

# New data on Mustelidae (Carnivora) from Southeast Asia: *Siamogale thailandica*, a peculiar otter-like mustelid from the late middle Miocene Mae Moh Basin, northern Thailand

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**Abstract** We report new dental remains of Mustelidae from the late middle Miocene of Mae Moh Basin, northern Thailand, improving the poor fossil record of the family in Southeast Asia. *Siamogale thailandica* is a poorly known mustelid, previously recorded from just a single tooth. Here we present over a hundred new specimens attributable to this species. *S. thailandica* shows a combination of primitive and convergent features of the dentition that makes its original subfamilial assignment to Lutrinae doubtful. Evidence from the dental morphology suggests that it belongs to a bunodont otter-like mustelid that evolved in convergence with “true” otters (Lutrinae) toward a semi-aquatic way of life. Autapomorphic features such as the height and the position of the m1 metaconid and the shape of the P4 lingual shelf make *S. thailandica* unique among Mustelidae. The morphology of this species is mostly similar to *Mionictis* species and *Lartetictis dubia*, reported in the Miocene of North America and Europe, respectively. These similarities could imply immigration events to Thailand in the early or middle Miocene. Alternately, the lineage leading

to *Siamogale* might have deeper origins from an endemic early Miocene Southeast Asian mustelid.

**Keywords** Mustelidae · *Siamogale thailandica* · Miocene · Mae Moh · Thailand

## Introduction

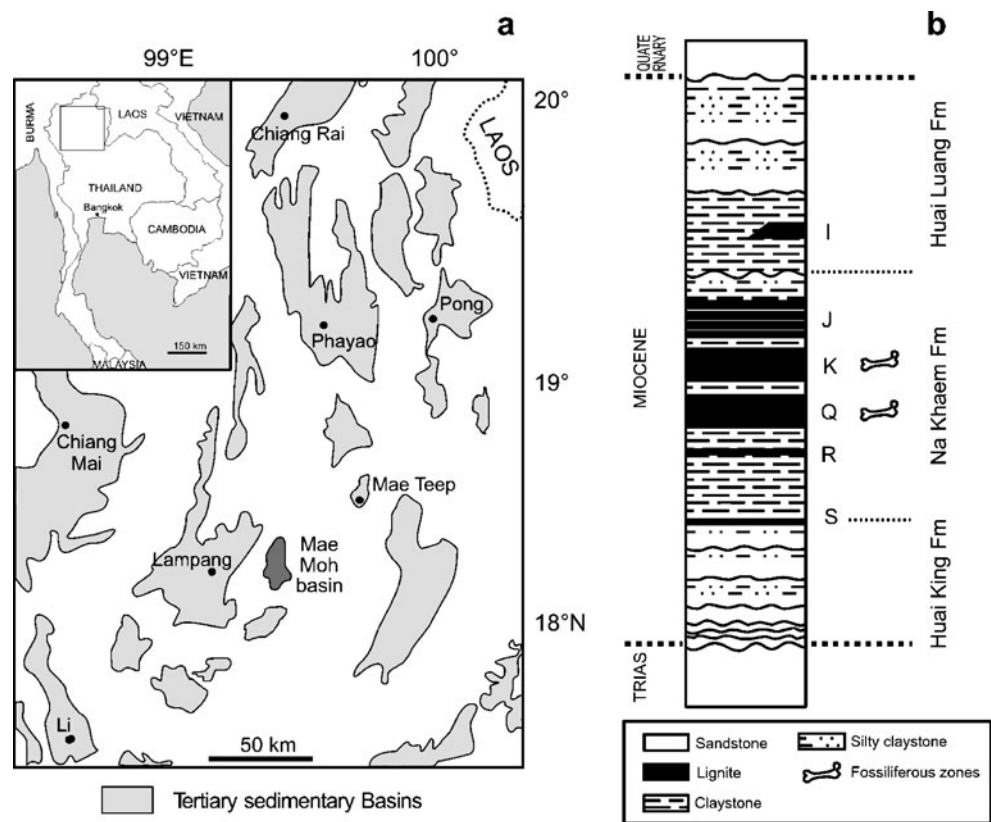
Northern Thailand comprises numerous intramontane basins that have yielded a rich and diversified Neogene mammalian fauna, including fossil hominoid (Chaimanee et al. 2003). One of these basins, the Mae Moh Basin, has provided one of the richest Miocene vertebrate fossil record of Southeast Asia, with several mammal taxa: mustelid and amphicyonid carnivorans, elephantoid, and deinothere proboscideans, a rhinocerotid, a cervid, a palaeochoerid, suids, rodents, a sivaladapid, and an undescribed tarsiid primate (Von Koenigswald 1959; Ginsburg et al. 1983; Ducrocq et al. 1994, 1995; Peigné et al. 2006; Chaimanee et al. 2008; Chavasseau 2008; Chavasseau et al. 2009). The basin is located in the Lampang province, approximately 26 km east of Lampang city (Fig. 1a). The Tertiary sedimentological filling of Mae Moh has been estimated by biostratigraphy to range from the middle part of the middle Miocene to the early late Miocene (Ginsburg and Tassy 1985; Ducrocq et al. 1995). Recent magnetic polarity stratigraphy investigations dated this sequence to the late middle Miocene, from 14.2 to 12.1 Ma (Benammi et al. 2002; Coster et al. 2010). The richest mammal-bearing formation of the basin, the Na Khaem Formation, is constituted by lacustrine and fluvial claystones, mud-

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**Fig. 1** Mae Moh Basin: location in northern Thailand (a) and simplified stratigraphic log representing the *Siamogale* bearing layers of the Na Khaem Formation. Modified from Coster et al. (2010; b)



stones, and siltstones, interbedded with fossiliferous layers of lignites (named R, Q, K, and J from the base to the top, Fig. 1b; see Benammi et al. 2002 and Coster et al. 2010 for more detailed sedimentology and stratigraphy). Fossil mammals mainly occur in the Q and K coal layers, estimated by magnetostratigraphy to 13.4 and 13.2 Ma, respectively (Coster et al. 2010).

With about 25 genera and 70 extant species, the Mustelidae is the largest and the most diversified family among Carnivora. The earliest mustelids *Paragale* and *Plesiogale* are reported from the early Miocene of Europe (Wolsan 1993; Wang et al. 2004). Although the Miocene fossil record of the family is abundant in Eurasia, Africa, and North America, especially in the Late Miocene (Savage 1978; Baskin 1998; Ginsburg 1999), it is still very scarce in Southeast Asia, where only two species are reported from Thailand: *Siamogale thailandica* and one indeterminate species (Ginsburg et al. 1983; Ducrocq et al. 1995). The description of *S. thailandica* was based on a single isolated tooth, a left m1. Due to this poor material, the anatomical comparison and the relationships of this species with other mustelids have been very limited since its discovery (Ginsburg and Tassy 1985; Willemsen 1992; Ginsburg and Morales 1996; Pickford 2007; Thewissen and Bajpai 2008). New field campaigns conducted by a Thai-French team (Department of Mineral Resources of Bangkok, Thailand and University of Poitiers, France) in the Mae

Moh Basin yielded more than a hundred dental specimens belonging to *S. thailandica* in the Q and K lignite layers. This new material is particularly significant because it brings enough additional morphological information to throw light on the morphological affinities and the subfamilial assignment of *S. thailandica* within Mustelidae. This would ultimately improve our knowledge of the early evolutionary history of this family in Southeast Asia.

## Material and methods

The specimens of *S. thailandica*, more than a hundred isolated teeth and mandible and maxilla fragments, are stored at the Department of Mineral Resources, Bangkok, Thailand (DMR). The comparative material includes specimens of Miocene, Pliocene, and Pleistocene Mustelidae housed in different institutions: American Museum of Natural History, New York, NY, USA; Muséum National d'Histoire Naturelle, Paris, France (MNHN); Institut International de Paléoprimateologie, Paléontologie Humaine: Évolution et Paléoenvironnements, Poitiers, France; and Staatliches Museum für Naturkunde von Stuttgart, Stuttgart, Germany (SMNS). Measurements of the Mae Moh specimens were taken with a digital caliper to the nearest 0.1 mm. Abbreviations for the dentition measurements are c, lower canine; Hhypo, hypoconid height; Hmeta, metaconid height;

Hpara, paraconid or paracone height; Hproto, protoconid or protocone height; L, maximum mesiodistal length; Llab and Lling, labial and lingual maximum mesiodistal length of M1; LtrigoLab, labial maximum mesiodistal length of m1 trigonid; LtrigoLing, lingual maximum mesiodistal length of m1 trigonid; m, lower molar; M, upper molar; MlabDling, maximum distance between mesiolabial corner and distolingual corner of M1; MlingDlab, maximum distance between mesiolingual corner and distolabial corner of M1; p, lower premolar; P, upper premolar; W, maximum linguolabial width; Wtalo, maximum linguolabial width of m1 talonid; and Wtrigo, maximum linguolabial width of m1 trigonid. Taxonomy follows McKenna and Bell (1997).

## Systematics

Order Carnivora Bowdich, 1821

Suborder Caniformia Kretzoi, 1943

Family Mustelidae Fischer, 1817

Genus *Siamogale* Ginsburg et al. 1983

*Original diagnosis (translated in English from Ginsburg et al. (1983): pp. 954):* Lutrine slightly smaller than the European otter; m1 with low and anteriorly tightened trigonid, hugely enlarged talonid, metaconid going down backward with a gentle slope as in *Mionictis* and extending toward the talonid back in a marked padding on top of the talonid hollow; low hypoconid extending backward by a thin crest.

*Emended diagnosis:* Mustelidae with double-rooted lower premolars and P3 that lack accessory cusps; p1 lost; broad and long basined talonid of m1; low trigonid; metaconid nearly at the same position and height as protoconid; metaconid directly connected to an entoconid crest that encloses the talonid until joining the low hypoconid; talonid outline rounded or subsquared; main cusp of p4 higher than m1 paraconid; P4 with a short shearing blade, a tiny parastyle, and a cup-shaped protocone mesially situated with respect to the paracone; lingual shelf moderately developed with a thin hypoconal crest distal to the protocone; M1 with a broad distolingual expansion, a crescent-shaped protocone, and a small metaconule just lingual to the metacone; enamel markedly crenulated on the m1 talonid basin and on the lingual parts of P4 and M1.

*Type species:* *S. thailandica* Ginsburg et al. 1983

*S. thailandica* Ginsburg et al. 1983

*Holotype:* TF 6316, left m1 (original figured in Ginsburg et al. (1983), pp. 954; cast in MNHN collections).

*Type locality and stratigraphic ranges:* Q and K coal layers of the Na Khaem Formation, age estimated between 13.4 and 13.2 Ma (Coster et al. 2010), Mae Moh Basin (Thailand), late middle Miocene (14.2–12.1 Ma; Benammi et al. 2002; Coster et al. 2010)—Tunggurian of the Asian Land Mammal Age (Qiu and Qiu 1995).

*Other referred specimens:* TF 6284, left mandible (c-m2; p2 alveolus, broken m1, and c); TF 6285, left maxilla (P4); TF 6286, right m1; TF 6287, left m1; TF 6288, left maxilla (P4); TF 6289, right P4; TF 6290, left M1; TF 6291, right m1; TF 6292, right mandible (p3–m1; broken m1 and m2 alveolus); TF 6293, left m1; TF 6294, left M1; TF 6295, right M1; TF 6296, left maxilla (P3–M1; broken P4); TF 6297, right P4; TF 6298, right mandible (p4–m1; p3 alveolus); TF 6299, right m2; TF 6300, right m2; TF 6301, left m2; TF 6302, left mandible (p3–m1; p2 and m2 alveoli); TF 6303, right m2; TF 6304, left m1; TF 6305, right P4; TF 6306, left maxilla (P2–P4; P3 alveolus and broken P4); TF 6307, right M1; TF 6308, left m2 (broken); TF 6309, right mandible (m1–m2); TF 6310, left mandible (p2–p4); TF 6311, left M1 (broken); TF 6312, left P4; TF 6313, right m1; TF 6314, left P4; TF 6315, right maxilla (P4–M1) plus other specimens of *S. thailandica* and fragments of isolated canines, premolars and mandibles of indeterminate Mustelidae stored at the DMR.

*Remarks:* These specimens are assigned to the same species in spite of some variations of tooth size (Table 1) and shape (e.g., the M1 distolingual border) because (1) these ranges of variations can agree with those of extant species of Mustelidae (Alcala et al. 1994; Wolsan et al. 1985; Wolsan 1988, 1989; Baryshnikov et al. 2003), (2) all these remains have been discovered in the same fossiliferous levels, separated by a maximum range of 200,000 years (Benammi et al. 2002; Coster et al. 2010).

*Diagnosis:* As for the genus.

*Differential diagnosis:* Differs from *Mionictis* and *Lartetictis* by a more prominent and more mesial m1 metaconid, a broader m1 talonid, a lower hypoconid, and a shorter P4 shearing blade. Differs from *Mionictis* by the position of the M1 metaconule, located lingually to the metacone. Differs from *Lartetictis* by a subequal importance of paracone and metacone of M1 and a less developed P4 hypoconal crest.

## Description

*Mandible:* The ascending ramus displays a deep masseteric fossa, less marked than in *Lutra* but more developed than in *Meles* (Fig. 2 a). The coronoid process is rounded, as in the genera *Enhydra* and *Meles*, and wide at its dorsal rim. Its dorsal and rostral part, where inserts the temporalis muscle, is slightly convex in labial view. It is placed rostrally with respect to the angular process. This latter process is slender and curved lingually to form the ventral outline of the medial pterygoid muscle area, visible in lingual view (Fig. 2 b). The internal mandibular foramen is distal to the tooth row and located below the alveolar plane. A thin ventral groove for the attachment of the digastric muscle is

**Table 1** Measurements (in millimeters) of the lower and upper teeth of *S. thailandica*, Q and K coal layers of the Na Khaem Formation, Mae Moh Basin (Thailand), late middle Miocene

Specimen	Measurements	<i>n</i>	Min.	Max.	Mean	SD
c	L	1	7.2			
	W	1	5.3			
p2	L	1	6.8			
	W	1	3.9			
p3	L	5	6.5	8.2	7.48	0.74
	W	5	3.7	5	4.4	0.47
p4	L	11	8.4	10.6	9.44	0.8
	W	12	4.4	6.7	5.42	0.72
m1	L	29	13.9	18	16.04	1.08
	W	27	7.3	9.8	8.51	0.68
	Wtrigo	28	6.8	9.8	8.2	0.76
	Wtalo	28	7.3	9.8	8.53	0.67
	Hpara	24	3.8	6.1	4.89	0.6
	Hmeta	13	4.7	6.1	5.31	0.4
	Hproto	12	5.6	7.2	6.24	0.48
	Hhypo	16	3.4	5.1	4.12	0.47
	LtrigoLab	22	8.2	10.2	9.21	0.52
	LtrigoLing	21	8.7	12.2	10.84	0.83
m2	L	10	6.9	11.1	8.5	1.27
	W	9	6.8	9.6	8.3	0.78
P2	L	1	5.2			
	W	1	2.9			
P3	L	1	7			
	W	1	4.1			
P4	L	15	11.1	13.5	12.08	0.76
	W	18	8.5	11.1	9.68	0.74
	Hpara	11	5.8	7.6	6.67	0.56
	Hproto	18	3.2	4.8	3.82	0.45
M1	Llab	19	8.5	12	9.73	0.84
	Lling	22	10.9	15.9	13.26	1.3
	W	16	12.3	17.8	14.53	1.52
	MlingDlab	19	11.3	15.5	12.93	1.25
	MlabDling	18	15.5	20.1	17.47	1.25

*n* number of specimens, *Min.* minimum, *Max.* maximum, *SD* standard deviation

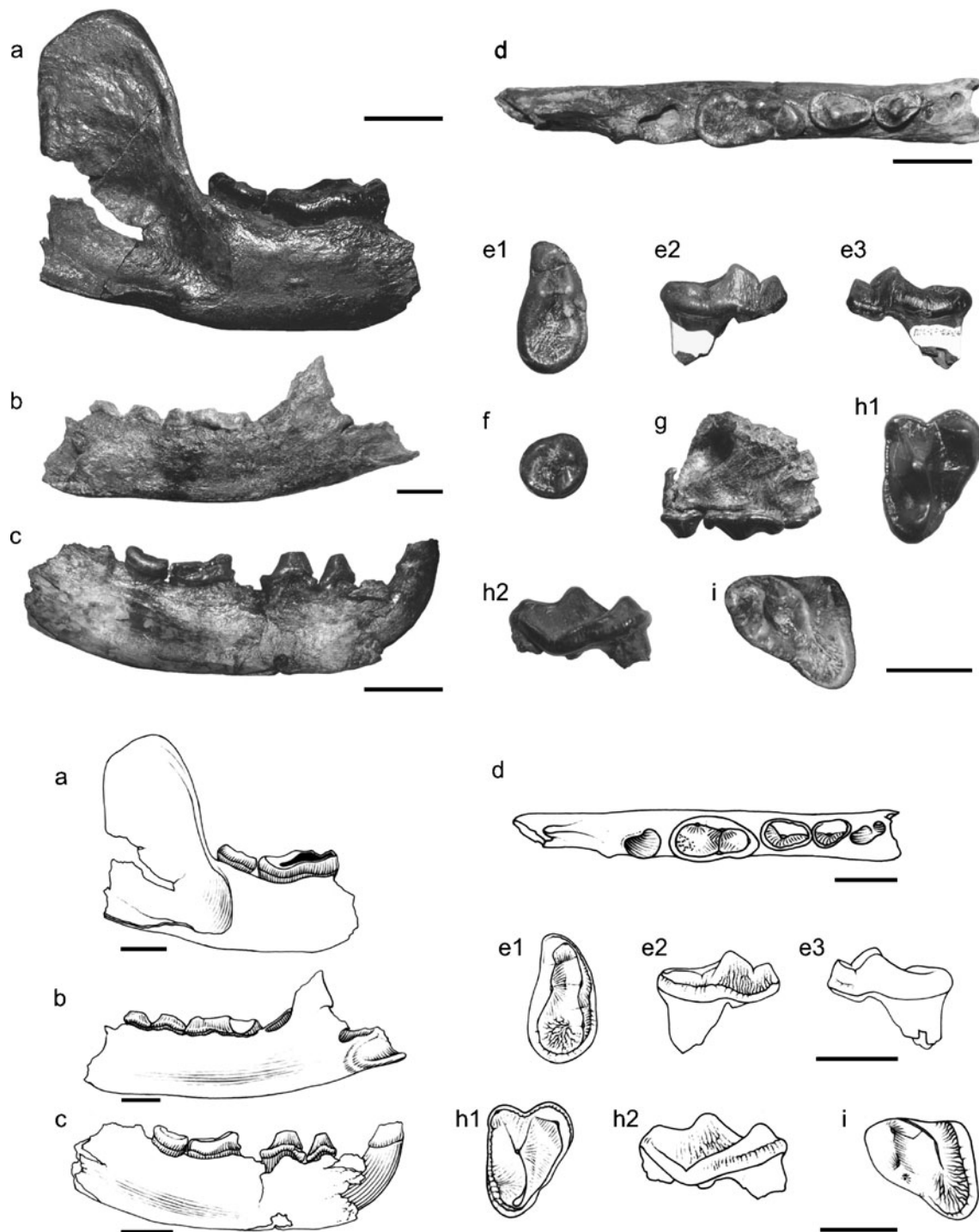
visible below p4–m2 in the lingual side of the mandible (Fig. 2 b, c). The tip of the articular condyle is not preserved. The horizontal ramus bears two mental foramina: one below the position of p2 and another below the position of the mesial part of p4.

**Lower teeth:** The dental formula for the lower dentition is ?1.3.2. The teeth are closely set together (Fig. 2 a–d). Only one mandible is preserved with the base of a canine crown (i.e., TF 6284; Fig. 2 c). This canine is slightly less long than the p4, and its root is curved toward the labial

side of the mandible. There is no p1. The premolars, doubled-rooted, lack accessory cusps. They are asymmetrical in lateral view: The main cusp is located mesially, the distal cingulum is more developed than the mesial one, and the former has a swelling shelf shape. These extended cingula create a broad occlusal surface. The size of these teeth and the height of the main cusp increase from p2 to p4 (Table 1). The p4 main cusp is higher than the m1 paraconid. The m1 are often preserved on the mandibles, but most of the teeth are isolated (Fig. 2 e1–e3). The m1 paraconid is the smallest cusp of the trigonid, and the protoconid is slightly higher than the metaconid (Table 1). The paraconid is nearly lingually oriented. The protoconid is slightly mesial with respect to the metaconid. The three cusps of the m1 trigonid are very close to each other. The carnassial notch and the lingual opening (between the paraconid and the metaconid) are weak. The metaconid and the protoconid are separated by a shallow notch. A distal crest extends with a gentle slope from the tip of the metaconid to join the entoconid crest of the talonid. The talonid is broader than the trigonid. The former is basined and has a rounded to subsquared shape. It is enclosed by a low and smooth entoconid crest which appears continuous from the distal crest of the metaconid to the labial hypoconid. This hypoconid is low and it is the unique cusp of the talonid. It is located at the distal base of the protoconid, from which it is separated by a weak notch. Enamel crenulations of m1 are mainly visible on the hollow talonid. The m2 is single-rooted (Fig. 2 b, d). Its root is concave in labial view. Its crown base arises slightly above the level of the premolars and the m1 (Fig. 2 a, c). The protoconid is the unique visible cusp (Fig. 2 f). It is labial and medial to slightly mesial. A small crenulated basin extends lingually to the protoconid. The outline, triangular to subcircular in shape, is formed by a wide and smooth crest, lower at the region of the basin.

**Maxilla:** Only TF 6296 (Fig. 2 g) shows an infraorbital foramen. This foramen is extended above the region of contact between P3 and P4 until the mesial part of P4 in lateral view. It has a wide diameter and is oval in mesial view.

**Upper teeth:** Within all the specimens, only P3, P4, and M1 are preserved. The P3 is double-rooted (Fig. 2 g). Like the lower premolars, it is asymmetrical, with a single cusp located mesially and a weak distal cingulum, which protrudes toward lingual part of the maxilla. Teeth are also closely set together. P4 lacks a carnassial notch, a derived feature found in most mephitids and mustelids (Wolsan 1993). The shearing blade is short. The paracone is the highest cusp of the tooth, nearly twice higher than the protocone (Fig. 2 h1–h2; Table 1). Two crests extend from its tip: One is oriented mesiolabially in direction of a low parastyle, and another is oriented mesiolingually in



**Fig. 2** *S. thailandica*, photographs and drawings of the most significant specimens. **a** TF 6309, right mandible (m1–m2) in labial view; **b** TF 6292, right mandible (p3–m1) in lingual view; **c** TF 6284, left mandible (c–m2) in lingual view; **d** TF 6302, right mandible (p3–m1) in occlusal view; **e** TF 6313, right m1 in occlusal

(**e1**), labial (**e2**) and lingual (**e3**) views; **f** TF 6299, right m2 in occlusal view; **g** TF 6296, left maxilla (p3–M1) in labial view; **h** P4 in occlusal (**h1**) and lingual (**h2**) views; **i** TF 6307, right M1 in occlusal views. Scale bar=1 cm

direction of the protocone basis. In mesial view, this last crest forms a V-shaped notch together with the mesiolabially crest coming down from the protocone. The protocone, more mesial than the paracone, is cup-shaped (i.e., the labial

surface is roughly plane whereas the lingual portion is convex). The lingual shelf is moderately developed. It shows a slight padding distal to the protocone, which is considered in this study as a hypoconal crest/crestiform hypocone



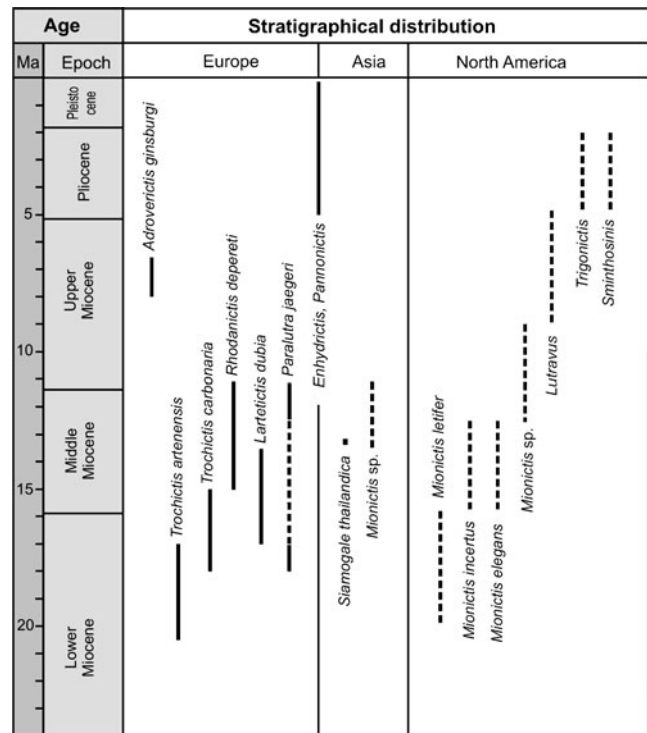
(Fig. 2 h2). A crest that originates from the distolingual face of the protocone joins the hypoconal crest at the level of the paracone position. The enamel is markedly crenulated on the lingual cingulum part near the shearing blade. The M1 has a prominent distolingual border. It forms a broad heel across the lingual third of the tooth (Fig. 2 i). As a result of this expansion, the distal border of the tooth shows like a medial constriction, and the maximal length of the M1 is more important than the P4 one (Table 1). The lingual cingulum is thick. There is no hypocone but a crescent-shaped protocone, which elongates distally and ends approximately to the middle of the tooth. A thin crest originates from the paracone for ending to the middle of the protocone. The paracone is slightly higher than the metacone, and its intracingular shelf (i.e., region located labially to the paracone) is slightly more extended than the metacone one. The two labial cusps are linked by a thin oblique crest. The enamel is mostly crenulated on the lingual part of the M1.

### Comparisons

*S. thailandica* displays a hypocarnivorous dentition (e.g., low m1 trigonid, wide and long basined talonid, lingual expansion of the upper teeth). Within Mustelidae, several taxa show a tendency of M1 enlargement, one of the most remarkable dental features of *Siamogale*. This is notably the case of Gulolinae and some Galictinae, Lutrinae, and otter-like or meline-like genera. The stratigraphic distributions of the main compared genera are reported in Fig. 3.

The distolingual expansion of M1 is particularly visible in the extinct Gulolinae (Gray, 1825) *Dehmictis*, *Plesio-gulo*, and *Iberictis* from the Miocene and Pliocene of Eurasia and in the extant genus *Martes*, known in Asia since the middle Miocene (Ginsburg 1999). In spite of the M1 shape, these taxa have a clearly more trenchant dentition than *Siamogale*, with, for example, a weak or absent P4 lingual shelf and a long opened trigonid with a low or nearly absent metaconid.

Some genera of the Galictinae (Reig, 1956) show a M1 with a distolingual expansion and a lingual shelf on P4 giving to the tooth a triangular shape. Baskin (1998) defined this group to have a wide m1 basined talonid and a metaconid connected to the entoconid crest of the talonid, as in *Siamogale*. They also show a tendency toward the loss of the p1 (García et al. 2008). The main difference between the galictines and *S. thailandica* is the longer and more opened m1 trigonid, with its slightly lower and more distal metaconid. This group includes the semi-aquatic Mustelidae *Lutravus*, from the Mio-Pliocene of North America after Baskin (1998) and the Plio-Pleistocene Eurasian *Enhydriactis* and *Pannonictis* after Pilgrim (1932a). The



**Fig. 3** Stratigraphic distributions of the main taxa used in comparison with *S. thailandica*, following Steininger (1999) for Europe, Qiu and Qiu (1995) for China, and Prothero (1998) for North America. The dotted lines indicate an uncertain distribution for the taxon

American Pliocene genera *Trigonictis* and *Sminthosinis* are also often considered as close to the extant galictines (e.g., Baskin 1998; see Fig. 3 for temporal and geographical distributions).

*Lutravus* is described by Baskin (1998) to have a short P4 shearing blade, a prominent M1 lingual cingulum, and a p4 without distal accessory cusp, as in *Siamogale*. But *Lutravus* differs from *Siamogale* in its M1, wider than long, because of the weak distolingual expansion of its tooth.

*Siamogale* resembles *Trigonictis* in its P4 triangular shape, which exhibits an incipient hypocone, the presence of a M1 metaconule just lingual to the metacone, the thick lingual cingulum, and the lack of accessory cusps on lower premolars. Nevertheless, in *Trigonictis*, the m1 trigonid is longer, with a reduced and more distal metaconid, the P4 protocone is nearly conical, the paracone is higher, the lingual shelf is less developed, and the M1 distolingual expansion is less prominent (Bjork 1970).

*Sminthosinis* is closely related to *Trigonictis* (Bjork 1970). The metaconid of m1 is approximately at the same position as the protoconid, like in *Siamogale*. P4 protocone is cup-shaped and wide but very reduced compared to *Siamogale*. It also differs from our Thai genus in its very moderate lingual shelf on P4, its lack of metaconule on M1, and its long m1 trigonid.

The genus *Enhydrictis* is similar to *Siamogale* with regard to its cup-shaped P4 protocone. Moreover, in *Enhydrictis galictoides*, the metaconid and protoconid are located about the same position as in *S. thailandica* (García et al. 2008). But the M1 is nearly rectangular; the metacone and its labial shelf are reduced; the m1 metaconid is low, more vertically connected to the talonid basin; the hypoconid is higher; and the p2 is single-rooted.

*Pannonictis* displays the same general morphological characters as *Enhydrictis*. *Pannonictis nestii* presents a P4 hypoconal crest and a more developed M1 distolingual expansion than the other species of the genus, making it closer to *Siamogale*. *Enhydrictis* and *Pannonictis* display, however, two roots on M1 whereas *Siamogale* M1 shows three roots.

*Paralutra*, known from the early middle Miocene of Europe, is the earliest representative of Lutrinae (Ginsburg 1999). This genus and notably the species *Paralutra jaegeri* (Fraas, 1862) have certainly the most important distolingual expansion on M1 within otters and shows a crenulated enamel, as in *Siamogale*. But the m1 talonid is shorter and narrower; the metaconid is smaller, more distal; and its distal part is not connected to the entoconid crest of the talonid. The P4 shows a high paracone and a distinct hypocone very close to the protocone. These features are clearly different from those observed in *Siamogale*.

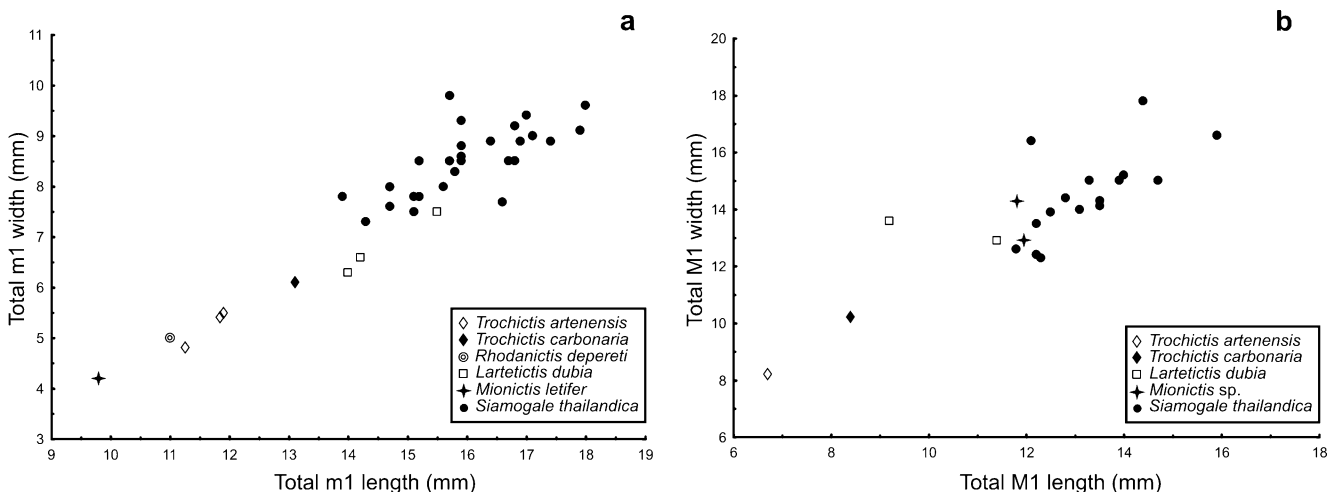
Some Miocene otter-like or meline-like forms of the Old and the New World are also compared to *Siamogale*. Strong similarities with the otter-like genus *Mionictis* have been suggested (Ginsburg et al. 1983; Willemsen 1992; Ginsburg and Morales 1996, 2000). *Mionictis* was originally represented in the Miocene of both North America and Europe. European species (*Mionictis dubia* de Blainville, 1841; *Mionictis artenensis* Ginsburg 1968; and *Mionictis ginsburgi* Alcala et al. 1994) were placed in this genus before

being moved to the genera *Lartetictis*, *Trochictis*, and *Adroverictis*, respectively (Ginsburg and Morales 1992, 1996).

*Adroverictis ginsburgi* is represented by a first upper molar from Spain (Alcala et al. 1994). The genus shows both a M1 mesiolingual and distolingual expansion, in conjunction with a crescent-shaped protocone, extended from the base of the paracone to the metaconule. These features are very different from those observed in *Siamogale*.

The American species of *Mionictis* and the European genera *Lartetictis* and *Trochictis* display several similarities with *Siamogale*: a low m1 trigonid, a metaconid connected with the entoconid crest of the talonid, a basined talonid surrounded by an entoconid crest and presenting a low hypoconid, a slightly reduced M1 metacone, a crescent-shaped protocone, and a distolingual expansion with thick lingual cingulum. The teeth have also enamel crenulations, notably visible on the m1 talonid and on the lingual development of the upper teeth. The lower and upper teeth measurements of *Siamogale*, *Mionictis*, *Lartetictis*, and *Trochictis* are reported in Fig. 4a, b and in Tables 2 and 3.

The monospecific genus *Lartetictis* extends from the early to the middle of middle Miocene in Europe (Heizmann and Morlo 1998; Ginsburg and Morales 2000). Its dental dimensions are close to those of *Siamogale* (Tables 2 and 3; Fig. 4a, b). In addition to the similarities cited above, the m1 talonid of *Lartetictis* is wide, and its M1 shows a metaconule, although slightly smaller than in *Siamogale* and a M1 distal border which is constricted just lingual to this metaconule, as in *Siamogale*. *Lartetictis* differs from it in a slightly smaller and more distal m1 metaconid, a longer P4 shearing blade, a more prominent P4 hypoconal crest, and a more extended intracingular shelf of the M1 paracone.



**Fig. 4** Scatter diagrams: total width versus total length of m1 (a) and M1 (b) of *S. thailandica* and the species of the genera *Trochictis*, *Rhodanictis*, *Lartetictis*, and *Mionictis*

**Table 2** Dental comparisons between *S. thailandica* and the Miocene European species of *Lartetictis*, *Trochictis*, *Rhodanictis*, and American species of *Mionictis*: lower teeth measurements (in millimeters)

Lower teeth		Lp2	Wp2	Lp3	Wp3	Lp4	Wp4	Lm1	Wm1	Lm2	Wm2
Fossil taxa	Specimens										
<i>Lartetictis dubia</i>											
MNHN Sa 801	Right mandible <sup>a</sup>		3	6.7	3.8	9.6	4.6	15.5	7.5		
MNHN Sa 802	Left p2 <sup>a</sup>	6.3	3.4								
SMNS 44427	Right mandible <sup>b</sup>	5.9	3.5	6.8	4	9.1	4.7	14.2	6.6		
	Left mandible <sup>b</sup>					8.9	4.7	14	6.3		
<i>Trochictis artenensis</i>											
MNHN Ar 21	Left mandible <sup>c</sup>	4.8	2.55	5.8	3.4	8.55	4.4	11.9	5.5	5.1	5.2
	Right mandible <sup>c</sup>			5.6	3.4	8.2	4.2	11.85	5.4		
MNHN Ar 22	Left m1 <sup>c</sup>							11.25	4.8		
MNHN Ar 2410	Right m2 <sup>c</sup>									5.6	5.15
<i>Trochictis carbonaria</i>											
MNHN SO 3010	Left mandible <sup>c</sup>			6.6	3.7	8.9	4.8	13.1	6.1		
MNHN Ba 3	Right mandible <sup>c</sup>					8.2	4.1				
<i>Rhodanictis depereti</i>											
MNHN M 5313b	Left mandible <sup>d</sup>	5	2.8	6	3.1	7.4	3.7	11	5		
<i>Mionictis incertus</i>											
A.M.18263	Right mandible <sup>e</sup>							12.3			
<i>Mionictis elegans</i>											
A.M.18267	Mandible <sup>e</sup>							11			
<i>Mionictis letifer</i>											
HC 484	Left mandible <sup>f</sup>					6.2	3	9.8	4.2		

<sup>a</sup> Ginsburg (1968)<sup>b</sup> Heizmann and Morlo (1998)<sup>c</sup> Ginsburg (2002)<sup>d</sup> Pilgrim (1932a)<sup>e</sup> Matthew (1924)<sup>f</sup> Cook and Mc Donald (1962)

The genus *Trochictis* is represented by two species, *Trochictis artenensis* and *Trochictis carbonaria*, from the early Miocene of France and Switzerland (Ginsburg 2002). Their teeth are smaller than those of *Siamogale* (Tables 2 and 3; Fig. 4a, b). The m1 talonid is narrower than in *Siamogale*, the metaconid is lower and located more distally, and the entoconid crest appears less smooth. The M1 lacks a metaconule and a medial constriction at the distal border of the tooth, so that it is nearly straight, unlike in *Siamogale*.

From the middle Miocene of France, *Rhodanictis depereti* was removed from the genus *Trochictis* (Ginsburg and Morales 2000). Although the m1 has a similar morphology and proportions with the other species of *Trochictis* (Tables 2 and 3; Fig. 4a), the M1 is nearly subsquared, with a moderate distolingual expansion, and the crescent-shaped protocone is connected to the metaconule, unlike in *Siamogale*. The P4 protocone,

cup-shaped, is similar to the *Siamogale* one, but the shearing blade is longer and the lingual shelf is reduced, no hypoconal crest being visible. *Rhodanictis* also differs from *Siamogale* by its interdental gap between premolars and the presence of a p1 and a distal accessory cusp on p4.

In the American species of *Mionictis*, only the lower dentition has been figured (Matthew 1924; Cook and McDonald 1962). The type species *Mionictis incertus* lacks p1, distal accessory cusps on premolars, and interdental gap between premolars, as *Siamogale*. However, the m1 talonid is narrower, the metaconid is lower and more distal, and the hypoconid is prominent. Harrison (1981) referred an undescribed partial skull from Texas to *Mionictis* sp. (F:AM 63296). Recently, the P4 and M1 of this specimen have been illustrated and briefly described in a taxonomical comparison (Tseng et al. 2009). These teeth are similar to the upper teeth of *Siamogale* in having



**Table 3** Dental comparisons between *S. thailandica* and the Miocene European species of *Lartetictis*, *Trochictis*, *Rhodanictis*, and American species of *Mionictis*: upper teeth measurements (in millimeters)

Upper teeth		LP1	WP1	LP2	WP2	LP3	WP3	LP4	WP4	LM1	WM1
Fossil taxa	Specimens										
<i>Lartetictis dubia</i>											
MNHN Sa 843	Left M1 <sup>a</sup>									11.4	12.9
SMNS 44427	Left maxillar <sup>b</sup>			5.6	3.1			12.3	9.5	9.2	13.6
<i>Trochictis artensis</i>											
MNHN Ar 2426	?Right P3 <sup>c</sup>					8.3	4.6				
MNHN Ar 2408	Right P4 <sup>c</sup>							11.5	8.5		
MNHN Ar 2409	Left M1 <sup>c</sup>									6.7	8.2
<i>Trochictis carbonaria</i>											
MNHN Ba 2978	Left M1 <sup>c</sup>									8.4	10.2
<i>Rhodanictis depereti</i>											
MNHN M 5313	Left maxillar <sup>d</sup>	2.8	2.4	5	2.7	6	3.4	9.5	6.7		
<i>Mionictis</i> sp.											
F:AM 63296	Left maxillar <sup>e</sup>			6.5	3.4	7.52	4.3	12.34		11.96	12.92
	Right maxillar <sup>e</sup>			6.16	3.26	7.48	4.26	12.3		11.82	14.28

<sup>a</sup> Ginsburg (1968)<sup>b</sup> Heizmann and Morlo (1998)<sup>c</sup> Ginsburg (2002)<sup>d</sup> Pilgrim (1932a)<sup>e</sup> Tseng et al. (2009)

a weak P4 hypoconal crest, a M1 paracone and metacone intracingular shelf nearly similarly developed, and a metaconule. Moreover, the M1 dimensions are close to those of *Siamogale* (Tables 2 and 3; Fig. 4b). But the P4 shearing blade is longer, the M1 paracone is higher, and the metaconule is more prominent and more labial. The associated mandible (F:AM 63298) shows a wide m1 talonid, as in *Siamogale*, but unlike *M. incertus*. Moreover, the m2 is more rounded than in *Siamogale*. These specimens of *Mionictis* sp. lack crenulated enamel, unlike *M. incertus* and *Siamogale*.

Thus, *S. thailandica* appears to be morphologically closer to the European *Lartetictis dubia* and the American *Mionictis* sp. However, several features as the height and position of the m1 metaconid and the development of the P4 make it distinctive and difficult to link with other known Mustelidae.

## Discussion

Apomorphies such as the lack of m3 and M2, and the lack of a carnassial notch on P4 in *S. thailandica* are present in Mustelidae and Mephitidae families (e.g., Tedford 1976; Wozencraft 1989; Baskin 1998). We suspect that the Thai species belongs to mustelids because they lack

extra roots on m1 and of a postprotocrista on M1, two derived features occurring in mephitids (Wang et al. 2004).

Concerning the subfamily, Ginsburg et al. (1983) placed *S. thailandica* within the Lutrinae as a specialized shellfish-eating otter. They based their attribution on the morphological features of the holotype, close to those present in Lutrinae (i.e., low closed trigonid, wide-basined talonid). They also took into account the morphological similarities of *Siamogale* with the genus *Mionictis*, considered as an otter, and notably with the European species *M. artensis*. This hypothesis will be followed in the few later publications related to *Siamogale* (Ginsburg and Tassy 1985; Willemsen 1992; Ginsburg and Morales 1996; Pickford 2007; Thewissen and Bajpai 2008). However, the morphology of the other dental remains of *S. thailandica*, especially the upper teeth, and the taxonomical changes of the European “*Mionictis*” species (Ginsburg and Morales 1992, 1996) make the subfamilial assignment of *Siamogale* doubtful and more complicated to establish.

According to recent molecular studies, Mustelidae are distributed into eight extant subfamilies: Taxidiinae (American badgers), Mellivorinae (honey badger), Melinae (badgers), Gulolinae (wolverine, martens), Helictidinae (ferret-badger), Galictinae (grisons and their allies), Mustelinae (weasels and their allies), and Lutrinae (otters; e.g., Koefli et al. 2008; Sato et al. 2009; Wolsan and Sato 2010).

The fossil group Leptarctinae is also considered as a mustelid subfamily (e.g., McKenna and Bell 1997; Baskin 1998). The crushing dentition tendency is observed in Leptarctinae, in badgers *sensu lato* (Taxidiinae, Helictidinae, Melinae), and in some Lutrinae and Galictinae.

The Miocene North American and Eurasiatic fossil group Leptarctinae includes members generally characterized by a more hypocarnivorous dentition than that of *Siamogale*, with notably quadrate and complex P4s and M1s (e.g., Lim 1999; Wang et al. 2004). The more singular genera *Kinometaxia* and *Schultzogale*, from the early Miocene of China and Nebraska, respectively, have a clearly more trenchant dentition compared to the other genera of the group but also compared to the Thai species (i.e., no lingual shelf and a long shearing blade on P4, transversely broad M1 with a small metacone and a wide intracingular shelf of the paracone; Lim and Martin 2000; Wang et al. 2004). Thus, *Siamogale* appears to be morphologically far from this subfamily.

Badgers *sensu lato* include relatively diverse Old World and New World forms. The Taxidiinae are known since the late Miocene and includes only three genera. *S. thailandica* differs from the extant *Taxidea* and the extinct *Pliotaxidea* in which the P4 has a well-developed hypocone and protocone, the M1 and m1 talonid have numerous cuspules, and the p4 shows an accessory cusp (Baskin 1998). The earliest genus of Taxidiinae, *Chamitataxus*, displays a long P4 shearing blade, a wide metaconule more distally located than in *Siamogale*, and lacks a crescent-shaped protocone. Morphological differences with *Siamogale* are too numerous to assign it to this subfamily.

The Helictidinae, currently represented by the Asian ferret-badger *Melogale*, are recognized as a distinct group of badgers but have no clear fossil representatives (e.g., Petter 1971; Sato et al. 2009). The teeth show a voluminous P4 similar to that of mephitids, a M1 wider than longer, without distolingual development, and bearing a longitudinal protocone, unlike in *S. thailandica*. Moreover, the m1 has a narrower and shorter talonid compared to the Thai species.

Considering only the dental material, *Siamogale* shows several features resemble those of Lutrinae, Melinae, and Galictinae. The connection of the m1 metaconid with the entoconid crest or entoconid is a morphological feature present in musteline-like forms including Galictinae, although this connection is often more abrupt than in *Siamogale*. This feature is absent in the Lutrinae, except in the genus *Mionictis*, its subfamilial position being doubtful. Other characters which are observed in *Siamogale*, as the closed low trigonid of m1, the elongated basined talonid, and the unreduced metaconid are convergent morphological tendencies seen in Lutrinae and Melinae (Baskin 1998). However, the talonid of Melinae shows numerous cuspules on its rim, and the metaconid is often located more distally with respect

to the protoconid, unlike in *Siamogale*. Some Galictinae also show a wide-basined talonid, but the metaconid is lower and more distal than in Lutrinae and in *Siamogale*. A P4 lingual shelf and a short shearing blade are developed by Melinae and Lutrinae. The Galictinae also present a lingual shelf but the protocone is generally more prominent and the shearing blade is longer than in *Siamogale*. The distolingual development of the M1 is a feature of Melinae and some Galictinae, but this development is generally in conjunction with a mesiolingual expansion for Melinae and the metacone tends to be reduced in Galictinae. Moreover, the oldest record of a distinctive badger, *Taxodon sansaniensis* from the early middle Miocene of France, shows a m1 talonid rim with several cuspules and a long P4 shearing blade while it has no M1 distolingual development yet. *Paralutra* is the unique genus of Lutrinae that displays a similar M1 development, but the lower dentition is more hypercarnivorous (see comparisons).

The dental pattern of the hypercarnivorous *Martes* is often considered as an ancestral morphological type for Mustelidae. Several groups of the family have evolved independently toward a crushing dentition. For *Siamogale*, this step implicated notably a reduction of the protoconid of m1 with an enlargement and lengthening of the talonid, a development of a lingual shelf and a cup-shaped protocone on P4, a reduction of the P4 shearing blade length, and an enlargement of the M1 metacone. Because of the lack of paleontological data and the problematic subfamilial assignment of fossil mustelids (notably for Helictidinae, Melinae, and Galictinae) and because of the primitive and convergent dental features of *S. thailandica*, we failed to find a subfamily for this species. A cladistic analysis integrating extant and extinct mustelids should be performed in a near future to test its position within the family. Until more data, notably cranial, are available, we suggest that *Siamogale* is an otter-like mustelid, certainly strongly dependent of water. Actually, most of the Carnivora specimens discovered in the lacustrine deposits of the Na Khaem Formation belong to this species. Its bunodont dental morphology and its horizontal worn tooth pattern suggest the consumption of hard items. We remark that mollusks and crabs are frequent in the sediments of the fossil coal layers, which could constitute a possible diet. Unfortunately, no postcranial elements are attributable to *Siamogale*, but its morphological affinities with *Lartectictis*, for which the postcranial bones seem to be adapted for a semi-aquatic way of life (Ginsburg 1968, 1999; Heizmann and Morlo 1998), can follow the otter-like hypothesis. According to the mustelid fossil record of Mae Moh, competition between *S. thailandica* and bunodont Lutrinae was unlikely, the only Miocene otters from Asia being confined in the Indian Subcontinent and in China (Lydekker 1884; Pilgrim 1932b; Qiu and Qiu

1995). Interestingly, several otter-like mustelid lineages, such as those of *Siamogale*, *Lutravus*, and *Enhydrictis*, occur in the Miocene and Plio-Pleistocene epochs, whereas the extant mustelids that inhabit freshwater and marine environments are nearly all included in the Lutrinae subfamily. Currently, the few semi-aquatic mustelids, such as the Mustelinae *Mustela vison* living near rivers and stream waters, can be forced to shift their diet when they are in competition with lutrines feeding on the same aquatic items (Larivière 1999; Bonesi et al. 2004). This could be partly explained by the more efficient aquatic adaptations for swimming and hunting preys underwater that might have been acquired by the Lutrinae during their evolution.

The geographic origin of *Siamogale* lineage is also questionable. The Mae Moh fauna usually appears close to taxa coming from other Miocene localities of northern Thailand and from the Siwaliks province of Pakistan (e.g., Ginsburg and Tassy 1985; Ducrocq et al. 1995; Chaimanee et al. 2008; see also Chavasseau 2008). However, some genera show possible close relatives in northern China and in North America or Europe (Peigné et al. 2006; Chavasseau 2008). Within the compared mustelids, the American *Mionictis* sp. and the European *Lartetictis* display the most similar morphology with *Siamogale*, thus suggesting a European or a North American immigration event before 13.4 Ma. Other geographic occurrences of *Mionictis* sp. are reported in the middle Miocene from Al-Sarrar (Saudi Arabia) and from Tunggur (China). However, the paucity of the material and the discovery, at Tunggur, of *Sthenictis neimengguensis*, a mustelid which might have been around the same size as *Mionictis*, render these occurrences very uncertain (Thomas et al. 1982; Qiu and Qiu 1995; Tseng et al. 2009; Wang, personal communication). According to the palynological studies and the Mae Moh fossil record, especially the rodents and the sivaladapid primate, Southeast Asia appears as a distinct biogeographic province in the middle Miocene (e.g., S epulchre 2003; Chaimanee et al. 2007, 2008). Added to the scarcity of the Mustelidae fossil record in that region and to the dental peculiar features of *S. thailandica*, a Southeast Asian endemic origin for *Siamogale* lineage cannot be ruled out.

## Conclusions

Many additional specimens of *S. thailandica* were collected in the Mae Moh Basin of northern Thailand. We suggest that this species is a bunodont otter-like mustelid, whose taxonomical position within the family is still unclear. After comparisons of its dental morphology with those of extinct and extant mustelids, we conclude that *Siamogale* displays more similarities with the early

and middle Miocene genera *Mionictis* and *Lartetictis*. If these genera are close relatives, it implies a European or a North American immigration event to Thailand before 13.4 Ma. Nevertheless, *Siamogale* shows peculiar morphological features, such as the shape of the P4 lingual shelf and the m1 metaconid position and height. Due to the scarcity of the fossil record of Mustelidae in Southeast Asia and the degree of endemism of this fauna, further fieldworks are necessary to find other representatives of this peculiar lineage.

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