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Florentin Cailleux, Yaowalak Chaimanee, Jean-Jacques Jaeger, Olivier Chavasseau. New Erinaceidae (Eulipotyphla, Mammalia) from the Middle Miocene of Mae Moh, Northern Thailand. *Journal of Vertebrate Paleontology*, 2020, 40 (3), pp.e1783277. 10.1080/02724634.2020.1783277 . hal-04198647

HAL Id: hal-04198647

<https://hal.science/hal-04198647>

Submitted on 7 Sep 2023

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New Erinaceidae (eulipotyphla, Mammalia) from the Middle Miocene of Mae Moh, northern Thailand

Journal of Vertebrate Paleontology 2020 40(3), e1783277

<https://doi.org/10.1080/02724634.2020.1783277>

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Abstract

The Galericinae are a group of Erinaceidae that are currently distributed in Southeast and Eastern Asia. Although galericines have an Asian origin, their fossil record in this region is scarce, which greatly limits the knowledge of the evolutionary history of this group. We describe here the first fossils of Eulipotyphla from the middle Miocene (13.4–13.2 Ma) of the Mae Moh Basin of northern Thailand, and assign the material to three taxa of Erinaceidae attributable to the Galericinae (*Galerix rutlandae*, *Lantanotherium anthrace*, sp. nov., and *Lantanotherium* sp.). The Mae Moh erinaceids present a *Lantanotherium*-*Galerix* association that is uncommon in the Miocene of Asia. *Galerix rutlandae* is a species formerly described in the Siwaliks of Pakistan and India, which reaffirms the strong affinities during the middle Miocene between the mammalian faunas of Southeast and Southern Asia. The discovery of two species of *Lantanotherium* in Mae Moh provides additional knowledge about the evolution in Asia of this widespread Miocene genus that had never been recorded in Southeast Asia. The presence of three Galericinae in Mae Moh Basin reinforces the hypothesis of a mainly closed and wet environment during the deposition of the K and Q lignite layers.

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Introduction

The geographic distribution of Recent species of the subfamily Galericinae (Erinaceidae, Eulipotyphla) is restricted to Southeast Asian rainforests (Corbet, 1988). Whereas the subfamily is represented by only a few extant species, the diversity of Galericinae was much higher in the fossil record. Lopatin (2006) dates the first occurrence of the Galericinae in the Middle Eocene of Asia based on the record of *Eogalericius*, *Microgalericius* and *Protogalericius*. The time of divergence between the Erinaceinae and the Galericinae was also placed in the Eocene on the basis on molecular data (Douady and Douzery, 2003; Bannikova et al., 2014). Galericinae are subsequently recorded from the upper Eocene to Pliocene in Europe. The lower Oligocene of North America is also characterized by the occurrence of *Ocajila makpiyahe*, a possible ancestor of some Miocene North American Galericinae identified as *Lantanotherium* (see Engesser, 1979). During the Miocene, an increasing diversity is observed. This is especially true for the tribe Galericipini, which is well diversified in Eurasia and also recorded in Africa (Butler, 1969, 1984; Senut et al., 1992). Well documented in the fossil record of Europe (Van den Hoek Ostende, 2001; Ziegler, 2006; Prieto et al., 2011; Furió and Alba, 2011), galericipines are rather poorly known in Southeast and East Asia, with records from only Pakistan (Zijlstra and Flynn, 2015), China (Li et al., 1983; Storch and Qiu, 1991), and in a single locality in Thailand (Mein and Ginsburg, 1997). Nevertheless, in the middle Miocene of Thailand, Ducrocq et al. (1995) noted the presence of an indeterminate Erinaceidae in Ban San King and Had Pu Dai, whereas Chaimanee et al. (2007) and Suraprasit et al. (2013) mentioned an undetermined Erinaceidae from the locality of Mae Moh. We describe here new specimens of Galericinae from Mae Moh, and provide further information on the evolution and diversity of Asian Galericinae. The new specimens complete numerous studies carried out in Thailand (e.g., Ducrocq et al., 1995; Mein and Ginsburg, 1997; Chaimanee et al., 2007), which contributed to a better understanding of the mammalian diversity and evolution recorded in the Miocene localities of Southeast Asia. Moreover, because extant Galericinae have fairly strict environmental preferences (Corbet, 1988; Furió and Alba, 2011) and possess body masses between those of rodents and small carnivores, they can provide additional paleoenvironmental information for Mae Moh locality during the middle Miocene.

Institutional Abbreviation—UPP MM, Mae Moh collection, Laboratoire Paléontologie Évolution Paléoécosystèmes Paléoprimatologie, UMR CNRS 7262 INEE, Université de Poitiers, Poitiers, France.

Geological setting

The Mae Moh Basin is one of the forty Cenozoic intermontane basins of northern Thailand (Packham, 1996; Morley et al., 2001) (see Fig. 1). It is the largest open pit coal mine of the country. Corsiri and Crouch (1985) have defined three formations in this basin, forming the Mae Moh Group: Huai King, Na Khaem, and Huai Luang. The Na Khaem Formation consists of fluviolacustrine sediments and four vertebrate-bearing fossiliferous lignite layers (J, K, Q, and R, from top to bottom), having delivered numerous mammalian taxa (Ducrocq et al., 1994, 1995; Songtham et al., 2005; Peigné et al., 2006; Chaimanee et al., 2007, 2008; Chavasseau et al., 2009; Grohé et al., 2010; Grohé, 2011; Suraprasit et al., 2011, 2013, 2014). Based on magneticpolarity stratigraphy, this section was dated between 14.2 and 12.0 Ma (Benammi et al., 2002; Coster et al., 2010). Within this section, the ages of the fossiliferous Q and K lignite layers, containing the new Galericinae material, were determined to be 13.4 and 13.2 Ma. The deposits were formed during a succession of temperate and tropical vegetation (Songtham et al., 2005). Nevertheless, the recovered flora showed an association of temperate and tropical pollens that may underline the fact that the Mae Moh Basin was close to the boundary between a tropical and a warm temperate climate (Sepulchre et al., 2009), thus potentially sensible to the numerous global climatic variations occurring during the late Miocene (see Billups and Schrag, 2003; Shevenell et al., 2004; Kelly and Goulden, 2008).

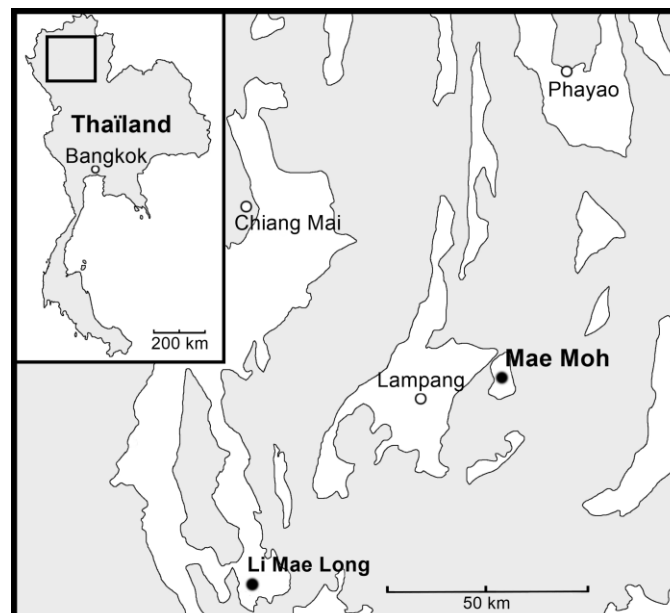


Figure 1. Map of Thailand showing the localities of Mae Moh and Li Mae Long. Tertiary deposits are here represented in white. Modified after Suraprasit et al. (2014).

Materials and methods

The studied material was discovered during two field seasons led by the Thai-French paleontological expedition in July 2008 and February 2009. Specimens comprising mandibles were collected directly from the coal seams. Measurements were taken with a digital micrometer (Mitutoyo 164-164) and follow the measurement methods of Klietmann et al. (2014). We follow Lopatin (2006) for the dental terminology. The studied material from Mae Moh locality is housed in the laboratory PALEVOPRIM – UMR CNRS 7262 INEE, Université de Poitiers, France.

The estimation of body mass followed the allometric equations of Legendre (1989) based on m1 dimensions. If Y is the body mass, X the multiplication of the length by the width, k is the slope, and Log(b) the intercept of the regression line: $\text{Log}Y = \text{Log}(b) + k\text{Log}(X)$. We especially used the corrected equation for insectivora that exclude outliers (Condylura, Talpa, Limnogale, and Tenrec). The equation parameters used (to obtain a 95% confidence interval of the body mass) are: $k = 1.8040$ and $\text{Log}(b) = 1.2430$ for the lower boundary and $k = 1.8860$ and $\text{Log}(b) = 1.3849$ for the upper boundary.

Systematic paleontology

Class Mammalia Linnaeus, 1758
Order Erinaceomorpha Gregory, 1910
Family Erinaceidae Fischer, 1814
Subfamily Galericinae Pomel, 1848

Remarks

Even if the phylogenetic analysis of Gould (1995) has not established the attribution of *Galerix* and *Lantanotherium* to the Galericinae, we consider here that the shared dental features of these genera are enough to include them among this subfamily. Thereby, we follow Corbet (1988) and use the concept of Galericinae Pomel, 1848, and not that of Hylomyinae Frost, Wozencraft and Hoffmann, 1991 (Engesser and Jiang, 2011). Thus, we do not follow the use of the concept Galericipidae (Bannikova et al., 2014), unlike Pavlova et al. (2018) and Abramov et al. (2018). This taxonomic elevation of Galericinae corresponds rather to an arbitrary change of definition, and we strongly suggest avoiding such taxonomic choice without compelling

arguments. Among the subfamily Galericinae, we consider here three tribes: Galericipini, Otohylomyini, and Hylomyini. We do not follow the concept of Galericipini sensu lato from Lopatin (2006), because it is too wide and probably paraphyletic, but instead we follow the concept of Van den Hoek Ostende (2001), who distinguished the tribe Galericipini (comprising the genera *Galerix*, *Parasorex*, *Deinogalerix*, and *Schizogalerix*) from the tribe Hylomyini (comprising *Hylomys*, *Neohylomys*, *Neotetracus*, *Echinosorex*, and *Podogymnura*). Among Galericipini, Van den Hoek Ostende (2001) also considered the genus *Tetracus* synonymous with *Galerix*. However, the subsequent description of the species *Tetracus daamsi* by Hugueneu and Adrover (2003) rendered this synonymy unlikely. *Tetracus* was confirmed to be a distinct genus of Galericipini by Van den Hoek Ostende and Doukas (2003) and Van den Hoek Ostende (2003a, 2018). We will also include here within the Galericipini the genera *Riddleria* Van den Hoek Ostende, 2003 and *Apulogalerix* Masini and Fanfani, 2013. The tribe Otohylomyini was recently created by Bannikova et al. (2014) due to the exclusion of *Otohylomys megalotis* (Jenkins and Robinson, 2002) from the tribe Hylomyini. The robustness of such a monospecific tribe should be further tested, but already presents a possible explanation for the peculiar anatomy of *Otohylomys*. Finally, concerning the tribe Hylomyini, we share the same doubt as Zijlstra and Flynn (2015) about the generic allocation of *Hylomys engesseri*. A revision of Hylomyini seems necessary to clarify this point.

Tribe Galericipini Pomel, 1848

Genus *Galerix* Pomel, 1848

Type Species—*Galerix exilis* (de Blainville, 1839).

Geographic and Stratigraphic Range—Lower to middle Miocene of Eurasia and Africa (Munthe and West, 1980; Li et al., 1983; Butler, 1984, 2010; De Jong, 1988; Van den Hoek Ostende, 2001; Prieto et al., 2011).

Diagnosis—From Van den Hoek Ostende (2001:686): “Small to large Galericipini. The $p2 \geq p3$. Protocone–metaconule connection present in at least part of the M1 and M2. Posterior cingulum of the M1 and M2 continuous in at least part of the specimens. P3 usually without hypocone.”

Galerix rutlandae Munthe and West, 1980

(Fig. 2)

Type Locality—H-GSP locality 18, Daud Khel, Punjab, Pakistan; Chinji Formation.

Geographic and Stratigraphic Range—Lower upper Miocene of Siwaliks of India (11–10 Ma; Cheema et al., 2000) and middle Miocene of Pakistan (14.3–11.6 Ma on the Potwar Plateau; Munthe and West, 1980; Zijlstra and Flynn, 2015).

Diagnosis—From Zijlstra and Flynn (2015:7): “A species of *Galerix* with the following combination of characters: size very small (comparable to *G. saratji*); hypocone absent on P3; metastyle crest on M1 weak and relatively posteriorly directed; protocone and metaconule on M1 and M2 almost always connected; connection between protocone and hypocone usually strong; metaconule on M1 and M2 usually with a short posterior arm that does not reach the posterolabial corner of the tooth; p1 two-rooted; p2 and p3 with distinct anterior cuspule; p3 larger than p2; p4 with poorly developed metaconid and with the paraconid elongated and crestlike; entoconid always connected to the posterior cingulum in m1 and usually in m2.”

Material—UPP MM-80, right p3 (L = 1.37, W = 0.82); UPP MM-81, right mandible fragment with p4 (L = 1.92, W = 1.16); UPP MM-82, right fragment of m1; UPP MM-83, right mandible fragment with m2 (L = 2.18, WTr = 1.52, WTa = 1.49) and m3 (L = 1.75, WTr = 1.11, WTa = 0.93); UPP MM-84, right mandible fragment. The material comes from layers K and Q of Mae Moh.

Estimated Body Mass—Between 72.5 g and 95.9 g (based on UPP MM-83 and the m1:m2 surface mean ratio of *Galerix rutlandae* calculated from Zijlstra and Flynn, 2015).

Description

The lower jaw is only known from incomplete specimens. Nevertheless, the corpus mandibulae is always straight and thin. One specimen shows a large mental foramen below the distal root of p3. The anterior teeth (i1 to p2) of *G. rutlandae* are not documented at Mae Moh. However, the alveoli of the p2 are partially fused. As deduced from the preserved p3, this tooth was larger than p2.

The third premolar is a narrow tooth with a slightly lingually placed and low paraconid. The protoconid is in a slightly mesial position. This tooth has a complete postcingulid. The gracile double-rooted p4 (Fig. 2) is elongated with an isolated and an almost conical paraconid. Its height is about half of the height of the protoconid. A low protocristid descends

mesiolingually from this cusp, leading to a weakly isolated metaconid. The height of this cusp is almost equal to the height of the paraconid. A metacristid connects the metaconid to the lingual part of the talonid. The latter, broad without cusps, is more compressed mesiodistally in its lingual part. A cingulid is present all along the distal margin of the tooth. A weak median bulge is present on the talonid.

The m1 is known at Mae Moh only by a talonid. The hypoconid is quite strong and connected to the protoconid by a mesiodistal oblique cristid. The talonid basin is open due to the lack of a strong entocristid. It has to be noted that the talonid basin is slightly notched between the entoconid and the metaconid. The postcingulid is connected to the entoconid and joins the lower lingual edge of the tooth. This connection could nevertheless be an artifact caused by the strong degree of wear.

The trigonid of m2 is broad, compressed mesiodistally, and is as long as the talonid. It is shallow and fairly closed. The paraconid is indistinguishable from the paralophid. The latter descends from the distolingual edge of the protoconid before turning posteriorly as a low crest. It ends on the lingual edge of the tooth without reaching the metaconid. This metaconid is the highest cusp of the tooth and is in a more mesial position than the protoconid. These two cusps are connected to each other by a metalophid (protocristid). The morphology of the talonid on m2 (Fig. 2) is similar to m1, even if the oblique cristid is lower. A complete buccal cingulid is present, and the postcingulid is connected to the entoconid.

The m3 (Fig. 2) is smaller and narrower than the m2. Like on m2, the trigonid is slightly higher than the talonid, and the metaconid is connected to the protoconid by the protocristid. The trigonid is moderately compressed mesiodistally. The low ridges of the talonid have a squared appearance in occlusal view. In addition to its smaller size, the m3 from Mae Moh presents a pronounced hypoconid, forming a vestibular swelling. The entoconid and hypoconid are high and connected to each other distally by the postcristid. The oblique cristid is straight, almost mesiodistally oriented. A robust lingual cingulid is present, especially between the hypoconid and the protoconid. Finally, there is no postcingulid.

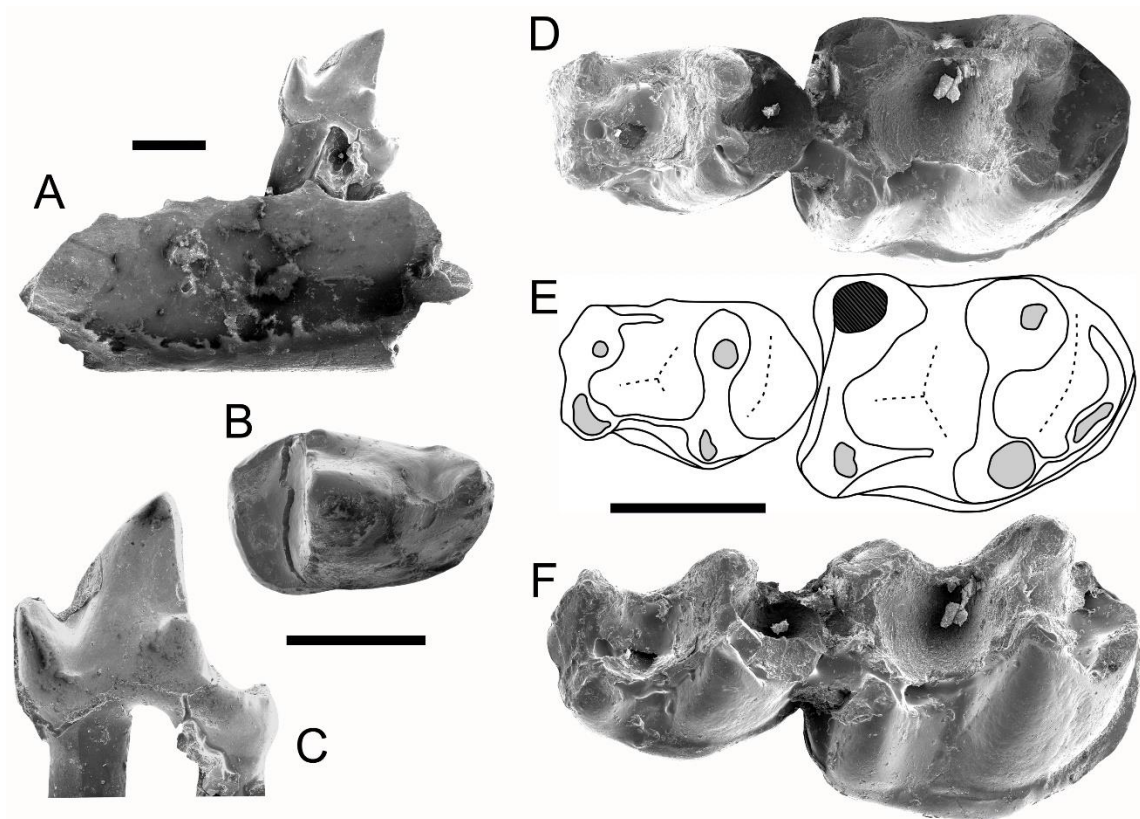


Figure 2. Specimens of *Galerix rutlandae*. A–C, UPP MM-81, right mandible fragment with p4: A, lingual view, B, occlusal view of p4, and C, lingual view of p4. D–F, UPP MM-83, right mandible fragment with m2–m3: D, occlusal view; E, interpretive drawing of the occlusal view; F, oblique buccal view. Scale bars equal 1 mm.

Genus *Lantanotherium* Filhol, 1888

Remarks—The name ‘Lanthanotherium’ is frequently used in the literature (e.g., Mein and Ginsburg, 1997; Storch and Qiu, 1991). However, the arguments of McKenna and Bell (1997) and Furió and Alba (2011) confirm the invalidity of that name and that ‘*Lantanotherium*’ is the valid, original spelling of the genus. *Lantanotherium* is usually considered as a Galericinae, but has not been univocally attributed to any tribe of Erinaceidae, probably because of the lack of studies on the relationships between the Oligocene and Miocene Erinaceidae. Storch and Qiu (1991) include *Lantanotherium* among the tribe Echinisoricini Cabrera 1925, a placement not followed by Gould (1995) and Furió and Alba (2011). We will refrain from classifying *Lantanotherium* in a tribe. However, we consider that this genus is closer to extant Hylomyini and Otohylomyini than the fossil representative of the Galericini (see also Furió and Alba, 2011).

Type Species—*Lantanotherium sansaniense* (Lartet, 1851). Geographic and Stratigraphic Range—Lower to upper Miocene of Europe (Crusafont et al., 1955; Engesser, 1972; Beaudelot and Crouzel, 1976; Ziegler, 2005a; Furió and Alba, 2011). middle to late Miocene of Asia (Li et al., 1983; Storch and Qiu, 1991; Jablonski et al., 2014), and North America (James, 1963; Engesser, 1979; Korth and Evander, 2016).

Diagnosis—From Gunnell et al. (2008:95): “m1 paralophid elongated; m2–3 trigonids open with hypoconid and entoconid each connected to trigonid by longitudinal ridge”; from Sabol (2005:435): “The extending protoconid posterior crest and posterior cingulid forming the entoconid of m1 indicate *Lantanotherium*, differing thus from other genera as follows: from *Galerix* by the shape and larger dimensions of the trigonid; from *Mioechinus* by the longer trigonid than talonid; from *Amphechinus* by smaller dimensions and proportionally by the wider trigonid.

Lantanotherium anthrace, sp. nov. (Figs. 3, 4)

Holotype—UPP MM-85, anterior part of the crushed skull of an individual preserving a right maxilla fragment with C (L = 1.53, W = 0.86), P1 (L = 0.88, W = 0.54), P2 (L = 1.16, W = 0.55), and P3 (Ldj = 2.16, W = 1.30); a right premaxilla with I1 (L = 1.39), I2 (L = 0.70) and I3, a left I1 (L = 1.39, W = 1.10); and a left mandibular fragment with i1 (L = 0.94, W = 0.76), i2 (L = 0.93, W = 0.78), i3 (L = 0.96, W = 0.66), c (L = 1.40, W = 0.97), p1 (L = 0.92, W = 0.56), p2 (L

= 1.09, W= 0.62), p3 (L = 1.41, W= 0.84), p4 (L = 1.86, W= 1.33), and m1 mesial root (Fig. 3). The holotype comes from layer K of Mae Moh.

Paratypes—UPP MM-86, right mandible fragment with i1 (L = 1.03, W= 0.68), i2 (L = 1.05, W= 0.64), i3 (L = 0.94, W= 0.64), c (L = 1.14, W= 0.99), p2 (L = 0.99, W= 0.64), p3 (L = 1.42, W= 1.01), p4 (L = 1.79, W= 1.27), and m1 (WTr = 1.52) (Fig. 4); UPP MM-87, right mandible fragment with i1 (L = 0.76, W= 0.82), i2 (L = 0.86, W= 0.76), i3 (L = 0.78, W= 0.65), and c (L = 1.07, W= 0.79); UPP MM-88, right i1 (L = 1.00, W= 0.66); UPP MM-89, right i3 (L = 0.93, W= 0.70); UPP MM-90, left mandible fragment with p2 (L = 0.96, W= 0.61), and p3 (L = 1.47, W= 0.82); UPP MM-91, right p2 (L = 0.91, W= 0.63); UPP MM-92, left mandible fragment with p3 (L = 1.35, W= 0.81), p4 (L = 2.00, W= 1.36), and m1 (L = 2.72, TWr = 1.45) (Fig. 4); UPP MM-93, left mandible fragment with p3 (L = 1.29, W= 0.94); UPP MM-94, right mandible fragment with p4 (L = 1.84, W= 1.16) and m1 (WTa = 1.65); UPP MM-95, right m1 (L = 2.83, WTr = 1.49, WTa = 1.69) (Fig. 4); UPP MM-96, right mandible fragment. Paratypes come from layers K and Q of Mae Moh.

Type Locality and Age—Mae Moh coal pit (K and Q layers), Mae Moh Basin, Thailand; middle Miocene (13.4–13.2 Ma).

Diagnosis—Small species of *Lantanotherium* (similar in size to *L. sanmigueli* Villalta and Crusafont, 1944 and *L. observatum* Korth and Evander, 2016) differing from all other species of this genus by the following combination of characters: upper incisors decreasing in size distally; I1 caniniform; lack of upper and lower post-canine diastema; presence of four lower premolars; premolars increasing in size distally; P1 and P2 with a talon elongated distally; strong P3 with a lingual expansion bearing no distinct protocone; p4 with a small metaconid.

Etymology—The specific epithet is derived from the Ancient Greek word ‘anthrax,’ meaning ‘coal.’ It is in reference to the mine of Mae Moh, largest coal mine of Thailand, where the remains were discovered.

Estimated Body Mass—Between 58.3 g and 76.4 g (UPP MM-95); between 51.4 g and 67.0 g (UPP MM-92).

Description

The premaxilla and the maxilla of *Lantanotherium anthrace*, sp. nov., are relatively complete but fractured (Fig. 3). The three incisors are decreasing in size and a small diastema is distinguishable between I1 and I2. There are no distinguishable diastemata on the maxilla.

The I1 is markedly caniniform, with a tall and anteroflexed cusp. The distal part of this cusp is compressed but without forming a ridge. Its basal section is oval. The I2 is more rounded than I1, subtriangular in buccal view, but slightly anteroflexed. Its height corresponds to half of the height of I1. I3 is a small and simple tooth composed only of a straight cusp.

The upper canine has a massive shape, with a strong mesiodistal elongation. Long and tall, it is characterized by its triangular crown in lateral perspective and its weak distal crest descending from the main cusp. This cusp is in a mesial position. There is no mesial bulge, and the mesial root is slightly stronger than the distal one.

P1 is a simple and elongated tooth with a narrower distal border. There is a small mesial bulge. A thin crest is distinguishable between the main cusp and the distal margin. P2 is longer than P1 but has the same shape. This double-rooted tooth has, as the P1, a mesial cusplet and a thin mesio-distal crest descending from the main cusp. The P3 is subequal in height to the canine and has a much bigger size than P1 and P2. The P3 is triple-rooted. The circular paracone is connected to the metacone by a straight crest. This tooth has a lingual expansion close to the paracone. A small lingual cingulum can be distinguished, but without bearing a protocone. There is a weak ectocingulum distal to the protocone. A bulge is present on the most mesial part of the tooth, corresponding to a small parastyle.

The mandible is gracile. The ascending ramus, partially preserved on one specimen (Fig. 4), is oblique and slightly curved distally. The mandible is distinguishable by a thick anterior body, which is not tapering before the symphysis. In *L. anthrace* the mandibular symphysis is long, reaching the middle of the p2. Four lower premolars are present. They increase in size gradually from front to back. A large mental foramen possessing an oval shape with an anteroposterior long axis in lateral perspective, present on two specimens, is located below the distal half of p2 and the mesial half of p3.

The i1 and i2 are subequal in size and are both larger than the i3. They have a fairly spatulate shape and are slightly projected forward. The i3 is lower and less spatulate. Moreover, unlike i1 and i2, it has a more pronounced distolingual slope. The lower canine is taller than the first three premolars. Oval in cross section, the canine is anteroflexed with a very short distal bulge.

The single-rooted p1 has a flat and oval shape, constituted by a circular cusp situated in the middle of the tooth. Its outline is slightly expanded distally. The root is circular and oblique. The small p2 is conical, without paraconid. Nevertheless, it is possible to distinguish a slight mesial bulge preceding it. A beginning of paralophid descends from the protoconid but does not reach this bulge. The p2 has a broad root. The p3 is proportionally quite large compared to p1 and p2. This double-rooted tooth exhibits a weak conical paraconid, near the mesiolingual border of the crown. The protoconid is conical. A short talonid is present but bears only a tiny hypoconid. The distal edge of the crown is quite broad and has a weakly marked cingulid, stronger in its median part. The p4 is weakly molarized and has a conical paraconid in a slightly lingual position. The paraconid is low and not isolated. From the lingual side of the conical protoconid descends a weakly developed protocristid leading to a small individualized metaconid, which is only half the height of the protoconid. The tooth has a relatively thick lingual cingulid. The talonid of the p4 is longer than that of the p3 and has a stronger postcingulid.

Lower molars are only known by m1. The trigonid is longer than the talonid. The metaconid and the protoconid are opposite to each other, the metaconid being in a slightly more mesial position. A weak isolated cingulid is located between the paraconid and the metaconid, partially closing the deep trigonid basin. The broad talonid basin is rather closed, because of a protruding entocristid only separated from the metaconid by a notch. Finally, the postcingulid is strong and joins the entoconid.

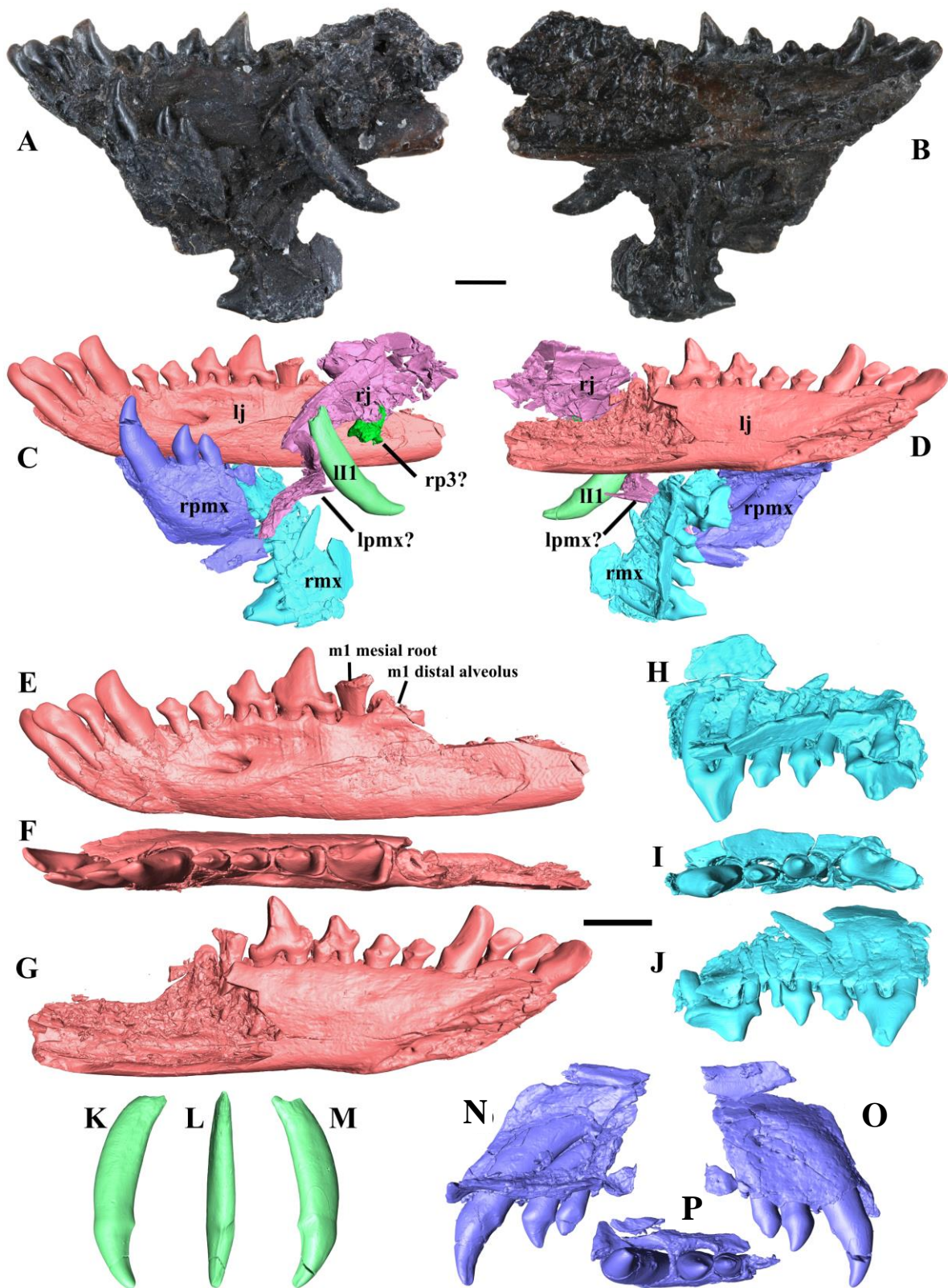


Figure 3. *Lantanotherium anthrace*, sp. nov., UPP MM-85, holotype, anterior part of the skull of a single individual. A, B, views of the bone assemblage. C, D, interpretation after CT-scan segmentation. E–G, extracted left jaw with i1–p4 in E, buccal, F, occlusal, and G, lingual views. H–J, extracted right maxilla with C–P3 in H, lingual, I, occlusal, and J, buccal views. K–M, extracted left maxilla with C–P3 in K, lingual, L, occlusal, and M, buccal views. N–O, extracted right maxilla with C–P3 in N, lateral, O, medial views. P, extracted right maxilla with C–P3 in lingual view. Scale bars = 1 cm.

extracted left I1 in K, buccal, L, distal, and M, lingual views. N–P, extracted right premaxilla with I1–I3 in N, lingual, O, buccal, and P, occlusal views. Abbreviations: lj, left jaw; II1, left first incisor; lpmx, left premaxilla; rj, right jaw; rmx, right maxilla; rp3, right third premolar; rpmx, right premaxilla. Scale bars equal 2 mm.

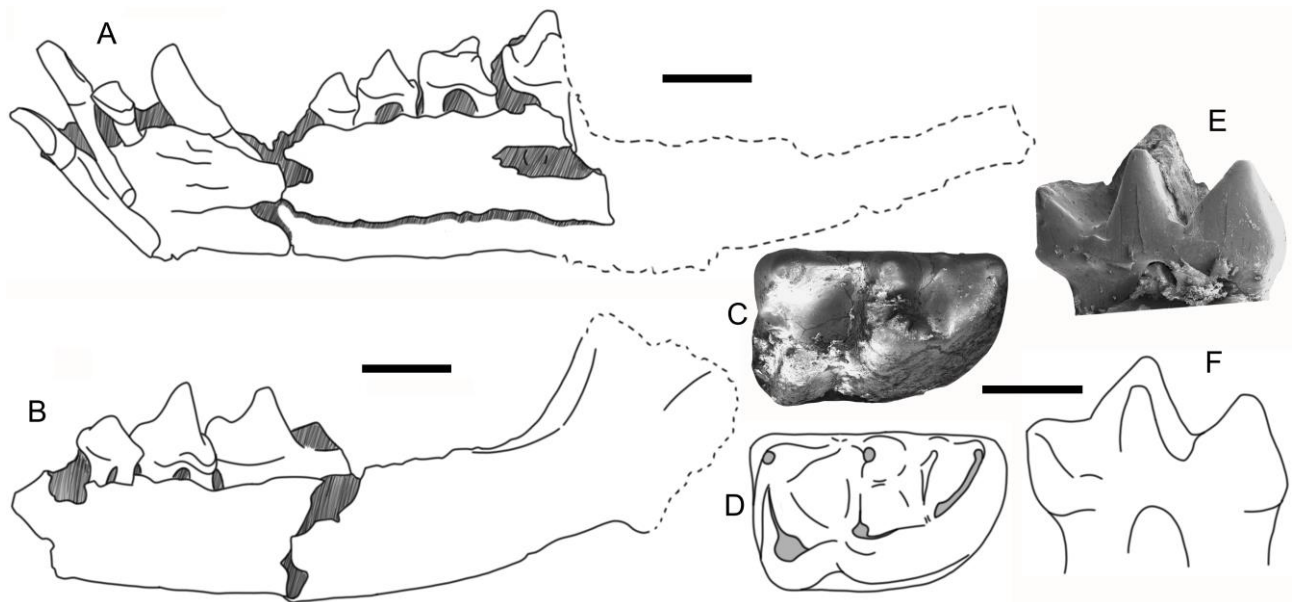


Figure 4. *Lantanotherium anthrace*, sp. nov., referred specimens. A, UPP MM-86, drawing of the right mandible fragment with i1–m1 in lingual view. B, UPP MM-92, drawing of the left mandible fragment with p3–m1 in buccal view. C–F, UPP MM-95, right m1: C, occlusal view; D, drawing of the occlusal view; E, lingual view; F, drawing of the lingual view. Scale bars equal 1 mm.

Lantanotherium sp.
(Fig. 5)

Material—UPP MM-98, right mandible fragment with p4 (L = 2.67, W = 1.62), m2 (L = 2.84, WTr = 1.85, WTa = 2.03), and m3 (L = 2.04, WTr = 1.53) (Fig. 5); UPP MM-99, left mandible fragment with p4 (W = 1.64) and m2 (L = 2.60, WTr = 1.73, WTa = 1.79); UPP MM-101, right mandible fragment with m1 (WTr = 1.75, WTa = 1.91) and m2 (L = 2.47, WTr = 1.72, WTa = 1.78); UPP MM-100, right mandible fragment with m1 (L = 3.06, WTr = 1.86, WTa = 1.99) and m2 (L = 2.41, WTr = 1.67, WTa = 1.81); UPP MM-102, left m3 (L = 1.87, WTr = 1.38, WTa = 1.18). The material comes from layer Q of Mae Moh.

Description

The mandible of *Lantanotherium* sp. (Fig. 5) is particularly robust because of a thick ramus. The ascending corpus is straight.

The strong p4 has a large size compared to the molars (Fig. 5). The paraconid is present but not isolated and is situated on the mesiolingual side of the tooth. The protoconid is massive and conical. On its distolingual side is a metaconid, higher than the paraconid. The metaconid constitutes an elongated bulge joining the distolingual edge of the tooth. The talonid is compressed and it apparently presents a low ridge in the distal border of the tooth.

The first lower molars are badly preserved. The trigonid is slightly longer than the talonid, but narrower. The paraconid is connected to the protoconid by a curved and robust crest. The protoconid and the metaconid are conical, particularly strong, opposite to each other and only connected by a low protocristid. The square talonid is characterized by a strong entocristid, separated from the metaconid by a notch. The entoconid and the hypoconid are both smaller than the protoconid and the metaconid. The oblique cristid is almost straight. The basin of the talonid is quite deep and almost closed. The postcingulid is connected to the entoconid in the only preserved m1. The m2 does not differ significantly from the m1. The trigonid is more mesiodistally compressed and the paraconid is not distinct from the paralophid. The postcingulid is frequently connected to the entoconid (three specimens out of four). The m2 from Mae Moh show a variable trigonid (Fig. 5): some specimens have a slight protoconid–metaconid connection due to the triangular base of the protoconid while others have a more rounded protoconid and no connection. The m3 of *Lantanotherium* sp. is especially broad, with a short and narrow talonid. Its dimensions are relatively small compared to m1 and m2. The

protoconid and metaconid are still the higher cusps of the tooth but have almost equal dimensions with the hypoconid. There is no postcingulid– entoconid connection.

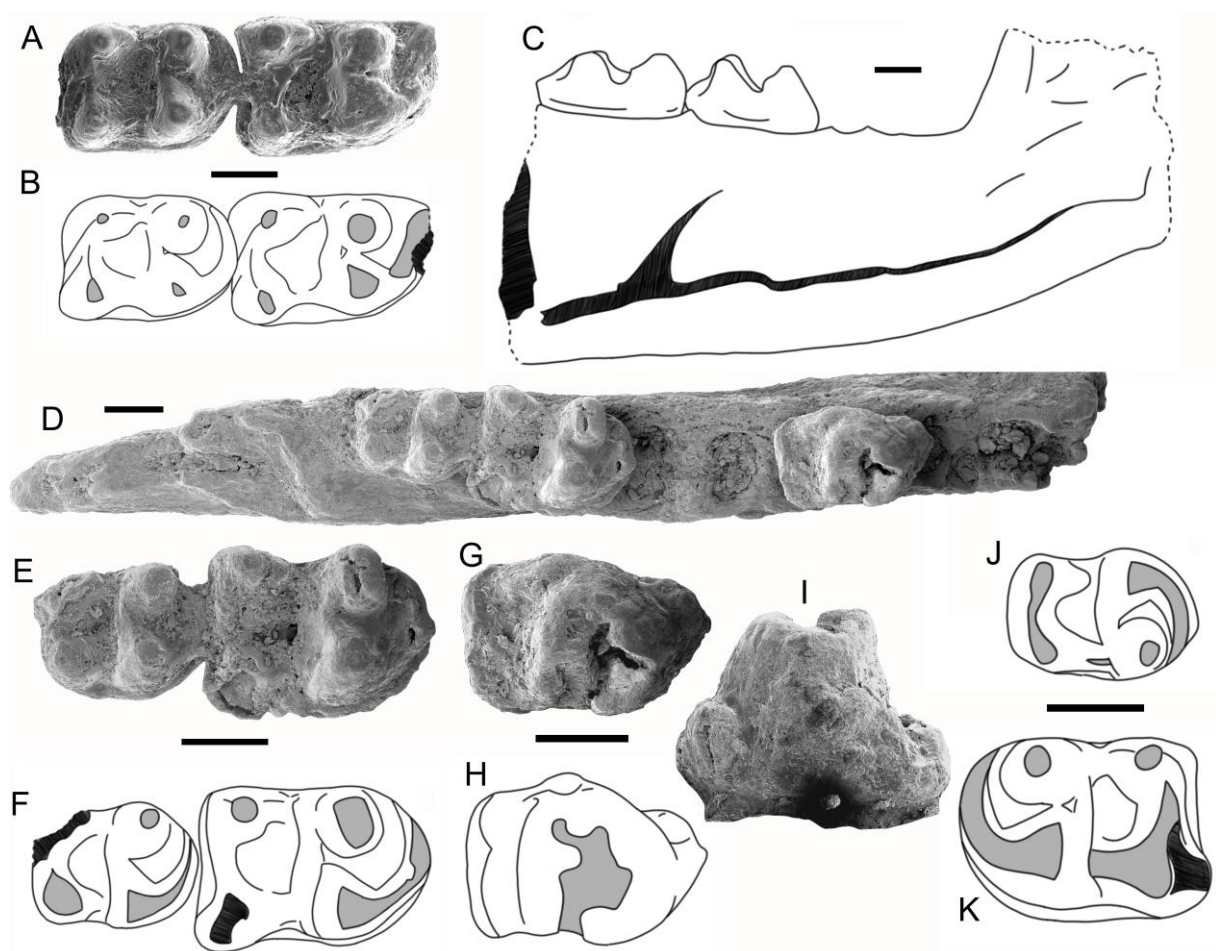


Figure 5. Specimens of *Lantanotherium* sp. from layer Q at Mae Moh. A–C, UPP MM-101, right mandible fragment with m1–m2: A, occlusal view of m1–m2; B, drawing of the occlusal view of m1–m2; C, drawing of the lingual view. D–I, UPP MM-98, right mandible fragment with p4, m2–m3: D, occlusal view of the mandible; E, occlusal view of m2–m3; F, drawing of the occlusal view of m2–m3; G, occlusal view of p4. H; drawing of the occlusal view of p4; I, lingual view of p4. J, UPP MM-102, drawing of the left m3 in occlusal view. K, UPP MM-99, drawing of the left m2 in occlusal view. Scale bars equal 1 mm.

Discussion

Biochronology, Faunal Composition, and Affinities

The presence of *Lantanotherium* and *Galerix rutlandae* at Mae Moh is not surprising considering that these genera are commonly found in the middle Miocene of Eurasia. However, the Mae Moh erinaceids provide the first firmly demonstrated co-occurrence of these genera in Asia. This association was proposed in the lower Miocene localities of Songlinzhuang and Shuanggou in the Xiacaowan Formation, China (Li et al., 1983). Nevertheless, according to Qiu and Qiu (1995:46), the presence of *Galerix* sp. in these sites is not confirmed because this “*Galerix* may be a species of *Lantanotherium*.” Despite several co-occurrences between the contemporaneous faunas of Mae Moh and the Tunggurian localities in China (e.g., the bovid *Eotragus*, the cervids *Stephanocemas* and *Lagomeryx* and the tragulid *Dorcatherium*), no Tunggurian record of *Lantanotherium* is known (Qiu and Qiu, 1995; Deng, 2006). In the Siwaliks of Pakistan, *Galerix* is a common genus but *Lantanotherium* has never been firmly identified, although its presence is suspected based on scarce material from the middle Miocene (Zijlstra and Flynn, 2015).

Galerix rutlandae is known in the Chinji Formation of the Siwaliks of Pakistan between 14.2 and 11.6 Ma in the localities of the Potwar Plateau (Zijlstra and Flynn, 2015). This further confirms previous claims (e.g., Chavasseau et al., 2009) that Na Khaem Formation is not only contemporaneous with the Chinji Formation but also presents notable faunal affinities with it.

There are no erinaceids in common between the Mae Moh and Li Mae Long faunas of Thailand. Li Mae Long was described as an early Miocene locality by Mein and Ginsburg (1997), but some studies suggest a middle Miocene age (Jaeger et al., 1985; Ducrocq et al., 1994) which is especially supported by the strong similarities between Li Mae Long and Mae Moh rodents (Chaimanee et al., 2007). Zijlstra and Flynn (2015) have noted that a few unidentified erinaceids from the middle Miocene Chinji Formation, dated between 13.4 and 12.3 Ma, showed affinities with the erinaceids of Li Mae Long. If confirmed, this would indicate even stronger affinities between the middle Miocene erinaceids of Pakistan and Thailand. Since species of Galericinae are known to have relatively wide biostratigraphic ranges, the completely different erinaceids fauna between Mae Moh and Li Mae Long localities could be simply a matter of spatial or environmental variation.

Environmental Implications of Erinaceidae from Mae Moh

Lantanothereium is often considered as a wetland indicator (Engesser, 1979; Furió and Alba, 2011). Furió et al. (2011a) have been able to confirm this environmental preference by observing a limit of the distribution of *Lantanothereium* in Europe during the Miocene, probably caused by lower rainfall in Southern Europe. Moreover, Zijlstra and Flynn (2015) noted that the appearance of *Galerix rutlandae* at 14.3 Ma coincided with an increase in Sciuridae diversity, and that the disappearance of the Galericipini from Siwaliks seems to be related with a more seasonal climate and the appearance of C4 plants. Therefore, these authors considered *G. rutlandae* as a Galericipinae living in close and humid environments, with no seasonality. This last parameter has been confirmed by Suraprasit et al. (2014) on the Mae Moh locality, due to the small variations of the $\delta^{13}\text{C}$ and the $\delta^{18}\text{O}$ values obtained from the teeth of the Rhinocerotidae *Gaindatherium* sp. and the Proboscidea *Stegolophodon* sp. Ducrocq et al. (1994) highlighted similar climatic conditions between Thailand and the Siwaliks of Pakistan from 16 Ma to 14 Ma, which probably enhanced the eastward dispersion of *Galerix rutlandae*. Despite their frequent presence in the Miocene, no coexistence of two species of *Lantanothereium* has been attested, except that of *L. dehmi* and *L. sawini* in North America (James, 1963). Suraprasit et al. (2013), based on carbon isotope analysis of tooth enamel of *Eotragus lampangensis*, suggest the presence of both closed forest habitats and open grassland in Mae Moh. The environmental fluctuation highlighted by Sepulchre et al. (2009) probably played a role in the preservation of two generalistic *Lantanothereium* and a more specialized *Galerix*.

Comments on *Galerix rutlandae* Variability and Phylogeny

The teeth from Mae Moh attributed to *Galerix rutlandae* are large but fall within the biometric range of the specimens from Pakistan. Zijlstra and Flynn (2015) note that only nine of the 22 specimens of p4 in their sample have a weak mesiodistal ridge on the talonid, which may correspond to the weak bulge found on the only p4 of Mae Moh. The metaconid of this tooth is less isolated than the specimens described in Pakistan. However, it may be problematic to consider this difference as relevant if we take into account the variability of this character in *Galerix exilis* highlighted by Ziegler (1983). The m2 has a postcingulid– entoconid connection, as do 12 of the 18 specimens described in Pakistan.

The genus *Galerix* is well documented in the Miocene European fossil record, where it is considered as an immigrant genus (Van den Hoek Ostende, 2001; Hugué and Adrover, 2003). However, the Asian fossil record of this genus is much scarcer. Whereas *Galerix* is attested in Anatolia among uppermost Oligocene deposits (De Bruijn et al., 1992; Van den

Hoek Ostende et al., 2019) and in Spain at 19.5 Ma (Larrasoaña et al., 2006; Ruiz-Sánchez et al., 2012; Furió et al., 2018), it is identified for the first time in Asia ca. 19 Ma (Zijlstra and Flynn, 2015) with *G. wesselsae*. This species is replaced in Pakistan between 14.3 Ma and 14.1 Ma by *G. rutlandae*, which is considered an immigrant species.

Even if the presence of a large p3 in *Galerix rutlandae* is unusual compared with species of *Galerix*, all the other features support this generic attribution. Moreover, mandibles of *Galerix exilis* where p3 are at least as large as p2 have already been observed in the localities of Steinberg and Goldberg (Ziegler, 1983), Sansan (Engesser, 2009), and in the Daroca-Calamocha area (F.C., pers. observ.). This characteristic is also present in *Galerix africanus* (Butler, 1956, 1984). The upper molar outline and the protocone–metaconule connection of *G. rutlandae* make it close to *G. remmertii* and *G. aurelianensis*, and, to a lesser degree, to *Galerix exilis*. Although Cheema et al. (1996) noted morphological similarities between *G. rutlandae* and *G. symeonidisi* from the middle Miocene of Europe, Zijlstra and Flynn (2015) point out that these common features are largely shared within the genus. For instance, the strong metaconid on p4 and the postcingulid–entoconid connection of m1 and m2 are also known in *G. remmertii* and *G. saratji*. Since the distribution of the Galericipini seems to imply two waves of dispersal to Europe during the early Miocene (the first with *Galerix remmertii* and *G. aurelianensis*, and the second with at least *Galerix symeonidisi*), it seems relevant to hypothesize the presence of a stock of *Galerix* in Asia during the early Miocene. Zijlstra and Flynn (2015) suggest the existence of a possible ancestor of *Galerix rutlandae*, in Central Asia, which is a relevant possibility. Considering these elements, *Galerix rutlandae*, *Galerix aurelianensis*, and *Galerix remmertii* probably share a common ancestor in Asia before 19 Ma.

***Lantanotherium*: Phylogenetic Hypotheses and Biogeographic History**

Affinities of *Lantanotherium anthrace*, sp. nov.

We have considered the possibility that *Lantanotherium* sp. and *Lantanotherium anthrace*, sp. nov., constitute a single highly variable species. Nevertheless, the Mae Moh material does not present any morphologically intermediate specimens, and the robust dental characteristic of *Lantanotherium* sp. are easily distinguishable from those of *L. anthrace*. The possibility of a sexual dimorphism was also taken into account. Only two examples of sexual dimorphism were highlighted in the fossil record of Erinaceidae, concerning *Proterix loomisi*/*P. bicuspis* (Bjork, 1975), and *Deinogalerix koenigswaldi* (Freudenthal, 1972; Butler, 1980;

Villier and Van den Hoek Ostende, 2011). However, in both cases, there is no evidence of a dimorphism in dental morphology. Thus, we consider here *Lantanotherium* sp. as a species distinct from *L. anthrace*.

Lantanotherium anthrace quickly appeared as a basal species of *Lantanotherium* sharing ancestral features with both European and North American species (Table 1). The thin mandible, the lack of a lower diastema, the presence of a weak p1 and the small size is only present in *L. anthrace* and *L. sanmigueli*, as described in Richardhof-Golfplatz and Götzendorf (Ziegler, 2005a). However, the presence/absence of the first premolar seems to be subject to intraspecific variation in Galericinae (Engesser, 1979), so that the lack of these teeth does not seem particularly informative with small samples. *Lantanotherium sanmigueli* is mostly found in Europe, but it is also recorded in several localities from Asia, such as Shuitangba (Jablonsky et al., 2014) in southern China. Because of morphological similarities and biogeographic distributions, the possibility of a close phylogenetic relationship between *L. sanmigueli* and *L. anthrace* should be considered seriously. To a lesser extent, the Thai species also shows shared features with *L. sawini* and *L. observatum* such as the absence of diastemata between premolars and a strong P3, even if these features are plesiomorphic. Finally, Chaimanee et al. (2007) noted that Mae Moh rodents show a high degree of endemism, visible in particular by a more primitive evolutionary stage. Endemism has been also observed by Latinne et al. (2013) in extant species of Thai Murinae and explained by the fundamental role of the karstic environments in the preservation of endemic species. The preservation of P1/p1, the presence of a relatively big P3 and the small size of *L. anthrace* could also be related to some endemism of this taxon in Thailand. This possibility is at least supported by the strong morphological similarities between *L. anthrace* and the extant *Otohyalomys megalotis*, which presents physiological adaptation to karstic environments (Jenkins and Robinson, 2002; Chernova et al., 2015).

Table 1. Comparison of the dento-gnathic features of the species of *Lantanotherium*.

Character/Species	<i>L. lactorense</i>	<i>L. sabinae</i>	<i>L. robustum</i>	<i>L. longirostre</i>	<i>L. sansaniense</i>	<i>L. sanmigueli</i>	<i>L. anthrace</i> sp. nov.	<i>L. sp.</i>	<i>L. dehmi</i>	<i>L. observatum</i>	<i>L. sawini</i>
Subgroup (supposed origin)	European	European	European	European	European	Asian	Asian	Asian	North American	North American	North American
Age	Early Miocene	Middle Miocene	Middle Miocene	Middle Miocene	Middle Miocene	Late Miocene	Middle Miocene	Middle Miocene	Late Miocene	Middle Miocene	Middle/Late Miocene
Distribution	France	France	France	Germany	Europe	Europe - China	Thailand	Thailand	USA	USA	USA
References	Baudelot and Crouzels, 1976; this paper	Mein and Ginsburg, 2002	James, 1963; this paper	Thenius, 1949; James, 1963	Viret, 1940; James, 1963; Engesser, 2009	Engesser, 1979; Storch and Qiu, 1991; this paper	This paper	This paper	James, 1963	Shotwell, 1968; Korth and Evander, 2016	James, 1963
m1 length (mm)	?	4.1	4.7	3.3	3.2 - 4.6	2.4 - 2.5	2.7 - 2.8	3.1	3.5 ^a	2.6 - 3.2	3.4
Largest upper incisor	?	?	?	I1	I1	I1	I1	?	?	I2	I2
Alignment of the upper incisors	?	?	?	?	Longitudinal		Longitudinal?	?	?	?	Transversal
P1/p1 size/presence	Small	Small	Absent	Small	Absent	Small	Small	?	?	Large	Large
Diastema between upper antemolars teeth	?	Yes	?	Yes	Yes	No	No	?	?	No	No
P3 relative size	?	?	?	Very small	Small	Variable	Large	?	?	Large	Large ^a
P3 distolingual development	?	?	?	Reduced	Reduced	Reduced/Cingulum	Cingulum	?	?	Distinct hypocone	Distinct hypocone
M1 metaconule-metacone connection	?	?	Weak	Absent	Often absent	Often Strong	?	?	?	Strong	Strong
M1 metaconule shape	?	?	Circular	Circular	Circular	Elongate	?	?	?	Elongate	Elongate
M1 distal cingulum	?	?	Narrow	Narrow	Wide	Wide	?	?	?	Narrow	Narrow
M3 metacone and hypocone	?	?	?	?	Distinct	Fused	?	?	?	Distinct?	Fused
Diastema between lower antemolar teeth	Yes	Yes	?	Yes	Yes	No	No	?	?	No	No
M1 distal cingulum	?	?	Reduced	Reduced	Expanded	Expanded	?	?	?	Reduced	Reduced
M3 metacone and hypocone	?	?	?	?	Separated	Fused	?	?	?	Distinct?	Fused
Diastema between lower antemolar teeth	Yes	Yes	?	Yes	Yes	No	No	?	?	No	No
p4 morphology	Medium	Medium	Large	Narrow	Narrow	Narrow	Narrow	Large	Large	Medium	Medium
General morphology of the lower molars			Robust	Slender	Slender	Slender	Slender	Robust	Robust	Slender?	Slender
m3 relative size		Medium	Small	Small	Small	Medium	?	Small	Small	Medium	Medium

^a Based on alveoli

Paleobiogeography of *Lantanotherium*

The evolutionary history of the genus *Lantanotherium*, although consisting of a large number of species, is still poorly understood (Furió and Alba, 2011). The inclusion in this genus of some species from North America by James (1963) and Shotwell (1968) has raised biogeographic issues. Whereas Gibert (1974, 1975) supports this incorporation on the basis of morphological similarities, Engesser (1979) suggests that the American species should be placed in the Oligocene genus *Ocajila*, arguing for an incoherent distribution because of the lack of Miocene material from Asia and for morphological differences between specimens from North America and Europe. The geographical argument of Engesser (1979) no longer seems valid since the suspicion of Viret (1940) about the presence of *Lantanotherium* in Asia was confirmed by the identification of this genus in China (Li et al., 1983; Storch and Qiu, 1991; Jablonski et al., 2014) and Central Asia (Lopatin, 1996). Engesser (1979) argued for strong differences in the upper dentition between the forms of the two continents. However, in 1979, only *L. sawini* was known by upper dentition in North America. The description of *L. observatum* by Korth and Evander (2016), morphologically close to *L. sawini*, corroborates that the North American specimens represent species of *Lantanotherium* that are plesiomorphic in several respects. This is especially the case for the presence of a more crescentic metaconule on M1 and M2. However, this crescentic shape is related to both the presence of a crest connecting the metaconule to the metacone and the presence of an elongated metaconule. Such a configuration is found also in *L. sanmigueli* from Can llobateres (F.C., pers. observ.). Concerning the M3, Engesser (1979) highlighted the more robust morphology of Eurasian species compared to *L. sawini*. This is indeed true for *L. sansaniense*, which always has a strong and isolated hypocone. However, *Lantanotherium sanmigueli* (from Lufeng, Montredon, and Can llobateres; F.C., pers. observ.) presents the same morphology as *L. observatum* and *L. sawini*, with the metacone and hypocone fused together as a curved loph. *Lantanotherium observatum* presents a P3 which is described as having a minute protocone. This poorly reduced P3 confirms the idea that *L. observatum* is less derived than the European species. Concerning the lower dentition, Engesser (1979) notes that the anterior dentition of *L. sawini* and *L. dehmi* are robust relative to the other species of the genus. However, the p4 of *Lantanotherium* sp. from Mae Moh also displays a robust morphology. Moreover, James (1963) observed similarities between the strong p4 of *L. dehmi* and *L. robustum*. Again, these shared features plead in favor of a presence of representatives of *Lantanotherium* in North America during the Miocene.

Korth and Evander (2016) summarized a few distinguishing features between the European and North American species of *Lantanotherium*. Unlike *L. sawini* and *L. observatum*, the European species of *Lantanotherium* exhibit a diastema between canines and premolars, I1/i1 larger than I2/i2, and a small or absent P1/p1. The European *L. sansaniense*, *L. longirostre*, and *L. sabinae* all possess a diastema between canines and premolars (James, 1963, Mein and Ginsburg, 2002). Nevertheless, *L. sanmigueli* and *L. anthrace* do not exhibit this feature, which may indicate an Asian origin of the former species. Based on these elements, to consider the presence of diastema as an autapomorphy of the European species seems relevant. In sum, the update of the arguments of Engesser (1979) with new material of *Lantanotherium* from Asia and North America leads to the recognition of a mostly plesiomorphic tooth pattern in Asian species (*L. anthrace* and *L. sanmigueli*). In this view, the most parsimonious scenario would be that *L. sanmigueli* dispersed from Asia to Europe during the late Miocene. Some features (large size, reduction of premolars, presence of diastemata) are mainly or even exclusively observed in the European species of *Lantanotherium*, which likely originate from an earlier wave of dispersal to Europe. Finally, we confirm that some features are only observed in *L. observatum* and *L. sawini* from North America (large I2/i2, strong P2/p2 compared to P1/p1).

The presence of *Lantanotherium* in North America raises questions from a climatic point of view because *Lantanotherium* preferred hot and humid environments (Furió and Alba, 2011; Furió et al., 2011a). The floristic data indicate that the Bering land bridge was dominated by deciduous taxa during the Miocene. However, thermophilic plants were able to expand in the coastal margins of North America during the global warming of the early Miocene (Tiffney and Manchester, 2001). Such environmental conditions may have been enough to allow *Lantanotherium* to disperse to North America. In addition, Engesser (1979) considered that the extant relict forms of Galericinae were representative of the ecology of all extinct species. This statement may be somewhat misleading since the Galericini apparently experienced an ecological radiation during the Miocene, resulting in eco-morphologically varied species (Van den Hoek Ostende, 2001, 2018) and locations in environments that do not correspond to tropical or sub-tropical zones (Luis and Hernando, 2000; Van den Hoek Ostende, 2003b; Van den Hoek Ostende and Doukas, 2003; Furió et al., 2011a, 2011b). Finally, several groups of Erinaceidae dispersed to North America in the latest Oligocene and early Miocene, viz. the Amphechinini, a group yet widespread throughout the Oligocene in Eurasia (Rich and Rasmusen, 1971; Rich, 1981; Lopatin, 2002; Ziegler, 2005b; Ziegler et al., 2007), the Brachyericinae, and the Erinaceini (Stevens, 1977; Rich, 1981; Lopatin and Zazhigin, 2003). Therefore, it is necessary

to consider the possibility that Asian representatives of *Lantanotherium* have joined one of these waves of migration through Beringia, presumably during the early Miocene.

Origin of *Lantanotherium*

The ancestry of *Lantanotherium* is still unclear. Shotwell (1968), Engesser (1979), and Korth and Evander (2016) hypothesized an American origin of *Lantanotherium* from the genus *Ocajila*. Although new specimens attributable to *Ocajila* were described by Korth (2009), this genus is represented only by a fragment of m1, m2, and m3. The occlusal profile of the lower molars of *Ocajila* is close to that of *Lantanotherium*. However, these poorly diagnostic molars also present some notable differences with the latter genus, such as a less elongated trigonid, the distinct hypoconulid on m1 and m2, and a quite long talonid on m3 (MacDonald, 1963). The presence of a hypoconulid on m1–m2 is only mentioned in early Erinaceidae such as *Changolestes* (Lopatin, 2006). Thus, we consider that a close relationship between *Lantanotherium* and *Ocajila* is unlikely. The latter genus could rather represent a first Oligocene migration of basal Galericinae in North America. Engesser (1979) suggested that the European forms of *Lantanotherium* may be linked to some European Oligocene genera such as *Tetracus* and *Neurogymnurus*. For now, the oldest occurrence of *Lantanotherium* is *Lantanotherium* sp. from the MN 3 of Beaulieu 2B, France (Aguilar et al., 2003). This leads to a wide biostratigraphical gap between *Lantanotherium* and these Oligocene genera. A direct ancestor–descendant relationship is also weakly supported because *Lantanotherium* seems to have an Asian origin.

It is true that *Tetracus* and *Neurogymnurus* exhibit some characters compatible with the morphologies known in *Lantanotherium*. Thus, *T. daamsi* exhibits a distinct metaconid on p4 like in *L. sansaniense* and *L. anthrace*, but unlike *T. nanus*. The morphology of the molars of *Lantanotherium* and *Tetracus daamsi* are also quite similar, *T. daamsi* lacking a metalophid and a hypoconulid, and having a pronounced entocristid on m1, a *Lantanotherium*-like paralophid morphology ('*Lantanotherium* type' paralophid of Lavocat, 1951), and a weak connection between protocone and metaconule on M1 (isolated metaconule in *Lantanotherium*). However, a link between *Lantanotherium* and *Tetracus* cannot be demonstrated because all the shared characters between these two genera likely correspond to plesiomorphic characters. In addition, some of the similarities noted between *Tetracus* and *Lantanotherium* are especially based on the species *L. piveteaui* (see Baudelot, 1972), which is a very doubtful species described from scarce and undiagnostic material (Furió and Alba, 2011) that could rather represent a taxon of *Galerix* (Van den Hoek Ostende et al., 2016), a close ally of *Tetracus*. *Neurogymnurus* has a

few shared morphological features with *Lantanotherium* and *Tetracus* on the lower dentition. However, *Neurogymnurus* also differs from these genera in several respects and displays numerous autapomorphies so that it should be reasonably excluded from the ancestry of *Lantanotherium*. *Neurogymnurus* could rather belong to a quite diversified Asian group, maybe related to some American species from the Oligocene (Butler, 1948) and *Pseudoneurogymnurus*.

Among the extant Galericinae, *Lantanotherium* shares numerous features with the recently described *Otohyalomys megalotis* Jenkins and Robinson, 2002. This is especially true for *Lantanotherium anthrace* and to a lesser degree for *Lantanotherium sanmigueli*. Based on molecular analyses, Bannikova et al. (2014) retrieved *O. megalotis* as the basal-most taxon among the extant Galericinae with an age of divergence from other galericines estimated between 42 Ma and 32 Ma. The phylogenetic relationships between *Otohyalomys megalotis* and the extinct Erinaceidae are still unclear especially because of the lack of in-depth dental descriptions and comparisons. Nevertheless, a close relationship between *Otohyalomys* and *Lantanotherium* seems plausible and should be tested further (F.C., under study).

Conclusions

The description of the first insectivores from Mae Moh significantly improves the knowledge of Miocene Thai microvertebrates and completes the taxonomic study of Mae Moh mammals. The abundant large mammal fauna from the layers K and Q of Mae Moh supports affinities already observed with contemporaneous faunas from Indo-Pakistan and China during the middle Miocene. Because *Lantanotherium* is not known in Tunggurian localities from the same age, both Eastern and Southern Asian influence can be recognized in the erinaceids from Mae Moh. The three recovered Galericinae strongly fit with the previous reconstruction of Mae Moh environment between 13.4 Ma and 13.2 Ma, apparently composed of humid, closed forest habitats with maybe some more open areas. The discovery of two species of *Lantanotherium* in Thailand is a new step to understanding the wide distribution of the Galericinae during the Miocene. The paleodiversity of *Lantanotherium*-like species brings several unsolved taxonomical questions, highlighting the importance of future in-depth morphological studies of *Lantanotherium*, *Ocajila*, *Otohyalomys*, and Hylomyini.

Acknowledgments

We thank the EGAT authorities for access to the mine of Mae Moh and scientific assistance, M. Rugbumrung (Department of Mineral Resources, Bangkok, Thailand) for field work and

preparation, K. Suraprasit (Chulalongkorn University, Thailand) for field work, A. Mazurier (Platform PLATINA, IC2MP, University of Poitiers) for CT-scan acquisitions, X. Valentin (PALEVOPRIM, University of Poitiers) for preparation, S. Passot (University of Lyon 1, France) for providing bibliographic resources, E. Béré (ImageUP, University of Poitiers) for SEM imaging, E. Robert (University of Lyon 1) and S. Jiquel (ISEM, University of Montpellier, France) for giving access to comparative material. We wish to express our deep gratitude to M. Furió and an anonymous reviewer who greatly improved the manuscript. This work has been supported by the Department of Mineral Resources (Thailand), the ANR-05-BLAN-0235, the ANR-09-BLAN-0238- 02-EVAH, the Fyssen foundation (grant to O.C.) and the UMR 7262 PALEVOPRIM (CNRS and University of Poitiers, France).

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