A new Late Eocene primate from the Krabi Basin (Thailand) and the diversity of Palaeogene anthropoids in southeast Asia

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According to the most recent discoveries from the Middle Eocene of Myanmar and China, anthropoid primates originated in Asia rather than in Africa, as was previously considered. But the Asian Palaeogene anthropoid community remains poorly known and inadequately sampled, being represented only from China, Myanmar, Pakistan and Thailand. Asian Eocene anthropoids can be divided into two distinct groups, the stem group eosimiiforms and the possible crown group amphipithecids, but the phylogenetic relationships between these two groups are not well understood. Therefore, it is critical to understand their evolutionary history and relationships by finding additional fossil taxa. Here, we describe a new small-sized fossil anthropoid primate from the Late Eocene Krabi locality in Thailand, Krabia minuta, which shares several derived characters with the amphipithecids. It displays several unique dental characters, such as extreme bunodonty and reduced trigon surface area, that have never been observed in other Eocene Asian anthropoids. These features indicate that morphological adaptations were more diversified among amphipithecids than was previously expected, and raises the problem of the phylogenetic relations between the crown anthropoids and their stem group eosimiiforms, on one side, and the modern anthropoids, on the other side.

1. Introduction

The Krabi locality has so far revealed only one large-sized anthropoid, Siamopithecus eocaenus [1–3]. According to its morphological characters, it was recognized as the largest known amphipithecid anthropoid. However, the anthropoid status of amphipithecids is still controversial. Authors have considered them as crown anthropoids [4–7], as sister group of the crown clade [8], as basal anthropoids [9–11] or as adapids [12,13]. However, their diversity is considerably limited compared with that of the African anthropoids. Here, we describe a maxilla fragment of a new small-sized fossil anthropoid primate from the Late Eocene Krabi locality, which shares several derived characters with the amphipithecids. It displays several unique dental characters, such as extreme bunodonty and reduced trigon surface area, that have never been observed in other Eocene Asian anthropoids. These features indicate that morphological adaptations were more diversified among amphipithecids than was previously expected, and raises the problem of the phylogenetic relations between the crown anthropoids and their stem group eosimiiforms, on one side, and the modern anthropoids, on the other side.

2. Krabi fauna and age

The Krabi coal mine is located in Krabi Province, Peninsular Thailand. It is the only Thai Palaeogene deposit yielding anthropoid primates. Many mammalian fossils have been collected from this locality during nearly three decades, mostly from the main coal seam, in three separate pits that were opened...
successively: Wailek, Bang Pudam and Bang Mark. It has yielded the most diversified Late Eocene land mammal community in southeast Asia, and it is therefore considered as a reference locality for this time period. The Krabi mammalian fauna consists of several original taxa: anthropoitheres largely dominate the fauna, being represented by several genera and species [14,15], while other taxa include tayassuids [16], suids [17], helohyids [18], ruminants [19,20], rhinocerotids [21,22], carnivores [23,24], baluchimyid rodents [25], megachirotetan bats [26] and dermopterans [27]. The faunal assemblage and local lithology indicate the occurrence of lakes, swamps and marshes surrounded by dense and forested vegetation [28].

Up to now, six distinctive primate taxa have been described from Krabi, including anthropoids and strepsirrhines. *Siamopithecus eocaenus* represents the most complete anthropoid primate yet discovered from Paleogene deposits in southeast Asia. It is represented by two mandible fragments, one fragment of maxilla and two maxillae with partial artits [1–3]. Its body mass was estimated at about 6–8 kg. *Siamopithecus* shares its anthropoid characters with *Pondaungia*, *Amphipithecus*, *Myanmarpithecus* and *Ganlea* from the Late Middle Eocene Pondaung Formation, Myanmar [1,5,29–31]. However, despite the number of synapomorphies shared with other crown anthropoids and the phenetic analysis of its facial anatomy, some authors are still reluctant to consider it as an anthropoid [32]. More recently, an isolated upper molar of a small amphipithecoid of body weight estimated about 300 g has been described [33]. Some strepsirrhine primates have also been described from this site, including a right mandible referred to *Wailekia orientale*, with body weight estimated at 1.5 kg, which was originally assigned to anthropoids because of its similarity in molar pattern to *Oligopithecus*, an African Oligocene anthropoid [34]. It was reinterpreted as a sivaladapid based on its resemblance to *Hoanghonius stehlini*, a Chinese Eocene strepsirrhine [35]. In addition, a nearly complete left mandible of a small adapiform, *Naungthanhoinis siamii*, revealed distinctive dental traits, including a double-rooted P3 and a molarized P4, with a body weight estimated at 365 g [36]. It has been referred to a new subfamily, the *Ekgmowechashalinae*, together with the Early Oligocene *Bugtipithecus* from Pakistan and the Early Miocene *Ekgmowechashala* from North America [37]. Moreover, there is an isolated lower molar referred to a large-sized adapid collected from a small lignite bed located about 20 m above the top of the main fossiliferous lignite layer and associated with the type-specimen of *Siamotherium krabiense* [14] that can be tentatively referred to *Wailekia cf. orientale*. The Krabi sediment has been accurately dated through magnetostratigraphic analysis, which, combined with the biochronological data obtained from fossil mammals, indicates a best correlation to magnetic chron C13r (34.78–33.73 Ma) or C12r (33.26–31.11 Ma) corresponding to a terminal Eocene age or an Early Oligocene age, according to the most recent calibration of the Eocene–Oligocene boundary (33.9 Ma) [38] (M. Benammi 2012, oral communication). But taking into account its similarity to the other Asian Middle–Late Eocene mammalian faunas and the absence of typical Oligocene taxa, we support a latest Eocene age for the Krabi locality (C13r: 34.78–33.73 Ma).

### 3. Systematic paleontology

Order Primates Linnaeus, 1758

Suborder Haplorhini Pocock, 1918

Infraclad Anthropoidea Mivart, 1864

Family Amphipithecidae Godinot, 1994

*Krabia* gen. nov.

**Type-species**: *Krabia minuta* sp. nov.

**Holotype**: MPFT-05-1, a maxillary fragment preserving the crowns of left P4–M2 (M3 represented only by small root fragment) and right M1–M2 (figure 1). The specimen is housed in Paleontology Collections, University of Poitiers, France. Tooth dimensions are given in table 1.

**Type-locality**: Krabi main coal seam, Bang Mark pit, Krabi Province, Peninsula Thailand.

**Age**: Latest Eocene.

**Diagnosis**: Small amphipithecoid anthropoid primates, similar in size to *Phenacopithecus*, much smaller than other Eocene amphipithecoid primates. Characterized by subtriangular upper molars having rounded corners, upper molars unwaisted, bunodont, low and vertical cusps, closed trigon, smooth enamel, absence of buccal cingulum, hypocone, paricone and conules, very strong and complete lingual cingulum, weak parastyle and metacone, and M2 buccal wall oblique with paracone more expanded buccally than metacone.

Diffs from other amphipithecoids (*Siamopithecus, Pondaungia, Ganlea, Myanmarpithecus* and *Bugtipithecus*) by the absence of buccal cingulum, hypocone, paricone and conules, presence of strong and complete lingual cingulum, smooth enamel, closed trigon, and weak parastyle and metacone.

Diffs from eosimiiforms (*Eosimi, Phenacopithecus, Bahinia, Philosimi* and *Afrasia*) by its broad and unwaisted upper molars, low cusp relief, absence of buccal cingulum and conules, more buccal position of its paracone and metacone, weak parastyle and metacone, strong and complete lingual cingulum and smaller trigon.

Diffs from omomyids and tarsids by less triangular shape of molar, no buccal cingulum, and no hypocone and conules.

Diffs from sivaladapids (*Guangxilemur* and *Hoanghoni*) by the absence of buccal cingulum, buccal shearing crests, mesostyle, hypocone, paricone and conules, weak parastyle and closed trigon.

**Etymology**: The genus name derived from Krabi Province and species name from its small size.

**Description**: *Krabia minuta* holotype is a maxilla fragment with five teeth preserved, left P4–M2 and right M1–M2. P4 and M2 are rather worn with little enamel left, indicating the rather old age of this individual. A remnant of a tiny lingual root fragment of left M2 is also present. Post-mortem deformation has altered the natural position of the teeth during life, so that the right and left tooth rows are no longer exactly symmetrical.

P4 is very worn. However, the overall outline is preserved. The buccal wall is longer than the lingual wall, as in the molars. Therefore, its outline is neither as rectangular nor as transverse as those of *Myanmarpithecus* and *Ganlea*. It bears two main cusps: a large and centrally located paracone on the buccal margin of the crown and a much smaller protocone on the lingual wall. Both seem to have been connected by a mesial crest resulting from fused preproto- cristae and hypoparacristae, as on the molars. The distal part of occlusal surface is completely worn, and no details can be observed. The lingual cingulum appears to be nearly continuous on the lingual margin of the crown and may have
joined parastyle and metastyle as on the molars. P₄ has three conical roots, two of which are small and located buccally, and one of which is large and located lingually (figure 1b).

M₁ is rather worn but clearly shows a broadly trapezoidal outline with a longer buccal wall, smooth and rounded corners. The crown is bunodont, bears smooth enamel and is unwaisted. The buccal wall is nearly straight, lacks a buccal cingulum, and is delimited by two weak styles, parastyle and metastyle, which are oriented in line with the two main buccal cusps. The paracone and metacone are situated near the buccal margin of the crown and are sub-equal in size. The lingual cingulum is strong and complete, joining parastyle to metastyle. At the latest stage of wear, the protocone becomes confluent with the lingual cingulum. M₂ has three roots, two small buccal (mesial is smaller than distal root) and one large lingual with a vertical groove (figure 1b).

M₂ shows similar morphology to M₁ but differs by its larger size, oblique buccal wall and more lingually located metacone. Postparacrista and premetacrista are short but well expressed. Parastyle and metastyle are very reduced, and located mesially and distally to the main buccal cusps. The protocone is the main cusp and is situated closer to the metacone. It is connected to the main buccal cusps by two crests, preprotocrista and postprotocrista. The former structure fuses with the hypoparacrista, yielding a continuous and elevated crest that joins the paracone. The postprotocrista connects the metacone, through the hypometacrista, isolating a rather deep but small trigon basin having a more or less rounded outline. This distal crest is less continuous than the mesial one and is more or less interrupted by a depression in its middle. The preprotocrista–hypoparacrista crest is higher and stronger than the distal one, but both connect the protocone to the apex of the two main buccal cusps. There are no conules, nor even any incipient trace of them. A strong, low and complete cingulum surrounds all but the buccal margin of the tooth, joining the parastyle to the metastyle. There is no evidence of hypocone and pericone. Numerous little enamel ridges link this lingual cingulum to the lingual wall of the protocone, a character also observed on upper molars of Bahinia. The enamel surface is smooth. M₂ has three roots (two buccal and one large lingual). The disto-buccal root is lingually displaced and all three roots bear a vertical groove on their internal side (figure 1b).

M₃ is represented by a tiny root fragment that can only be observed on micro CT scan images as shown in figure 1b,c.
(a) Comparison with other Asian anthropoids
Several Middle and Late Eocene anthropoid primates have been described from Asia, and among them seven originate from Pondaung Formation, Myanmar (Pondaungia, ‘Amphipithecus’, Bahinia, Myanmarpithecus, Eosimias, Ganlea and Afrasia [5,7,30,39–42], two from China (Eosimias and Phenacopithecus) [43–45], one from Thailand (Siamopithecus) [1–3] and two Early Oligocene anthropoid primates from Pakistan (Bugtipithecus and Philosimias) [4].

Small-sized Asian Palaeogene anthropoid primates Afrasia, Bahinia, Eosimias, Phenacopithecus and Philosimias are grouped within the Eosimiiformes [7]. This group is now considered as stem anthropoids [7,9,10]. Phylogenetic relationships within the amphipithecids have been studied by several authors [4–7,9,10,46]. Some phylogenies consider Siamopithecus as the most basal genus, followed by a dichotomy between Ganlea + Myanmarpithecus and Pondaungia + ‘Amphipithecus’. This topology led to the definition of a new subfamily for Siamopithecus (the Siamopithecinae) and to grouping the other Burmese taxa within the Amphipithecinae [5]. Other authors have obtained slightly different phylogenetic relationships within amphipithecids, but this group always remains monophyletic [4,5,7,10].

(i) Comparison with Eosimiiformes
*Krabi*a shares several characters with eosimiiforms, such as a closed trigon basin with a complete lingual cingulum, and the absence of hypocone and conules. But *Krabi*a differs from eosimiiforms by its broad and unwaisted molars, bunodont cusp pattern, absence of buccal cingulum and buccal stylar shelf, reduced area of its trigon basin, which is more elongated buccolingually in Bahinia, and the more buccal position of its paracone and metacone. But, as in Bahinia and Phenacopithecus, it develops complete mesial and distal crests connecting the protocone to the buccal cusps and lacks any trace of conules. It has a more complete and stronger lingual cingulum than *Afrasia* and it lacks the conule cristae (preparaconule and postmetaconule) that connect these conules to the parastyle and metastyle, respectively.

(ii) Comparison with Amphipithecidae
Compared with Siamopithecus, *Krabi*a shares several derived characters, such as the absence of a buccal cingulum, the position of the buccal cusps on the buccal edge, the absence of conules and the reduced metacone on M2. But *Krabi*a differs from Siamopithecus by the absence of a hypocone, complete lingual cingulum, stronger connection between protocone and buccal cusps, M1 smaller than M2, smooth enamel, and not slanted lingual and buccal walls. In Siamopithecus on M1–M2, the hypocone is firmly connected to the protocone by a distally oriented crest, neither distolingual nor buccal cingulum are present, the buccal and lingual faces of P4–M3 are well expanded bilaterally, and the paracone is pointed and much higher than the protocone on P4.

Amphipithecines are represented by three distinct genera so far restricted to the Eocene deposits of Myanmar: Pondaungia, Myanmarpithecus and Ganlea. They share many derived characters that unite them within the same subfamily but most of these characters concern the lower jaw, the lower dentition and especially the premolars. Upper premolars and molars of amphipithecines are represented by a smaller number of specimens than the lowers. However, some shared characters can be recognized, such as the reduction of the buccal stylar shelf, the buccal position of paracone and metacone, the reduction of styles and conules, the strong and continuous development of the lingual cingulum, and the strong development of the protocone–paracone connection.

*Krabi*a shares more similar characters with the small-sized amphipithecids (Myanmarpithecus and Ganlea) than with large-sized amphipithecids, such as bunodont cusps, complete lingual cingulum, and the absence of buccal cingulum, hypocone, pericone and conules. Ganlea, which is only known from one upper molar, displays main cusps with preprotocrista ending at the mesial end of paracone, without continuity with the hypoparacrista. A posterior bucco-lingual weak crest unites the hypometacrista issued from a reduced metacone to the distal extremity of the postprotocrista. This peculiar connection is also present in Pondaungia and Siamopithecus, but not in Myanmarpithecus. The protocone of Ganlea is located more lingually and the trigon basin appears to be rather larger, in contrast to that of Krabi*a. Also, the metacone is not displaced lingually as it is in Krabi*a. In addition, the lingual cingulum of Ganlea is weaker and incomplete, being interrupted behind the protocone. The P4 are more similar, both taxa showing a well-developed anterior connection between protocone and paracone, and a lingual position of the protocone. But they differ in their occlusal outline, the buccal part of Krabi*a P4 being notably longer than its lingual part. The same resemblances are shared with Myanmarpithecus. This taxon displays more resemblance with Krabi*a, possibly because it has kept more numerous amphipithecines plesiomorphic characters on its upper molars. Krabi*a is smaller than Bugtipithecus, an amphipithecid from Pakistan and differs from it by the absence of buccal cingulum, hypocone and metacone, unwaisted outline, and more bunodont cusps.

(b) Comparison with Asian Adapiformes
Sivaladapids have been reported from the Middle and Late Eocene of China (Honghominis, Rencunius and Guangxilemur), Myanmar (Paukkaungia and Khitanaungia) and Thailand (Wailekia), and from the Early Oligocene of Bugti, Pakistan (Guangxilemur) [34–36,47–50].

Several characters of Krabi*a upper molars distinguish them from those of sivaladapids. The buccal and lingual cingula of sivaladapid upper molar are well developed, but Krabi*a has only lingual cingulum well developed. There is a well-developed hypocone and a small pericone on
**Hoanghonius, Rencuntius and Guangxilemur upper molars, but these cusps are absent on Krabia.** The trigon basin on the upper molars of sivaladapids is not closed, as it is in Krabia, because the preprotocrista and postprotocrista are directed to parastyle and metastyle. The increased development of external shearing crests with strong parastyle and mesostyle in *Hoanghonius* and *Guangxilemur* contrast with the weak development and the reduced styles in *Krabia*. Sivaladapids’ upper molars, like those of *Hoanghonius* from the Late Eocene of China, display a very distinctive morphology with more largely open trigon, large trigon basin, and preprotocrista and postprotocrista that reach rather tiny conules but not paracone and metacone, strong postparacrista and premetacrista, often connected to a mesostyle, also connected to buccal cingulum. The lingual cingulum of sivaladapids is usually very complete and strong, as in *Krabia*, but often displays incipient hypocone and pericone, which are not present in *Krabia*. In *Guangxilemur*, the trigon is very wide, and preprotocrista and postprotocrista reach lingual cingulum just in front of parastyle and metastyle. In fact, only a very strong and complete lingual cingulum is shared between *Krabia* and the sivaladapids. Other Asian adapids display the more primitive bauplan of the upper molar: widely open trigon, preprotocrista and postprotocrista displaying a wide angle, and joining conules rather than buccal cusps. Most of the Asian adapids develop a distinct true hypocone on their lingual cingulum. In conclusion, there is no Asian adapid that displays tooth morphology similar to that of *Krabia*.

The body size of *Krabia* is estimated between 225 and 235 g. It is much smaller than those of *Weiilekia* and *Muangthanhnius*, the other strepsirrhines from the same locality (1200 and 365 g, respectively). A medium-sized sivaladapid, *Weiilekia* has been described from Krabi locality, but it is represented only by lower molars, which are larger than the upper molars of *Krabia* and display foliolar adaptations. M1 or M2 of an indet. amphipithecid (TF 3475) from Krabi coal mine shares a few similarities with those of *Krabia*, including its outline, the buccal position of paracone and metacone, the reduced parastyle and metastyle, and the complete lingual cingulum, whose development is nevertheless much more moderate. But the protocone is not connected to paracone and metacone, there is a distinct buccal cingulum, and there is a small hypocone developed on the posterior cingulum, which is connected to the protocone by a very distally oriented crest. It is mainly on the basis of that character, associated with the absence of conules, that this tooth was attributed to amphipithecids [32]. However, TF 3475 shares several characters with *Bugtilemur* such as complete lingual cingulum, buccal position of paracone and metacone, partial buccal cingulum and a disto-buccal crest issued from the protocone. But in *Bugtilemur*, this crest does not join a small hypocone, developed on the posterior cingulum, as on TF 3475. Another resemblance concerns the connection between metacone and protocone. A tiny hypometacrista joins the base of the buccal wall of the protocone at the middle, as on the holotype of *Bugtilemur*. The preprotocrista joins the parastyle and no conules are present as on TF 3475. The main difference between *Bugtilemur* and TF 3475 upper molar therefore concerns the development of an incipient hypocone and its connection to the protocone. According to these numerous similarities, we reallocate TF 3475 to the genus *Muangthanhnius*, which was so far only documented by a lower jaw fragment, and therefore to a strepsirrhine.

### 4. Phylogenetic analysis

In order to understand *Krabia*'s phylogenetic position within the evolutionary tree of primates, we performed a phylogenetic analysis based on a data matrix, including 33 taxa and 316 characters (see the electronic supplementary material). For the analysis, we used the characters and character states from previous phylogenetic analyses [5,7,51]. The parsimony analysis was undertaken using PAUP v. 4 b 10 [52]. A single most parsimonious tree was recovered with a length of 1278 steps, a consistency index of 0.37 and a retention index of 0.54.

*Krabia* is grouped within the Amphipithecinae, with *Ganlea* as a sister group (figure 2) on the basis of several shared derived characters, such as absence of buccal cingulum, paracronule and metaconule, and very reduced to absent hypocone on upper molars. *Myanmarpithecus* is reconstructed as the sister group of *Krabia* + *Ganlea*, while *Siamopithecus* and *Pondaungia* appear as more basal genera of a monophyletic amphipithecid family. The monophyly of Amphipithecidae has been confirmed by several phylogenetic analyses [4–7,10,11,53,54], which also pinpointed the basal position of *Siamopithecinae*. Recently, Coster et al. [11] have proposed a new interpretation concerning the dental homology of the hypocone of *Pondaungia*, interpreting it as a displaced metaconule. This interpretation had an immediate impact on the phylogenetic position of that group. In their new phylogenetic analysis, amphipithecids became basal anthropoids. However, the monophyly of amphipithecids is not affected and the cusp re-interpretation concerns only the most specialized amphipithecids. *Krabia minuta* is devoid of hypocone and metaconule, suggesting that the metaconule has been lost in this branch and that the disto-lingual cusp of its upper molars was either lost or never has developed, underlining again the high diversity shown by amphipithecids in their dental characters. Until now, the Amphipithecinae, to which *Krabia* is referred, have been considered endemic to central Myanmar. But the phylogenetic position of *Krabia* point out a larger distribution area within southeast Asia. However, owing to the lack of lower pre-molar and molar information, its phylogenetic position within Amphipithecidae is still a matter of uncertainty, as indicated by the low or moderate Bremer indices and bootstrap values, and will have to be confirmed by additional discoveries.

*Bugtilemur*, an Early Oligocene primate from Pakistan, originally allocated to the Amphipithecidae, appears here as the sister taxa of all crown anthropoids. Several other analyses confirm this position, even in those where the Amphipithecidae are excluded from the crown anthropoids [8,10,54]. This position, at the basis of catarrhines, platyrhines and amphipithecids, has also recently been obtained [11] and reinforces the scenario of a single Asian origin for these groups. In addition, it demonstrates the occurrence in Asia of a third distinct family of anthropoids that we propose to name the Bugtiplethiidae.

Finally, in all recent analyses, including the present one, amphipithecids appear to be clearly grouped within the anthropoids. Half of the above-mentioned phylogenetic analyses identify them as stem anthropoids, others as crown anthropoids, and therefore there is still no consensus concerning their position within the anthropoid tree, as indicated by the low Bremer indices. This uncertainty is due to the low number of fossils (mostly represented by
lower jaws), the absence of significative cranial remains and the scarce post-cranial remains.

5. Feeding adaptation

*Krabia minuta* is a small-sized anthropoid primate with an estimated body weight of 225–235 g on the basis of M1 area (left and right M1), according to the regression proposed by Bajpai *et al.* [54]. Its body weight estimates are therefore similar to those obtained for *Phenacopithecus* (235 g) by the same authors. Its body weight places *Krabia* below ‘Kay’s threshold’ of 500 g, below which primates cannot be obligate folivores owing to fundamental metabolic constraints [55]. *Krabia* displays a very peculiar molar morphology. Its molar structure has nearly no shearing and cutting devices, indicating that it could not have had an insectivorous or a folivorous diet. Its cusps are very rounded and low, and the connecting crests are reduced. Low cusp relief with neither postparacrista nor premetacrista reflects the relatively weak development of the principal shearing crests and suggests a diet consisting mainly of fruits or gum. According to the diet categories defined by Kay & Covert [55], *Krabia* falls within the exclusive frugivore or gummivore primates. However, the hard seed diet option cannot be eliminated. Small primates displaying exceptionally poor molar shearing crest development must be recognized by having exhibited the potential for hard seed predation, a widespread feeding adaptation among amphipithecids [56,57]. But as for gummivores, the contribution of hard seeds in its additional regime cannot

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**Figure 2.** Phylogenetic positions of *Krabia minuta* within Palaeogene anthropoids. Tree length = 1278 steps; consistency index = 0.37; retention index = 0.54. Numbers above and below the branches are bootstrap values and Bremer indices, respectively.
be recognized since there is no trace of its anterior dentition, which is very striking for *Ganlea* [5]. Its molar row size, with an increasing surface from $P^4$ to $M^2$, is unlike that of *Siamopithecus*, which has $M^1$ larger than $M^2$, an adaptation for increasing masticatory forces. Its pattern of tooth size increase corresponds to the pleiomorphic condition seen in most primates. Also, its enamel is smooth, as in *Eosimia*, *Phenacopithecus*, *Bahinia*, *Bugtipithecus* and *Philosimia*, differing from the wrinkled enamel of *Pondaungia*, *Ganlea*, *Myanmarpithecus* and *Siamopithecus*, all showing adaptations for hard food. Wrinkled enamel is usually interpreted as related to a diet consisting of hard seeds. According to its dental characters, a diet predominantly based on fruits or gum appears as the most plausible feeding adaptation for this new genus of amphipithecids. Enamel thickness could also bring further information, but the enamel–dentine limit of *Krabia* could not be recognized on the micro CT scan images. However, the wear surfaces suggest that it had rather thin enamel, an additional point suggesting a fruit- or gum-dominated diet.

6. Discussion and conclusion

The Krabi primate fauna consists now of two amphipithecid anthropoids (*S. eocaenus* and *K. minuta*), an enigmatic tarsidiiform and two strepsirhines (*Wailekia* and *Muangthanhiniius*). The upper molar (TF 3475) described as an amphipithecid indet. is here referred to *Muangthanhiniius* and one isolated tooth of a previously sivaladapid indet. to *Wailekia* sp. Therefore, the total number of identified Krabi primates is reduced to five instead of six. Among them, *Krabia* is unique by its dental adaptations. Its bunodont molars, absence of hypocone and pericone, reduced shearing crests, inflated lingual cingulum and its small trigon represent a unique character association for Eocene Asian anthropoids, which may suggest possible relationships with modern anthropoids or convergent evolution. Some of these dental features also occur in some extant platyrhines, but most of these differ by the development of a hypocone on the distal cingulum, a characteristic feature of most African crown anthropoids and/or by more developed buccal shearing crests. The diversity of dental morphology among Eocene southeast Asian anthropoids is striking, and suggests a more important adaptive radiation and a wider variety of diets that could be expected, but their morphological characters are unlike those of African crown anthropoids, which reduces the probability of a possible African origin [58]. One important point concerns the understanding of the relationships between the stem eosimiforms and the amphipithecids. Until now, there has been no described fossil which documents the transition between these two groups. Eosimiformes have narrow and waisted upper molars without hypocone and very acute cusps in relation to their predominantly insectivorous diet. All known amphipithecids have less waisted upper molars with bunodont cusps, suggesting different diets. *Krabia* occupies an extreme position among these amphipithecids in relation to its peculiar diet probably dominated by fruits or gum. But it shares some derived characters with *Bahinia*, the dentally most advanced eosimiform, such as closed trigon, reduction or absence of conules, and direct connections between the protocone and the buccal main cusps. But the lack of information concerning the anterior and lower dentition of *Krabia* does not allow interpretation of these few characters as homoplastic features or shared derived characters. *Siamopithecus* displays very primitive lower premolars, more similar to those of eosimiforms than to those of amphipithecines. All these resemblances support a possible relationship between the eosimiforms and the amphipithecids, but the fossils bridging this gap have not yet been discovered and should be found in Early Eocene or Early Middle Eocene deposits. The importance of some characters, like the development of the hypocone, is still enigmatic. Eosimiforms have no hypocone. *Myanmarpithecus* has a small incipient true hypocone, differentiated from distal cingulum. *Siamopithecus* has a strong hypocone, related to the distal cingulum. *Krabia* has no hypocone and *Ganlea* has an incipient hypocone. *Pondaungia* and ‘Amphipithecus’ develop a disto-lingual cusp whose homology is debated. It has been interpreted as a true hypocone [59], as a pseudo-hypocone derived from the splitting of the protocone [60] and, recently, as a lingually displaced metacone [11]. Only *Bugtipithecus* develops a strong true hypocone, a character present in all African crown anthropoids. Therefore, only Asian anthropoids with true hypciones derived from distal cingulum can be taken into account to bridge the gap between Asian and African anthropoids. With the exception of *Bugtipithecus*, no Asian fossil can presently be considered to represent an ancestor of African crown anthropoids, and more discoveries have to be made in southeast Asia to complete the evolutionary history of the crown anthropoids.

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