

# A new amphicyonid (Mammalia, Carnivora, Amphicyonidae) from the late middle Miocene of northern Thailand and a review of the amphicyonine record in Asia

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## Abstract

Recent field research conducted in the middle Miocene basin of Mae Moh, northern Thailand, allow discovering dental remains of a new amphicyonid (Mammalia, Carnivora, Amphicyonidae). A thorough comparison with all known Asian and non-Asian Miocene genera of Amphicyonidae supports the assignment of these specimens to a new amphicyonine, *Maemohcyon potisati* gen. et sp. nov. We propose the first review of the fossil record of the Amphicyoninae and we discuss the possible geographic origin and phylogenetic relationships of this new taxon. It appears that *Maemohcyon* does not have close relationships with contemporary (*Amphicyon*, *Pseudocyon*, *Ischyrocyon*, *Pliocyon*) or earlier (*Ictiocyon*, *Pseudarctos*, *Cynelos*, *Ysengrinia*) genera. We suggest that the *Maemohcyon* lineage probably arrived much earlier than 13 Ma (age of Mae Moh fauna) and evolved in this insulated region until the late middle Miocene.

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## 1. Introduction

Numerous Cainozoic basins have been discovered in northern Thailand since more than forty years ago (see Chaodumrong and Chaimanee, 2002, Fig. 1). Most of them have yielded a rich and diversified fauna and flora of Miocene age, among which mammals are the best-documented vertebrates with approximately 40 taxa (Ducrocq et al., 1994; Ducrocq et al., 1995). One of these basins is the coal deposit of Mae Moh, east of Lampang, 500 km north of Bangkok (Fig. 1). This small basin is 9 km wide, 16 km long, up to 900 m deep, and contains the largest open cast mine in Thailand, ca 8 km east–west and 7 km

north–south. The Mae Moh basin tectonic evolution has been extensively studied (Morley et al., 2001) and the deposit consists of three formations: Huai King, Na Khaem and Huai Luang formations. Only the Na Khaem Formation has yielded fossils of mammals. It is approximately 420 m thick and contains the main coal seams of the basin, interbedded with lacustrine claystones, mudstones and sandstones (Fig. 2). Research conducted in Mae Moh by other Thai–French teams since 1980 have yielded a poor faunal record so far, compared with localities like Mae Long in the Li Basin: two elephantoid proboscideans, *Stegolophodon* cf. *latidens* and a distinct but indeterminate species that may be an amebelodontid; an indeterminate Rhinocerotini cf. *Gaioatherium*; an indeterminate cervid; and two mustelid carnivorans (*Siamogale thailandica* and an indeterminate species) (Ginsburg et al., 1983; Ginsburg and Tassy, 1985; Tassy et al., 1992; see also Ducrocq et al., 1995). Based on the evolutionary level of the fauna, the age

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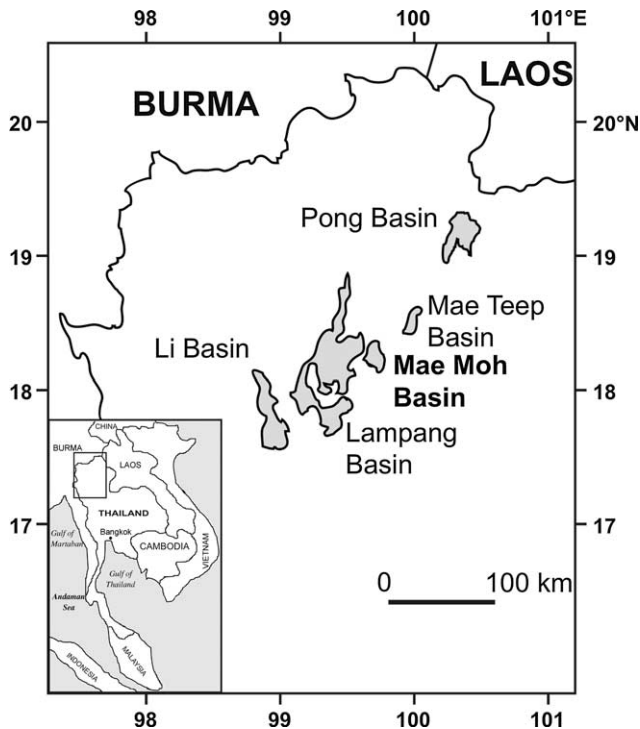


Fig. 1. Map showing the location of the Mae Moh mine, within the Miocene Basin of Northern Thailand (from Chaodumrong and Chaimanee, 2002).

of the Mae Moh fauna ranges from the middle part of the middle Miocene to the early late Miocene (Ginsburg and Tassy, 1985; Ducrocq et al., 1995). On the basis of paleomagnetic data, Benammi et al. (2002) have proposed an age of 12.8 Ma (i.e. late middle Miocene) for the member K1 of the K-lignite seam (see Fig. 2). During a field

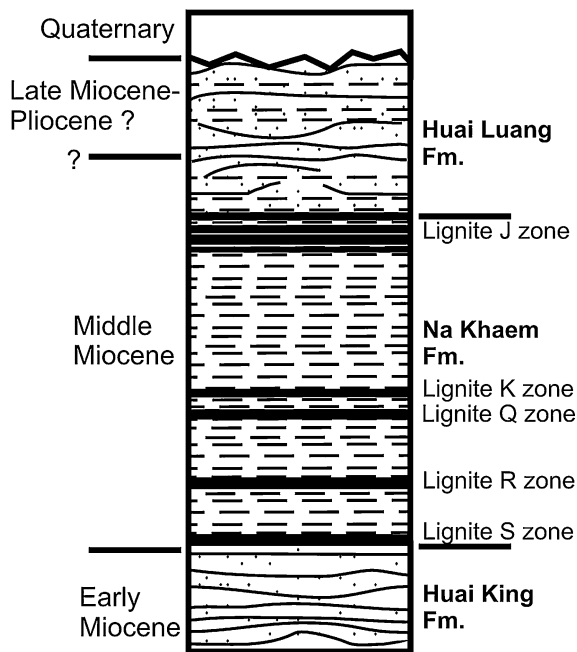


Fig. 2. Stratigraphic log of the Mae Moh mine, modified from Morley et al. (2001).

campaign in July 2000, dental remains of a large amphicyonid carnivoran were discovered from this member. This record is particularly significant because the Miocene Carnivora are poorly represented in Southeast Asia to date. Only three taxa (two mustelids and cf. *Amphicyon* sp.; Ducrocq et al., 1995) have been recognized from the Miocene of Thailand. In particular, the family Amphicyonidae is scanty in Asia while it displays a great diversity and a wide geographic distribution in Europe and North America, especially during its most important early-middle Miocene radiation (Hunt, 1996, 1998; Ginsburg, 1999). The new amphicyonid from Mae Moh represents an important discovery in the evolutionary and biogeographic context of this family; it is also the first well-documented species from Southeast Asia. So far, indeterminate remains of a small, amphicyonid-like species from the middle Miocene of Ban San Klang (Pong Basin, northern Thailand) assigned to cf. *Amphicyon* sp. (Ducrocq et al., 1995) and a lower incisor from the early Miocene of Hangmon (Sonla Province, northern Vietnam) assigned to *Amphicyon* cf. *giganteus* (Ginsburg et al., 1992) have been assigned to this family. In addition, the amphicyonid from Mae Moh potentially represents the latest known record of the Amphicyonidae in eastern Asia; no taxa younger than 13 Ma have been previously described from this area (Hunt, 1996). Qiu (2003) mentions *Amphicyon* sp. from the Chinese localities of Lufeng and Yuanmo (about 8 Ma), but this remains to be confirmed.

Abbreviations used in the text are as follows: MNHN, Muséum national d'Histoire naturelle, Paris; NHM-M, Natural History Museum, London; TF, Thai Fossil deposited in the Geological Survey Division, Department of Mineral Resources, Bangkok; YPM, Yale Peabody Museum of Natural History, Yale University, New Haven. Throughout the text, lower cases are used for the lower teeth and upper cases for the upper teeth.

In this paper, we use the standard dental terminology proposed by Smith and Dodson (2003), e.g. lingual/labial and mesial/distal in designating the tooth directions.

## 2. Description

A small fragment of the mandible is preserved but does not provide any significant information. The canine preserves a large part of its crown. It is most similar to, but slightly more slender than, that of *Amphicyon major* from Sansan (middle Miocene, France). It has a sharp distal ridge and a strong mesiolingual keel with a wrinkled rim. The p4 is elongated and about the height of the m1 paraconid; the distolingual part of the crown is not preserved. The mesial border of p4 is markedly concave and displays a slightly prominent crest near the crown basis. A trenchant, moderately high, distal accessory cusp is present; it is separated from the main cusp by a deep, slit-like notch. There is a short distal

cingulid bearing a small, sagittally oriented, prominent crest. The cingulid is not distinct on the crown. The m1 paraconid is low and slender and it has mesially tapered lingual and labial faces; this cusp has a straight, nearly vertical mesial border and a short blade. The m1 protoconid is particularly tall and markedly more robust than the paraconid. Its distal face is oriented forwards relatively to the cervix plane. The angle formed by the paraconid and protoconid blades is close to 180°. The metaconid is a small blunt cusp located up on the distolingual face of the protoconid; it reaches about the height of the paraconid in lingual view. In occlusal view, the metaconid is distinctly distal to the protoconid tip, but is not visible in labial view. A shallow notch separates the protoconid and the metaconid. The largest width of m1 is across the trigonid/talonid boundary. The talonid is long (about one third of the m1 total length) and is formed by a tall, trenchant, and sagittally oriented hypoconid crest that extends slightly labially from the protoconid face; the greatest height of the hypoconid is approximately at the two-thirds of the talonid length. In labial view, the hypoconid crest makes a right angle with the distal face of the protoconid. The distal face of the talonid is particularly high and vertical, at a right angle with the cervix plane of the tooth. There is no prominent crest or an entoconid present at the low lingual border. The talonid basin is shallow and displays a marked groove that is roughly sagittally oriented and lingually located, distal to the metaconid. A prominent crest closes up the talonid distally. The cingulid is only marked distolabially. The two m2s do not preserve their roots and only the right one has a complete crown. This is a large tooth and its trigonid is markedly wider than that of m1. The protoconid is a large, pyramidal cuspid with three prominent crests extending from its tip. The mesial crest gently curves lingually and reaches the vestigial paraconid, which only forms an extremely low and transversely short crest. The distal protoconid crest marks the distolabial face of this cusp, then reaching the talonid. The lingual protoconid crest forms a deep V-shaped notch together with the labial crest rising from the metaconid tip. The latter cuspid is relatively well developed in comparison with that on m1. It is much smaller than the m2 protoconid, however, and only slightly distal to it. The basis of the mesial face of the m2 metaconid displays a modestly prominent crest, but the latter does not reach the vestigial paraconid. The distal face of the trigonid is distinctly concave, especially between the metaconid and protoconid; in lateral view, the distal faces of these cusps are strongly oriented forwards. The m2 talonid is slightly shorter than the trigonid and it tapers backwards, especially lingually. The hypoconid crest is tall and wide, and occupies the labial half of the talonid. In labial view, the crest makes a right angle with the protoconid distal face. A low crest is present distolingually but it is short and does not

extend mesially. The trigonid basin is shallow and mesiolingual. The cingulid is developed in the mesio- and distolabial corners (Fig. 3).

For measurements see Table 1.

### 3. Discussion and comparisons

The occurrence, in North America, of the probable sister group of the Oligocene European Haplocyoninae (i.e. Temnocyoninae) and the presence on those two continents of the amphicyonines *Cynelos*, *Ysengrinia*, *Pseudocyon*, and *Amphicyon* (Hunt, 1998, Fig. 11.3; Hunt, 2002) demonstrate that several dispersals from Eurasia to North America occurred during the early Oligocene-middle Miocene interval. The identification of some European genera, like *Cynelos*, *Ysengrinia*, *Amphicyon*, and *Agnotherium*, in the early and middle Miocene of Africa (Hunt, 1996; Morales et al., 1998, 2003) further supports that amphicyonids also participate in the faunal dispersals as a result of the Africa–Eurasia contact around the Oligo-Miocene boundary. Recent floristic data from Thailand (Chaimanee et al., 2003) also support the existence of faunal and floral dispersal corridors between Africa and Eurasia, in particular between Africa and Southeast Asia during the middle Miocene. In Asia, a lack of intensive field exploration prevents the discovery of intermediate taxa that should connect New and Old World lineages.

The amphicyonid from Mae Moh differs from cf. *Amphicyon* sp. from Ban San Klang, Thailand. The latter, if an amphicyonid, would represent a very small, new species. The Mae Moh amphicyonine also differs from *A. cf. major* from Hangmon, Vietnam, which is a much larger species. The Mae Moh mine therefore, yields a new form for the Southeast Asian Miocene. The reduction of p4 and the enlargement of m2, both relatively to m1, the development of the labially located m1 hypoconid crest and, on m2, of a well-developed and distinct protoconid–metaconid–hypoconid support an assignment to the subfamily Amphicyoninae. This subfamily is distinguished from others (Daphoeninae, Haplocyoninae, Temnocyoninae, and Thaumastocyoninae) in having greatly enlarged M2–3/m2–3 relative to M1/m1 (Hunt, 1998; personal data). In addition, amphicyonines differ from daphoenines (e.g. *Daphoenictis*, *Daphoenodon*), haplocyonines (e.g. *Haplocyon*, *Haplocyonoides*), and temnocyonines (*Temnocyon* and *Mammacyon*) in having more reduced anterior premolars (p1–3, P1–3), and m2 enlarged relative to m1. In addition, amphicyonines differ from haplocyonines and temnocyonines in having a P4 with a more reduced protocone, an M1 with a crescent-shape and not isolated protocone (see Hunt, 1998). In addition, amphicyonines differ from thaumastocyonines (*Thaumastocyon* and *Agnotherium*) in having an M1 with a less prominent paracone and metacone compared to the protocone and a less reduced lingual part (metaconid,

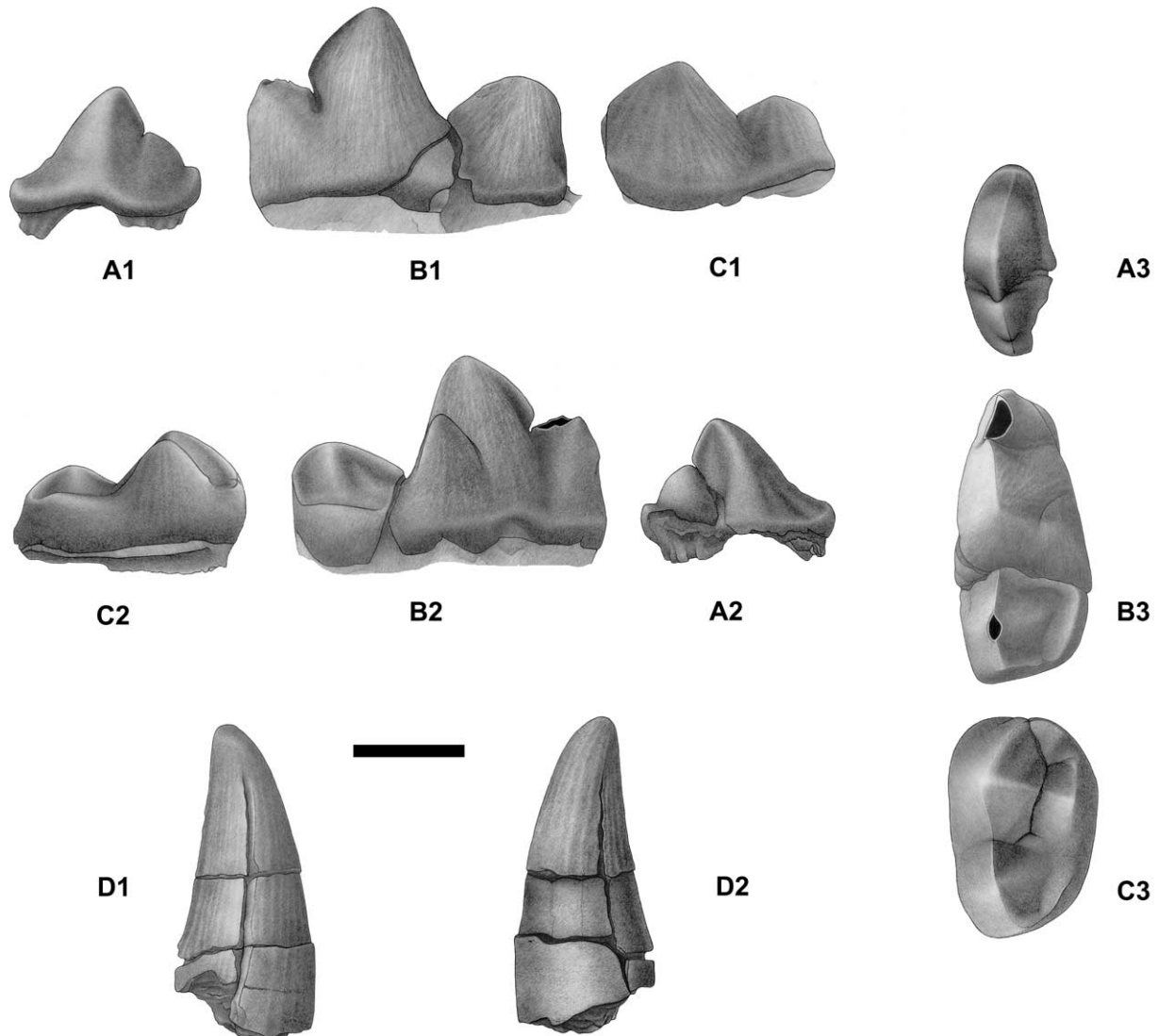


Fig. 3. *Maemohcyon potisati* gen. et sp. nov., TF 6210, holotype. Left p4 in A1, labial, A2, lingual, and A3, occlusal view; left m1 in B1, labial, B2, lingual, and B3, occlusal view; right m2 (reversed) in C1, labial, C2, lingual, and C3, occlusal view; left canine in D1, lingual, D2, labial view. Scale = 1 cm.

entoconid) on the lower molars (Ginsburg, 1999; personal data).

### 3.1. Comparison with Asian Amphicyoninae

In Asia, nearly all amphicyonids belong to the Amphicyoninae. Most taxa are assigned to the genus *Amphicyon* but *Arctamphicyon*, *Ysengrinia*, and cf. *Cynelos* are also present. Through time, many Miocene amphicyonids have been assigned to the wastebasket genus *Amphicyon* without justification. In Europe, approximately 70 late Oligocene and Miocene specific names have been assigned to this genus (Kuss, 1965). Recent works, however, recognize 3–10 valid species of *Amphicyon* from this continent (Viranta, 1996; Ginsburg, 1999; Hunt, 2003), 3 species from North America (Hunt, 2003) and 1 species from Africa (Morales et al., 1998, 2003). The Asian *Amphicyon* species almost certainly represent different lineages and need to be

re-investigated, as previously pointed out (Hunt, 1998; Wang et al., 1998). According to Raza et al. (1984, p. 592) ‘probably none of the large Siwalik amphicyonids truly belong to *Amphicyon*’. It has therefore, been necessary to include in this study all previously described Asian specimens assigned to *Amphicyon*. Also, in order to place the Mae Moh amphicyonine in a more general context, we propose the first review of the fossil record of the Amphicyoninae from Asia, on the basis of the literature and personal data. Fig. 4 presents the stratigraphic distribution of the Asian Amphicyoninae discussed below.

Three middle Miocene amphicyonines from China have been described and illustrated. Unless noticed, the recent contributions of Qiu and Qiu (1995) and Wang et al. (1998) have served as our main stratigraphic references. *Amphicyon confucianus*, described by Young (1937), is based on a fragmentary right hemimandible with p3, m1 and belongs to the Shanwang Local Fauna, early middle Miocene in age



Table 1

Comparison of dental measurements (mm) and proportion between *Maemohcyon potisati* gen. et sp. nov. and Asian species of *Amphicyon*; some non-Asian species discussed in the text are included

	p4	m1	m2	Lp4/Lm1	Lm2/Lm1
<i>Maemohcyon potisati</i>					
TF 2610 (holotype)	16.8×7.7	27.4×12.3	20.3×13.6	0.61	0.74
<i>Amphicyon confucianus</i>					
Holotype mandible <sup>a</sup>	(20.4)	38.0×17.5	–	(0.54)	–
<i>Amphicyon cooperi</i>					
NHM-M 12341 (holotype)	–	32.5×16.5	–	–	–
<i>Amphicyon palaeindicus</i>					
GSI D 225 and 226 <sup>b</sup>	–	31.0×11.9	21.0×13.7	–	0.70
MPM N-76-6 <sup>c</sup>	–	–	17.2	–	–
<i>Amphicyon pithecophilus</i>					
NHM-M 1557	–	33.0×15.8	–	–	–
GSI D 30 <sup>b</sup>	–	–	23.1×16.0	–	–
<i>Amphicyon shahbazi</i>					
GSI D 110 (lectotype) <sup>d</sup>	21.5×13.0	30.0×18.0	20.5×13.0	0.72	0.68
NHM-M 12339	–	27.3×14.0	17.5×12.5	–	0.64
NHM-M 12340	–	31.0×15.0	–	–	–
<i>Amphicyon sindiensis</i>					
GSI D 25 (holotype) <sup>b</sup>	–	–	19.9×13.5	–	–
<i>Amphicyon tairumensis</i>					
AMNH 26606 (holotype) <sup>e</sup>	14.0×7.5	28.0×13.0	–	0.50	–
<i>Amphicyon ulungurensis</i>					
IVPP-V 7731 (holotype) <sup>g</sup>	–	(41.0)×19.5	29.6×21.4	–	0.72
<i>Amphicyon galushai</i> <sup>g</sup>					
F:AM H409-3044	19.7×10.0	32.2×15.7	18.5×13.8	0.61	0.57
UNSM 25-11-11-38	18.2×10.4	–	19.4×13.3	–	–
F:AM 25407	18.5×10.0	31.1×16.5	19.7×15.9	0.59	0.63
F:AM 25406	17.5×9.6	30.2×16.1	20.6×15.4	0.58	0.68
<i>Amphicyon frendens</i>					
Mean <sup>g</sup>	19.8	36.3	25.9	0.55	0.70
<i>Amphicyon ingens</i>					
Mean <sup>g</sup>	22.6	40.6	30.5	0.55	0.73
<i>Amphicyon major</i>					
MNHN-Sa 36	18.6×9.6	35.1×16.6	25.5×17.7	0.53	0.73
MNHN-Sa 45	–	32.0×15.0	–	–	–
MNHN-Sa 37	8.9	30.4×14.2	21.4×16.0	–	0.70
MNHN-Sa 35	19.0×10.1	36.9×17.3	–	0.51	–
MNHN-Sa 34	–	35.6×17.3	24.0×17.1	–	0.67
MNHN-Sa 13974	16.5×9.6	30.3×14.0	21.3×16.0	0.54	0.70

Data for *A. ingens* and *A. frendens* (N>11) are numerous and only the mean (from data in Hunt, 2003) is provided.

<sup>a</sup> Young (1937).

<sup>b</sup> Pilgrim (1932).

<sup>c</sup> West et al. (1978).

<sup>d</sup> Pilgrim (1912).

<sup>e</sup> Colbert (1939).

<sup>f</sup> Qi (1989).

<sup>g</sup> Hunt (2003).

(about 16 Ma; Qiu, 2003). In comparison with the Thai material, *A. confucianus* has a much larger size (m1 total length = 38 mm), a more forwardly oriented m1 protoconid that results in a distinctly more open angle between the distal face of this cusp and the hypoconid crest, and probably a shorter p4. Colbert (1939, Fig. 7) created *Amphicyon tairumensis* on the basis of a subcomplete left hemimandible with p3-m1 from the Tunggur Formation, probably contemporaneous with the Mae Moh fauna (the Tunggur Local Fauna is late middle Miocene in age). Unfortunately, the teeth are very worn and the m1 paraconid

is not preserved. Despite that and a similar size, *A. tairumensis* possesses a proportionally wider and much shorter p4 relatively to m1 length than in the Thai species (Table 1). *Amphicyon ulungurensis* is known from the middle Miocene of the Karamagay (=Halamagai) Formation in the Junggar Basin (Xinjiang Autonomous Region, China); the fauna from Karamagay belongs to the Tunggur Local fauna. *A. ulungurensis* is a huge species, most comparable to *A. major*; it is known only by the type specimen, a fragment of right hemimandible with partial m1 talonid and m2–3 described by Qi (1989, Fig. 1). The size

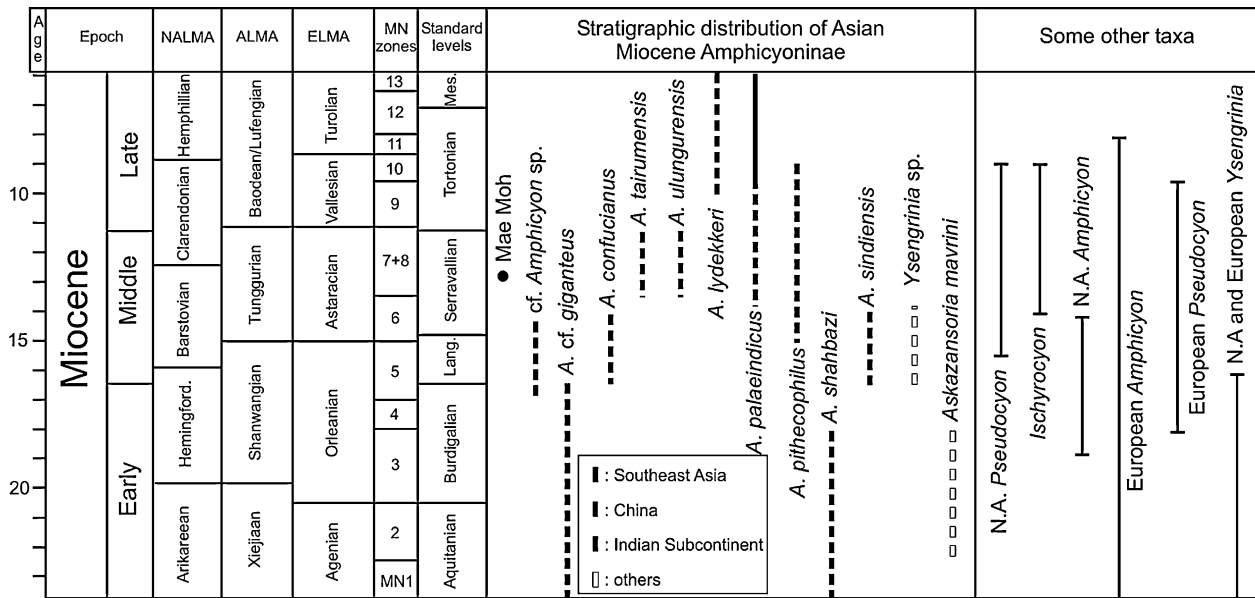


Fig. 4. Stratigraphic distribution of the Amphicyoninae in Asia. The biochronological scale is based on Prothero (1998) for NALMA (North American Land Mammal ages), Qiu and Qiu (1995) for ALMA (Asian Land Mammal ages), and Steininger (1999) for ELMA (European Land Mammal ages), the MN zones, and the standard levels. See text for the distribution of Asian taxa. The distribution of some non-Asian taxa is included for comparison (data from Viranta, 1996; Hunt, 1998, 2003; Ginsburg, 1999; Morales et al., 2003). Dotted lines indicate an uncertain stratigraphic distribution.

difference is the most significant distinction between the Chinese and the Thai species; however, the measurements and illustration provided by Qi (1989, Fig. 1) further indicate that the former has a less elongated m2 with a talonid that tapers less backwardly than the latter (see Table 1). *A. ulungurensis* is approximately the size of *A. confucianus* but the single type specimens of these two species document a different portion of the mandible that cannot be directly compared. *Amphicyon* cf. *major* is also mentioned but not described from the Tongxin basin (Hunt, 2003).

The systematic status and the stratigraphic origin of the amphicyonids from the Indian Subcontinent are much more confused than in China. The amphicyonid remains from this area are particularly difficult to date. On the one hand, the fragmentary nature of the type specimens (often a single isolated tooth) results in a very divergent assignment of the hypodigm specimens (e.g. Lydekker, 1884; Forster-Cooper, 1923; Matthew, 1929; Pilgrim, 1932). On the other hand, the specimens from the 'old collections', and especially those found during Lydekker's and Pilgrim's expeditions, are rather difficult to date and/or their geographic origin is imprecisely known. This is due to, first, the lack of stratigraphic and/or geographic information and, second, the difficulty in correlating the geological formations through Pakistan and India. For instance, until the early 1990's, fossils from the Bugti Hills of Pakistan were believed to be early Neogene in age by many authors, though Pickford (1988) argued for an apparent mixture of Oligocene and early Miocene taxa. Recent field campaigns have, however, demonstrated that the age of the 'Bugti bone

beds' ranged from the early Oligocene to the late Miocene (Welcomme and Ginsburg, 1997; Welcomme et al., 2001). Nearly 60 years after the description of the first amphicyonid from the Indian Subcontinent (*Amphicyon palaeindicus* Lydekker, 1876), Pilgrim (1932) proposed the first review of all known amphicyonids from this region. He selected a type specimen for each genus and species. Pilgrim also proposed a diagnosis and provided the hypodigm and a description of the taxa. Pending a modern review of the Amphicyonidae from the Indian Subcontinent and to avoid a useless and complicated systematic discussion of each specimen which is beyond our present scope, we use the work of Pilgrim (1932) as our main systematic source. It is important to note, however, that the assignment of the so-called 'referred specimens' in Pilgrim (1932) is provisional; the specific association of the lower and upper dentitions remains to be confirmed later.

*Arctamphicyon lydekkeri* was created by Pilgrim (1910) on the basis of an m1 found in the Dhok Pathan horizon (sensu Pilgrim, 1932) near Padhri, Potwar Plateau, northern Pakistan. This tooth is, however, an upper tooth (right M2) as first pointed out by Matthew (1929). In 1932, Pilgrim identified it as an M1 and created the genus *Arctamphicyon* for this species on the basis of the morphological and proportional differences between this tooth and an M2 (the single additional tooth referred at that time to the species; Pilgrim, 1932, Pl. 2, Fig. 8) compared with the *Amphicyon* species. From the illustration provided by Matthew (1929, Fig. 18, left); Pilgrim (1932, Pl. 2, Fig. 7), there is no doubt that the holotype of *A. lydekkeri* is an M2. The holotype and the only additional specimen are therefore, both M2.

The features of *Arctamphicyon lydekkeri* mentioned by Pilgrim (1932) indicate a typical morphology for an M2: ‘inner border [...] only slightly shorter than outer border’, crown low and flattened, with low cusps, ‘paracone much stronger than metacone’, ‘inner cingulum crenulated, very broad and just as strongly developed on the anterior as on the posterior side, continuing in an outward direction so as almost to join up with the external cingulum’. The holotype and paratype M2s may belong to the same species, which is supported by an identical proportion, a small size difference (within the variation range of, e.g. *Amphicyon major*; Ginsburg, 1961, Fig. 3), and rather poor morphological differences. These two teeth do not display any significant difference relative to *Amphicyon* that would justify a generic distinction. We therefore, state that the generic distinction made by Pilgrim is based on invalid morphological differences. *Arctamphicyon* must be regarded a junior synonym of *Amphicyon*. A direct study of this material and that recently recorded but not described from the Potwar Plateau (Pilbeam et al., 1979) would be necessary to confirm the status of *Amphicyon lydekkeri*. No comparisons are possible with the Mae Moh species.

*Amphicyon palaeindicus* is also based on an isolated tooth, an M2 discovered at Kushalgarh, near Attock (Potwar Plateau, northern Pakistan), described and illustrated by Lydekker (1876, Pl. 7, Fig. 5; 1884, Pl. 32, Fig. 8). The holotype cannot be compared to the Mae Moh individual but Pilgrim (1932, Pl. 1, Figs. 9, 12, not 7, 8) also referred to *A. palaeindicus*, a fragmentary mandible with left m1–m2 and right m1 collected around Chinji (southern Potwar Plateau, northern Pakistan). Colbert (1935), Figs. 38–40) illustrated some lower teeth, a right m1 from Chinji and a right m2 from Bhandar beds, in the Dhok Pathan zone. The exact age of these specimens cannot be determined because the Chinji region includes several fossiliferous localities ranging from ca. 15 Ma to ca. 9 Ma (biostratigraphic zones 1–5; Pilbeam et al., 1979). The species has also been described from the Dang Valley fauna, western Nepal, which is correlated with the Chinji fauna (West et al., 1978) of late middle Miocene in age (Antoine et al., 2003). It has also been recorded but not described in the Potwar Plateau from two biostratigraphic interval-zones, 9.5–7.4 Ma and 7.4–5.3 Ma (Barry et al., 1982). *Amphicyon palaeindicus* may therefore, range from the late middle Miocene to the latest Miocene; it is probably stratigraphically later than the Mae Moh amphicyonine. Compared with the lower teeth assigned to *A. palaeindicus* by Pilgrim (1932); West et al. (1978), the lower dentition of the Thai species differs by the lesser elongation of m1 and m2 (see Table 1) and by an m1 with a shorter paraconid blade, a talonid and a trigonid similar in width, and an m2 with a talonid that tapers more distally.

*Amphicyon pithecophilus* was created by Pilgrim (1932) on the basis of an isolated M2 from Chinji Village. Referred specimens used for comparison in this study are two fragmentary mandibles, one with right dp4 and m1 from

Nurpur (Lydekker, 1884: pl. 32, Fig. 5), one with a left m2 from Chinji (Pilgrim, 1932: pl. 2, Fig. 4), and a partial isolated m1 also from Chinji (Pilgrim, 1932: pl. 2, Fig. 1). As pointed out above, the material from the Chinji area may range from ca 15 to 9 Ma. The stratigraphic origin of the specimen from Nurpur (NHM-M 1557, cast of the original) is unknown. On this specimen, which is a juvenile individual, the m1 is incompletely erupted and does not permit precise measurements. Nevertheless, the carnassial displays some similarities to that of the Mae Moh species: a tall trigonid with a subvertical labial face (especially the protoconid one), a paraconid and a protoconid blade making a very open angle, resulting in a greater elongation of the tooth, and a prominent hypoconid crest. Beside a larger size, however, NHM-M 1557 differs from the Mae Moh amphicyonine in having a more lingual (roughly distal to the metaconid/protoconid notch) and better developed hypoconid crest, along with a well-developed entoconid crest.

When Pilgrim (1912) created *Amphicyon shahbazi*, he described two poorly preserved right mandibular fragments from the ‘Bugti stage of the Gaj series’ of Chur Lando (=Lundo Chur, southern syncline of Gandoi of the Zin Range, Bugti Hills, Pakistan). It is important to note that the ‘Gaj series’ of Pilgrim now corresponds to the Chitarwata Formation (Downing et al., 1993). At Lundo Chur, known fossil-bearing layers range from the basal late Oligocene (fossiliferous level F; Welcomme et al., 2001, Figs. 3, 4; Antoine et al., 2003, Fig. 2) to the middle Miocene (fossiliferous level W; Welcomme et al., 2001, Figs 3, 4; Antoine et al., 2003, Fig. 2). No amphicyonid remains have been found from the recent excavations. In the review of Indian amphicyonids, Pilgrim (1932) selected the right mandibular ramus with p3–m2 as the ‘holotype’ of the species (which is a lectotype, however). In addition to a second fragmentary mandible with partial m1 and m2 (paralectotype), which is part of the syntype, Pilgrim (1932) also assigned to *A. shahbazi* an M1, a fragment of maxilla with P4, an isolated m1, and provisionally a fragmentary right mandible with partial p4, m1–m2 (NHM-M 12339) and a right m1 (NHM-M 12340). All specimens but the first-mentioned m1 come from the Bugti Hills. The latter tooth was found north of Basal near Attock (Potwar Plateau, northern Pakistan) in the Lower Murree Formation, believed to be early Miocene in age, though much older than 18 Ma in the northern Potwar Plateau (Barry et al., 2002). The stratigraphic age of this carnassial suggests an early Miocene age for the material from the Bugti bone beds. The lectotype and paralectotype mandibles from Lundo Chur differ from the Thai species by a less reduced m2 and, especially, a longer p4 proportionally to m1, a p4 markedly shorter than m2 (this is the opposite in the Mae Moh species), and a p4 (on the lectotype) lacking a distal accessory cusp (Pilgrim, 1912, p. 12). NHM-12339 and NHM-M 12340 are morphologically very different from each other and cannot be assigned to the same species.

NHM-M 12339 differs from the Mae Moh amphicyonid in having a well-marked cingulid on teeth (especially on the distal part of p4, on both sides of m1 paraconid, on the labial face of the m1 talonid and, at least, on the labial face of m2), a much wider p4 (relatively to m1), a less elongated m1 partly resulting from the oblique orientation of the paraconid blade, a less reduced m1 metaconid, a much more reduced m2 (relatively to m1) that displays a more rectangular outline due to a wider talonid, a less reduced paraconid, a longitudinally less developed protoconid, and a more basined talonid with a less prominent hypoconid crest. The m1 from NHM-M 12340 shares with NHM-M12339 the presence of a well-developed cingulid, especially on the labial face of the talonid, and a poorly developed hypoconid crest. NHM-M 12340 differs from both the Mae Moh specimen and NHM-M 12339, however, in having a lower and more obliquely oriented paraconid blade, a more backwardly oriented mesial face of the paraconid, and an obliquely oriented hypoconid crest (instead of being parasagittal) that rises more lingually on the trigonid distal face, below the metaconid-protoconid notch.

*Amphicyon cooperi*, described by Pilgrim (1932), is only known by the holotype, an isolated and unworn m1 (NHM-M 12341) collected, as the syntype mandibles of *A. shahbazi*, from the 'Bugti stage of the Gaj series' (Pilgrim, 1932) in the Bugti Hills, late Oligocene to early Miocene in age (see above). An early Miocene age for this tooth is probable, however, based on the record of *A. cf. cooperi* (no description is provided) from zones 4 and 6 of the Dera Bugti synclinal that are correlated with the early early and late early Miocene, respectively (Antoine et al., 2003). Beside a larger size, the type of *A. cooperi* differs from Mae Moh amphicyonine in having an obliquely oriented paraconid blade (in particular the paraconid labial face) that results in a lesser elongation of the trigonid. Moreover, *A. cooperi* also displays a lower metaconid (relatively to the paraconid) and a much shorter talonid with a more marked lingual crest, a small entoconid and entoconulid, and a markedly less prominent hypoconid.

*Amphicyon sindiensis* was created by Pilgrim (1932) on the basis of a fragment of right mandible with m2 discovered in the basal beds of the Manchar Formation of the Sind Province, Pakistan (early middle Miocene in age; Raza et al., 1984) and an isolated m2 for which Pilgrim (1932, p. 14) only provided some dimensions. On the mandible, m2 has a similar size and proportion to those of the Mae Moh m2, but differs in having a subquadrate outline, especially in the mesio- and distolingual corners, a less reduced and more transversely developed paraconid, and a talonid with a less reduced entoconid and a lingual rim that tapers less distally.

Other amphicyonines are also recorded but not described by Raza et al. (1984) from the Sind, southern Pakistan: cf. *Cynelos* sp. (localities 7, 12) from the uppermost Gaj Formations (Oligocene) in sections along the Gak River, cf. *Cynelos* sp. (locality 2) and cf. *Amphicyon* sp. (localities 2,

6, 16) from the Manchar Formation in a section at Bhagothoro, indeterminate genus and species of Amphicyonidae (locality 2) from the Basal Manchar Formation. Pilbeam et al. (1979), studying the Potwar Plateau (mainly Chinji and Khaur regions), also mentioned but not described *Amphicyon* sp. from the Chinji, Nagri, and Dhok Pathan formations, i.e. between 14.2 Ma and ca 7 Ma.

The only Asian specimen assigned to *Ysengrinia* has been recorded from Japan. The material consists of a right M1 from Korematsu Formation, Bihoku Group, southwestern Japan; the locality is early middle Miocene in age (Kohno, 1997). The systematic status of this specimen has been discussed by Hunt (2002) who suggests a closer affinity with the advanced *Cynelos* from North America. Although the assignment of an isolated tooth remains difficult, the comparison with MNHN-SG 393 (paralectotype of *Ysengrinia gerandiana*; Peigné and Heizmann, 2003, p. 44) and YPM 10061 (holotype of *Ysengrinia americana*; Hunt, 2002) indicates a clear difference of morphology. The most prominent difference is the larger difference between the mesiodistal length of the labial (paracone–metacone) and the lingual half of M1 in *Ysengrinia* from Europe and North America relative to *Ysengrinia* from Japan. No comparison is possible with our material. A second *Ysengrinia* record is known from the early Miocene of Askazansor Formation in Betpakdala Steppe, South Kazakhstan (Bonis et al., 1997). Recently, this material has been erected as a new genus and species, *Askazansoria mavrini* (Kordikova, 2001). The holotype and single specimen is a fragment of right maxillae with P4-M2; no comparisons are possible with our material. We also mention the endemic *Aktaucyon brevifacialis* from the early Miocene of Kazakhstan (Kordikova et al., 2000), which has been assigned to the Daphoeninae (Hough, 1948). This species is represented by the single holotype, a fragment of left maxilla that cannot be directly compared with our material.

From our analysis, not only does the Thai species represent an unknown taxon from Asia, there is also moreover no potential ancestor for the Mae Moh amphicyonid so far described from this continent.

### 3.2. Comparison with non-Asian Amphicyoninae

Faunal and/or floral exchanges have been demonstrated between Africa and southern Asia, and between Eurasia and North America (through Asia). Amphicyonines have always been part of these migration events. Genera such as *Amphicyon*, *Cynelos* and *Ysengrinia* are found in each of these continents; *Pseudocyon* is known from Europe and North America. According to Qiu (2003), a few faunal exchanges took place between Eurasia and North America around 13 Ma. Hunt (1998) additionally mentioned several migrations of amphicyonids between North American and Eurasian between ca 15.5 and 14 Ma. Whether the amphicyonid from Mae Moh is part of one of these middle



Miocene intercontinental migrations between the Old and New World is discussed here through a more complete comparison with non-Asian taxa.

The genus *Cynelos* is a basal amphicyonid that includes numerous species from the late Oligocene and early Miocene of Europe (Peigné and Heizmann, 2003), from the mid-early to early middle Miocene of North America (Hunt, 1998) and from the early Miocene of Africa (Savage, 1965; Schmidt-Kittler, 1987). No *Cynelos* species is contemporaneous with the Mae Moh taxon. Compared to TF 2610, the European species of *Cynelos* are smaller in size, tend to reduced p4 relatively to m1 but do not enlarge m2 like in the species of *Amphicyon*, and also have an m1 talonid with a more developed entoconid, a more pronounced basin, a more rectangular m2 with a wider talonid (not tapering backward), and a less prominent hypoconid. The North American species of *Cynelos* document a clear trend toward increasing size, but have a morphology that is not much different from that of the early Miocene species from Europe: m2–3 not enlarged like in *Amphicyon*, m2 rectangular, and, for the early middle Miocene species, m1 talonid with a centrally placed hypoconid (Hunt, 1998). The African *Cynelos euryodon* and *C. macrodon* are poorly known. The lower dentition is known only from isolated lower molars of *C. euryodon*. Compared to the lower carnassials from Songhor (Schmidt-Kittler, 1987, text-Fig. 3) and Napak (Savage, 1965, text-Figs. 53–54), TF 6210 is much larger, has a more obliquely oriented metaconid distal face, and a more developed hypoconid. The paratype of the species, a right m1 (NHM-M 19085, studied from a cast MNHN-unnumbered) also displays a lower protoconid and shallower talonid basin. TF 2610 clearly stands apart from all the *Cynelos* lineages that evolved in Europe, Africa, and the New World (see Table 2 for measurements).

The genus *Ysengrinia* is documented from Europe by three late Oligocene and early Miocene species (Peigné and Heizmann, 2003); the only North American species, *Ysengrinia americana* (Wortman, 1901), ranges between ca. 23 and 19 Ma (Hunt, 2002, p. 9). The carnassial of *Ysengrinia* species is morphologically close to that of the Thai specimen. Nevertheless, the *Ysengrinia* species differ in having a much more reduced m2 relatively to m1 (Table 2). In addition, except for *Ysengrinia* sp. from Japan (see also end of Section 3.1.), the latest *Ysengrinia* species, *Y. valentiana* from Spain (European Mammal Zone MN 4; Belinchón and Morales, 1989) and *Y. ginsburgi* from Arrisdrift, Namibia (Morales et al., 2003) are late early Miocene to basal middle Miocene in age.

Our specimen differs from the type species *Amphicyon major*. Basically, the *Amphicyon* species are distinguished by the robustness and overall shape of the p4 and the lower molars that, for Hunt (1998, p. 213), adequately defined a ‘swollen inflated appearance’. This morphology is particularly clear from a mesial or distal view of *Amphicyon* teeth, which shows that the lingual and, in particular, the labial

faces of p4 and the labial face of the m1-2 trigonid are obliquely oriented, whereas they are nearly vertical in the Thai specimens. In addition to this fundamental distinction, the *Amphicyon* lineages tend to have a more reduced p4 relatively to m1, a less elongated m1 with a more distal metaconid, an m2 with a metaconid not distal to the protoconid, a more rectangular outline due to a wider talonid, and a talonid not tapering distal. The Mae Moh species cannot be attributed to *Amphicyon*, although the development of its m2 relatively to m1 is within the range of variation observed in, e.g. the population of *A. major* from the French locality of Sansan (European Mammal Zone MN 6, slightly older in age than Mae Moh). The North American *Amphicyon* lineage (three species) follows the same trend: increasing size, reduction of p4 and enlargement of m2 (see Hunt, 2003; Table 1). The species from Mae Moh thus differs from the earliest species *A. galushai* by the enlargement of m2 and from the latest species *A. frendens* and *A. ingens* by a smaller size and a less reduced p4.

The genus *Pseudocyon* (especially the type species *P. sansaniensis*) is well distinguished from our material as well, in having a more reduced p4 and m2 relatively to m1, and an m2 talonid lacking a prominent hypoconid crest. *Pseudocyon* is also distinguished by the presence of a mesial and distal accessory cusp on p4 (Hunt, 1998). The holotype of *P. sansaniensis* (MNHN-Sa 207) lacks a mesial accessory cusp, however, that indicates some variation for this feature. In North America, *Pseudocyon* is partially contemporaneous with Mae Moh species, ranging from 15.5 Ma to ca 9 Ma. Known materials are very similar to that from Europe in having, e.g. a small p4 and an m2 with mesially shifted trigonid cusps and a low, flat, and long talonid (Hunt, 1998). These features markedly distinguish the Mae Moh amphicyonine from the North American *Pseudocyon*.

Other non-Asian Amphicyoninae are endemic taxa to Europe, North America, or Africa. The Miocene European amphicyonine *Ictiocyon* Crusafont et al. (1955), and, in particular *Pseudarctos* Schlosser, 1899 are morphologically very different from the material described here. These genera are known by much smaller and more ursoid species that display a more hypocarnivorous dentition than that of the species from Mae Moh.

Two endemic amphicyonine genera are known from North America, *Pliocyon* (Matthew, 1918) and *Ischyrocyon* (Matthew and Gidley, 1904). The type species of *Pliocyon*, *P. medius*, is based on a partial skull (Matthew 1918, Figs. 2, 3) that cannot be compared with our material. Additional materials are recorded, yet undescribed, from the late early Miocene and middle Miocene of North America (Berta and Galiano, 1984; Hunt, 1998); some dimensions are provided for one individual by Berta and Galiano (1984, Table 1). A second species, *P. robustus*, is known by a partial left mandible with c, p2–p3, m1 from the middle Miocene (either Barstovian or Clarendonian) of Florida (Berta and Galiano, 1984, Fig. 1). This specimen differs from our

Table 2

Comparison of dental measurements (mm) and proportion between *Maemohcyon potisati* gen. et sp. nov. and species of *Ysengrinia*, *Cynelos*, *Pseudocyon*, *Pliocyon*, and *Ischyrocyon*

	p4	m1	m2	Lp4/Lm1	Lm2/Lm1
<i>Maemohcyon potisati</i>					
TF 2610	16.8×7.7	27.4×12.3	20.3×13.6	0.61	0.74
<i>Cynelos crassidens</i>					
MNHN-QU 9254 (holotype)	13.4×6.3	17.0×8.5	9.2×7.0	0.79	0.54
<i>Cynelos piveteaui</i>					
MNHN-QU 9268 and 9269 (holotype)	14.8×(7.0)	21.4×10.2	13.3×9.5	0.69	0.62
<i>Cynelos quercensis</i>					
MNHN-QU 9250 (holotype)	14.3×7.2	21.2×10.0	11.7×8.0	0.67	0.55
<i>Cynelos lemanensis</i>					
Mean	14.1×6.7	21.0×9.5	14.1×9.7	0.69	0.68
<i>Cynelos helbingi</i>					
Mean	13.4×7.0	23.8×10.6	14.3×9.5	0.53	0.62
<i>Cynelos schlosseri</i>					
Mean	10.3×5.2	16.9×7.6	10.1×7.6	0.61	0.60
<i>Cynelos rugosidens</i>					
BSP-1881-IX-581 (lectotype)	–	19.6×8.8	12.7×8.8	–	0.65
<i>Cynelos</i> sp.					
CM 2200 <sup>a</sup>	–	21.3×9.3	–	–	–
<i>Cynelos caroniavorus</i>					
M CZ 3931 (holotype) <sup>b</sup>	10.0×4.5	15.0×7.0	9.0×7.0	0.67	0.60
<i>Cynelos sinapius</i>					
AMNH 9358 (holotype) <sup>c</sup>	–	–	27.1×18.1	–	–
<i>Cynelos euryodon</i>					
NHM-M 19085 (paratype) <sup>d</sup>	–	20.8×8.9	–	–	–
SO-1107 <sup>d</sup>	–	18.2×7.9	–	–	–
SO-5668 <sup>d</sup>	–	20.2×9.4	–	–	–
<i>Y. gerardiana</i>					
FSL 213828 (lectotype)	15.3×8.2	24.5×11.4	–	0.62	–
<i>Y. tolosana</i>					
MNHN-BTA 131 (cast of holotype)	17.1×9.4	28.0×12.9	16.0×13.2	0.61	0.57
NMB-Pa 951	18.5×9.4	29.4×14.7	17.5×13.0	0.63	0.60
MNHN-ALL 1 (cast)	18.4×10	26.8×14.7	16.2×13.8	0.69	0.60
<i>Ysengrinia depereti</i>					
MNHN-Ch 258 (cast of holotype)	–	30.7×14.8	18.5×15.0	–	0.60
<i>Ysengrinia ginsburgi</i>					
MGSN AD 133 (holotype)	14.5×7.8	27.2×12.0	17.0×11.5	0.53	0.63
MGSN AD 311'97		29.2×13.5			
<i>Ysengrinia americana</i>					
F:AM 54147 (paratype) <sup>e</sup>	20.4×9.6	28.8×14.4	17.7×13.1	0.71	0.61
UNSM 26584 <sup>e</sup>	16.6×10.1	27.9×14.9	16.7×12.3	0.59	0.60
<i>Pseudocyon sansaniensis</i>					
MNHN-Sa 207 (holotype)	15.2×8.5	29.7×13.2	17.8×13.0	0.51	0.60
<i>Pseudocyon steinheimensis</i>					
SMNS 4808 (holotype)	13.2×7.9	30.3×14.0	19.4×14.0	0.44	0.64
<i>Pliocyon robustus</i>					
UF 24013 (holotype) <sup>f</sup>	19.5a	33.2×14.8	21.5a	(0.59)	(0.65)
<i>Pliocyon medius</i>					
F:AM 54319 <sup>f</sup>	16.7×9.5	28.2×14.8	16.8	0.59	0.60
<i>Ischyrocyon gidleyi</i>					
AMNH 10671 (type of <i>I. gidleyi</i> ) <sup>g</sup>	<20.0	40.0	31.0	<0.50	0.78
AMNH 10802 (type of <i>I. hyaenodus</i> ) <sup>h</sup>	24.0×14.0	45.0×21.0	28.0×17.0	0.53	0.62
PPHSM 2155 (type of <i>I. walkerae</i> ) <sup>i</sup>	21.0×10.5	38.8×16.4	24.5×17.0	0.54	0.63
UCMP 26792 (type of <i>I. mohavensis</i> ) <sup>j</sup>	22.6×11.7	44.0×16.6	24.0a	0.51	0.55
SDSM 53274 <sup>k</sup>	19.7×11.4	41.2×19.1	26.7×19.5	0.48	0.65
SDSM 5685 <sup>k</sup>	20.3×10.9	41.4×19.5	27.3×18.9	0.49	0.66
SDSM 571 <sup>k</sup>	19.8×10.3	38.0×16.4	24.5×16.6	0.52	0.64

a, Alveolus only; numbers in brackets are estimated.

<sup>a</sup> Hunt (1972).

<sup>b</sup> White (1947).

<sup>c</sup> Gazin (1932).

<sup>d</sup> Schmidt-Kittler (1987).

<sup>e</sup> Hunt (2002).

<sup>f</sup> Berta and Galiano (1984).

<sup>g</sup> Matthew (1902).

<sup>h</sup> Matthew and Gidley (1904);

<sup>i</sup> Johnston and Christian (1941).

<sup>j</sup> Stock and Furlong (1926).

<sup>k</sup> MacDonald (1960).

material in having an m1 with a more backwardly placed metaconid and a talonid with a more pronounced entoconid crest. From dental measurements (Table 2), our material is distinguished from the species of *Pliocyon* by an enlarged m2 relatively to m1 (more so in *P. robustus* than in *P. medius*). According to Hunt (1998), the dentition of *Pliocyon* is similar to that of *Cynelos* and may be regarded as a derivative of this lineage. Ranging from 14 to 9 Ma, *Ischyrocyon* is a partially contemporaneous genus of the Mae Moh amphicyonine, as are *Pseudocyon* and, possibly, *Pliocyon robustus* (see above). *Ischyrocyon* may have evolved from the North American *Pseudocyon* or *Cynelos* (Hunt, 1998); it is a derived amphicyonid that tends to develop a more trenchant dentition than that of *Pseudocyon* and *Cynelos* species. A single species, *I. gidleyi*, is recognized (see Hunt, 1998). Measurements and/or illustrations of several specimens (mainly Clarendonian), including the type specimen of *I. gidleyi* and that of some junior synonyms of this species (see Hunt, 1998) have been used as a comparison (Table 2). In addition to a much larger size (but Barstovian specimens have the size of TF 6210; Hunt, 1998), *I. gidleyi* differs from the Mae Moh species in having a wider and more reduced (relatively to m1) p4. The type of the species *I. hyaenodus*, a left mandible of a juvenile individual with dp3 and the nearly complete permanent tooththrow (i3-m2) erupting (Matthew and Gidley, 1904, Figs. 1 and 2) also displays additional morphological differences: no distal accessory cusp on p4, m1 lacking a metaconid and having a centrally placed hypoconid.

Two endemic species are known from Africa. *Afrocyon burolleti* Arambourg, 1961 is based on a fragment of a left mandible with p4-m3 (MNHN-not numbered) from Gebel Zelten, Libya (Arambourg, 1961, Fig. 1), the age of which ranges from late MN 3 (Savage, 1989) to late MN 4 (Mein, 1989, Table 1). The main distinction of the tooth of the genus is the double-rooted m3, which is not preserved from Mae Moh. The dentition of the type specimen of *A. burolleti*, in particular the crown of the molars, is poorly preserved and prevents a detailed comparison. The second species, *Myacyon dojambir*, is based on a fragment of right mandible with m1-2, unerupted m3, from the Vallesian locality of Oued Mya 1, southern Algeria (Sudre and Hartenberger, 1992). *Myacyon dojambir* differs from the Thai species by a much larger size and by the reduction of m2 relatively to m1.

### 3.3. Systematics of the Mae Moh Amphicyoninae

The above comparison indicates that the Amphicyoninae from Mae Moh has no known close relatives in Asia. Although still fragmentary known, the Thai species stands apart from all the contemporaneous amphicyonine genera as well (e.g. *Amphicyon*, *Pseudocyon*, *Pliocyon*, *Ischyrocyon*). Moreover, a clear distinction has been demonstrated with the earlier genera *Ictiocyon*, *Pseudarctos* and, to lesser

extent, with *Cynelos* and *Ysengrinia*. We therefore, propose a new name in order to distinguish this species, the systematic of which is as follows:

Order Carnivora Bowdich, 1821  
 Suborder Caniformia Kretzoi, 1943  
 Infraorder Arctoidea Flower, 1869  
 Family Amphicyonidae Trouessart, 1885  
 Subfamily Amphicyoninae Trouessart, 1885  
*Maemohcyon potisati* gen. et sp. nov.

*Etymology.* Generic name: from Mae Moh, in reference to the type locality, and from the latin *-cyon*, meaning dog. Specific name in reference to M. Somsak Potisat, general director of the Department of Mineral Resources, Bangkok.

*Holotype.* TF 6210, fragment of left hemimandible with m1, and isolated left fragmentary canine, p4, m2 lacking its distalmost part, and right m2. All teeth are unworn and belong to a single, young adult individual and are housed in the Department of Mineral Resources, Bangkok.

*Additional referred material.* None.

*Differential diagnosis.* Mid-sized amphicyonine differing from the typical species of *Amphicyon* (mainly European and North American species, see text) by teeth that do not display the diagnostic ‘swollen inflated appearance’ (Hunt, 2003, p. 82) and by a less reduced p4 relatively to m1 (compared with middle Miocene *Amphicyon*) and an enlarged m2 relatively to m1 (compared to early Miocene *Amphicyon*). Compared to *Cynelos*: m1 talonid with a less developed entoconid and a less pronounced basin; much enlarged (relatively to m1), less rectangular m2 with a narrower talonid that tapers distally and a more prominent hypoconid. Compared to *Ysengrinia*: much enlarged m2 relatively to m1, m2 broader than m1 (except in *Y. depereti*). Compared to *Pseudocyon*: less reduced p4 and enlarged m2 (both relatively to m1), m2 with trigonid cuspids not mesially shifted (trigonid longer than talonid) and with a prominent hypoconid crest. Compared to *Pliocyon*: enlarged m2 relatively to m1. Compared to *Ischyrocyon* (especially late Miocene specimens): narrower and less reduced (relatively to m1) p4; distal accessory cusp present on p4, m1 retaining a metaconid and having a labially placed hypoconid.

*Type locality and horizon.* Mae Moh mine; the material comes from the K1 member in the Lignite K-zone, Na Khaem Formation (see Morley et al., 2001; Benammi et al., 2002 for details; Fig. 2 herein).

## 4. Conclusions

The family Amphicyonidae is poorly known in Asia. The new form described here is therefore, a significant discovery that improves our knowledge of the family on this continent. Our study demonstrates that *Maemohcyon* gen. nov. has no close relationship with the known

contemporaneous amphicyonines; it is, in addition, distinct from all earlier amphicyonine genera. Thus, if resulting from a non-Asian immigration, the *Maemohcyon* lineage probably arrived much earlier than 13 Ma in the Mae Moh area and evolved in this insulated region until the late middle Miocene. This hypothesis would be, however, better supported if the Asian fossil record was satisfactory, which is not the case. Within the earlier taxa of Amphicyoninae, *Ysengrinia* and *Pliocyon* display the most similar morphology, only differing by a reduced m2 (relatively to m1). Only the former genus is not endemic; it is known from Europe, Africa, and North America (the record from Japan remains to be confirmed). Deriving the lineage of *Maemohcyon* from *Ysengrinia* implies an enlargement of m2, which is the same trend followed by the *Amphicyon* lineages. The systematic relationships of the Mae Moh species remain particularly difficult to determine, however, due to the fragmentary nature of the known material. Additional documents of *Afrocyon burolleti* from Libya, *A. tairumensis* from China, and *A. sindiensis* from Pakistan are also necessary for a thorough comparison with *Maemohcyon potisati*.

This study is the first review of the fossil record of the Amphicyoninae. We agree with Raza et al. (1984); Hunt (1998) that most, if not all, Asian *Amphicyon* species must be excluded from this genus. More especially, species from the Indian subcontinent (e.g. *A. shahbazi*, *A. cooperi*, *A. sindiensis*), though not well known, display a diversified morphology and may belong to a genus of their own. At a generic level, Asian amphicyonines show a similar level of endemism to that in Europe and North America (*Askazansoria*, *Maemohcyon*, and possible endemic taxa from Indian subcontinent as well).

The Amphicyonidae are well known from western Europe and North America and there are many evidences of several migrations events between these continents during the early and middle Miocene. However, the poor fossil record of Asia prevents us from finding taxa that would connect those from Europe and North America. The new species described here appears to be the result of one of these migration events. However, we fail to recognize the closest ancestor of *Maemohcyon*, which remains to be discovered. The hypothesis of an Asian origin for *Maemohcyon* cannot be ruled out, because it cannot be really tested due to the poor fossil record. In any case, the lineage of *Maemohcyon* probably diverged much earlier than the late middle Miocene, from an ancestor that may resemble *Ysengrinia*. This ancestorship remains to be confirmed later.

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