An astonishing example of convergent evolution toward carnivory: *Siamosorex debonisi* n. gen., n. sp. (Mammalia, Lipotyphla, Soricomorpha, Plesiosoricidae) from the latest Oligocene of Thailand

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ABSTRACT

Paleogene faunas from Southeast Asia are rare and mainly represented by those from Krabi (late Eocene, Thailand) and Pondaung (middle Eocene, Myanmar). The late Oligocene locality of Nong Ya Plong (Thailand) was discovered recently and has so far yielded mammalian remains representing the orders Carnivora, Dermoptera, Rodentia, and Perissodactyla. A new genus and species from this locality (*Siamosorex debonisi* n. gen., n. sp.) of the soricoid family Plesiosoricidae is described. The material consists of lower dentitions only. The species differs from other plesiosoricids in being larger to much larger (except compared to some species of *Plesiosorex*) and in having a shallow masseteric fossa; i2 enlarged, not procumbent but upright and caniniform, with a deep mesiolingual groove; elongated, double-rooted p3 and p4, similar in length but p3 with simple crown and p4 semimolariform with a reduced paraconid, a high, distinct metaconid, and a short talonid; lower molars decrease in size strongly from m1 to m3; elongated molars with the talonid markedly narrower and shorter than the trigonid, tall and open trigonid, especially in m1, entoconid and hypoconid not individualized, entocristid lower than the oblique cristid, and metaconid taller than paraconid in m1, subequal to the paraconid in m2. *Siamosorex debonisi* n. gen., n. sp. was approximately the same size as small species of *Mustela* (Carnivora) and probably preyed on small vertebrates and arthropods. There is some support for the presence of a venom delivery apparatus in *S. debonisi* n. gen., n. sp. The origin of *Siamosorex* n. gen. is unknown, although this genus may have some relationships with the genus *Butselia* from the early Oligocene of western Europe.

KEY WORDS
Mammalia,
Lipotyphla,
Soricomorpha,
Plesiosoricidae,
Southeast Asia,
Oligocene,
convergent evolution,
carnivory,
venom delivery apparatus,
new genus,
new species.

RÉSUMÉ

Un surprenant exemple de convergence évolutive vers la carnivorie : Siamosorex debonisi *n. gen., n. sp. (Mammalia, Lipotyphla, Soricomorpha, Plesiosoricidae) de l'Oligocène terminal de Thaïlande.*

Les faunes paléogènes d'Asie du Sud-Est sont rares et représentées principalement par celles de Krabi (Éocène supérieur, Thaïlande) et Pondaung (Éocène, Myanmar). La localité oligocène supérieur de Nong Ya Plong (Thaïlande), récemment découverte, a livré jusqu'à présent des restes de mammifères appartenant à des Carnivora, Dermoptera, Rodentia et Perissodactyla. Un nouveau genre et espèce (*Siamosorex debonisi* n. gen., n. sp.) de la famille soricoïde Plesiosoricidae est décrit de cette localité. Le matériel comprend uniquement des dentures inférieures. L'espèce diffère des autres plésiosoricidés par les caractères suivants : taille plus grande à beaucoup plus grande (sauf par rapport à certaines espèces de *Plesiosorex*) ; fosse massétérine peu profonde ; i2 développée, non orientée vers l'avant mais redressée et caniniforme, avec un sillon mésio-lingual profond ; p3 et p4 allongées, biradiculées, à peu près de même longueur, p3 simple et p4 semi-molariforme avec un paraconide réduit, un métaconide haut, distinct et réduit et un talonide court ; forte diminution de taille de m1 à m3 ; molaires allongées avec un talonide bien plus étroit et plus court que le trigonide, haut et ouvert, surtout sur m1 ; entoconide et hypoconide non individualisés ; entocristide plus basse que la crête oblique ; métaconide plus haut que le paraconide sur m1, de même hauteur sur m2. *Siamosorex debonisi* n. gen., n. sp. était approximativement de la taille des petites espèces de *Mustela* (Carnivora) et chassait probablement de petits vertébrés et des arthropodes. La présence d'un appareil à venin chez *S. debonisi* n. gen., n. sp. est envisagée. L'origine de *Siamosorex* n. gen. n'est pas connue, bien que ce genre puisse être lié au genre *Butselia* de l'Oligocène inférieur d'Europe occidentale.

MOTS CLÉS
Mammalia,
Lipotyphla,
Soricomorpha,
Plesiosoricidae,
Asie du Sud-Est,
Oligocène,
évolution convergente,
carnivorie,
appareil à venin,
genre nouveau,
espèce nouvelle.

INTRODUCTION

The Palaeogene vertebrate record from Southeast Asia is quite poor compared to other Asian regions (especially China and Mongolia). In their exhaustive review of the Palaeogene record of mammals in Asia, Russell & Zhai (1987) reported only two mammalian localities from Myanmar (in the Pondaung and Pegu Formations) containing about 20 taxa, of which many were indeterminate. During the past two decades, however, the mammalian record from this region has much improved in quantity of taxa, although it mainly results from intensive field work in two places, the Pondaung Formation (middle Eocene of Myanmar; Benammi *et al.* 2002; Tsubamoto *et al.* 2002) and Krabi (latest Eocene; Ducrocq *et al.* 1995; Benammi *et al.* 2001). Localities in the Pondaung Formation yielded about 50 mammalian taxa (Tsubamoto *et al.* 2005) and additional new taxa were recently published (Métais 2006; Métais *et al.* 2006, 2007; Beard *et al.* 2007; Egi *et al.* 2007, 2008; Peigné *et al.* 2007). The latest published faunal list for Krabi is quite old and comprised 27 mammal taxa (Ducrocq *et al.* 1995), but with the inclusion of numerous recent discoveries, more than 40 taxa of mammals have now been recognized from Krabi (see revised faunal list in Appendix 1). The richness and diversity of mammals from these two formations or localities rank them among the most remarkable sites in Asia. Palaeocene and Oligocene terrestrial faunas are much scarcer, if not totally unknown. The recent discovery of a late Oligocene fauna at Nong Ya Plong (Fig. 1), Thailand, is therefore very important in this context (Marivaux *et al.* 2004; Peigné *et al.* 2006a). Thailand is the only country in the Southeast Asia to document faunas from both the Eocene and the Oligocene, while the Miocene basins of northern Thailand also yielded very rich and diverse faunas (see, e.g., Ducrocq *et al.* 1995; Peigné *et al.* 2006b; Chaimanee *et al.* 2007, 2008).

In the present contribution, we describe a new genus and species of Insectivora Bowdich, 1821 from Nong Ya Plong that represents a unique example of morphological convergence with true carnivorans. Yet this species belongs to the Plesiosoricidae Winge, 1917, a poorly known insectivoran family that belongs to the early offshoots in the first radiation of Soricomorpha Gregory, 1910 (Lopatin 2006). This family includes small carnivore-like taxa ranging from the middle Eocene to the late Miocene in North America, Europe, and Asia. Lopatin (2006: fig. 1) recognized two subfamilies, the Butseliinae Quinet & Misonne, 1965 and the Plesiosoricinae Winge, 1917, which have mutually exclusive geographic and stratigraphic ranges. The material described here represents the most southerly record of the family in Asia and, if we are correct in assigning it to the Butseliinae, the latest record for this subfamily.

Fig. 1. — Geographical map of South-east Asia showing the vertebrate fossil locality of Nong Ya Plong.

MATERIAL AND METHODS

The material consists of three individuals represented by well-preserved, nearly complete lower dentitions found in the coal mine of Nong Ya Plong, Thailand (Fig. 1) during a summer field trip by a joint French-Thai team (Department of Mineral Resources of Bangkok and University of Montpellier) in 2001. This locality has thus far yielded a poor fauna comprising four species of mammals: a rodent, *Fallomus ladakhensis* Nanda & Sahni, 1998, a rhinocerotid

Diceratherium sp. cf. *D. lamilloquense* Michel, 1983, a musteloid carnivoran *Chaprongictis phetchaburiensis* Peigné, Chaimanee, Yamee, Srisuk, Marandat & Jaeger, 2006, and a cynocephalid dermopteran (*Dermotherium chimaera* Marivaux, Bocat, Chaimanee, Jaeger, Marandat, Srisuk, Tafforeau, Yamee & Welcomme, 2006) that indicate a late Oligocene age for the fauna (Marivaux *et al.* 2004, 2006; Peigné *et al.* 2006a). The material was found in a lignite block and prepared in the Institut des Sciences de l'Évolution, University of Montpellier, France. After study all of the material will be stored in the Department of Mineral Resources, Bangkok.

Measurements have been taken with a Measurescope Nikon.

Dental nomenclature follows Lopatin (2006: fig. 3).

ABBREVIATIONS

BSP	Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich;
GSP-UM	Geological Survey of Pakistan, Islamabad and Quetta, casts at University of Michigan Museum of Paleontology;
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing;
JG	Landesmuseum Joanneum, Graz;
KE	Kapchagay Geological Expedition, Ministry of Ecology and Natural Resources, Almaty, Kazakhstan;
KU	Kansas University, Museum of Natural History, Lawrence;
MAFI	Hungarian Geological Institute, Budapest;
MF	Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow;
MN	Mammal Neogene, biozone of the European continental biochronological scale for the Neogene (see Mein 1999);
MNHM	Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland;
MP	Mammal Palaeogene, reference level of the European continental biochronological scale of the Palaeogene (see Sigé & Legendre 1997);
NHMW	Naturhistorische Museum, Vienna;
NMB	Naturhistorische Museum, Basel;
PIN	Paleontological Institute of the Russian Academy of Sciences, Moscow;
PSS	Palaeontology and Stratigraphy Section, Institute of Geology, Mongolian Academy of Sciences, Ulan-Bator;
SDSM	Museum of Geology, South Dakota School of Mines and Technology, Rapid City;
SHM-CP	Srisuk House Museum, Cha Prong;
SMF	Forschungsinstitut und Naturmuseum Senckenberg, Francfort;
SMNS	Staatliches Museum für Naturkunde, Stuttgart;
UCMP	Museum of Paleontology, University of California, Berkeley;
UNSM	University of Nebraska State Museum, Lincoln;
USNM	National Museum of Natural History, Washington, DC.

SYSTEMATICS

Superorder INSECTIVORA Bowdich, 1821
Order LIPOTYPHLA Haeckel, 1866
Suborder SORICOMORPHA Gregory, 1910
Superfamily SORICOIDEA Fischer, 1817

Family PLESIOSORICIDAE Winge, 1917

Classification above the family follows Lopatin (2006: S384). This choice might seem arbitrary, but there is currently no consensus on the phylogeny of insectivorans (Symonds 2005; Lopatin 2006).

Genus *Siamosorex* n. gen.

TYPE SPECIES. — *Siamosorex debonisi* n. sp. by monotypy and present designation.

ETYMOLOGY. — The genus name refers to Siam, old name of Thailand, and *-sorex*, Latin for mouse.

DIAGNOSIS. — Plesiosoricid of large size that differs from most other plesiosoricids in being larger to much larger (except compared to some species of *Plesiosorex* Pomel, 1848) and having a shallow masseteric fossa; i2 enlarged, not procumbent but upright and caniniform, with a deep, mesiolingual groove; p3 and p4 elongated, double-rooted, of similar length; p3 with simple crown and p4 semimolariform with a reduced paraconid, a high, distinct metaconid, and a short talonid; molars show a strong decrease in size from m1 to m3; molars elongated with talonid markedly narrower and shorter than the trigonid, trigonid tall and open, especially in m1, entoconid and hypoconid not individualized, entocristid lower than oblique cristid, and metaconid taller than paraconid in m1, subequal to it in m2.

DISTRIBUTION AND AGE. — Nong Ya Plong, Thailand, late Oligocene (see Marivaux *et al.* 2004; Fig. 1).

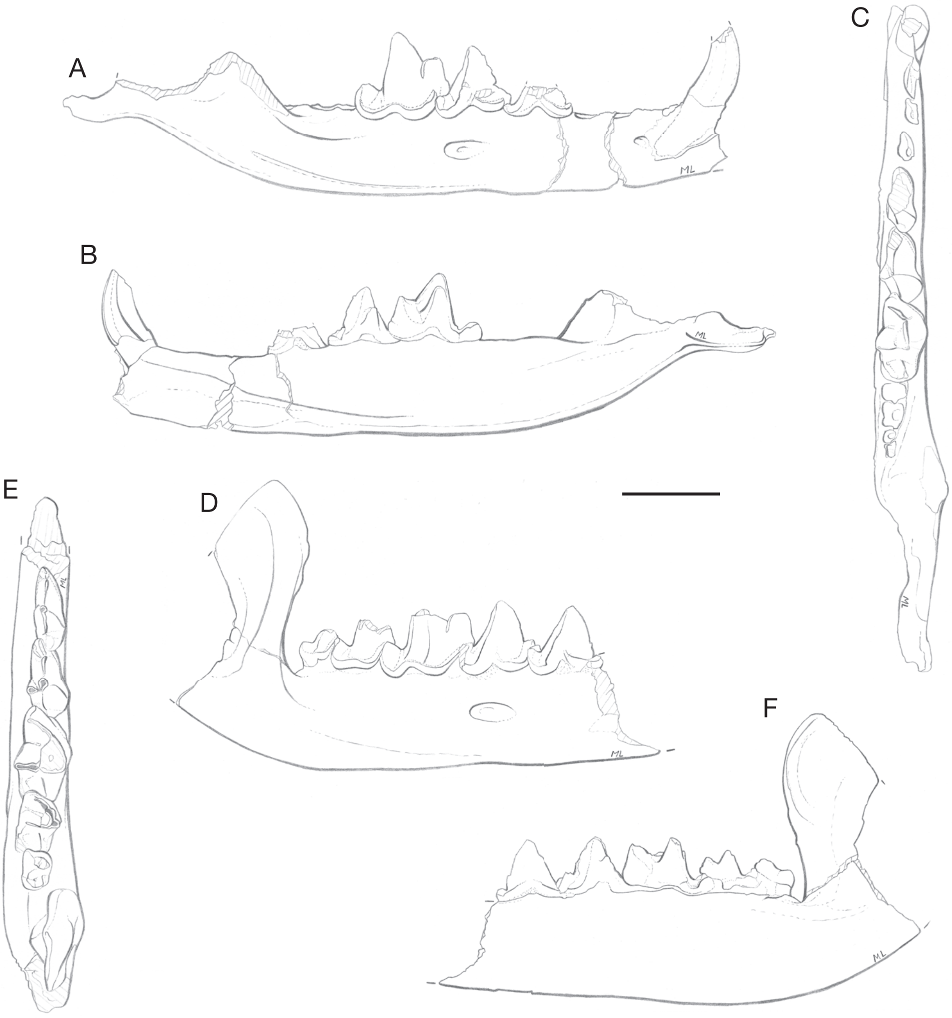

Fig. 2. — *Siamosorex debonisi* n. gen., n. sp. from Nong Ya Plong, Thailand, hemimandibles with teeth: **A**-**C**, SHM-CP 677, holotype, incomplete right hemimandible with broken c and p3, p4-m1 in buccal (**A**), lingual (**B**), and dorsal (**C**) views; **D**-**F**, SHM-CP 234, paratype, fragment of right hemimandible with p3-m3 in buccal (**D**), dorsal (**E**), and lingual (**F**) views. Scale bar: 5 mm.

Siamosorex debonisi n. sp.

Holotype. — SHM-CP 677, incomplete right hemimandible with i2, partial p3, p4-m1, isolated i1, i3, m2, and isolated left m3 located very near the mandible in the same block of sediment and probably belonging to the same individual (Fig. 2A-C; 3; 4A-C).

Paratypes. — SHM-CP 327, fragmentary left hemimandible with p4-m2; SHM-CP 234, fragmentary right hemimandible with p3-m3 (Fig. 2D-F; 4D-F).

Type locality. — Cha Prong pit of Nong Ya Plong coal mine, Province of Phetchaburi, Thailand.

Diagnosis. — As for the genus.

Etymology. — Named for Louis de Bonis (IPHEP, University of Poitiers) in recognition of his many contributions to the paleontology of carnivorous fossil mammals.

Distribution and age. — As for the genus.

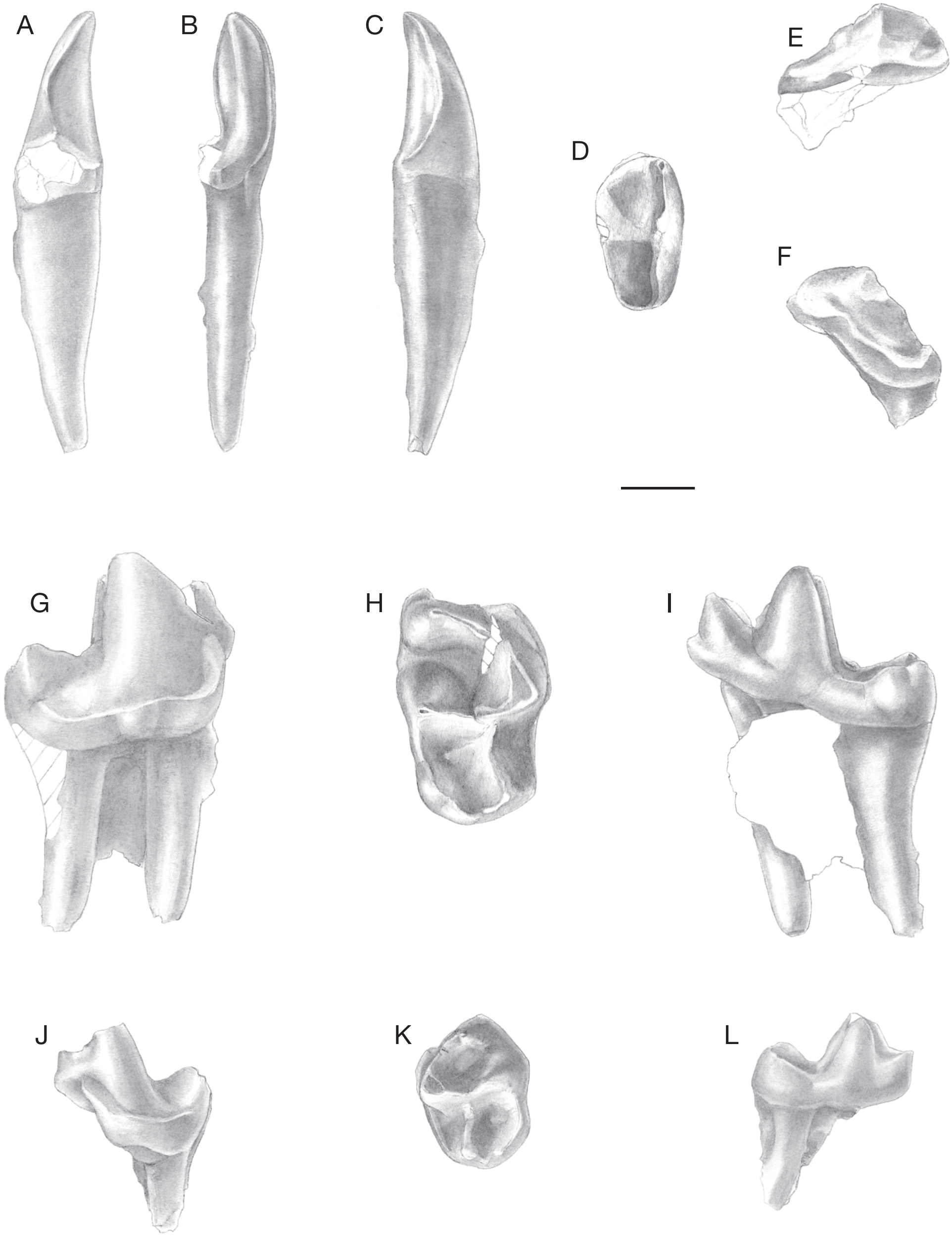

FIG. 3. — *Siamosorex debonisi* n. gen., n. sp. from Nong Ya Plong, Thailand, detailed drawings of isolated teeth, SHM-CP 677, holotype: **A**-**C**, (?)left i1 in distal (**A**), lingual (**B**), and mesial (**C**) views; **D**-**F**, (?)right i3 in occlusal (**D**), labial (**E**), and lingual (**F**) views; **G**-**I**, right m2 in buccal (**G**), occlusal (**H**), and lingual (**I**) views; **J**-**L**, left m3 in buccal (**J**), occlusal (**K**), and lingual (**L**) views. Scale bar: 1 mm.

DESCRIPTION

Mandible (Fig. 2)

The mandibular body is slender and has approximately the same depth throughout its length. It is shallow, with a maximum depth similar to or lower than the height of the protoconid of m1.

The symphysis is poorly marked, which suggests that the hemimandibles were not closely attached together. A shallow but distinct longitudinal groove is present on the lingual face of the corpus, from the level of m3 to the symphysis; it is slightly buccally positioned posteriorly, then ventral beneath p4-m1, and lingual throughout its anterior part. There are two mental foramina. A small one is visible beneath the anteriormost border of p2 and a larger one, which opens forwards, is located beneath the main cuspid of p4. In dorsal view, the root of the coronoid process appears to be laterally located relatively to the tooth row; it has its anterior border at the level of the distal rim of the distal alveolus of m3. A prominent crest is present on the lingual surface of the mandible, posterior to the m3. There is a distinct retromolar space. SHM-CP 234 (paratype) preserves most of the coronoid process, which is tall and oriented slightly forwards, making an acute angle with the ventral border of the mandible. The masseteric fossa is very shallow. The angular process is completely preserved in the holotype. It is slender, elongated, and weakly hooked dorsally. The insertion area for the *M. pterygoideus lateralis* is developed in the form of a shallow and elongated depression that faces mediodorsally. The internal crest that separates this area from that for the *M. pterygoideus medialis* is strong. The ventral surface of the angular process is horizontally oriented and displays an expanded surface for the insertion of the *M. masseter superficialis*.

Dentition (Figs 3; 4)

The dentitions are almost unworn and represent young adults with permanent dentition. The i1 (Fig. 3A-C) is laterally compressed; the main cuspid is lanceolate and slightly procumbent, with a curved lateral ridge. No accessory cuspids are preserved, but the concave distal margin of the main cuspid suggests that a distal accessory cuspid may have been present and separated from the main cuspid by a deep notch. The incisor root is about twice the length of the crown. In plesiosoricids (except in *Ernosorex* Wang & Li, 1990), the enlarged incisor is the i2. In the Thai species too, this tooth is very large, caniniform, and slender, but it is not procumbent and has a slightly trenchant distal rim (Fig. 4A-C). A deep groove, triangular in cross-section, and covered by enamel, is present in a mesiolingual position (Fig. 4A). An isolated antemolar present near the mandible SHM-CP 677 in the lignite block (Fig. 3D-F) is here identified as an i3, based on its great resemblance to the i3 of the type species of the genus *Plesiosorex*, *P. soricinoides* (Blainville, 1840) from the mid-Oligocene of Saint-André (e.g., Viret 1946: fig. 1). This is a small and transversely compressed tooth, with a somewhat trenchant longitudinal crest; its crown is asymmetrical and markedly projected forwards relative to the root. The tooth row is straight and there is no diastema between the teeth. The alveolar margin between the i3 and p3 is poorly preserved in the material (Fig. 4C). We distinguish 3 or 4 alveoli, but it is not possible to determine whether c, p1, and p2 were all present and how many roots they had. The p3 and p4 are double-rooted and morphologically similar (Fig. 4). They are tall, slender, and have a piercing protoconid, trenchant rims, with the mesial rim slightly convex and the distal rim slightly concave, a reduced paraconid, a short trenchant distal talonid, and a distinct buccal cingulid. These teeth are much taller than the m1 paraconid. The p4 differs from p3 in being slightly larger and semimolariform: it has a slightly larger paraconid and a highly placed, small metaconid closely pressed against the mesiolingual surface of the protoconid. The m1 is marginally longer than p4 (Fig. 4; Table 1). The trigonid is composed of a tall protoconid, a much lower paraconid, and a conical metaconid, reduced but taller than the paraconid. The paraconid and protoconid shearing blades make an obtuse angle; the carnassial notch is moderately deep. The metaconid is separated from the paraconid by a deep valley and is placed lingually to the protoconid. The distal face of the trigonid is oriented slightly forwards. The talonid is much lower, narrower, and shorter than the trigonid. There are no individualized cuspids. The oblique cristid is trenchant, taller than the entocristid, and meets the distal surface of the trigonid at the protocristid notch. The talonid basin is shallow. The ectocingulid is distinct and especially well developed at the contact with p4 (precingulid). The m2 (Figs 3G-I; 4D-F) is double-rooted and much

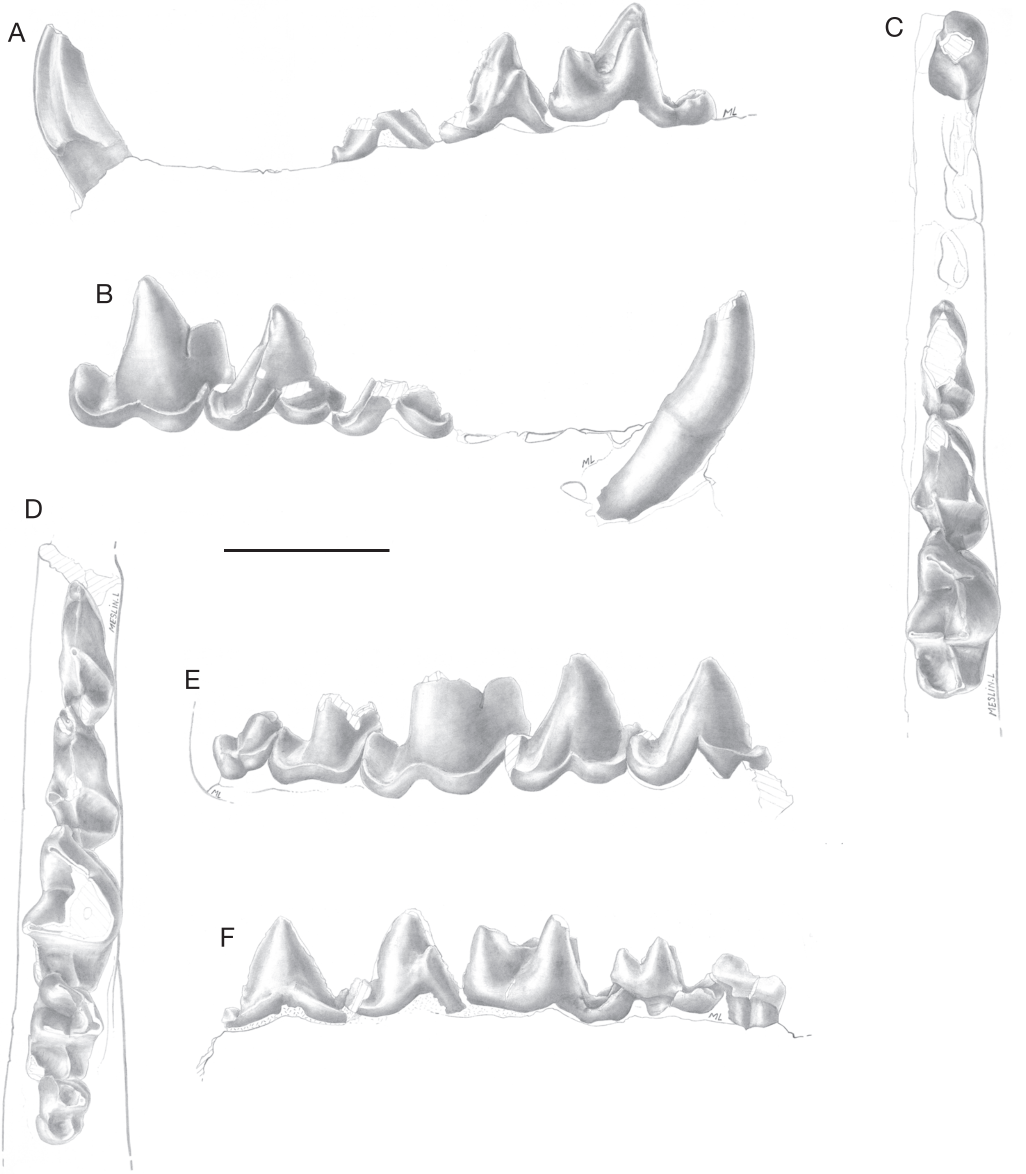

FIG. 4. — *Siamosorex debonisi* n. gen., n. sp. from Nong Ya Plong, Thailand, detailed drawings of dentitions: **A**-**C**, SHM-CP 677, holotype, broken c and p3, p4-m1 in lingual (**A**), buccal (**B**), and occlusal (**C**) views; **D**-**F**, SHM-CP 234, paratype, p3-m3 in occlusal (**D**), buccal (**E**), and lingual (**F**) views. Scale bar: 5 mm.

more reduced (especially much lower) than m1. Its overall morphology is similar, however, except for some details. Thus, it differs from m1 in being less elongated and in having a less open trigonid, a shallower carnassial notch, a metaconid as tall as the protoconid, a longer talonid, and a more developed precingulid. The m3 (Figs 3J-L; 4D-F) is double-rooted in the holotype, but may have

TABLE 1. — Measurements (in mm) of dentitions of *Siamosorex debonisi* n. gen., n. sp., compared to those of Palaeogene plesiosoricids. Abbreviations: **E. Eocene**, early Eocene; **E. Oligo.**, Early Oligocene; **Fm**, Formation; **L**, greatest length; **Lm1-3**, alveolar length of m1 to m3; **L. Oligo.**, Late Oligocene; **M. Eocene**, middle Eocene; **NYP**, Nong Ya Plong; ***Pseudo.***, *Pseudoneurogymnurus*; **wmax**, greatest width. Notes: **1**, based on drawing in Butler (1972); **2**, from Lopatin (2006); **3**, from Wang & Li (1990); **4**, from Gureev (1979); **5**, from Russell & Gingerich (1981).

Specimen	**Locality**	**Measurements**												
		i2		**p3**		**p4**		**m1**		**m2**		**m3**		**Lm1-3**
		L	**w**	**L**	**w**	**L**	**w**	**L**	**wmax**	**L**	**wmax**	**L**	**wmax**	
***Siamosorex debonisi*, L. Oligo.**														
SHM-CP 234	NYP			4.16	1.52	4.21	1.72	4.9	2.7	3.31	2	2.14	1.47	
SHM-CP 677	NYP	2.02	1.6	3.54	1.4	4	1.7	4.75	2.45	3.05	1.98	1.96	1.5	8.51
SHM-CP 327	NYP					3.67	1.73	4.31	2.36	2.72	1.8			
***Butselia biveri*[1], E. Oligo.**														
priv. coll. Ford	Isle of Wight									2.2	1.7			
***Ordolestes ordinatus*[2], E. Eocene**														
PIN 3104/952, holotype	Tsagan-Kushu							2.7	1.6					
PIN 3104/953	Tsagan-Kushu							2.55	1.5					
PIN 3104/954	Tsagan-Kushu							2.5	1.5					
PIN 3104/956	Tsagan-Kushu									2.1	1.5	1.7	1	
PSS 20-1242	Tsagan-Kushu							2.6	1.5					
***Ernosorex jilinensis*[3], M. Eocene**														
IVPP V 8796	Huadian Fm.					1.6	1.28	2.08	1.6					
***Pseudo. schevyrevi*[4], M. Eocene**														
no number	Konurkura									2	1.5			
***Pseudo. zhchikvadzei*[4], M. Eocene**														
no number	Konurkura									1.65	1.25			
***Pakilestes lathrius*[5], M. Eocene**														
GSP-UM 122	Kuldana Fm.							1.3	0.9					
GSP-UM 146	Kuldana Fm.					1.15	0.8							

partly fused roots in SHM-CP 234 (see Fig. 4F) and has the same basic structure as the other molars. The trigonid is tall, the metaconid is as tall as the protoconid, the carnassial notch is weakly pronounced; the talonid is lower and narrower than the trigonid, and has an oblique cristid taller than the entocristid. The ectocingulid and the precingulid are strongly developed.

The molars decrease in dimensions from m1 to m3, the more so between m1 and m2 than between m2 and m3. Furthermore, from m1 to m3, the molars shorten, the molar trigonid becomes less dominant relative to the talonid (the ratio of trigonid length relative to total length decreases from m1 to m3; Table 1), trigonid cuspids form a more and more closed triangle and tend to be less prominent and less well individualized from one another.

DISCUSSION

FAMILIAL ASSIGNMENT OF *SIAMOSOREX DEBONISI* N. GEN., N. SP.

The Soricoidea (*sensu* Lopatin 2006) includes three families: the Nyctitheriidae Simpson, 1928, the Plesiosoricidae Winge, 1917, and the Soricidae Fischer, 1817. The assignment of our material to the family Plesiosoricidae is based on the presence of specialized carnivorous teeth, a semimolariform p4, an m1 much larger than m2, which is much larger than m3, the presence, on the molars, of a tall trigonid with a low paraconid, a tall metaconid well separated from the protoconid, a carnassial notch, a low, narrow, and short talonid with poorly defined cuspids, low mandibular body with a tall and forwardly inclined coronoid process. Plesiosoricids clearly differ from soricids. They have a double-

TABLE 2. — Measurements (in mm) of dentitions of *Siamosorex debonisi* n. gen., n. sp., compared to those of *Plesiosorex* spp. Abbreviations, same as in Table 1 and; **LF**, Local Fauna; **Ulm-West**, Ulm-Westtangente; **Wann.**, Wannemacher. Notes: **1**, from Ziegler (1990); **2**, from Thenius (1949); **3**, from Engesser (1972); **4**, from Seemann (1938); **5**, from Ziegler & Mörs (2000); **6**, from Rzebik-Kowalska (1993); **7**, from Schötz (1989); **8**, from Ziegler (1998); **9**, from Engesser *et al.* (1981); **10**, from Ziegler (2005); **11**, from Mayr & Fahlbusch (1975); **12**, from Ziegler (2006); **13**, from Franzen *et al.* (2003); **14**, from Engesser & Storch (2008); **15**, from Kordikova (2000); **16**, from Wilson (1960); **17**, from Emry & Eshelman (1998); **18**, from Martin & Lim (2004); **19**, from Hall (1929); **20**, from Green (1977); **21**, from Martin & Green (1984).

Specimen	**Locality**	**Measurements**												
		i2		**p3**		**p4**		**m1**		**m2**		**m3**		**Lm 1-3**
		L	**w**	**L**	**w**	**L**	**w**	**L**	**wmax**	**L**	**wmax**	**L**	**wmax**	
***Siamosorex debonisi*, L. Oligocene**														
SHM-CP 234	NYP			4.16	1.52	4.21	1.72	4.9	2.7	3.31	2	2.14	1.47	
SHM-CP 677	NYP	2.02	1.6	3.54	1.4	4	1.7	4.75	2.45	3.05	1.98	1.96	1.5	8.51
SHM-CP 327	NYP					3.67	1.73	4.31	2.36	2.72	1.8			
***P.* cf. *soricinoides*^{1}, E. Miocene**														
SMNS 44733	Ulm-West							3.6	1.9	2.5	1.71			7.9
SMNS 44738	Ulm-West					2	1.26	3.67		2.64	1.74			
SMNS 44739	Ulm-West					2.13	1.46	4	2.35	2.98	2.05			
SMNS 44740	Ulm-West			1.26	1.04									
SMNS 44742.1	Ulm-West			1.29	1.05									
SMNS 44742.2	Ulm-West					2	1.35							
SMNS 44742.3	Ulm-West											1.84	1.41	
coll. Wann. UW2	Ulm-West					2.15	1.37	3.66	2.24	2.77	1.94	1.79	1.39	7.85
***P. styriacus*, M. Miocene**														
JG 1480, holotype^{2}	Schönegg							3.9	2.2	2.9	2			
NHMW^{2}	Voitsberg					2.4	1.6	3.8	2.3					
NMB no number^{3}	Rümikon							3.52	2.66					
***P. germanicus*, M.-L. Miocene**														
Type^{4}	Viehhausen, Aumeister, Günzburg	2.1	1.2					3.8-4.8	2.3-2.4					
Hambach material^{5}	Hambach					2.28	1.49	3.8-4.39	2.24-2.5	2.54-2.93	1.96-2.16	2.03-2.21	1.53-1.72	
MF/2141/1^{6}	Belchatow							3.95	2.28					
MF/2141/3^{6}	Belchatow									2.95	2.23			
MF/2141/4^{6}	Belchatow											2.75	1.76	
BSP 1980 IX 232^{7}	Massendorf					2.41	1.37							
BSP 1980 IX 223^{7}	Massendorf							3.77	2.63					
BSP 1980 IX 224^{7}	Massendorf							3.77						
BSP 1980 IX 226^{7}	Massendorf									2.63	1.96			
BSP 1980 IX 227^{7}	Massendorf									2.74				
BSP 1980 IX 228^{7}	Massendorf									2.66	2.13			
BSP 1980 IX 229^{7}	Massendorf									2.48	2.07			
BSP 1980 IX 230^{7}	Massendorf											1.63		
BSP 1980 IX 231^{7}	Massendorf											1.78		
***P.* aff. *germanicus*^{8}, M. Miocene**														
1997z0007/0002/1	Oberdorf 4						1.4							
1997z0007/0002/5	Oberdorf 4							3.81	20.7					
1997z0007/0002/6	Oberdorf 4									2.49	1.85			
1997z0007/0002/7	Oberdorf 4											2.21	1.52	
***P.* cf. *germanicus*^{9}, M. Miocene**														
no number	Vermes 1					2.62	1.62							
no number	Vermes 1											2.14	1.56	
***P. schaffneri*, L. Miocene**														
NMB Al. 149, holotype^{3}	Anwil	1.76				3.12	1.52	5.23	2.88	2.64	2.44	2.4	1.76	

Specimen	Locality	Measurements												
		i2		p3		p4		m1		m2		m3		Lm 1-3
		L	w	L	w	L	w	L	wmax	L	wmax	L	wmax	
MAFI V20516[10]	Rudabánya					2.34	1.67	4.6	2.79					
MAFI V20517[10]	Rudabánya					2.44	1.9							
MAFI V 20579[10]	Rudabánya											2.38	1.74	
MAFI V 20580[10]	Rudabánya											2.14	1.59	
***P.* aff. *schaffneri*[11], L. Miocene**														
BSP 1973 XIX 84	Hammerschmiede									2.76	2.17			
BSP 1973 XIX 85	Hammerschmiede											2.1	1.55	
***P. evolutus*[12], L. Miocene**														
2004z0182/0002	Schernham			2.15	1.67									
2004z0182/000	Schernham					3.04	2.21							
2004z0182/0000	Schernham					2.87	2.18							
2004z0182/0003	Schernham					2.84	2.02							
2004z0182/0004	Schernham							5.31	3.11					
2004z0182/0005	Schernham									3.28	2.69			
2004z0182/0000	Schernham									3.35				
2004z0183/0001	Götzendorf 1-6							5.19	2.9					
2004z0183/0000	Götzendorf 5								2.72					
2004z0183/0000	Götzendorf 1											2.31	1.84	
***P. roosi*[13], L. Miocene**														
MNHM PW2002/10005-LS	Eppelsheim							4.92	2.72	3.20	2.28			
***P. martinii*[14], L. Oligocene**														
SMF 2005/320	Oberleichtersbach									2.20	1.80			
SMF 2005/317-319, 321												1.80	1.20	
***P. aydarlensis*[15], M. Miocene**														
KE-AktI-366	Aktau Mountains									2.90	2.10			
KE-AktI no number	Aktau Mountains											2.16		
***P. coloradensis*[16], E. Miocene**														
KU specimens	Quarry A, Martin Canyon Fm	1.5	1	1.8	1.2	2.3-2.50	1.3-1.6	3.9-4.0	2.5-2.6	2.7-3.1	2.2-2.5			8.5
***P.* cf. *coloradensis*[17], E. Miocene**														
USNM 475857	Pollack Farm LF							3.8	2.3					
***Plesiosorex greeni*[18], E. Miocene**														
UNSM 200031	UNSM Coll. Loc. BX-7							4.8	2.5	2.8	2.3			
***P. latidens*[19], M. Miocene**														
UCMP 29603, holotype	Esmeralda Fm, Fish Lake Valley					1.8				3	2.4	2.5	1.7	9
***P. donroosai*[20], M. Miocene**														
SDSM 8537, holotype	Feyereisen Gap, Springer LF					3	2.15	5.5	3.7	4.5	3.25			11.8
***P. obfuscatus*[21], M. Miocene**														
SDSM 8669	BBQII, Rosebud Fm					1.35	1	2.3	1.35					
SDSM 8670 (= 11 m1)	BBQII, Rosebud Fm							2.1-2.3	1.2-1.5					
SDSM 8671 (= 11 m2)	BBQII, Rosebud Fm									1.75-2.09	1.09-1.38			
SDSM 8672 (cf.) (= 11 m2)	BBQII, Rosebud Fm									1.45-1.62	0.99-1.20			

rooted p3 (in *Butselia* Quinet & Misonne, 1965, *Ernosorex*, *Siamosorex* n. gen., and *Plesiosorex* Pomel, 1848, except in some species such as *P. soricinoides*; Viret 1946: fig. 1), the i2, not the i1, enlarged and caniniform, molars that decrease strongly in size towards the rear and that have a relatively taller trigonid and more reduced entocristid, a posterior mental foramen below p4 (at least primitively in plesiosoricids), while it is below m1 or m2 in true shrews (Lopatin 2006), a rounded coronoid process tip unlike the typically acute process of the Soricidae, including the earliest members such as *Soricolestes* Lopatin, 2002. Plesiosoricids differ from the Nyctitheriidae in the structure of p4, which is semimolariform, the reduction of the hypoconulid in the molars, and the strong reduction in size of molars from m1 to m3.

COMPARISONS (TABLES 1; 2)

According to some recent classifications, the Plesiosoricidae includes six genera: *Pakilestes* Russell & Gingerich, 1981, *Ernosorex*, *Butselia*, *Pseudoneurogymnurus* Gureev, 1979, *Ordolestes*, Lopatin, 2006, and the type genus *Plesiosorex* (= *Meterix* Hall, 1929 = *Hibbarderix* Martin & Green, 1984; see Gunnell *et al.* 2008). Except for the type genus *Plesiosorex*, these taxa are known only from a few fragmentary dentitions. The genus *Ernosorex*, who was originally assigned to the Soricidae, then to the Changlelestidae Tong & Wang, 1993. It was then assigned to the Plesiosoricidae in e.g., McKenna & Bell (1997), followed by Lopatin (2006: S367), who still recognized the Changlelestinae as a basal subfamily of the Erinaceidae. It must be noted that the assignement of *Pakilestes lathrius* Russell & Gingerich, 1981, *Pseudoneurogymnurus zhchikvadze* Gureev, 1979, and *Plesiosorex obfuscatus* (Martin & Green, 1984) to the Plesiosoricidae, being not based on non-ambiguous morphological features, remains to be confirmed (R. Ziegler pers. comm.).

The two species of *Pseudoneurogymnurus* (*P. schevyrevii* Gureev, 1979 and *P. zhchikvadze* Gureev, 1979), Konurkura Formation, Zaysan Depression, Kazakhstan (middle Eocene; Gabunia & Chkhikvadze 1997) are known from isolated upper teeth and the m2 (Gureev 1979). The author does not provide a description, but the dental measurements indicate that these species have a proportionally much wider m2 than in *Siamosorex debonisi* n. gen., n. sp. Although the size of the species of *Pseudoneurogymnurus* is not easy to compare based on a single isolated tooth, it is worth noting that they have the smallest m2 in the family Plesiosoricidae (see Tables 1; 2), suggesting either a more reduced m2 relative to the other teeth or an overall more reduced body size than in other plesiosoricids.

Pakilestes lathrius Russell & Gingerich, 1981 is known from a right lower molar, probably an m1, the trigonid of a left ?m2, and possibly a p4 from Kohat, Kuldana Formation, Pakistan (early middle Eocene; Russell & Gingerich 1981; Gingerich 2003). This species shares some features with our material, such as molars with a short talonid on which cuspids are low, approximately of equal height, and poorly developed. However, besides its much smaller size (Table 1), *P. lathrius* differs from *S. debonisi* n. gen., n. sp. in having much less elongated teeth, a p4 with a more developed talonid, an m1 with a lower angle between the para- and protocristid, a wider talonid, and a cristid obliquid that meets the distal surface of the trigonid more lingually.

Ernosorex jilinensis Wang & Li, 1990 is known only by its holotype, a fragmentary mandible with i1-2, c, p4-m1 from the middle Eocene of Member III, Huadian Formation, Jilin Province, China (Wang & Li 1990). The m1 of this species is approximately half the length of that of *Siamosorex debonisi* n. gen., n. sp. (Table 1); its body size was estimated to approximately 40 g (Lopatin 2006: table 46). *Ernosorex* differs from *Siamosorex* in many features: lower incisors having totally different proportions, with an enlarged i1 and a reduced i2, both with accessory cusplets; much wider p4 and m1; absence of metaconid in p4; m1 talonid much wider than the trigonid and proportionally much longer, with a distinct entoconid and hypoconid; m2 possibly wider than m1. The proportions of the incisors, in particular the presence of an enlarged i1 instead of an enlarged i2, differ markedly from the condition observed in other plesiosoricids, which raises questions about the familial assignment of *Ernosorex jilinensis*. It is worth to know that Tong & Wang (1993) included *Ernosorex* in the family Changlelestidae. While they considered it to belong to the Soricomorpha, Lopatin (2006) placed this family as a basal family of the Erinaceidae (Lopatin 2006: fig. 59).

Butselia biveri Quinet & Misonne, 1965 is based on upper molars (M1 and M2) from the early Oligocene site of Hoogbutsel, Belgium (Quinet & Misonne 1965); recent fieldwork in a new locality close to Hoogbutsel, Boutersem TGV (Smith 2004), has yielded lower teeth that may allow a better comparison with our material when published (R. Smith pers. comm.). This species is otherwise reported from at least three levels in the Yarmouth-Bouldnor Cliff locality (Isle of Wight, England), Hamstead Member, Bouldnor Formation, England (early Oligocene, MP 21; Hooker *et al.* 2004: fig. 1). One of these records is from the lower Hamstead Member, belonging to pre-Grande Coupure faunas; the other two records are from the upper Hamstead Member representing post-Grande Coupure faunas; the Grande Coupure is a turnover event in European faunas that took place at, or soon after, the Oligocene-Eocene boundary (see Hooker *et al.* 2004). A part of these remains is illustrated and partly described in Butler (1972: figs 1, 4a), but *Butselia biveri* from the Isle of Wight remains poorly known. The material figured in Butler (1972) represents isolated teeth (M2, p4, m1 trigonid, m2) and an incomplete hemimandible with m2 from different individuals. Besides being smaller, *B. biveri* differs from *S. debonisi* n. gen., n. sp. in having a p4 with a protoconid proportionally taller relative to its length, a longer and more developed paraconid, and a larger metaconid; molar trigonids more closed, which results from a metaconid sets closer to the paraconid; in m2, the metaconid is lower than the protoconid (subequal in *S. debonisi* n. gen., n. sp.).

Ordolestes ordinatus Lopatin, 2006 is based on material from the early Eocene of Tsagan-Khushu, Mongolia (Lopatin 2006): an isolated m1 (holotype), 3 isolated m1s, a fragmentary mandible with m2-3, and an m1 previously assigned to cf. *Hyracolestes* (Russell & Dashzeveg 1986: text-fig. 9d, e). This species, the body size of which was estimated to approximately 50 g (Lopatin 2006: table 46), is much smaller than *S. debonisi* n. gen., n. sp. (Table 1). In addition, it differs in showing a lesser marked size decrease from m1 to m3 (with especially a much less reduced m3) and in having an m1 protoconid taller relative to the tooth length, a metaconid more reduced (than the protoconid) in m2 and m3, and an incomplete cingulid on the buccal surface.

Plesiosorex is by far the best-known genus of plesiosoricids, although fossils remain extremely rare in small mammal assemblages (Ziegler 1999). It is represented by 13 species, ranging from the mid-Oligocene (MP 26) to the late Miocene (MN 10) in North America and Eurasia. Appendix 2 provides the age and distribution of these species and Table 2 lists dental measurements. Evolutionary trends in the genus include increasing size, displacement of the posterior mental foramen to a more posterior position, reduction of the ectocingulid, elongation of m1 trigonid, and increase in the sharpness of cusp(id)s and ridges (Franzen *et al.* 2003). This trend is therefore correlated with an increased cutting function. The Thai species clearly differs from *Plesiosorex* spp. in showing a much more developed cutting function in the dentition and in having a caniniform i2 not procumbent but vertical, with a deep longitudinal groove along the lingual surface, a double-rooted p3 (presumably plesiomorphic), a much more elongated and slender p4 with a more reduced metaconid, lower molars on which the talonid is relatively shorter and markedly narrower than the trigonid, with weakly defined hypoconid and entoconid, the latter being lower than the former. Additional distinctive features include the presence of a (posterior) mental foramen located beneath the posterior root of p4 (as in the Oligocene *Plesiosorex soricinoides*, but unlike the Miocene species of *Plesiosorex* in which this foramen is more posteriorly located).

Lopatin (2006) divided the Plesiosoricidae into two subfamilies, the Plesiosoricinae Winge, 1917 and the Butseliinae Quinet & Misonne, 1965. The morphology of *S. debonisi* n. gen., n. sp. agrees with the diagnosis of the subfamily Butseliinae (including *Butselia*, *Ordolestes* and *Pakilestes*), and differs from the Plesiosoricinae in its high and clearly detached metaconid in p4 and its reduced entoconid in the molars (the entoconid is taller than the hypoconid in the Plesiosoricinae).

DENTAL MORPHOLOGY AND DIET

The strong decrease in size from m1 to m3 and the emphasis on the m1 shear are typical of true carnivores (Carnivora), but the presence of a metaconid cuspid in a distolingual position in p4, a posterior mental foramen below p4, an enlarged i2, and an antemolariform i3 are unknown in taxa from this order. On the contrary, all the above-mentioned characters are found in plesiosoricid lipotyphlans (except *Ernosorex*, the i1 of which is enlarged). Among the most distinctive characters of *Siamosorex debonisi* n. gen., n. sp. are the development of p3 and p4 and the morphology and vertical orientation of the caniniform i2, which are convergent with many carnivorans. Antemolars are generally more reduced and less elongated in other plesiosoricids (*Plesiosorex*, *Pakilestes* and *Ernosorex*). In the best known genus *Plesiosorex*, the i2 is also enlarged, but it is always procumbent as in *P. coloradensis* (e.g., Wilson 1960: fig. 11a), *P. latidens* (e.g., Hall 1929: fig. 1f), *P. schaffneri* (Engesser 1972: fig. 7), *P. donroosai* (Green 1977: fig. 1), *P. greeni* (Martin & Lim 2004: fig. 1), and *P. soricinoides* (Blainville 1840: pl. 11).

The presence of a deep groove on the mesiolingual surface of the enlarged i2 is an autapomorphy of *S. debonisi* n. gen., n. sp. The precise function of such a groove is unknown, though it may be related to the diet of the animal. Its position, on the lingual side of a lower incisor, its extension, very probably along the entire tooth height (although its apex is missing), and its depth suggest that it could be related to a venom apparatus in which it would serve as a gutter for conducting poisonous saliva. Toxic saliva is rare in placental mammals. It is known only from a few species of Lipotyphla belonging to the shrew genera *Neomys* Kaup, 1829, *Blarina* Gray, 1838, and to the genus *Solenodon* Brandt, 1833. However, only the species of the latter genus display modified grooved incisors associated with venom delivery (Orr *et al.* 2007). In fossil mammals, there are only four published examples for which grooved teeth were related to venom delivery: the soricine *Beremendia fissidens* (Petényi, 1864) and *Dolinasorex glyphodon* Rofes & Cuenca-Bescós, 2009 from early Pleistocene sites located in the Sierra de Atapuerca, Spain (Cuenca-Bescós & Rofes 2007; Rofes & Cuenca-Bescós 2009), the pantolestid *Bisonalveus browni* Gazin, 1956 and an indeterminate mammal from the Palaeocene of Alberta, Canada (Fox & Scott 2005). But many extant mammals (primates, bats, carnivores) do have anterior grooved teeth (mostly canines), despite the fact that they are non-venomous taxa (Folinsbee *et al.* 2007; Orr *et al.* 2007: table 1). Inference of venom delivery in fossil taxa can therefore not be supported only based on the presence of grooved teeth. Nevertheless, at least two pieces of evidence support such an inference for *Siamosorex* n. gen., *Beremendia* Kormos, 1934, and *Dolinasorex* Rofes & Cuenca-Bescós, 2009: first, as in the extant *Solenodon* spp. (Orr *et al.* 2007; Folinsbee *et al.* 2007), the grooved teeth in these fossil taxa are the i2s; and second, these fossil taxa and *Solenodon* are phylogenetically related and belong to the soricomorph Lipotyphla. At any rate, this hypothesis remains to be confirmed by the presence of skeletal evidence usually associated to the presence of venom glands such as palatal or mandibular fossae. In addition we acknowledge that it is almost equally plausible that the incisor groove in *Siamosorex* n. gen. and, perhaps, *Beremendia* and *Dolinasorex* from Atapuerca, is not correlated to any particular diet or function, as in primates, suids, and hippos (Folinsbee *et al.* 2007).

Given the dental morphology of *Siamosorex debonisi* n. gen., n. sp., its diet probably included a relatively high proportion of small animals such as arthropods and small vertebrates. Based on m1 length, this species reached approximately the size of the smallest species of the carnivoran genus *Mustela* (*c.* 0.3 kg), being only marginally smaller than, e.g., the slender mongoose *Galerella sanguinea* (Rüppell, 1835) (0.35-0.9 kg; Taylor 1975).

PALEOBIOGEOGRAPHY

Except for *Plesiosorex aydarlensis* Kordikova, 2000 from the early-middle Miocene of Kazakhstan, the Asian species of the Plesiosoricidae are early to middle Eocene in age (*Pseudoneurogymnurus*, *Pakilestes*, *Ernosorex* and *Ordolestes*). The family therefore originated probably in Asia, *Ordolestes* from the early Eocene of Mongolia being the earliest known member. There is then a gap of some 10 million years before the family occurs in western

Europe, with *Butselia* from the early Oligocene of England and Belgium and *Plesiosorex* from the mid-Oligocene to the late Miocene. *Plesiosorex* was quite a successful genus, with an extended stratigraphic and geographical distribution, dispersing to North America during the early Miocene. Evidence of this migration event could be represented by *P. aydarlensis* from Kazakhstan. European plesiosoricids were long seen as a part of the many taxa that dispersed from Asia into Europe, an event known as the Grande Coupure. The Asian origin of European plesiosoricids, in particular *Butselia*, was, however, recently debated, based on remains of *Butselia* found from pre-Grande Coupure deposits in England (Hooker *et al.* 2004). The discovery of a plesiosoricid, a possible relative to *Butselia*, *Ordolestes* and *Pakilestes* (Butseliinae), from the late Oligocene of Thailand, could result in a more complicated paleobiogeographical scenario. The morphology of *Siamosorex debonisi* n. gen., n. sp. is so distinct from that of the other butseliines that its origin remains unclear. *Butselia biveri* could be the closest relative of the Thai species, but the lower dentition of this species is thus far too poorly known to support such a relationship. The Plesiosoricidae remains a poorly known family. The fragmentary nature of the fossil record of most of the included taxa, with the notable exception of the type genus of the family *Plesiosorex*, prevent us from making a detailed phylogenetic analysis of this family. In addition, taxa such as, e.g., *Ernosorex*, the incisor morphology of which strongly differs from that of the other plesiosoricids, could prove to belong to another lipotyphlan group when better known.

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APPENDIX 1

Revised faunal list of mammals from Krabi; for other vertebrates, taxa new to add to the faunal list of Ducrocq *et al.* (1995), consist of three testudinoid turtles (Claude *et al.* 2007). Assignment of *Wailekia* to the Sivaladalipdae is based on Qi & Beard (1998), that of *Siamopithecus* to the Amphipithecidae on Kay (2005). The presence of true Mustelidae and Procyonidae (Ducrocq *et al*. 1995) in the Krabi fauna is not confirmed by a preliminary analysis of the material by one of us (SP). This analysis also allows us to distinguish at least 10 different species of Arctoidea. Egi *et al*. (2008) recently reported the presence of one mustelid and one or two taxa related to *Cephalogale*; the record of a true mustelid from late Eocene sediments remains to be confirmed, however.

Dermoptera (1 species)
  Cynocephalidae
    – *Dermotherium major* Ducrocq, Buffetaut, Buffetaut-Tong, Jaeger, Jongkanjanasoontorn & Suteethorn, 1992

Insectivora (1 species, possibly 2)
    – Family indet. 1
    – ?Family indet. 2

Megachiroptera (1 species)
    – Pteropodidae gen. et sp. indet. (see Ducrocq *et al.* 1993)

Primates (6 species)
  Adapiformes
    – *Muangthanhinius siami* Marivaux, Chaimanee, Tafforeau & Jaeger, 2006
  Sivaladapidae
    – *Wailekia orientale* Ducrocq, Jaeger, Chaimanee & Suteethorn, 1995
    – *Wailekia* sp. (= cf. *Hoanghonius* sp. in Suteethorn *et al.* 1988; see Ducrocq *et al.* 1995)
  Amphipithecidae
    – *Siamopithecus eocaenus* Chaimanee, Suteethorn, Jaeger & Ducrocq, 1997 (= Anthropoidea gen. et sp. nov. *in* Ducrocq *et al.* 1995)
    – ?Amphipithecinae indet. (see Ducrocq *et al.* 2006)
  Family indet.
    – Gen. et sp. indet. cf. Tarsiidae or Omomyidae (see Ducrocq *et al.* 2006)

Rodentia (5 species)
    – *Baluchimys krabiense* Marivaux, Benammi, Ducrocq, Jaeger & Chaimanee, 2000 (= Ctenodactyloidea indet. *in* Ducrocq *et al.* 1995)
    – Baluchimyinae sp. nov.
    – Sciuridae indet. (= Family indet. 1 in Ducrocq *et al.* 1995)
    – Anomaluroidea indet. (= Family indet. 2 *in* Ducrocq *et al.* 1995)
    – Ischyromyidae indet.

Artiodactyla (13 species)
  Tayassuidae
    – *Egatochoerus jaegeri* Ducrocq, 1994
  Suidae
    – *Siamochoerus banmarkensis* Ducrocq, Chaimanee, Suteethorn & Jaeger, 1998 (= Suidae gen. et sp. nov. *in* Ducrocq *et al.* 1995)
  Entelodontidae
    – Entelodontidae gen. et sp. indet.
  Lophiomerycidae
    – *Krabimeryx primitivus* Métais, Chaimanee, Jaeger & Ducrocq, 2001 (= Lophiomerycidae gen. et sp. nov. *in* Ducrocq *et al.* 1995)
  Tragulidae
    – *Archaeotragulus krabiensis* Métais, Chaimanee, Jaeger & Ducrocq, 2001 (= ?Tragulidae gen. et sp. nov. *in* Ducrocq *et al.* 1995)
  ?Tragulidae
    – *Krabitherium waileki* Métais, Chaimanee, Jaeger & Ducrocq, 2007
  Helohyidae
    – *Progenitohyus thailandicus* Ducrocq, Chaimanee, Suteethorn & Jaeger, 1997
  Anthracotheriidae
    – *Siamotherium krabiense* Suteethorn, Buffetaut, Helmcke-Ingavat, Jaeger & Jongkanjanasoontorn, 1988
    – *Anthracotherium chaimanei* Ducrocq, 1999
    – *Anthracokeryx thailandicus* Ducrocq, 1999
    – *Anthracohyus* sp. (see Ducrocq 1999; = Anthracotheriinae gen. et sp. nov. Ducrocq, 1995 *in* Ducrocq *et al.* 1995)
    – *Bothriogenys orientalis* Ducrocq, 1999
    – *Atopotherium bangmarkensis* Ducrocq, Chaimanee, Suteethorn & Jaeger, 1996 (= ?Agriochoeridae gen. et sp. nov. *in* Ducrocq *et al.* 1995)

Perissodactyla (2 species)
  Rhinocerotidae
    – ?*Guixia* sp. cf. *G. simplex* (see Antoine *et al.* 2003) (= ?Hyracodontidae gen. et sp. nov. *in* Ducrocq *et al.* 1995)
    – *Siamolophus krabiense* Ducrocq, Chaimanee, Jaeger & Métais, 2006 (= Helaletidae gen. et sp. nov. *in* Ducrocq *et al.* 1995)

Carnivora (13 species)
  Nimravidae
    – *Nimravus* sp. cf. *N. intermedius* (see Peigné *et al.* 2000)
    – *Hoplophoneus* sp. (see Peigné *et al.* 2000)
  Miacidae
    – *Miacis thailandicus* Ducrocq, Buffetaut, Buffetaut-Tong, Helmcke-Ingavat, Jaeger, Jongkanjanasoontorn & Suteethorn, 1992
    – Arctoidea indet. 1 to 10

APPENDIX 2

Species of *Plesiosorex* Pomel, 1848, age and distribution.

Plesiosorex soricinoides (Blainville, 1840), type species: Chaufours (= Chauffours, type locality, France, latest Oligocene, MP 29; Blainville 1840) (Hugueney (1997) noticed that the type is from Cournon, MP 28-29, while Viret [1940] stated that it is from either Cournon or Chauffours), Marseille-Saint-André (France, mid-Oligocene, MP 26; Viret 1946), Ulm-Westtangente (cf., Germany, early Miocene, MN 2; Ziegler 1990), Chaveroche (= Chavroches, cf., France, early Miocene, MN 2; Viret 1940).

Plesiosorex styriacus (Hofmann, 1892): Schönegg (type locality, Austria, early Miocene, MN 4; Thenius 1949), Voitsberg (Austria, early Miocene, MN 4; Thenius 1949), Rümikon (illustration only, Switzerland, middle Miocene, MN 5; Engesser 1979: plate 5, fig. a, an M1, not an m1 as indicated), Oberdorf 3 (cf., Austria, early Miocene, MN 4; Ziegler 1998).

Plesiosorex germanicus (Seemann, 1938): Viehhausen (type locality, Germany, middle Miocene, MN 5), Aumeister (Germany, late Miocene, MN 9), Günzburg (Germany, middle Miocene, MN 5) (Seeman 1938), Belchatow (Poland, middle Miocene, MN 5; Rzebik-Kowalska 1993), Langenau 1 (Germany, early Miocene, MN 4; Sach & Heizmann 2001), Hambach 6C (Germany, middle Miocene, MN 5; Ziegler & Mörs 2000), Vermes (cf., Switzerland, middle Miocene, MN 5; Engesser *et al.* 1981), Oberdorf 4 (aff.; Germany, early Miocene, MN 4; Ziegler 1998).

Plesiosorex schaffneri Engesser, 1972: Anwil (type locality, Switzerland, middle Miocene, MN 7/8; Engesser 1972), Rudabánya (Hungary, late Miocene, MN 9; Ziegler 2005), Hammerschmiede (aff., Germany, late Miocene, MN 9; Mayr & Fahlbusch 1975).

Plesiosorex aydarlensis Kordikova, 2000: Aktau Mountains (type locality, Kazakhstan, early-middle Miocene, MN 4/5; Kordikova 2000).

Plesiosorex roosi Franzen, Fejfar & Storch, 2003: Eppelsheim (type locality, Germany, late Miocene, MN 9; Franzen *et al*. 2003).

Plesiosorex evolutus Ziegler, 2006 from Schernam (type locality, Austria, late Miocene, MN 10; Ziegler 2006), Götzendorf (Austria, late Miocene, MN 10; Ziegler 2006).

Plesiosorex martinii Engesser & Storch, 2008: Oberleichtersbach (type locality, Germany, late Oligocene, MP 30; Engesser & Storch 2008).

Plesiosorex sp. is also recorded from Grosslappen (Germany, late Miocene, MN 9, partly described in Engesser 1979), Stixneusiedl (Austria, late Miocene, MN 10; Ziegler 2006), La Chaux 7 (Switzerland, early Miocene, MN 2; Weidmann *et al.* 2003), Messen (Switzerland, early Miocene, MN 2; Engesser 1976), Boudry-La Fabrique (Switzerland, late Oligocene, MP 28; Mojon *et al.* 1985), Boudry I (Switzerland, early Miocene, MN 2; Mojon *et al.* 1985), Alsótelekes (Hungary, late Miocene; Mészáros 1999), and Bayraktepe (Turkey, late Miocene, MN 9; Engesser & Ziegler 1996).

Green (1977) proposed that *Meterix* Hall, 1929 is a junior synonym of *Plesiosorex* Pomel, 1848, a suggestion that has been followed by recent authors (McKenna & Bell 1997; Gunnell *et al.* 2008). Thus *Plesiosorex* is the sole genus of the family present in the New World, with five species (see Gunnell *et al.* 2008 for a review of the distribution; and Martin & Lim 2004, for additional species): *P. latidens* (Hall, 1929), *P. coloradensis* Wilson, 1960, *P. donroosai* Green, 1977, *P. obfuscatus* (Martin & Green, 1984), and *P. greeni* Martin & Lim, 2004. *Plesiosorex coloradensis* is the best known North American species of the genus. North American species of *Plesiosorex* range from the late Arikareean to the late Clarenfordian (mid-early to mid-late Miocene), with a possible extension to the late Hemingfordian (terminal Miocene) (Gunnell *et al.* 2008). The junior synonymy of *Hibbarderix* (including the species *Hibbarderix obfuscatus*) with *Plesiosorex* suggested by McKenna & Bell (1997) and Gunnell *et al.* (2008) remains to be confirmed, however, as *Hibbarderix obfuscatus* may belong to the Erinaceidae Fischer, 1817 (R. Ziegler pers. comm.).