FACS buffer [phosphate-buffered saline (PBS), 1% FBS, and 0.02% NaN_3, at pH 7.4)]. Subsequently, the cells were directly stained with fluorescein isothiocyanate–or phycoerythrin-conjugated mouse monoclonal antibodies to CD83 (Immunotech, Marseille, France), CD1a, CD86, HLA-DR (PharMingen, San Diego, CA), or CCR6 (R&D Systems) at 24°C for 1 hour at a final concentration of 5 μg/ml in FACS buffer. As a negative control, DCs were stained with isotype-matched irrelevant antibodies. Thereafter, the cells were washed twice with FACS buffer and twice with PBS, resuspended in PBS containing 1% paraformaldehyde, and analyzed with a flow cytometer (Coulter or FACScan Epics Analyzer).

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A New Primate from the Middle Eocene of Myanmar and the Asian Early Origin of Anthropoids

J.-J. Jaeger,[1] Tin Thein,[2] M. Benammi,[1] Y. Chaimanee,[3] Aung Naing Soe,[4] Thit Lwin,[4] Than Tun,[5] San Wai,[5] S. Ducrocq[1]*

A new genus and species of anthropoid primate, *Bahinia pondaungensis* gen. et sp. nov., is described from the Yashe Kyitchaung locality in the Late Middle Eocene Pondaung Formation (Myanmar). It is related to *Eosimias*, but it is represented by more complete remains, including upper dentition with associated lower jaw fragment. It is interpreted as a new representative of the family Eosimiidae, which corresponds to the sister group of the Amphipithecidae and of all other anthropoids. Eosimiidae are now recorded from three distinct Middle Eocene localities in Asia, giving support to the hypothesis of an Asian origin of anthropoids.

Anthropoid primates are represented during the Eocene in Southeast Asia by three derived genera, which belong to a monophyletic group, the Amphipithecidae (*1*). Two of them, *Amphipithecus* and *Pondaungia*, are recorded from the Late Middle Eocene Pondaung Formation in Myanmar, and *Siamopithecus* has been described from the Late Eocene Krabi Formation in Thailand (*2*). However, these forms give little information concerning their origins. *Eosimias* is a much more primitive primate known from the Middle Eocene of China (*3–5*), and its systematic position is debated; some authors recognize it as a basal anthropoid, therefore supporting an Asian origin of the group (*3, 4*), while others interpret it as having possible affinities with tarsiiformes (*6*). Some have even doubted its anthropoid nature (*7*).

During the November 1998 fieldwork organized in the frame of the Myanmar-French Pondaung Expedition Project, we recovered the remains of a new small primitive anthropoid, *Bahinia pondaungensis* gen. et sp. nov., at the Yashe Kyitchaung locality in Central Myanmar. The fossils (two fragmentary maxillaries and a broken lower jaw) were collected from a carbonate nodule in a reddish clay level which also yielded a complete lower jaw of *Amphipithecus mogaungensis* in the same stratigraphical level (*1*). The stratigraphic sequence shows normal magnetic polarity (*8*).

Systematics: Suborder Anthropoidea Mivart, 1864; Family Eosimiidae Beard *et al.*, 1994; *Bahinia pondaungensis* gen. et sp. nov.

Holotype: Left and right maxilla and associated jaw fragment. The right maxilla [National Museum of Myanmar Primate (NMMP) 15], shows I^{1-2}, C, P^{2-3}, broken P^4, M^{1-2} (Fig. 2A), and the premaxillary-maxillary suture (Fig. 1). The left maxilla (NMMP 14) (Fig. 2B) displays I^{1-2}, C, P^{2-4}, M^{1-2}, and broken M^3. The two maxillaries were separated in the nodule by carbonate matrix; thus, they belong to a single individual. The fragmentary right lower jaw (NMMP 16) (Fig. 2C) preserves the posterior part of the socket for canine and P_2-M_1.

Horizon and locality: Late Middle Eocene of Pondaung Formation, Yashe Kyitchaung locality (Primate Resort), Bahin village, Myaing Township.

Diagnosis: Very small anthropoid primate with dental formula 2.1.3.3. Two upper incisors vertically implanted with I^1 slightly larger than I^2 (judging from the remaining roots), strong vertical upper and lower canine with rounded crown sections, reduced and single-rooted P_2, P_3 as large as P_4, simple with their crown obliquely orientated and high protoconid, M_1 with low paraconid, metaconid widely separated from protoconid, and buccodistally projecting hypoconulid. Very reduced P^2, broad upper molars with well-developed cingulum surrounding the crowns, very slight hypocone swelling on M^1 and M^2 and strongly reduced paraconule and metaconule, lingually bent paracone and metacone on M^2. Mesiodistally reduced M^3. Differs from *Eosimias* species by its larger size, less reduced P_2, more simple P_4 and P^3, M_1 with less oblique cristid obliqua and trigonid only slightly higher than talonid, and by its upper molars with very small conules. Differs from *Catopithecus* and *Oligopithecus* by the retention of P^2_2, its single-cusped P_4, its P_{3-4} of about the same size, its hypoconid non-twinned with entoconid on lower molars, its upper premolars without inner cusps, and by its broader upper molars with only very slight hypocone swelling. Differs from *Proteopithecus* by its deeper lower jaw, its P_2 smaller than P_3, its more simple P_4, its M_1 paraconid in mesiolingual position and non-twinned hypoconulid and entoconid, its upper premolars lacking an inner cusp, and by its upper molars without well-developed hypocone (dimensions in Table 1).

Etymology: Genus name after Bahin village, and species name after the stratigraphic

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[1] Institut des Science de l'Evolution, Université Montpellier-II, case 064, 34095 Montpellier cedex 5, France. [2] Department of Geology, University of Pathein, Myanmar. [3] Department of Mineral Resources, Geological Survey Division, Paleontological Section, Rama VI Road, Bangkok 10400, Thailand. [4] Geology Department, University of Yangon, Yangon, Myanmar. [5] Office of Strategic Studies, Ministry of Defence, Yangon, Myanmar.

*To whom correspondence should be addressed. E-mail: ducrocq@isem.univ-montp2.fr

level (Pondaung Formation), where the specimen was discovered.

Although *Bahinia* possesses several characters that can be observed in adapiforms and omomyids (for example, strongly developed lingual cingulum on upper molars as in *Sivaladapis*, large and vertical canine, loss of $P^1{}_1$, and unfused symphysis as seen in adapiforms, single-rooted and reduced P_2 as in omomyids and tarsiers), these features can also be seen in archaic anthropoids (*3–5*). However, the combination of the symphyseal structure, the deep horizontal ramus, the obliquely oriented $P_{3\text{-}4}$ with their mesial root somewhat more labial than the distal one, the M_1 trigonid with protoconid enlarged and widely separated from the metaconid, the vertically implanted upper incisors, and the weakly developed hypocone on upper molars justifies placement of *Bahinia* within basal anthropoids.

Bahinia has a symphyseal region that is dorsoventrally deep and anteroposteriorly abbreviated, thus resembling other anthropoids, including amphipithecids (*1*), whereas the symphysis in adapiforms and omomyids is much lower and procumbent. Similarly, the retention of three lower and upper premolars is a feature shared between *Bahinia* and the African anthropoids *Proteopithecus* and parapithecids, and *Amphipithecus*, although some derived adapiforms (*Mahgarita*) have attained the single-rooted P_2 condition. On the other hand, the obliquely oriented $P_{3\text{-}4}$ in *Bahinia* also occurs in parapithecids and in the Asian *Eosimias* and *Amphipithecus*. The trigonid configuration of M_1 observed in *Bahinia* with an enlarged protoconid well separated from the smaller and slightly distal metaconid is common in anthropoids but very unusual in adapiforms and omomyids in which both cusps are similar in size and closer to each other. The lower and upper canine of *Bahinia* are very large and have a circular section, and the upper incisors (judging from the remains of roots) are vertically implanted with the central incisor larger than the lateral one. This configuration is similar to that of the archaic anthropoid *Catopithecus* and later anthropoids and adapiforms but unlike that of omomyids, in which the lateral upper incisor is larger and the canine small (*9, 10*). The shape of the incisors in *Bahinia* cannot be inferred from the available remains. In addition, the vertically implanted incisors in *Bahinia* contrast with the forward-jutting front teeth of omomyids. Finally, *Bahinia* is characterized by broad upper molars with a strongly developed basal cingulum and poorly developed hypocone on its distolingual part. The continuous lingual cingulum is present in propliopithecines and oligopithecines, as well as some parapithecids. Most of Eocene and Oligocene anthropoids from North Africa display a well-defined hypocone, and *Oligopithecus* possesses upper molars with a small crestiform hypocone, resembling that of *Bahinia*. In sum, *Bahinia* displays a combination of mandibular and dental characters that precludes it from adapi-

Table 1. Dental measurements (in millimeters) of *B. pondaungensis*. Length from C to M/1, 11.4 mm; length from I1/ to M2/, 17.8 mm. Asterisks indicate minimal values.

	Length	Width
r P/2	1.8	1.6
r P/3	2.6	2.0
r P/4	2.6	2.3
r M/1	3.0	2.4
r I1/	1.2	1.3
r I2/	1.2	0.8
r C	3.3	2.9
r P2/	1.5	1.8
r P3/	2.3	3.0
r P4/	1.7*	3.6*
r M1/	2.9	4.1
r M2/	3.0	4.2
l C	3.0	3.0
l P2/	1.6	1.4
l P3/	2.6	2.9
l P4/	2.2	3.5
l M1/	3.0	4.2
l M2/	3.0	4.3

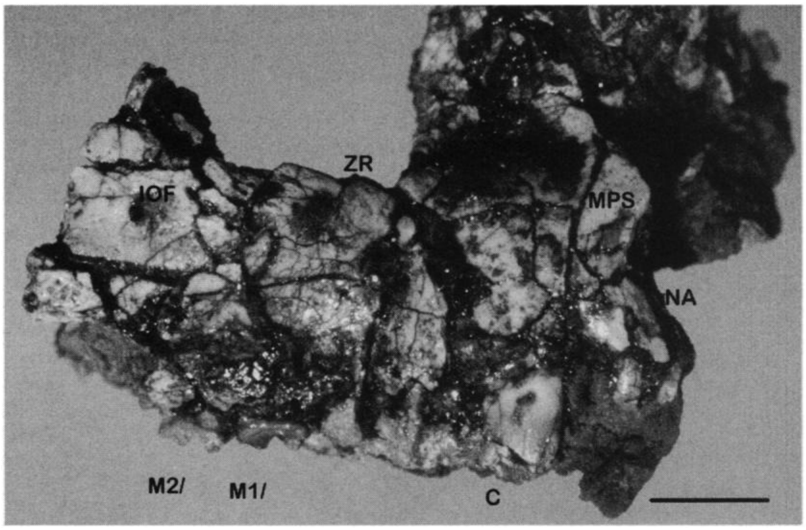

Fig. 1. *Bahinia pondaungensis* gen. et sp. nov., right maxillary in labial view showing position of the infraorbital foramen (IOF), the zygomatic root (ZR), the maxillary-premaxillary suture (MPS), and of the nasal aperture (NA). Scale bar, 5 mm. Photo by P. Aventurier, (Gamma).

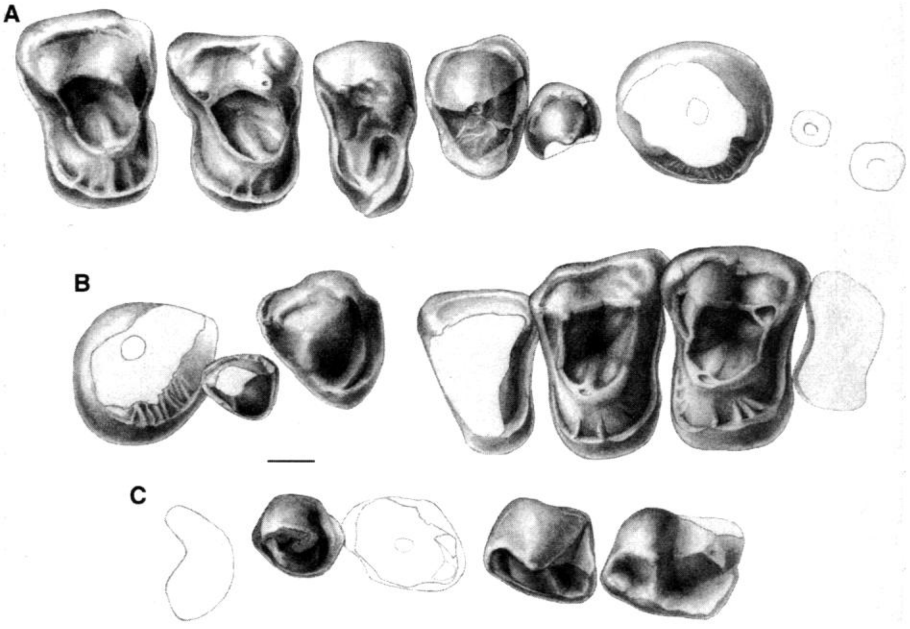

Fig. 2. *Bahinia pondaungensis* gen. et sp. nov. (**A**) Occlusal view of right maxillary (NMMP 15). (**B**) Occlusal view of left maxillary (NMMP 14). (**C**) Occlusal view of right dentary (NMMP 16). Scale bar, 1 mm (drawings by L. Meslin).

forms and omomyids and reinforces the hypothesis that *Bahinia* is a basal anthropoid.

Although *Bahinia* shares several characters with anthropoids (*11*) (the very deep horizontal ramus of the lower jaw; the small but distinct medial hypoconulid; the bent protocone and protoconid of P^4_4 and M^1_1; the nonwaisted P^3 and P^4; upper molars with strong lingual cingulum, extremely reduced paraconule and metaconule, and with strong pre- and postprotocone crista; the uninterrupted and sharp metacrista), its primitive retentions are extremely important because they allow one to reconstruct the hypothetical ancestral dentition and molar structure of anthropoids and therefore to infer their origins. However, *Bahinia* exhibits three features that seem to have appeared first in the evolution of the group: the depth of the lower jaw, the obliquity of the lower premolars relative to the longitudinal axis of the tooth row, and the development of the metacrista.

Bahinia is very likely more related to *Eosimias* than to any other anthropoid, with which it shares the association of vertical lower canine, loss of P_1, single-rooted and reduced P_2, large P_3 and P_4 with the similar obliquely orientated crown with a small hypoconid and talonid basin, similar lower M_1 structure, and broad and waisted upper molars with strongly developed basal cingulum and very weak or even absent hypocone. However, several differences between both genera fully justify the erection of the new Myanmar taxon: *Bahinia* is significantly larger, with its weight estimated from M_1 and M^1 size of approximately 400 g (*12, 13*), and its P_2 is less reduced with its crown obliquely directed and somewhat wider than long. P_3 is also larger and more similar to P_4 than in *Eosimias*, and there is no labial cingulid on P_3 and P_4. The P_4 of *Bahinia* does not have paraconid or metaconid cusp, its M_1 shows a more mesially directed cristid obliqua, and its entoconid is not mesially displaced as in *Eosimias*. Therefore, *Bahinia* confirms the anthropoid nature of the Eosimiidae, which might represent the sister group of the more advanced Asian Amphipithecidae (*1*) and of all other anthropoids.

Bahinia can be distinguished from *Tarsius eocaenus* (*3*) and *Xanthorhysis* (*14*) by its M_1, with the trigonid and talonid about the same width, the hypoconulid situated closer to the hypoconid, the metaconid lower than the protoconid, the entoconid more distal relative to the hypoconid (except in *Xanthorhysis*), and by the less developed entocristid (except in *Xanthorhysis*). *Xanthorhysis* further differs from *Bahinia* in its more reduced P_3, its P_4 with metaconid, and in its well-developed buccal cingulid of all lower cheek teeth. Comparison with extant *Tarsius* shows many differences, indicating a more derived status for *Bahinia* for most of the dental characters. For instance, the lower premolars of *Tarsius*, especially P_3 and P_4, are much smaller and are aligned with the tooth row, whereas they are oblique in *Bahinia*. The P^{3-4} of *Bahinia* are not waisted. Modern *Tarsius* dentition also shows specialized characters which are not shared with *Bahinia*, and resemblances between both taxa therefore concern only primitive characters which are numerous in *Tarsius*, thus suggesting that if *Bahinia* originated from a tarsiid ancestor, the divergence very likely occurred well before the middle Eocene. *Afrotarsius*, a Fayum tarsiiform (*15*), has been recently related to Eosimiidae (*16*). However, *Afrotarsius* displays lower molars with much more acute cusps, a more protruding shelf-like paraconid, a metaconid opposite to the protoconid, a mesiodistal cristid obliqua, a strong labial cingulum, and a more distal entoconid.

On the other hand, *Bahinia* exhibits a combination of features that distinguishes it from most omomyids and adapiforms and that is rather reminiscent of the condition in tarsiids: strongly developed lower canine, rather rectangular and short M_1, broad and lingual paraconid not closely connate with metaconid, tall hypoconid, and distinct entocristid. Also, the anterior upper dentition of *Bahinia* more closely resembles that of *Tarsius* rather than that of omomyids.

We have recognized only four derived characters that we consider as autapomorphic for *B. pondaungensis*: the large size of the P_3 (nearly as large as P_4), the reduction of the conules on upper molars (which may be related to the development of sharp-crested cheek teeth adapted to specialized feeding habits of *Bahinia*), the lingually bent paracone and metacone of M^2, and the strong mesiodistal reduction of M^3.

The set of primitive characters with derived anthropoid features in *Bahinia* is unique for an Eocene primate. It is especially the case for the structure of the upper molars, with a continuous cingulum without differentiation of a true hypocone (also characterizing *Eosimias*), and for the development of the parastyle, of the cingular and of the metastylar shelf of the upper molars, which are characters that are only found among the late Paleocene [*Altiatlasius* (*17*)] and Early Eocene primates [*Altanius*, *Teilhardina* (*18*)]. On the lower molar, the retention of a cuspidate paraconid also represents a primitive character. Regarding these features, retained for some 20 million years, *B. pondaungensis* appears as a "Middle Eocene living fossil." Its evolutionary stage is indicative of an extremely old age of differentiation for the anthropoids, as already suggested (*4, 19, 20*), and more strongly supports tarsiid than adapiform or omomyid affinities for the earliest anthropoids.

Africa has a diverse fossil record of anthropoids starting from the Middle Eocene (*19, 20*). However, the Eosimiidae are the most primitive group of anthropoids recorded so far, and their widespread occurrence in Asia supports an origin for that clade on that continent. Another point concerns the phylogenetic relationships between the Asian and African anthropoids. Several primitive anthropoid taxa have been described from the Fayum (*20*). They indicate that Africa was also an important center of radiation of anthropoids during the Eocene. The sister-group relationships between Eosimiidae and Amphipithecidae are likely, but their relationships with the Oligopithecidae, Propliopithecidae, Parapithecidae, Platyrrhini, and Catarrhini now have to be re-examined. Additional Eocene African anthropoids must be discovered in order to establish these relationships. Finally, several other Asian Eocene primates, including *Kohatius* (*21*), *Panobius* (*22*), *Lushius* (*23*), *Wailekia* (*24*), and *Hoanghonius* (*25*), show some overall resemblances with *Bahinia*, but they have been previously attributed either to Adapidae or to Omomyidae. However, the occurrence of these primates in the Eocene of Asia seems to testify to a highly diversified Eocene Asian radiation of anthropoid and nonanthropoid primates equivalent to that of the African Late Eocene anthropoids (*20*).

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26. B. Marandat prepared the material and L. Meslin drew Fig. 2. Photograph is from P. Aventurier (Gamma). Our thanks go to the Fyssen and the Singer-Polignac Foundations. This is publication ISEM 99-079.

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