with regard to M/2 in *Amphipithecus* (M/3 was considered to be longer than M/2 in *Pondaungia*, as emphasized by Jaeger et al. [15]). However, the two holotypes did not share any tooth in common, making comparisons impossible, so that it was wrongly considered that *Amphipithecus* was of small size and *Pondaungia* of large size. Takai et al. [28] compared 21 characters of the lower jaw and teeth of these two genera, considered in the traditional way. Among these characters, only two were mentioned for differentiating *Amphipithecus* and *Pondaungia*: the relative length of molar trigonid versus talonid, and the length of M/3 versus M/2. In our opinion, such characters are not relevant for justifying a generic separation: according to Chaimanee et al. [5], enamel crenulations are also present on the M/3 (NMMP 7) of samples previously attributed to *Amphipithecus*, as are duplicated metaconids (interpreted as a paraconid and a metaconid by Ciochon and Holroyd [6]). Chaimanee et al. (o.c.) concluded that these peculiar shared characters may indicate very close phylogenetic relationships or even sexual dimorphism within a single species. Here we show that only metric differences separate two sets of individuals that display similar morphology. The holotype of *Pondaungia cotteri* corresponds to the small individuals and that of *Amphipithecus pondaungensis* to the large ones. M/3 are extremely variable in size as in most mamma-

lian taxa. According to the morphological identity and to the amount of their metric differences, these two sets are interpreted here as male and female of one single species.

3. Description of the new specimens

NMMP 24 (Fig. 1A–C) is an undeformed right lower jaw with complete corpus and a portion of the proximal ascending ramus. This specimen bears alveoli of I/1 and I/2, canine, roots of P/2 and P/3, P/4, M/1–M/3. All premolars and molars are very worn out, and enamel is preserved only on the canine and M/3. This jaw is quite similar in size and shape to another jaw (NMMP 17) attributed to *Pondaungia cotteri* by Chaimanee et al. [5]. NMMP 17 having been already extensively described by these authors, we will here describe additional features exhibited by the new specimen. Contrary to NMMP 17, NMMP 24 is not laterally crushed and its remarkable preservation confirms some formerly observed features such as: the depth of the corpus, the presence of strong superior and weaker inferior transverse tori, the important thickness of the superior transverse mandibular torus, the strong parabolic shape of the dental arcade, the strong concavity of the tooth row in lateral view, the depth of the masseteric fossa, and the strong superior and inferior masseteric ridges. The depth of the corpus remains constant from the canine to the M/3. The symphysis is large, vertical, unfused and the strong transverse superior torus extends posteriorly to the P/3 level. A deep genio-glossal fossa separates the upper torus from a less important lower torus. The symphyseal angle measures 65° while the planum alveolare angle measures 32° (Fig. 2). The symphysis bears much rugosity on the symphyseal surface and its section bears resemblance with that of some Miocene hominoids. Two mental foramina are present, one below the root of P/2 and the second between P/3 and P/4, midway between the alveolar margin and the inferior side of the corpus. Alveoli of I/1 and I/2 are present, showing buccolingually elongated trapezoidal root sections. The alveolus of I/1 is much larger than that of I/2 and the mesial wall of the canine is flat and slightly concave, thus indicating that I/2 was very close to the canine distally and I/1 mesially, that probably formed an anterior complex – a rather similar morphological structure

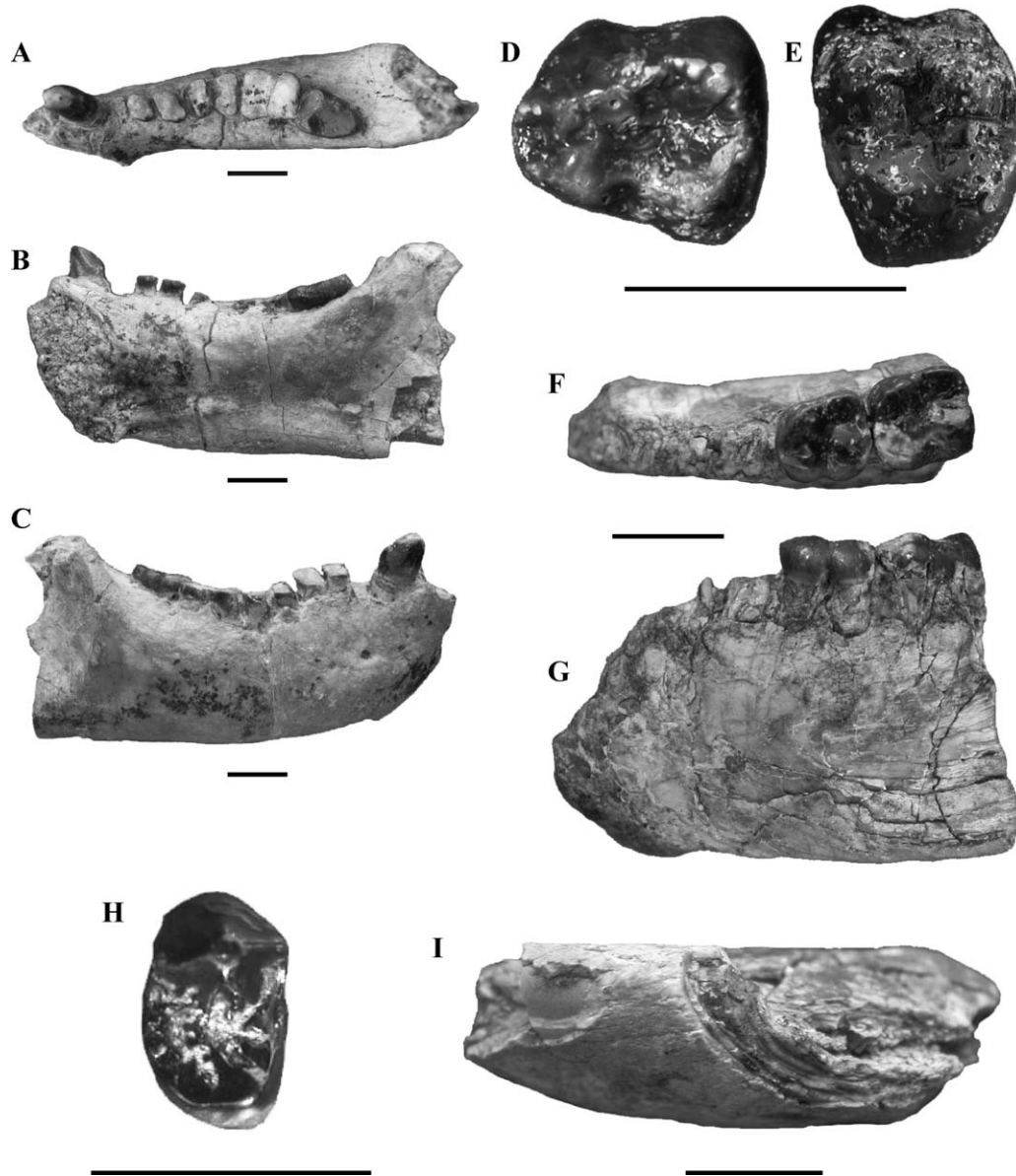


Fig. 1. New specimens of *Pondaungia cotteri*. (A) Occlusal view of NMMP 24, right lower jaw with C-M/3 from Paukkaung 2; (B) lingual view of NMMP 24; (C) buccal view of NMMP 24; (D), NMMP 25, left M/1 from Lema Kyitchaung in occlusal view; (E) NMMP 35, left M1/ from Lema Kyitchaung in occlusal view; (F) occlusal view of NMMP 38, left lower jaw with M/1-M/2 from Saba Pondaung; (G) buccal view of NMMP 38; (H) NMMP 22, right P4/ from Lema Kyitchaung in occlusal view; (I) NMMP 5, right lower jaw with M/2–M/3 showing growth arrest lines.

Fig. 1. Nouveaux spécimens de *Pondaungia cotteri*. (A) Vue occlusale de NMMP 24, mâchoire inférieure droite avec C-M/3 de Paukkaung 2; (B) vue linguale de NMMP 24; (C) vue buccale de NMMP 24; (D) NMMP 25, M/1 gauche de Lema Kyitchaung en vue occlusale; (E) NMMP 35, M1/ gauche de Lema Kyitchaung en vue occlusale; (F) vue occlusale de NMMP 38, mâchoire inférieure gauche avec M/1-M/2 de Saba Pondaung; (G) vue buccale de NMMP 38; (H) NMMP 22, P4/ droite de Lema Kyitchaung en vue occlusale; (I) NMMP 5, fragment de mâchoire inférieure droite avec M/2–M/3 montrant des lignes d'arrêt de croissance.

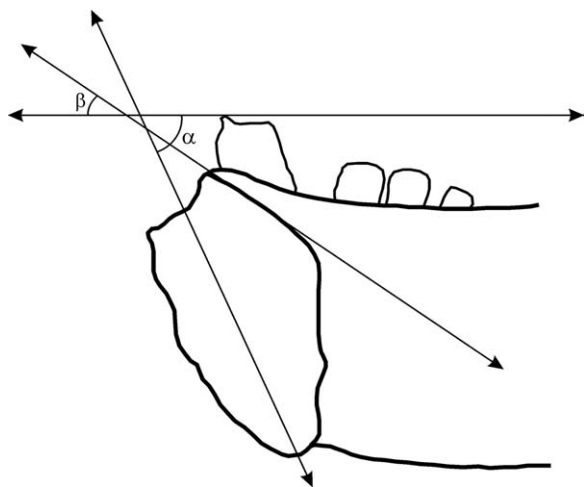


Fig. 2. Mandibular symphysis of *Pondaungia cotteri* (NMMP 24) and estimation of the symphyseal (α) and planum alveolare (β) angles.

Fig. 2. Symphyse de *Pondaungia cotteri* (NMMP 24) et estimation des angles de la symphyse (α) et du planum alveolare (β).

occurring for instance also in *Soriacebus*, a Miocene South American platyrrhine anthropoid [9]. However, among anthropoids from the Oligocene of the Fayum region of Egypt [17], I/2 is larger than I/1 in several genera (a basic anthropoid character), although the lower incisors of some taxa (such as *Qatrania*, *Serapia*, *Simonsius*) are still unknown [23]. Although the reduction of I/2 is not systematically depicted in most anthropoids, such a character observed in the Myanmar fossils may be considered as derived inasmuch as it occurs in cercopithecoids [26]. This character can, therefore, not be used to exclude *Pondaungia* from the anthropoids. The incisors were rather erect than procumbent with respect to their root orientation and the verticality of the symphysis. The canine is of moderate size and represents the first known complete lower canine of that genus. Its crown is oval in cross section. It bears a mesiodistally oriented apical wear facet on its apex, a buccal facet made by the upper canine, which displays many oblique striations and a tiny distal talonid cusplet. Its buccal and distolingual walls are convex and bear no cingulid. Its apical wear facet is the result of the wear produced by the upper incisors, because the lower canine has apparently taken the function of an incisor. The very worn premolars and molars display differently oriented wear facets: directed buccally for premolars and lingually for molars.

NMMP 38 [Fig. 1F, G] is a left mandibular fragment showing well preserved M/1-M/2, root sections of anterior teeth, and the lower part of the symphysis. The mesial part of the jaw is broken obliquely, and displays a section of the I/1 root near its extremity, very deeply rooted in the symphysis. There is no evidence of the root section of I/2, which suggests that the former belong to I/1, and that I/2 is reduced with shorter root, as observed on NMMP 24. The long axis of the canine root section measures 3.08 mm. The crown of M/2 is broken distally and displays an enamel section. On this specimen as well as on NMMP 33, the enamel appears to be radial without decussating prisms and cusps show also a very low dentine penetrance. M/1 shows three small dentine pits (but not M/2) and the elevation of the horizontal branch measures 17.5 mm under the distal part of M/2, and 9.50 mm of maximum thickness. Regarding the wear facets and the size of jaw, when compared to other samples, it might be expected that NMMP 38 belonged to an adult individual.

NMMP 33 (not figured) is a very worn M/1, with only small enamel patches on the talonid.

NMMP 25 (Fig. 1D) is an unworn M/1, which displays all details of its occlusal surface. The trigonid is mesiodistally long because the distal metaconid cusp is very posteriorly located. The mesial metaconid cusp has the same elevation that the distal one and both are connected to the protoconid, thus isolating a small fovea, just behind the mesial fovea. The protocristid encloses the trigonid mesially and joins the apex of the mesial metaconid. There is no trace of paraconid. Ciochon and Holroyd [6] have interpreted the mesial metaconid as a paraconid. However, on most *Pondaungia* and on some *Amphipithecus* first and second molars, mesial metaconids have the same elevation as the distal metaconids, whereas in most mammals, including primates, the paraconid is more and more reduced from M/1 to M/3. This led us to interpret this cusp as a result of the duplication of the original metaconid and not as a paraconid, which is unknown among large Amphipithecidae and in *Myanmarpithecus*. Both buccal and lingual main cusps are strongly slanted, but the trigonid cuspids are considerably more slanted than the talonid ones. The talonid is only slightly lower than the trigonid. The straight cristid obliqua joins the distal slope of the protoconid, which is slightly higher than both metaconids. The entoconid is reduced, occupying a more distal position relative to the hypoconid. The

mesial arm of the entoconid is connected to the distal arm of the distal metaconid, isolating with the cristid obliqua, a deeply rounded talonid basin. A small enamel swelling occurs in the distal part of the talonid basin. By the fact that this swelling is closer to the hypoconid than to the entoconid, and that its distal part is connected to the distobuccal cingulid, it could correspond to a minute hypoconulid. The buccal cingulid does not completely surround the buccal side of the tooth, and it is interrupted at the level of the hypoflexid. Thick enamel crenulations occur in the talonid basin. NMMP 25 differs from other specimens referred to *Pondaungia* by the absence of a notch separating both the mesial and distal metaconids. In our interpretation, the trigonid elongation observed in the lower molars of *Pondaungia* results from the duplication of the metaconid. It is therefore a derived feature, as suggested by Godinot [13]. The presence/absence of the hypoconulid is a disputed matter, but NMMP 25 as well as NMMP 38 demonstrates that a vestigial hypoconulid can occur on very pristine M/1's of *Pondaungia*, thus indicating that it has been reduced or lost during the course of evolution.

The right P4/, NMMP 22 (Fig. 1H), is the only complete P4/ of *Pondaungia* recorded to date. It is transversely elongated with a rectilinear mesial wall and a convex distal margin. The slanted paracone is the highest and largest cusp. The preparacrista reaches mesially a low parastyle and the postparacrista, which is low, reaches distally a low metastyle. The protocone is low and mesial. It is connected to the paracone by a curved crista obliqua. The preprotocrista reaches mesially the parastyle and the distal cingulum joins the metastyle. Although larger in size, NMMP 22 is very similar in shape to the P/3 (NMMP 12) from Pangan [25].

NMMP 35 (Fig. 1E) corresponds to an unworn left M1/. The paracone is slightly larger than the metacone. A tiny paraconule is present at mid distance between paracone and protocone. The metaconule is well distinct between the metacone and the hypocone. These three cusps are located on a transverse line buccolingually oriented. The hypocone is about as high as the protocone and is connected to it by a distinct postprotocrista. Like in crown anthropoids, the buccal wall of the paracone is salient with respect to the metacone wall. A cingulum surrounds the tooth almost completely. It is very shallow on the buccal side and be-

comes progressively more developed towards the lingual side. However, it is interrupted on the lingual wall of the protocone. The postcingulum links the hypocone and the lingual cingulum. The preprotocingulum joins a tiny parastyle cusp. Some broad enamel crenulations develop within the trigon basin. The central fovea is extremely small.

4. Discussion

The increasing amount of material indicates a wider range of variation than formerly expected, that significantly modifies the classical understanding of the taxonomy of these South Asian primates. As a matter of fact, several characters, which were basically considered as diagnostic, are shared by both genera. For instance, it is the case for the enamel crenulations, a diagnostic character for *Pondaungia* [21], which occur on nearly all specimens, with the exception of *Amphipithecus mogaungensis* holotype. The same holds true for the duplicated metaconid [5], which is found on the lower molars of small and large-sized specimens, with the exception of the holotype of *A. mogaungensis* (AMNH 32520). However, the strongest argument is the amazing morphological resemblance between homologous teeth attributed to small and large forms. Remaining differences between these two sets concern only metric characters, as the length and width of teeth, including M/3 [28], the elevation and section surface of lower jaws. The differences of tooth size concern mostly the breadth of the teeth. To analyse more in details these differences, we have undertaken the measure of the occlusal surfaces of the molars. As those initiated by Ducrocq [8], these measurements were made with a video camera and managed by Optimas 6.5 software. Between the small and the large sized individuals, according to the previous classical interpretation that *Amphipithecus* was small-sized and *Pondaungia* large-sized, (NMMP 6, 7 and 30 where considered to represent small individuals and NMMP 2, 17, 25 and 38 to represent large individuals), we obtained a mean ratio value of 1.27 between occlusal surfaces of the M/1 of these two sets (Table 1) and a mean ratio value of 1.26, by including *Amphipithecus* holotype among the set of large individuals. Actually, this holotype displays metric characters of its M/1 and of its jaw elevation and section that clearly fits

Table 1

M/1 surfaces of *Pondaungia cotteri* (mesio-distal maximum length × bucco-lingual maximum breadth) and correlative body mass estimates of individuals.

Surface des M/1 de *Pondaungia cotteri* (longueur maximale mésio-distale × largeur maximale bucco-linguale) et estimations de la masse corporelle des individus.

Specimens	M/1 area (mm ²)	Gingerich (g)	Conroy	
			all Primates (g)	anthropoids (g)
AMNH 32520 Holotype <i>A. mogaungensis</i>	35.05	7566	7224	7817
NMMP 2	34.97	7537	7195	7789
NMMP 6	28.16	5250	4889	5543
NMMP 7 left	30.43	5976	5615	6262
NMMP 7 right	31.09	6193	5832	6475
NMMP 30	29.62	5714	5352	6003
NMMP 17	41.02	9841	9567	10009
NMMP 25	37.95	8641	8326	8857
NMMP 38	35.34	7672	7332	7919

with those of the other large individuals (see measurements in Colbert, 1937). Concerning the M/3/M/2 ratio, the specimens previously referred to *Pondaungia* (large individuals) display values ranging from 0.76 (holotype) to 0.95, while the so-far-considered *Amphipithecus* (small individuals) values range from 0.63 to 0.65 (NMMP7) (Table 2). NMMP 30 displays an intermediate value of 0.73. Only the holotype of *P. minuta* shows an extreme ratio of 1.11, but this high value may be related to the absence of enamel cap on M/2, which makes all surface estimations of that tooth highly questionable. Mandibular depth of the holotype of *Amphipithecus* shows a value of 19.5 mm measured under M/1 (in Colbert, 1937), significantly higher

compared to that of *Pondaungia* holotype value of 12.3 mm measured under M/2 (Table 3). For all these reasons, there is no argument left and no other basis (there is no observable molar trigonid length difference) to consider that small individuals belong to *Amphipithecus* and large individuals to *Pondaungia*. To the contrary, reference to the holotypes demonstrates the opposite: *Pondaungia cotteri* holotype represents a small individual and *Amphipithecus pondaungensis* holotype a large one. However, they otherwise share exactly the same morphological characters. Therefore, on the basis of these evidences, there is no reason anymore to distinguish two different genera. In addition, there is no strong basis to refer the two sets to

Table 2

M/2 and M/3 areas of *Pondaungia cotteri* calculated from their outlines and M/3/M/2 ratios.

Surfaces des M/2 et des M/3 de *Pondaungia cotteri* calculées d'après leurs circonférences et rapports M/3/M/2

Specimens	M/2 area (mm ²)	M/3 area (mm ²)	Ratio M3/M2
NMMP 1	44.32	38.1	0.86
NMMP 3	46.13	38.62	0.84
NMMP 5	47.99	41.98	0.87
NMMP 7 left	35.49	23.16	0.65
NMMP 7 right	34.84	22.02	0.63
NMMP 17	44.75	42.45	0.95
NMMP 24	42.45	35.93	0.85
NMMP 30	32.43	23.89	0.73
GSI D 201 Holotype <i>P. cotteri</i>	32.07	24.42	0.76
NMMP 4 Holotype <i>P. minuta</i>	26.89	29.98	1.11

Table 3

Measurements of mandible depth of *Pondaungia cotteri* below M/2. Mesures de la hauteur de la mandibule de *Pondaungia cotteri* sous M/2

Specimens	Mandible depth below M/2 (mm)
AMNH 32520 Holotype <i>A. Mogaungensis</i>	19.5
GSI D 201 Holotype <i>P. Cotteri</i>	12.3
UCMP 120377	16.3
NMMP 1	18.65
NMMP 3	18.78
NMMP 5	17.18
NMMP 6	13.79
NMMP 7 left	15.71
NMMP 7 right	15.4
NMMP 17	19.41
NMMP 24	18.53
NMMP 30	13.51
NMMP 38	17.07

different species, if taking in account the possibility of a strong sexual dimorphism, which is common among extant and fossil anthropoids [18]. Following that conclusion, which has been already expressed by Chaimanee et al. [5], and which is here strengthened by additional data, only one species, *Pondaungia cotteri* Pilgrim 1927 – according to priority rule – is present among the large amphipithecids of the Pondaung Formation. However, the hypothesis of a sexual dimorphism as strong as among Miocene hominoids in an Eocene Anthropoid deserves additional investigations. Among the methods for estimating sexual dimorphism in fossil species of an unsexed assemblage, the means method [22] is considered to perform relatively well. According to that method, an undifferentiated sample (here represented by extrapolated body weights) is divided into two sets of values at the mean of body weights of the total sample. The means of these divided sets are then used to calculate the dimorphism estimate [22]. We thus tried to estimate the amount of body mass sexual dimorphism, in hypothesizing that individuals with the smallest teeth were female and those with the larger teeth were males. In our analysis, canines could not be used, because only one upper (NMMP 12) and one lower canine (NMMP 24) are known. From the M/1 surface (mesio-distal maximum length \times bucco-lingual maximum breadth) the body mass of each individual has therefore been estimated using three different regression equations, that of Gingerich et al. [11] for Primates and those of Conroy [7] for all Primates and for Anthropoids (Table 1). By using the means method to estimate dimorphism, we obtained three close values of 1.39 (Conroy, only anthropoids), 1.46 (Conroy, all Primates) and 1.42 (Gingerich). Such values are in the range of most extant anthropoid groups. Among platyrrhines, *Saimiri sciureus* (1.39), *Ateles geoffroyi* (1.342) or *Miopithecus talapoin* (1.335), among catarrhines *Presbytis (Trachypithecus) entellus* (1.48), *Colobus quereza* (1.36), and *Macaca fuscata* (1.44) all display similar values [22]. Less extreme sexual dimorphism is also known among Eocene adapids for canines and body mass [10], and among Paleogene anthropoids from North Africa (Fayum localities), notably for *Catopithecus* and *Proteopithecus* [27]. In that respect, the plausible sexual dimorphism implied by our interpretation is quite compatible with what is measured on anthropoids of modern aspect. This observation represents an

additional anthropoid feature for characterising the Amphipithecidae. Our interpretation contrasts therefore with those proposed by previous authors. For instance, Takai et al. [29] consider that ‘small-type’ and ‘large-type’ *Pondaungia* as sympatric with *Amphipithecus mogaungensis*, supposing sympatry between three morphologically identical primates, the sizes of which are largely overlapping. Geological age differences inducing evolutionary changes can be excluded, because all Pondaung primate localities fall within the same palaeomagnetic zone [2]. Even if limited diachronism between the different localities cannot be precluded, it appears that the largest individuals (NMMP 17) have been discovered in the same locality and level (Tandaung Kyitchaung, Mogaung) as the smallest specimen (NMMP 6).

Our new interpretation leads therefore to the following taxonomic reappraisal:

- genus *Pondaungia* Pilgrim, 1927
- type-species: *Pondaungia cotteri* Pilgrim, 1927
- holotype: GSI D201–203, interpreted here as belonging to a female individual
- type-locality: roadcut near Pangan village, central Myanmar
- age and distribution: late Middle Eocene, Pondaung Formation, Myanmar.

Emended diagnosis. Large and strongly dimorphic amphipithecoid primate, of the size of the extant platyrrhine *Alouatta palliata*, with very massive and short jaws, subvertical symphysis with upper transverse torus strongly developed, and strong parabolic shaped dental arcades; lower jaw deep with nearly constant depth between P/3 and M/3; I/2 smaller than I/1, closely appressed to the canine, forming an anterior complex; large and spatulate I1/, stout projecting upper canine without mesial groove; reduced lower canine involved with the incisors into a morpho-functional complex; three upper and lower premolars, with premolar row length very reduced relative to molar row length; premolars very short mesiodistally and wide buccolingually; P2/2 reduced and single rooted; upper premolars with unwaisted and oval occlusal profile; lower premolars obliquely oriented with respect to the tooth row; buccally oriented wear for premolars, lingually for molars; molar enamel radial, without Hunter–Schreger bands, smooth to strongly crenulated; slanted buccal and lingual cusps with reduced occlusal

surfaces; upper molars with hypocone showing a pre-hypocrista linked to the postprotocrista; continuous lingual cingulum; reduced upper M3/; lower molars with talonid as elevated as trigonid and with straight cristid obliqua. Paraconid and hypoconulid absent, with occasionally duplicated metaconid; M/3 extremely variable in size, but with crown area always smaller than M/2.

Pondaungia cotteri Pilgrim, 1927.

Diagnosis: as for the genus.

Synonyms: *Amphipithecus mogaungensis* Colbert, 1937, which is now considered as a representative of a male of *Pondaungia cotteri*; *Pondaungia savagei* Gunnell et al., 2002, also interpreted here as a male of *Pondaungia cotteri*.

In that respect, we attribute to *Pondaungia cotteri* the following samples: NMMP1, 2, 3, 5, 6, 7, 12, 17, 18, 19, 22, 24, 25, 29, 30, 33, 34, 35, 38, 40, 41, UCMP 120377, GSI D201–202–203, AMNH 32520.

The specimens with the largest molars, AMNH 32520, NMMP 1, 2, 3, 5, 17, 22, 24, 25, 34, 35 and 38 are interpreted here as males. Samples NMMP 6, 7, 30 and GSI (D201–202–203) are interpreted as females.

If our interpretation of a highly dimorphic unique species would be refuted in the future, then two sympatric species would have to be taken in account, a small one, *Pondaungia cotteri*, Pilgrim 1927 and a larger one, *Pondaungia mogaungensis* (Colbert 1937). There would be therefore no justification left to create a new large species of *Pondaungia*.

The case of *Pondaungia minuta* Jaeger 1998 holotype remains unsolved. Its M/3/M/2 area ratio (1.11) is unlike any other specimen of *Pondaungia* (see comment on the previous page) and the metric of its lower jaw also differs significantly from all other *Pondaungia* samples by its extremely small dimensions. However, most of the diagnosis characters of *Pondaungia* lower jaw are present (concave tooth row in lateral view, convex tooth row in occlusal view, position of the foramen mentale). On the available evidence, we cannot make decision between two conflicting interpretations. Either it represents an abnormal small sized female of *Pondaungia cotteri*, or it corresponds to a different species, what corresponds to its current status.

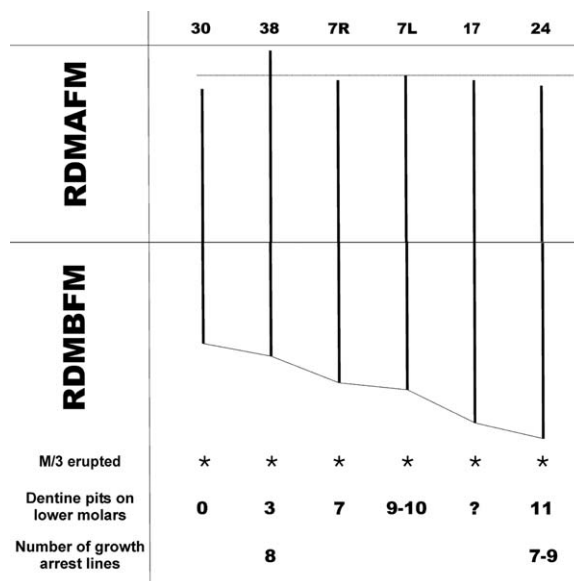


Fig. 3. Correlation between mandibular depth, tooth wear stages and number of growth arrest lines in some specimens of *Pondaungia cotteri*. RDMBFM: Relative depth of the mandible below the foramen mentale. RDMAFM: Relative depth of the mandible above the foramen mentale.

Fig. 3. Corrélation entre la hauteur de la mandibule, le degré d'usure des dents et le nombre de lignes d'arrêt de croissance sur quelques spécimens de *Pondaungia cotteri*. RDMBFM: Hauteur relative de la mandibule sous le foramen mentale. RDMAFM: Hauteur relative de la mandibule au-dessus du foramen mentale.

5. Palaeobiology and life history of *pondaungia cotteri*

As a means of estimating individual age of the different specimens referred to *Pondaungia cotteri*, we have taken into account the elevation of the corpus, and for the tooth wear, the number of dentine pits. The elevation of the lower jaws has been measured above and below the foramen mentale (the most distal foramen in the cases where two foramina are present). In Fig. 3, it can be observed that the elevation of the corpus is relatively constant above the foramen mentale and that most differences in elevation affected the lower part of the corpus under the foramen mentale. In order to assess the importance of age-effect on that last variable, we counted the number of dentine pits on the lower molars. The smallest jaw, NMMP 30, has no dentine pit. It is followed by NMMP 38 with three pits on M/1 only, then by NMMP 7, with 7 to 10 dentine pits, respectively, and finally by the eldest NMMP

24 with 11 dentine pits. When molars were flat worn, we counted four dentine pits for each molar. As such, the tooth wear patterns are well-correlated with the elevation of the lower jaws, especially with the elevation of the jaw below the foramen mentale. We also noticed that all specimens, even the smallest one, display an erupted M/3, even in the absence of any dentine pit on the anterior dentition and on the first molar. We thus conclude that the M/3 probably erupted very early in that species. Therefore, this character cannot be used as an indicator of the age of an individual. We also drew attention to fragmentary specimens, which display partial (NNMP 5, NMMP 24) or complete (NMMP 3, NMMP 5, NMMP 38) sections of the corpus. Most of these sections display growth arrest lines (LAGs), which separate bone layers of irregular thickness (Fig. 11) and which can be particularly easily observed in the lower part of the horizontal branch, under the mandibular canal. These structures are the consequence of primary concentric bone deposition followed by interruptions of the remodelling process. They represent temporary perturbations in skeletal growth and are usually interpreted as annual increments formed in response to seasonal variability in the environment [19]. If they correspond to annual cycles (which seems the most likely hypothesis [3]), then they represent a way to assess the minimum age of each individual that displays these LAGs. They are most recognizable on NMMP 5, on which at least nine LAGs occur, which could mean that this individual was more than nine years old. They are less visible on NMMP 24. However, on the lateral part of the angular region, close to the angular process, eight to nine regularly spaced LAGs can be observed under reflecting light. On NMMP 38, five LAGs can be seen under the mandibular canal. On NMMP 3, at least five LAGs can be observed. From Fig. 3, it appears that a possible correlation exists between the LAGs number and the estimated ages of these specimens on the basis on tooth wear and lower corpus depth. This suggests that reconstructions of growth curves of these individuals are possible. Also, it appears that the oldest individuals could have had longevity of over 10 years, which is in agreement with available data concerning the longevity of living primates of similar body size. For instance, observed life spans of non-human primates are over 20 years for living primates of equivalent weight [24].

In conclusion, *Pondaungia cotteri* appears as a medium sized primate, displaying strong sexual dimor-

phism in its body mass as well as in its dental and bony structures, with molar cusps showing a low relief, low dentine penetrance and rather thick radial enamel. The jaws are shortened and the mandibular corpus is very deep, allowing the insertions of strong masticatory muscles. The length of the lower jaws is greatly reduced in order to develop maximum pressure during the power stroke on the middle of the tooth row. The molars are extremely robust, with small occlusal surface compared to the basal crown surface, bearing anvil-like structures as on *Siamopithecus* [4]. Some of these characters are also present among extant and fossil seed-eating hominoids [16]. However, among these more recent taxa, the eruption of the third lower molar is delayed, and the molars display a strong gradient of wear between M/1 and M/3. In *Pondaungia*, we have shown that M/3 erupts quite early during its growth, because no lower jaw with unerupted M/3 has been discovered so far, and because NNMP 30 displays a complete tooth row (including M/3) without any dentine pit on any tooth. In that respect, if the specialization of *Pondaungia* corresponds to that of a nut or seedeater, it appears to have developed this adaptation in a peculiar way. Either the M/3 are involved lately in the chewing process or the enamel is considerably thicker compared to other molars. It is also possible that such a situation results from the combination of both processes. The seasonal deposit of bone layers is probably related to stress induced by food shortages due to strong seasonality, and it can hardly be attributed to other kinds of physiological perturbations since it occurs on nearly all specimens, which display partial or complete sections of mandibular corpus.

Furthermore, paleobotanical data indicate seasonality because of the occurrence of growth rings in several fossil woods, but the amount of data is not yet sufficient to conclude, and studies are still in progress. Geological and sedimentological data, such as well developed mud-cracks at the interfaces between clay levels and sand bodies, or the development of abundant pedogenic carbonate concretions, present in many fossiliferous overbank deposits, are also indicative of strong seasonality of the Pondaung paleoclimate during the deposition of these fossiliferous beds [1].

It is therefore possible to infer from all these data that *Pondaungia cotteri* was coming to river shores to drink and that it was feeding on some kind of hard food, as for example nuts produced by some variety of

palm trees, which are usually abundant in corresponding extant tropical environments. However, its unique lower anterior dentition, made of canines and incisors closely pressed together, cannot yet be interpreted functionally, because it remains insufficiently known. It may indicate a very peculiar feeding adaptation, with no extant equivalent. Some dental characters are shared with parapithecids, as the reduction of incisor area, waisted lower molar in occlusal view and parabolic tooth row. Additionally, several other characters are shared with the hominids: nearly vertical symphysis and incisors, very short and deep jaws and strongly parabolic tooth rows. Resemblance to parapithecids could indicate phylogenetic relationships but evidence is lacking, pending further discoveries. Hominid characters are interpreted here as the result of parallel evolution and do not testify to phylogenetic relationships with them. They rather correspond to an adaptation of a primate for surviving in a strong seasonal climate with annual food shortage periods. Such characters, shared with parapithecids and with hominids may nevertheless reinforce their anthropoid affinities. However, some authors have considered [6] that amphipithecids are in fact adapiform primates that have independently acquired several anthropoid characters. The recent discovery of a talus [20] referred by its size to a small individual (now interpreted as a female of *Pondaungia cotteri*) and displaying all the characters expected from an anthropoid makes this interpretation much less probable. Parallel evolution can affect teeth, jaws and talus independently, but the probability that anthropoid characters developed in parallel in independent structures as teeth and talus would represent a truly remarkable example of homoplasy! We rather consider that the Amphipithecidae are true anthropoids and that their inclusion in that group leads to a more extended definition, as the discoveries in the Late Eocene of Fayum have already demonstrated. Our definition of the anthropoids is summarized in Table 4.

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Table 4

List of anthropoid characters.

Liste des caractères d'anthropoïdes

Lower dentition

- symphysis unfused to fused, nearly vertical with strong upper torus and weak lower torus
- nearly vertical symphysis with vertical lower incisors
- strong canines
- single rooted P/2
- P/3-P/4, with their long axis oblique to the molar row and with posterolingual expansion
- P/4 with well developed metaconid
- trigonid and talonid of lower molars nearly of similar height
- basally inflated crowns with bunodont low cusps
- presence of labial cingulid (often reduced)
- M/3 area reduced relative to M/2 area
- M/3 trigonid wider than talonid
- Paraconid reduced to absent
- Protoconid higher than metaconid (*Eosimias*)
- Hypoconulid in medial position, small to very large
- Cristid obliqua straight
- Talonid of lower molars lingually closed
- X facet present

Upper dentition characters

- Upper incisors spatulated
- Stout projecting upper canine
- Upper Premolars unwaisted with oval outlines, with protocone on P3/-P4/
- Lingual cingulum well developed
- Labial cingulum weak to strong
- Conules present, weakly to strongly developed
- Expanded M2/ labial wall of paracone
- Paracone higher than meracone (*Eosimias*)

Cranial characters

- Metopic suture fused
- Postorbital closure
- loss of stapedia artery
- middle ear pneumatization
- lacrimal bone in orbit
- tympanic ring fused to the lateral wall of the auditory bulla

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