



General Palaeontology, Systematics, and Evolution (Vertebrate Palaeontology)

## First record of Entelodontidae (Mammalia, Artiodactyla) from the late Eocene of Southeast Asia



### *Premier enregistrement d'un Entelodontidae (Mammalia, Artiodactyla) dans l'Éocène supérieur d'Asie du Sud-Est*

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#### ABSTRACT

We describe two entelodontid upper premolars that were recovered from the late Eocene of the Krabi coal mine in southern Thailand. The size and morphology of the material suggest that it can be referred to *Entelodon* aff. *E. gobiensis*, a species known from the late Eocene to the early Oligocene of northern Asia and southern China. The Thai material documents for the first time the southernmost occurrence of entelodontids in Asia during the Paleogene and also suggests that Eocene Southeast Asian mammal localities might potentially yield further entelodontid remains mostly associated with selenodont ungulates.

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#### R É S U M É

Nous décrivons deux prémolaires supérieures d'entelodontidé découvertes dans la mine de lignite d'âge Éocène supérieur de Krabi, en Thaïlande méridionale. Les dimensions et la morphologie de ce matériel suggèrent qu'il peut être rapporté à *Entelodon* aff. *E. gobiensis*, une espèce connue de l'Éocène supérieur à l'Oligocène inférieur d'Asie septentrionale et du Sud de la Chine. Ces restes fossiles de Thaïlande documentent, pour la première fois, l'existence la plus méridionale d'entelodontidés en Asie durant le Paléogène et suggèrent que les localités à mammifères fossiles éocènes d'Asie du Sud-Est pourraient potentiellement livrer d'autres restes d'entelodontidés associés principalement à ceux d'ongulés sélénodontes.

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## 1. Introduction

The late Eocene fauna of Krabi, in southern Thailand, has been known for its diversified and rich vertebrate community (for example, Antoine et al., 2003; Benammi et al., 2001; Chaimanee et al., 1997; Ducrocq, 1999; Ducrocq

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et al., 1992, 1995, 1996, 1998, 2006; Métails et al., 2001, 2007) that led to increase our knowledge of the early Paleogene vertebrate faunas of Southeast Asia. Artiodactyls are particularly abundant and represented by at least 12 distinct taxa, including suoids, anthracotheres, and ruminants. However, the occurrence of an entelodontid artiodactyl in the late Eocene Krabi fauna of Thailand has been mentioned (Ducrocq et al., 1995), but the corresponding material was never published. It is therefore important to describe and identify this additional taxon.

The Entelodontidae are a group of middle to large size artiodactyls characterized by their complete bunodont dentition, mandibular tubercles, jugal flanges and didactyl limbs that appeared during the late-middle Eocene in Asia before dispersing to North America in the late Eocene and to Europe after the “Grande Coupure”. The group became extinct at the end of the Oligocene in Eurasia and during the early Miocene in North America (Foss, 2007). They were not very abundant in the Asian vertebrate faunas although they were widely distributed from Georgia to Japan and from Kazakhstan to southern China (Brunet, 1979; Lucas

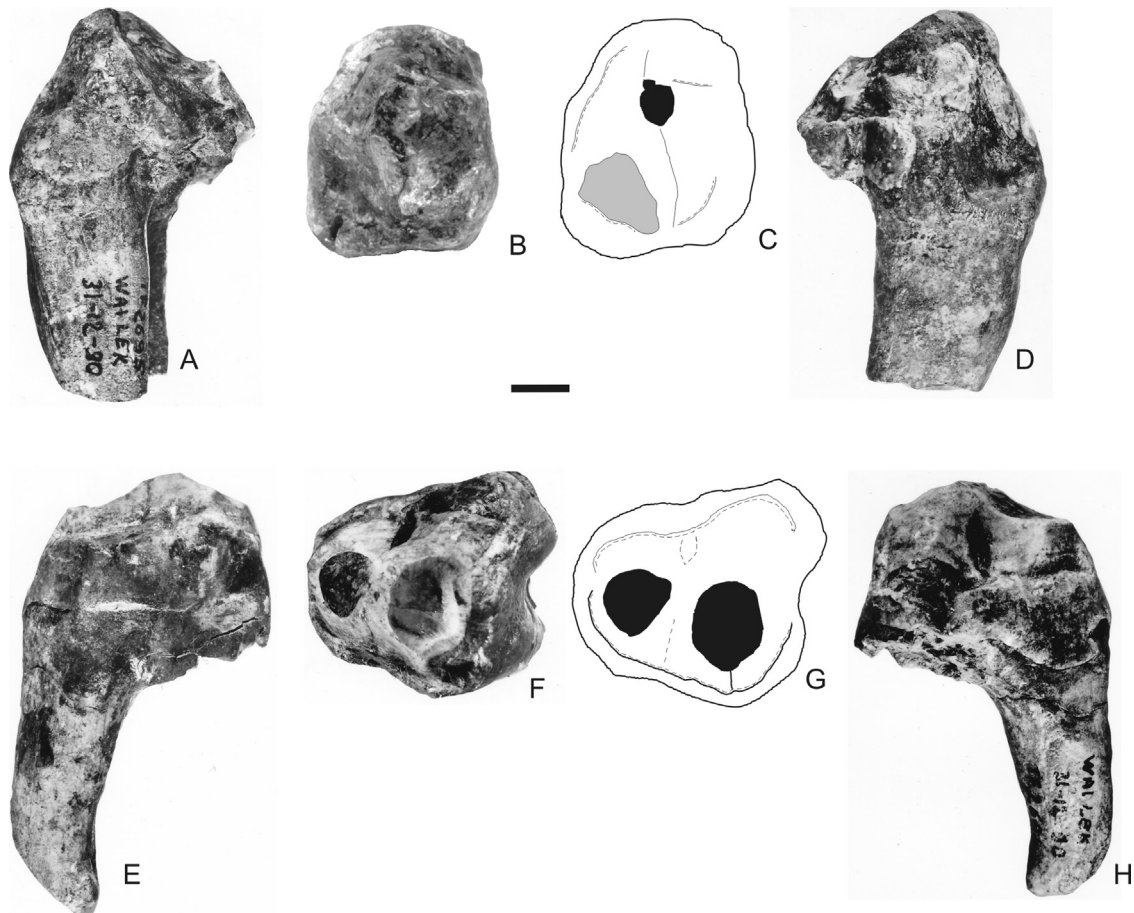
and Emry, 1996, 1999; Tsubamoto et al., 2015), but never recorded in Southeast Asia so far.

The classification of entelodontids has been revised several times over the past years (Brunet, 1979; Foss, 2007; Lucas and Emry, 1996, 1999; Vislobokova, 2008) and we will adopt here the one from Foss (2007). The abbreviations used in the text are *L* = premolar length, *W* = premolar width and TF = Thai Fossil. All fossils described here are housed in the Department of Mineral Resources, Bangkok, Thailand.

## 2. Description

Two associated upper premolars (P3 and P4) have been collected from the upper coal seam in the Wai Lek mine, Krabi Basin that very probably belong to the same individual.

The left P3 (TF 2695) is a massive tooth, taller than P4 with a triangular occlusal outline, but a small part of the mesial end is missing (Fig. 1A–D). The paracone occupies most of the crown and is slightly slanted lingually. The distolingual corner of the premolar is protruding and lower



**Fig. 1.** *Entelodon* aff. *E. gobiensis* from the late Eocene of Krabi, Thailand. A–D. TF 2695, left P3 in buccal (A), occlusal (B and C), and lingual (D) views. E–H. TF 2694, left P4 in distal (E), occlusal (F and G), and mesial (H) views. Scale bar equals 1 cm.

**Fig. 1.** *Entelodon* aff. *E. gobiensis* de l'Éocène supérieur de Krabi, Thaïlande. A–D. TF 2695, P3 gauche en vue buccale (A), occlusale (B et C) et linguale (D). E–H. TF 2694, P4 gauche en vue distale (E), occlusale (F et G) et mésiale (H). La barre d'échelle représente 1 cm.

than the rest of the crown and there is a large wear surface on the distolingual face of the tooth. The mesiodistally oriented postparacrista and the preparacrista are marked. The cingulum is weakly developed on all sides of the crown. The premolar possesses one mesial root and two distal fused roots ( $L=32.3$  mm;  $W=27.9$  mm).

The left P4 (TF 2694) is complete except for its two buccal roots that are broken away (Fig. 1E–H). The occlusal outline of the crown is subtriangular and wider than long. The paracone and the protocone are about the same size and closely appressed and a slight groove separating both cusps can be observed on the distal face. The protocone is slightly more mesially situated than the paracone and it seems to be very slightly bent distally. A cingulum is present mesially and distally, it is interrupted lingually and very weak buccally. There is no parastyle, but a very slight spur of enamel occurs on the distobuccal corner of the crown at the end of the postparacrista. The occlusal wear facet of the paracone is slanting buccally and that of the protocone is slanting lingually. There is no crest except for a very slight and short postparacrista ( $L=27.1$  mm;  $W=31.6$  mm).

The structure of both premolars does not match that of anthracothere corresponding teeth: the P3 is more massive, its pre- and postparacrista are in a longitudinal axis and it displays a distolingual wear surface; the P4 has cusps very close to each other, its mesiobuccal and distobuccal crests are weakly expressed, there is no preprotocrista and the wear facets are slanted. The general massive morphology and bunodonty of both premolars rather indicates that they belong to an entelodontid.

### 3. Discussion

Four genera of entelodontids have been identified in Asia (Lucas and Emry, 1996, 1999; Tsubamoto et al., 2011; Vislobokova, 2008): *Brachyhyops* Colbert, 1937 (middle Eocene of China; late Eocene of China, Mongolia and Kazakhstan), *Eoentelodon* Chow, 1958 (middle Eocene of China, Mongolia and possibly Kazakhstan), *Entelodon* Aymard, 1846 (late Eocene of Mongolia, China and Japan; early Oligocene of China and Kazakhstan), and *Paraentelodon* Gabunia, 1964 (late Oligocene of Georgia, Kazakhstan and China). Among the oldest Asian taxa, *Brachyhyops* and *Eoentelodon* both differ from the Krabi specimen by their much smaller size, and *Brachyhyops* further displays much slenderer P3 and P4, the latter tooth having a mesial and distal waisting absent on the P4 from Krabi, a reduced protocone and stronger cingula (upper teeth are unknown for *Eoentelodon*). Several species of the genus *Entelodon* have been described in the Paleogene of Asia but only two of them have been retained by different authors (Brunet, 1979; Lucas and Emry, 1996): *E. gobiensis* (Trofimov, 1952) and *E. dirus* Matthew and Granger, 1923. *Entelodon dirus* is a very large species from the early Oligocene of Mongolia known only by a M3 and a lower jaw preserving p2–m3, but the Krabi premolars are too small to be referred to this species. On the other hand, the species from Krabi is similar in size with *Entelodon gobiensis* (late Eocene and early Oligocene from Kazakhstan, Mongolia, China and Japan) and it shares with it the two fused posterior roots and the

slightly lingually slanted paracone on P3, and the paracone and protocone of similar size and straight to convex buccal edge on the P4. However, both Thai premolars have less developed cingula, the P3 is more massive with a wider mesial part, and the P4 has a distal wall less convex. *Paraentelodon* is a late Oligocene giant form (Lucas and Emry, 1999) that also differs from the Krabi specimens by its slenderer P3 with a less developed distolingual corner and distal cingulum, and by its squarer P4 without a protruding mesiobuccal corner.

Vislobokova (2008) described a fragmentary lower jaw preserving m2–3 from the middle Eocene of Khaichin Ula II in Mongolia that she assigned to *Proentelodon minutus*, a new primitive entelodontid of very small size. Although this form markedly differs from that of Krabi by its dimensions, we agree with Tsubamoto et al. (2011) that it probably cannot be attributed to the Entelodontidae because of the occlusal structure of its lower molars that also retain a paraconid and an enlarged hypoconulid lobe on m3, both features being unknown in entelodontids.

The premolars from Krabi and those of *Entelodon magnum* Aymard, 1846 have a similar size, but some differences can be noted: the Thai P3 is wider and more massive, with a better developed distolingual corner of the crown. The P4 from Krabi also displays less developed lingual and distal cingula and its mesiobuccal corner is more buccally displaced than in the European species. *Entelodon antiquus* Repélin, 1919 has somewhat smaller premolars with a slenderer P3 curved buccally and a P4 with a protocone markedly smaller than the paracone and better developed cingula. Finally, *Entelodon deguilhemi* Repélin, 1918 from the early Oligocene of western Europe is a form larger than that of Thailand that can be distinguished from it by its longer and narrower P3 with better developed cingula and its P4 with a more rounded distal edge and a paracone more distally slanted.

The available dental material from Krabi makes a precise attribution difficult. Indeed, the P3 and P4 are not the most diagnostic teeth in entelodontids and some features that distinguish the Thai material from other Asian taxa cannot be used in systematics. Actually, Brunet (1979) has shown that a mesial waisting on P4 (a character that often differentiates the Thai P4 from that of other genera) was variable within a species. However, the only Eocene Asian species that is morphologically and metrically closer to the Krabi species is *E. gobiensis*, although the peculiar structure of the massive P3 with its enlarged distolingual shelf and weakly expressed cingula on both the P3 and P4 suggest that the Krabi taxon might belong to a distinct species of *Entelodon*. In the absence of additional material, we prefer to refer the entelodontid from Krabi to *Entelodon* aff. *E. gobiensis*.

### 4. Conclusions

The discovery of an entelodontid in late Eocene sediments of southern Thailand is noteworthy not only because it increases the number and diversity of taxa in the Krabi fauna, but it also documents the southernmost record of the family in Asia. Indeed, the most meridional known occurrence of entelodonts in Asia is *Entelodon* sp. in the late Eocene Caijiachong Formation in Yunnan, South China

(Wang and Zhang, 1983). Only Eocene to early Oligocene taxa have been recorded as far as South China, the late Oligocene genus *Paraentelodon* being known only from the northern part of the landmass (Lucas and Emry, 1999). There is now evidence that representatives of the Entelodontidae occupied a wider area than previously thought, the Asian *Entelodon* having so far occurred in Kazakhstan, Mongolia, China, Japan, and Thailand. The Entelodontidae were not as abundant in the Asian fossil record as the large bunodont anthracotheres (representatives of this group being another major component of Paleogene faunas), possibly because of their similar paleoecological adaptations and diet that led them to compete with each other (according to Joeckel, 1990, the jaw morphology and tooth structure and wear of entelodonts were compatible with a diet based on resistant or hard food items). As a matter of fact, when entelodontids are recognized in Asian Paleogene mammal faunas, they are almost always associated with selenodont anthracotheres or other ungulates that specialized in fibrous vegetation, but not with large bunodont forms (Russell and Zhai, 1987; Tsubamoto et al., 2015) that likely had an omnivorous diet. This might also explain why entelodonts were more frequent in North America than in Europe and Asia (Brunet, 1979; Foss, 2007): during the Cenozoic, most of the New World large ungulates that could have competed with the entelodonts were herbivorous and only very few Eocene and Oligocene medium to large size taxa were bunodont (for example the anthracothere *Heptacodon* and tayassuids). Now that entelodonts have been unambiguously identified at low latitudes in South Asia, it is likely that dental or even postcranial elements attributed to representatives of this family might be recovered from other recently discovered Eocene southern localities like Na Duong in Vietnam (Ducrocq et al., 2015), which might help to improve our knowledge on the origin and evolution of Eurasian taxa.

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## References

- Antoine, P.-O., Ducrocq, S., Marivaux, L., Chaimanee, Y., Crochet, J.-Y., Jaeger, J.-J., Welcomme, J.-L., 2003. Early rhinocerotids (Mammalia, Perissodactyla) from South Asia and a review of the Holarctic Paleogene rhinocerotid record. *Can. J. Earth Sci.* 40, 365–374. <http://dx.doi.org/10.1139/e02-101>.
- Aymard, A., 1846. *Essai monographique sur un nouveau genre de mammifère fossile trouvé dans la Haute-Loire, et nommé Entelodon*. *Ann. Soc. Agric. Puy* 12, 227–267.
- Benammi, M., Chaimanee, Y., Jaeger, J.-J., Ducrocq, S., 2001. Eocene Krabi Basin (southern Thailand): paleontology and magnetostratigraphy. *Bull. Geol. Soc. Am.* 113, 265–273. [https://doi.org/10.1130/0016-7606\(2001\)113<0265:EKBSTP>2.0.CO;2](https://doi.org/10.1130/0016-7606(2001)113<0265:EKBSTP>2.0.CO;2).
- Brunet, M., 1979. Les grands mammifères chefs de file de l'immigration oligocène et le problème de la limite Éocène-Oligocène en Europe. *Éditions de la Fondation Singer-Polignac, Paris*.
- Chaimanee, Y., Suteethorn, V., Jaeger, J.-J., Ducrocq, S., 1997. A new late Eocene anthropoid primate from Thailand. *Nature* 385, 429–431. <http://dx.doi.org/10.1038/385429a0>.
- Chow, M., 1958. *Eoentelodon*, a new primitive entelodont from the Eocene of Lunan, Yunnan. *Vert. Palasiatica* 2, 30–36 (English 30–34; Chinese 35–36).
- Colbert, E.H., 1937. Notice of a new genus and species of artiodactyl from the upper Eocene of Wyoming. *Am. J. Sci.* 33, 473–474.
- Ducrocq, S., 1999. The late Eocene Anthracotheriidae (Mammalia, Artiodactyla) from Thailand. *Paleontographica A* 252, 93–140.
- Ducrocq, S., Buffetaut, E., Buffetaut-Tong, H., Helmcke-Ingavat, R., Jaeger, J.-J., Jongkanjanasontorn, Y., Suteethorn, V., 1992. A lower Tertiary vertebrate fauna from Krabi (South Thailand). *Neues Jahrb. Geol. Paläontol. Abh.* 184, 101–122.
- Ducrocq, S., Chaimanee, Y., Suteethorn, V., Jaeger, J.-J., 1995. Mammalian faunas and the ages of the continental Tertiary fossiliferous localities from Thailand. *J. SE Asian Earth Sci.* 12, 65–78.
- Ducrocq, S., Chaimanee, Y., Suteethorn, V., Jaeger, J.-J., 1996. An unusual anthracotheriid artiodactyl from the late Eocene of Thailand. *Neues Jahrb. Geol. Paläontol. Mh.* 7, 389–398.
- Ducrocq, S., Chaimanee, Y., Suteethorn, V., Jaeger, J.-J., 1998. The earliest known pig from the late Eocene of Thailand. *Palaeontology* 41, 147–156.
- Ducrocq, S., Chaimanee, Y., Jaeger, J.-J., Métais, G., 2006. A new ceratomorph (Perissodactyla, Mammalia) from the late Eocene of Southeast Asia. *J. Vert. Paleontol.* 26, 1024–1027. <http://dx.doi.org/10.1080/02724634.1999.10011130>.
- Ducrocq, S., Benammi, M., Chavasseau, O., Chaimanee, Y., Suraprasit, K., Phan Dong Pha, Vu Le Phuong, Phung Van Phach, Jaeger, J.-J., 2015. New Anthracotheriidae (Cetartiodactyla, Mammalia) from the Paleogene of northeastern Vietnam: biochronological implications. *J. Vert. Paleontol.* 35, e929139. <http://dx.doi.org/10.1080/02724634.2014.929139>.
- Foss, S.E., 2007. Family Helohyidae. In: Prothero, D.R., Foss, S.E. (Eds.), *The Evolution of Artiodactyls*. The Johns Hopkins University Press, Baltimore, pp. 85–88.
- Gabunia, L.K., 1964. Benarskaya fauna oligosensenykh pozvonochnykh [Benara fauna of Oligocene vertebrates]. *Akademiya Nauk Gruzinskoy SSR Institut Paleobiologii Izdatelstvo "Metsnierba", Tbilisi [Russian]*.
- Joeckel, R.M., 1990. A functional interpretation of the masticatory system and paleoecology of entelodonts. *Paleobiology* 16, 459–482. <http://dx.doi.org/10.1017/S0094837300010198>.
- Lucas, S.G., Emry, R.J., 1996. Late Eocene entelodonts (Mammalia: Artiodactyla) from Inner Mongolia, China. *Proc. Biol. Soc. Washington* 109, 397–405.
- Lucas, S.G., Emry, R.J., 1999. Taxonomy and biochronological significance of *Paraentelodon*, a giant entelodont (Mammalia, Artiodactyla) from the late Oligocene of Eurasia. *J. Vert. Paleontol.* 19, 160–168. <http://dx.doi.org/10.1080/02724634.1999.10011130>.
- Matthew, W.D., Granger, W., 1923. The fauna of the Houldjin Gravels. *Am. Mus. Novit.* 97, 1–6.
- Métais, G., Chaimanee, Y., Jaeger, J.-J., Ducrocq, S., 2001. New remains of primitive ruminants from Thailand: evidence on the origin of traguloids. *Zool. Scripta* 30, 231–248. <http://dx.doi.org/10.1046/j.0300-3256.2001.00071.x>.
- Métais, G., Chaimanee, Y., Jaeger, J.-J., Ducrocq, S., 2007. Eocene bunoselenodont Artiodactyla from southern Thailand and the early evolution of Ruminantia in South Asia. *Naturwissenschaften* 94, 493–498. <http://dx.doi.org/10.1007/s00114-007-0218-2>.
- Repélin, J., 1918. Sur de nouvelles espèces du genre *Entelodon* Aymard (*Elotherium* Pomel, *Archaeotherium* Leidy, *Oltinotherium* Delfortrie, *Pelonax* Cope). *C. r. hebdom. séances Acad. sci. Paris* 166, 397–400.
- Repélin, J., 1919. Sur les espèces ou mutations nouvelles du genre *Entelodon* Aymard. *Bull. Soc. géol. France* 19, 11–14.
- Russell, D.E., Zhai, R., 1987. The Paleogene of Asia: mammals and stratigraphy. *Mem. Mus. Nat. Hist. Nat., Paris* 52, 1–488.
- Trofimov, B.A., 1952. Novyye entelodontidy iz Mongolii i Kazakhstana [New entelodonts from Mongolia and Kazakhstan]. *Akademiya Nauk SSSR Trudy Paleontologicheskii Institut* 41, 144–154 [Russian].
- Tsubamoto, T., Koda, Y., Hasegawa, Y., Nabana, S., Tomida, Y., 2015. Paleogene mammals from the Iwaki Formation in Japan: their implications for the geologic age and paleobiogeography of this formation. *J. Asian Earth Sci.* 108, 18–32. <http://dx.doi.org/10.1016/j.jseas.2015.03.049>.

- Tsubamoto, T., Saneyoshi, M., Watabe, M., Tsogtbaatar, K., Mainbayar, B., 2011. The entelodontid artiodactyl fauna from the Eocene Ergilin Dzo Formation of Mongolia with comments on *Brachyhyops* and the Khoer Dzan locality. *Paleont. Res.* 15, 258–268, <http://dx.doi.org/10.2517/1342-8144-15.4.258>.
- Vislobokova, I.A., 2008. The oldest representative of Entelodontidea (Artiodactyla, Suiformes) from the middle Eocene of Khaichin Ula II, Mongolia, and some evolutionary features of this Superfamily. *Palaeont. J.* 42, 643–654, <http://dx.doi.org/10.1134/S0031030108060105>.
- Wang, B., Zhang, Y., 1983. New finds of fossils from Paleogene of Qujing, Yunnan. *Vert. Palasiatica* 21, 119–128.