New discoveries of hyaenodontids (Creodonta, Mammalia) from the Pondaung Formation, middle Eocene, Myanmar – paleobiogeographic implications

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ABSTRACT

The Pondaung fauna includes approximately 50 species of mammals, including five species of creodonts, of which four have been described. The best known species, *Kyawdawia lupina* Egi *et al.*, 2005, was recently described based on a fragmentary skull, heavily worn dentitions and postcranial material. On the basis of the Pondaung creodont taxa, previous phylogenetic analyses have suggested a paleobiogeographic Africa-Asia connection during the Eocene, hence a close phylogenetic relationship between Afro-Arabian and Southeast Asian taxa (so-called "Afro-Asian proviverrines" by previous authors). Here, we doubt the natural existence of such a clade on the basis of new hyaenodontid material discovered in the Pondaung Formation, including localities from which creodonts were previously unknown. The new material consists of well preserved, mostly unworn dental remains of two species: 1) *Kyawdawia lupina* documented here by teeth, or portions of teeth unavailable or poorly preserved in the hypodigm of this species; and 2) Hyaenodontidae sp. indet. Thanks to this material and to a direct study of a great number of hyaenodontids, we analysed the arguments supporting a relationship between Asian and African taxa. This relationship is not supported by our analysis due to: 1) previous character misinterpretations resulting partly from the poor preservation of the hypodigm; and 2) configuration of the data matrix in the previous phylogenetic analysis with important characters and taxa missing. Consequently, the alleged paleobiogeographic connection between Asia and Africa in the Eocene appears to be much less supported than previously thought.

KEY WORDS
Mammalia,
Creodonta,
Southeast Asia,
systematics,
paleobiogeography,
Africa-Asia relationships.

RÉSUMÉ

Nouvelles découvertes de hyaenodontidés (Creodonta, Mammalia) de la Formation Pondaung, Éocène moyen, Myanmar : implications paléobiogéographiques.

La faune de Pondaung inclut environ 50 espèces de mammifères, comprenant cinq espèces de créodontes dont quatre ont été décrites. L'espèce la mieux connue, *Kyawdawia lupina* Egi *et al.*, 2005, a été récemment décrite sur du matériel crânien fragmentaire, des dentures très usées et des éléments post-crâniens. En se basant sur ces créodontes de Pondaung, une récente analyse phylogénétique suggère une connexion paléobiogéographique entre l'Afrique et l'Asie au cours de l'Éocène, donc une relation de proche parenté phylogénétique entre les créodontes d'Afro-Arabie et ceux d'Asie du Sud-Est (d'où le nom « Afro-Asian proviverrines » donné à cet ensemble par de précédents auteurs). Dans cet article, nous remettons en question l'existence naturelle de ce clade sur la base d'un nouveau matériel de créodontes découvert dans la Formation Pondaung, notamment dans des localités qui n'en avaient pas encore livré jusqu'à présent. Ce nouveau matériel inclut les restes dentaires très bien préservés de deux espèces : 1) *Kyawdawia lupina* représenté par des dents complètes ou fragmentaires qui n'étaient pas ou mal documentées dans l'hypodigme de l'espèce ; et 2) Hyaenodontidae sp. indet. Grâce à ce matériel et à l'étude directe d'un grand nombre de Hyaenodontidae, nous avons analysé les arguments en faveur d'une relation de parenté proche entre les créodontes d'Afrique et ceux d'Asie. Cette relation n'est pas confirmée en raison : 1) d'une mauvaise interprétation des caractères, résultant en partie de la mauvaise conservation du matériel hypodigme ; et 2) de l'absence de caractères et/ou de taxons clés dans la matrice de données de l'analyse phylogénétique discutée. En conséquence, la prétendue connexion paléobiogéographique entre l'Asie et l'Afrique à l'Éocène apparaît bien moins soutenue que précédemment supposé.

MOTS CLÉS
Mammalia,
Creodonta,
Asie du Sud-Est,
systématique,
paléobiogéographie,
relations Afrique-Asie.

INTRODUCTION

The Pondaung Formation of Central Myanmar is exposed in the Chindwin-Irrawaddy basins, and is characterized by a succession of marine and continental deposits. This formation is mainly composed of cyclic sequences of sandstones and variegated clays whose association suggests a fluvio-deltaic environment (Aung Naing Soe *et al.* 2002). The Pondaung Formation is lithologically divided into a "Lower Member" that consists of coarse-grained sandstones, siltstones, and conglomerates, and an "Upper Member", composed of variegated clays and sandstones. Most of the mammal fossils have been collected from the lower half of the "Upper Member" (Aung Naing Soe 2004). In its north-south section, the Pondaung Formation is sandwiched between the overlying late Eocene Yaw Formation and the marine clays of the underlying early middle Eocene Tabyin Formation (Aye Ko Aung 1999). A middle-late Eocene age of the Pondaung Formation was previously established on the basis of faunal correlations with Chinese and North African faunas (Holroyd & Ciochon 1994), but recent geochronological evidence has definitely attributed the mammal-bearing strata to the late middle Eocene. Both fission track analyses of zircon grains from a tuff bed in the Paukkaung section (Fig. 1) and paleomagnetic studies of the Bahin section (Fig. 1) suggest an age of about 37 Ma (Benammi *et al.* 2002; Tsubamoto *et al.* 2002). Twenty seven fossiliferous localities ("Kyitchaung" in Myanmar language) have been recognized in the Pondaung Formation and they are distributed in three areas: Pangan, Bahin, and Mogaung (Fig. 1). According to Aung Naing Soe (2004), the mammalian-bearing sediments exposed in these three areas were probably contemporaneously deposited, although some authors (e.g., Hla Mon 1999) suggested that fossil localities in Mogaung might be stratigraphically older than those in Bahin and Pangan.

The Pondaung fauna has long been known mainly for its abundant fossil mammals such as artiodactyls (e.g., Pilgrim 1928; Ducrocq *et al.* 2000; Métais *et al.* 2000; Métais 2002; Tsubamoto *et al.* 2005), perissodactyls (Colbert 1938), rodents (Dawson *et al.* 2003; Marivaux *et al.* 2005), creodonts (see below), and especially primates (Pilgrim 1927; Colbert 1937; Ciochon *et al.* 1985, 2001; Jaeger *et al.* 1998, 1999; Takai *et al.* 2001; Shigehara *et al.* 2002), which make it one of the most diversified Eocene land mammal faunas of South Asia. The most recently published list of the Pondaung fauna includes nearly 50 species of mammals (Tsubamoto *et al.* 2005: table 2).

The present contribution deals with the hyaenodontid Creodonta, which represents the single most diversified mammalian order of predators in Pondaung. Although these are well documented in the Eocene of North America (Gunnell 1998) and Europe (Morlo & Habersetzer 1999), the fossil record of hyaenodontid creodonts – with the exception of the subfamily Hyaenodontinae Leidy, 1869 (genus *Hyaenodon* Laizer & Parieu, 1838 and close relatives) of Kazakhstan and Mongolia (Dashzeveg 1964, 1985; Lange-Badré & Dashzeveg 1989; Lavrov 1996, 1998; Morlo & Nagel 2006) – remains poor in Asia throughout the stratigraphic distribution of the order, and in particular during the Eocene (see, e.g., Russell & Zhai 1987; Kumar 1992; Egi *et al.* 2005). Besides hyaenodontines, Asian Eocene hyaenodontid creodonts include taxa previously assigned to *Pterodon* Blainville, 1839, Hyainailourinae Pilgrim, 1932 (emended senior synonym of Pterodontinae Polly, 1996). Now, none are placed in that genus and most are no longer interpreted as hyainailourines: "*Pterodon*" *exploratus* Dashzeveg, 1985 was regarded to be a junior synonym of *Hyaenodon incertus* Dashzeveg, 1985 by Morlo & Nagel (2006), "*Pterodon*" *hyaenoides* Matthew & Granger, 1925 and "*Pterodon*" *rechetovi* Dashzeveg, 1985 were assigned to Hyaenodontinae by Lavrov (1996, 1998), who also erected the genus *Neoparapterodon* on the latter species. The only species still thought to belong to Hyainailourinae is "*Pterodon*" *dahkoensis* Chow, 1975, for which Egi *et al.* (2007) erected the new genus *Orienspterodon*. While Lavrov (1996, 1998) interprets it on its uniqueness among all hyaenodontids, for Holroyd (1999) and Egi *et al.* (2003, 2007) it represents the most plesiomorphic hyainailourine genus, thereby ignoring *Francotherium* Rich, 1971 from MP 10 of Mancy that was assigned to Hyainailourinae by Polly (1996).

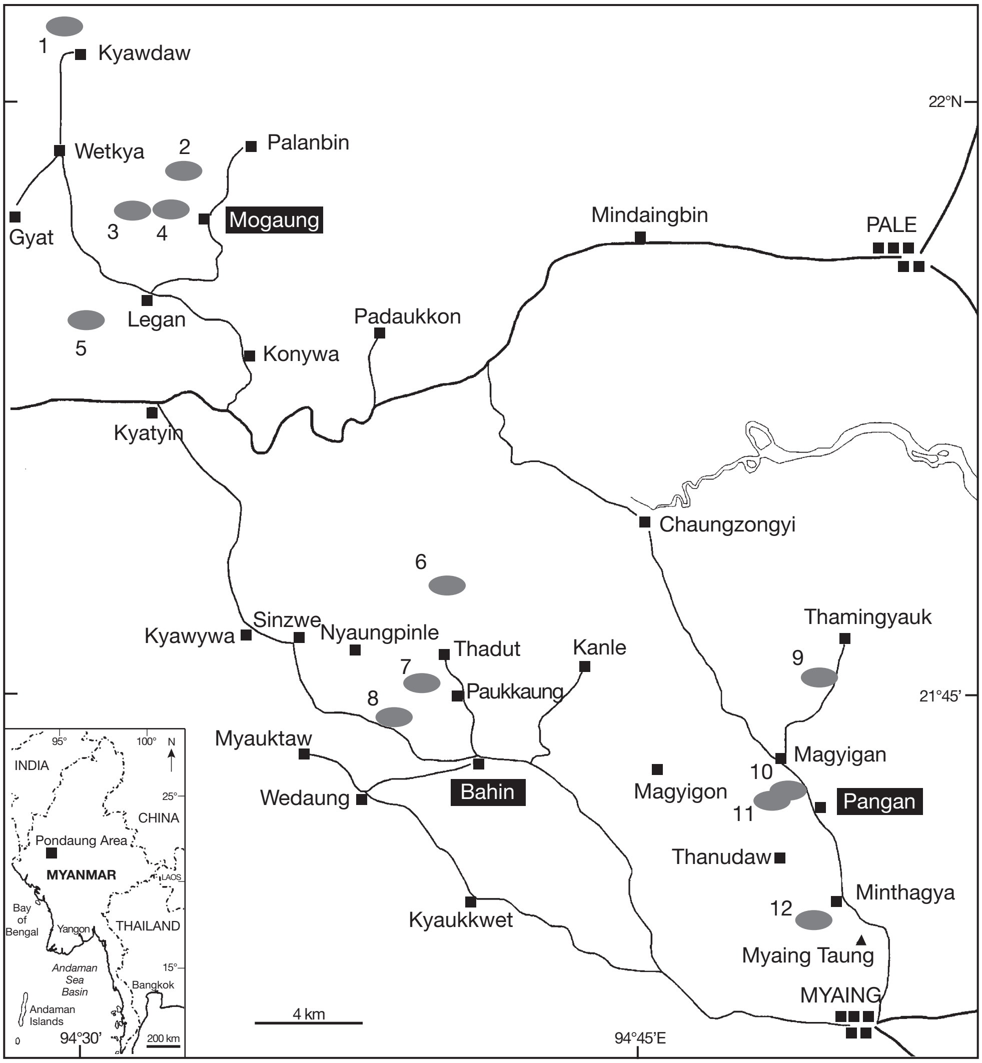

FIG. 1. — Geographical map of the Pondaung area (Myanmar) showing the vertebrate fossil localities in the Pondaung Formation that have yielded creodont material; in these names, "Kyitchaung" means "locality" in Myanmar language: **1**, Kyawdaw Kyitchaung (Kdw); **2**, Thandaung Kyitchaung (Tdg); **3**, Kyaukmagyi Kyitchaung (Kmi); **4**, Lema Kyitchaung (Lma); **5**, UCMP V83106; **6**, fossiliferous site 2 km N of Thadut (*Oriensopterodon*); **7**, Paukkaung Kyitchaung (Pk 2); **8**, Yarshe Kyitchaung (Yse); **9**, Thamingyauk Kyitchaung (Tmk); **10**, Pangan Kyitchaung (Pgn); **11**, Taungnigyin Kyitchaung (= Pangan 2; Pgn 2); **12**, Myinthagya Kyitchaung (Mta). Modified after Aung Naing Soe (2004).

Among other hyaenodontid subfamilies, the Limnocyoninae Wortman, 1902 is represented in the Asian Eocene by *Prolimnocyon chowi* Meng, Zhai & Wyss, 1998 from the Bumbanian (latest Paleocene or earliest Eocene; see Bowen *et al.* 2005). Other citations of middle Eocene Asian limnocyonines are *Prolaena parva* Xu, Yan, Zhou, Han & Zhang, 1979 and "*Thinocyon*" *sichowensis* Chow, 1975, with the latter probably not being a creodont at all (see Morlo & Gunnell 2003). Also recorded is "*Limnocyon* sp." from the Shanghuang fauna (Tsubamoto *et al.* 2004).

Proviverrine hyaenodontid creodonts are very rarely recognized in the Asian Eocene. Slightly younger in age than *Prolimnocyon chowi* are *Arfia langebadreae* and ?*Prototomus* sp., described by Lavrov & Lopatin (2004). From the early to middle Eocene, *Paratritemnodon* Ranga Rao, 1973 from the Indian subcontinent is well known (Ranga Rao 1973; Kumar 1992; Thewissen *et al.* 2001). Also, the first Asian species of *Sinopa* is of late middle Eocene age (Schaal *et al.* in press). Other citations of Asian proviverrines were tentative: ?*Tritemnodon* sp. from Hetaoyuan (Gao Yu 1976; Egi *et al.* 2004) in fact, belongs to the hyaenodontine *Propterodon* Martin, 1906 (Tong & Lei 1986). Questionable *Sinopa* sp. is cited from the Hetaoyuan fauna (Gao Yu 1976; Tong & Lei 1986) and the Naran fauna, Naran-Bulak Formation (Tsubamoto *et al.* 2004).

According to Tsubamoto *et al.* (2005: table 2) and Egi *et al.* (2007), five taxa of creodonts are present in the Pondaung fauna, but only four species have been described so far (Egi & Tsubamoto 2000; Egi *et al.* 2001, 2004, 2005, 2007), including new genera and species: *Yarshea cruenta* Egi et al., 2004, *Kyawdawia lupina* Egi *et al.*, 2005 (cited as Proviverrinae gen. et sp. nov. 1 or 2 in Tsubamoto *et al.* 2005: table 2), *Orienspterodon dahkoensis* (Chow, 1975), and Proviverrinae indet. Here, we describe dental remains of a new, large species of hyaenodontid creodont, and new dental remains of the hyaenodontid *Kyawdawia lupina* from the Pondaung Formation discovered by the French-Myanmar team during many successive field seasons since 1998. A part of the new material assigned to *K. lupina* comes from localities that had not previously yielded creodonts. The new remains represent mostly unworn teeth that reveal details partly obscured by the worn dentition of the hypodigm. The new material is significant in documenting the relatively great size variation of *Kyawdawia lupina* and allows a revision of the diagnosis of this rare hyaenodontid. We also re-assess a previously suggested paleobiogeographic scenario that implies an Africa-Asia connection during the Eocene.

ABBREVIATIONS AND TERMINOLOGY

Measurements were made to the nearest 0.1 mm; for upper teeth, measurements were made following the method illustrated in Lavrov (1996: fig. 3b). We follow Smith & Dodson (2003) for anatomical notation and orientation of dentitions.

Institutional abbreviations

AMNH	American Museum of Natural History, New York;
KU	Kyoto University;
NMM	National Museum of Myanmar, Yangon;
UCMP	University of California, Museum of Paleontology, Los Angeles;
UM	University of Michigan Museum of Paleontology, Ann Arbor.

SYSTEMATICS

Order CREODONTA Cope, 1875
Family HYAENODONTIDAE Leidy, 1869

Subfamily PROVIVERRINAE Schlosser, 1886

The specimens described here are classified as proviverrines, although this stem group is at least paraphyletic (Polly 1996; Morlo & Gunnell 2003) if not subsuming completely unrelated clades. Proviverrines lack the apomophies of other hyaenodontid subfamilies, with the Hyainailourinae and the Hyaenodontinae both differing by, e.g., the lack or strong reduction of metaconid on m3 and reduction of the talonid on the lower molars (see Polly 1996). However, separation of subfamilies is not always clear, which is why single taxa have been moved from one to another (e.g., *Dissopsalis*, see Polly 1996).

Kyawdawia lupina Egi, Holroyd, Aung Naing Soe, Takai & Ciochon, 2005

HOLOTYPE. — NMMP-KU 0042, 0043, 0044, 0784, 0785, and 1661 (acronyms used by Egi *et al.* 2005): cranial and mandibular fragments with subcomplete permanent dentition and various incomplete postcranial bones (see Egi *et al.* 2005 for a precise description of the holotype). All of these specimens represent a single individual from Kyawdaw according to Egi *et al.* (2005). However we add here M3s, which are not listed in the holotype definition (these teeth belong to the type specimen NMMP-KU 0042; see Egi *et al.* 2005: fig. 1A, C) but in the description of the holotype dentition by Egi *et al.* (2005: 340).

TYPE LOCALITY. — Kyawdaw, Pondaung Formation, late middle Eocene of central Myanmar.

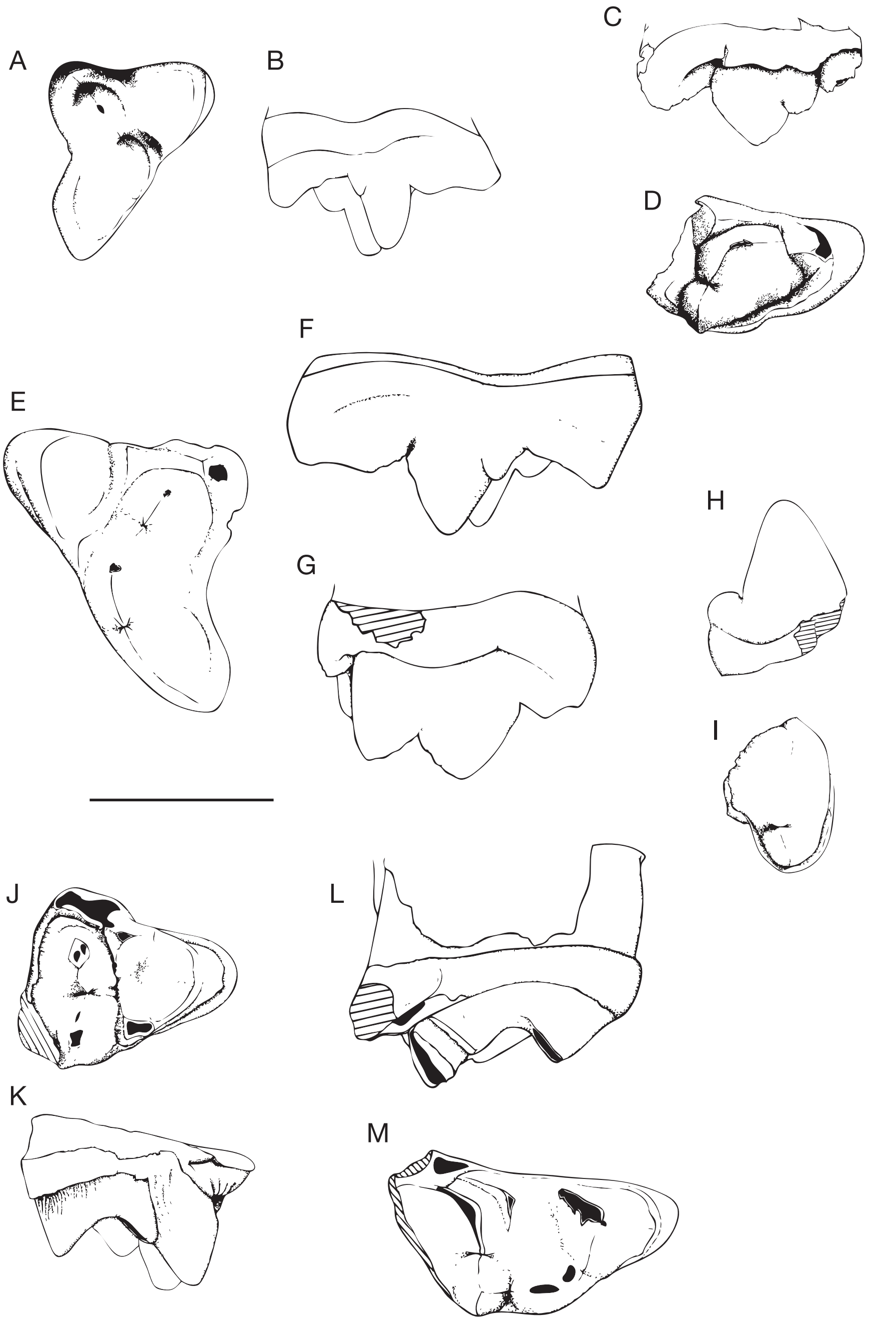

FIG. 2. — **A**-**K**, *Kyawdawia lupina* Egi *et al.*, 2005 from Pondaung Formation, Myanmar. From Bahin: NMM Bhn-1040, right M1 in occlusal (**A**) and labial (**B**) views; from Thandaung: NMM Tdg-801, fragment of left M3 in distal (**C**) and occlusal (**D**) views; left M2 in occlusal (**E**), lingual (**F**) and labial (**G**) views; NMM Tdg-802, fragment of right P4 in labial (**H**) and occlusal (**I**) views; from Kyaukmagyi: NMM Kmi-500, fragment of right M2 in occlusal (**J**) and lingual (**K**) views; **L**, **M**, Hyaenodontidae indet. from Pondaung Formation, Myanmar. From Thamingyauk: NMM Tmk-500, subcomplete right M3 in mesial (**L**) and occlusal (**M**) views. Scale bar: 1 cm.

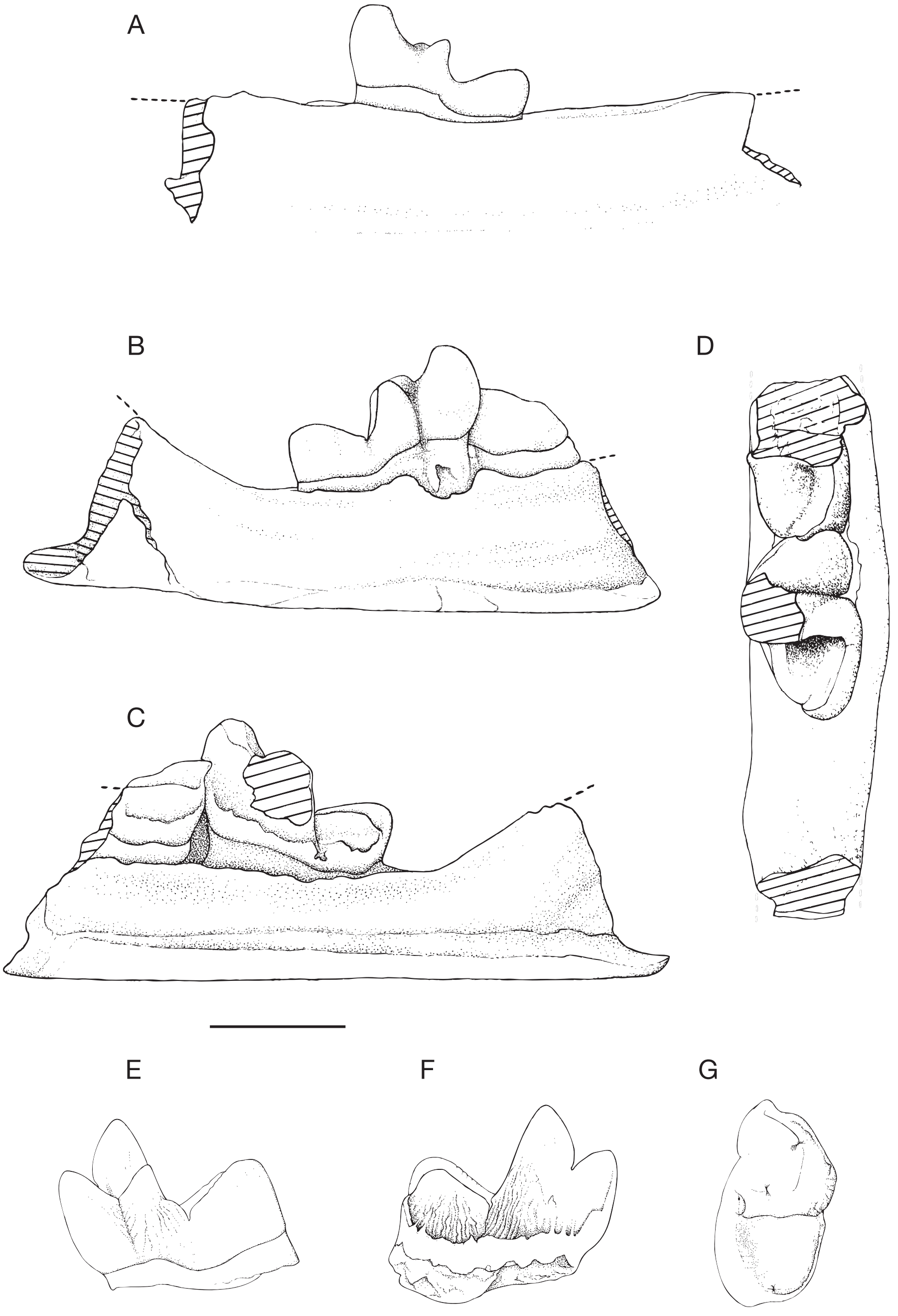

FIG. 3. — *Kyawdawia lupina* Egi *et al.*, 2005 from Pondaung Formation, Myanmar. From Bahin: NMM Bhn-2000, fragment of right hemimandible with m3 in lingual view (**A**); from Paukkaung: NMM Pkg-1050, fragment of left hemimandible with m2 talonid and m3 in lingual (**B**), labial (**C**) and occlusal (**D**) views; NMM Pkg-1051, right m2 in lingual (**E**), labial (**F**) and occlusal (**G**) views. Scale bar: 1 cm.

NEW REFERRED MATERIAL AND LOCALITIES (Fig. 1). — From Bahin: NMM Bhn-1040 (left and right isolated M1, Fig. 2A, B), NMM Bhn-2000 (fragment of right hemimandible with m3 with broken protoconid, Fig. 3A); from Thandaung: NMM Tdg-800 (left M2, Fig. 2E-G), NMM Tdg-801 (fragment of left M3, Fig. 2C, D), NMM Tdg-802 (fragment of left P4, Fig. 2H, I); from Paukkaung 2 (Pk 2): NMM Pkg-1050 (fragment of left hemimandible with m2 talonid and m3 with broken protoconid, Fig. 3B-D), NMM Pkg-1051 (isolated right m2, Fig. 3E-G); from Kyaukmagyi: NMM Kmi-500 (fragment of right M2, Fig. 2J, K).

DISTRIBUTION AND AGE. — The material of *K. lupina* was collected from many localities of the Pondaung Formation, Myanmar (Fig. 1), which dates to the late middle Eocene. In Mogaung area: Kyawdaw (Kdw), which is the type locality near the village of Kyawdaw; UCMP locality V 83106, located about 5.6 km southwestern from Mogaung; and 1 unspecified locality near Kyawdaw. In Bahin area: Paukkaung-2 (Pk 2), near the village of Paukkaung, and several unspecified localities near Paukkaung/Bahin. In Pangan area: Pangan-1 (Pgn 1) and Pangan 2 (Pgn 2). New specimens described here come from the Bahin area, and from Thandaung (Tdg) and Kyaukmagyi (Kmi), both located in the Mogaung area (Fig. 1).

DESCRIPTION OF THE NEW MATERIAL

Compared with the holotype specimen, the study of which is based on a resin cast made by one of us (SD), the new material is both better preserved and less worn, although it is less complete since the holotype documents the major part of the tooth rows. The measurements of the new material described in the present study and those from the hypodigm are presented in Table 1 (upper dentition) and Table 2 (lower dentition). The P4 lacks its mesial and mesiolingual portions but the tooth was probably longer than it is high (height is greater than length on p4; Egi *et al.* 2005). The cingulum is developed on the talon of P4, which is crest-like. Although the tooth is not completely preserved lingually, it is clear that the protocone lobe was not as developed as in some other proviverrines (e.g., *Masrasector* Simons & Gingerich, 1974, *Cynohyaenodon* Filhol, 1873), and that the lingual bulge was poorly developed; these are derived characters of the species (Egi *et al.* 2005). The M1 (NMM Bhn-1040) is small and approximately the size of that in the holotype (see Table 1). On the contrary to the latter, the M1 from Bahin is very well preserved. The paracone and metacone are about the same height, the former being smaller in diameter/length than the latter. Both cusps are connated at their base, with their upper portion being separated by a deep valley and a shallow notch. The protocone is much lower than the paracone and metacone, but it has a wide and triangular-shaped base and marked crista. It is widely separated from the labial cusps by a deep basin. A small paraconule and a vestigial metaconule are distinct. The metastyle blade is elongated, low and separated from the postmetacrista by a deep notch. The cingulum is distinct but poorly developed all through the lingual face and it is labially more marked. A small parastyle is present in the mesiolabial corner. The M2 from Thandaung (NMM Tdg-800) is a large morphological replica of the M1, although both are easily distinguishable. On M2 the paracone and metacone are still of similar height, with the metacone base larger than the paracone one; the V-shaped valley that separates the two cusps is, however, more open than in M1. The metaconule is larger and the cingulum is more mesially developed than in M1. The fragmentary M2 from Kyaukmagyi (NMM Kmi-500) preserves the paracone, the metacone, the protocone and the conules; it is slightly smaller than NMM Tdg-800, with a slightly stronger cingulum around the protocone. The M3 from Thandaung (NMM Tdg-801) compares well with that of the holotype; both specimens preserved the same labial portion of this tooth and are of similar length. The tooth from Thandaung is, however, a fresh one while that of the holotype is horizontally abraded. Size and morphology of NMM Tdg-801 match those of the corresponding tooth of the holotype, especially in the size of the parastyle and the paracone, which is larger than the metacone, and the two cusps being widely fused except for their apex. Because of the wearing pattern, conules are not distinct in the holotype but, on the M3 from Thandaung, a metaconule and a paraconule are present, the former being the largest.

The lower dentition is documented by fragmentary hemimandibles with m2 talonid, m3 with broken protoconid (NMM Bhn-2000 and NMM Pkg-1050), and an isolated m2 (NMM

Pkg-1051), which represent three individuals. Both teeth have a cingulid developed on the labial face, which is particularly prominent mesiolabially on the paraconid ("precingulid" of Van Valen 1994). The isolated m2 from Paukkaung is particularly interesting because the tooth was previously known only from the holotype, in which it is much worn. In contrast NMM Pkg-1051 is a fresh, perfectly preserved tooth. The trigonid is tall, with a protoconid much taller than the paraconid, although the two cuspids are about the same mesiodistal length. In addition, the protoconid height is much greater than the trigonid length (see measurements in Table 2). The mesial face of the paraconid is slightly convex, displays a prominent ridge and, at its base, a strong precingulid. The metaconid is reduced and lower than the paraconid; the two cuspids are separated by a V-shaped valley that is prolongated by a distinct groove on the lingual face of the tooth. The metaconid shows a prominent ridge along its distolingual face. The distal face of the trigonid is nearly transversely oriented, with the distal faces of the metaconid and protoconid being at the same level. The talonid is as wide as the trigonid but slightly shorter; the talonid basin is deep. The cristid obliqua is labial, and its maximum height is located distally at the level of the hypoconid. The entocristid is longer than the cristid obliqua and it is curved lingually. There is no distinction between an entoconid and a hypoconulid. The latter is separated mesially from the metaconid and distally from the hypoconid by a notch. The enamel on the labial face of the protoconid and the talonid, above the cingulid, is clearly wrinkled. NMM Pkg-1051 has a strong cingulid along its labial face. The m2 talonid is also preserved, but very worn, in NMM Pkg-1050, it shows the same shape as in NMM Pkg-1051 and the similarly developed labial cingulid. The m3s in NMM Bhn-2000 and NMM Pkg-1050 do not preserve the protoconid; the tooth is also more worn in the former than in the latter. Relative to that of m2, the talonid of m3 is distinctly narrower than the talonid, which is mainly due to a more centrally placed cristid obliqua. In addition, compared to m2, m3 has a slightly more reduced metaconid and a more triangular-shaped talonid, with an entocrista that is clearly less curved and distally more prominent relative to the cristid obliqua. Nevertheless, the trigonid/talonid length ratio and the development of the labial cingulid are similar in m2 and in m3.

COMPARISONS AND DISCUSSION

Our comparisons are based on a direct study of a great number of proviverrine hyaenodontids by at least one of us (SP and/or MM). Egi *et al.* (2005) support a relationship of *Kyawdawia* Egi *et al.*, 2005 to the proviverrines *Masrasector* and *Paratritemnodon* (but see the following discussion on character misinterpretations in that analysis), partly based on the presence of a distally extended labial cingulid on m3, which was said to be an autapomorphy of this clade. However, an extended labial cingulid is also known from: 1) the European monospecific *Proviverra* Rütimeyer, 1862 (but not *Lesmesodon* Morlo & Habersetzer, 1999, even if both genera were coded as a single taxon by Egi *et al.*); 2) the North American *Sinopa* and monospecific *Proviverroides* Bown, 1982 (Morlo & Habersetzer 1999), taxa close to *Prototomus* Cope, 1874 (see Gunnell 1998; Morlo & Gunnell 2003); 3) Laurasian *Arfia* Van Valen, 1965 (see Gingerich 1989); and 4) the apterodontine hyaenodontid *Apterodon* Fischer, 1880 (see Lange-Badré & Böhme 2005). The character description, however, is correct in stating that the labial cingulid surrounding the hypoconid extends to the distal tooth margin. This is not the case in *Proviverra*, but it is in *Sinopa*, *Proviverroides*, *Arfia*, *Paratritemnodon*, *Yarshea* Egi *et al.*, 2004, and *Masrasector*, and also in *Apterodon*. The character thus cannot be interpreted as an autapomorphy of the proposed Afro-Asian proviverrine clade (see Fig. 4A). The character is present on the specimens described and referred to here as *Kyawdawia*; these remains differ from *Masrasector* and *Paratritemnodon* by their much larger size.

The new material described here reveals a great range of size variation. Compared to most of the known proviverrines, *Kyawdawia lupina* is a large species, especially after *Dissopsalis* Pilgrim, 1910 has been removed from Proviverrinae and included in Hyainailourinae (Polly 1996), partly based on the tooth eruption sequence of its sister-taxon *Buhakia* Morlo, Miller & El-Barkooky, 2007. Body size

TABLE 1. — Measurements (in mm) of the upper dentition of *Kyawdawia lupina* Egi *et al.*, 2005. Abbreviations: **L**, labial length; **W**, labiolingual width; **LL**, lingual length; **ML**, metastylar length; *, mean of right and left teeth.

		Bhn-1040*	**Tdg-800**	**Tdg-801**	**Kmi-500**	**Holotype**
M1	L	13.1				12.7
	W	11.3				11.7
	LL	15.3				15.5
	ML	5.6				
	L/W	1.16				1.09
M2	L		17.1			17.3
	W		16.1		13.8	17.0
	LL		22.2			23.0
	ML		8.0			8.4
	L/W		1.06			1.02
M3	L			8.4		9.0

is one of the characters used by Egi *et al.* (2005: character 1) in their character matrix. According to these authors, m1-3 length is greater than 47 mm in *K. lupina* (character state and threshold previously used by Barry 1988) which is based on the holotype. Adding each of the molar length gives 47 mm while (due to overlapping of the molars) m1-m3 length is 44.9 mm only in the holotype right hemimandible NMMP-KU 1661 (see Egi *et al.* 2005: 342); lower dentition measurements of the holotype in Egi *et al.* (2005: table 1) should refer to NMMP-KU 1661, not NMMP-KU 0042, which corresponds to the maxilla, cranial and postcranial fragments. In the material described here, the upper teeth are larger (M1 and M2) or slightly smaller (M3) than the holotype (Table 1). Compared to the size variation of, e.g., the proviverrine-like hyainailourine (Polly 1996; Morlo *et al.* 2007) *Dissopsalis carnifex* Pilgrim, 1910 (Barry 1988: table 1), this size difference is not large, however. On the contrary, the size difference between the newly referred lower dentition and the material previously described by Egi *et al.* (2005) is much greater (the m3 NMM Bhn-2000 is only 67% the size of the holotype), although the proportion of lower molars (L/Wtrigo, Ltal/Ltrigo in Table 2) is not much different if the large variation observed in the hypodigm is taken into account. Among other early to middle Eocene hyaenodontids, a similar size variation of lower molar length is present in: the North American proviverrines *Arfia shoshoniensis* (Matthew, 1915), where m3 length varies between 8.2 mm (AMNH 15747) and 12.5 mm (AMNH 15743), and *Prototomus phobos* Gingerich & Deutsch, 1989, where m2 length varies between 5.3 mm (UM 92614) and 7.4 mm (UM 79358) (MM unpublished data); and the limnocyonine *Thinocyon velox* Marsh, 1872 (Morlo & Gunnell 2003). Large size variations of about 30% are also known from Oligocene *Hyaenodon* (Mellett 1977; Lange-Badré 1979; Morlo & Nagel 2006). Various modern carnivorans may also display such a great range, such as *Felis sylvestris*, where m1 length variation reaches 72% (N = 9; SP unpublished data) or *Meles meles* where m1 and m2 length variations are up to 74 and 66%, respectively (N = 131; Abramov & Puzachenko 2005).

There are additional, morphological differences between the description of Egi *et al.* (2005) and our observations of the holotype and new material described here. According to these authors, the paracone of the M1 and M2 of *K. lupina* (represented only by the holotype in their study) is slightly lower than the metacone (character 11), but slightly larger in basal diameter (character 12 in Egi *et al.* 2005: 340, table 5); for the latter character, *Kyawdawia* is coded "0: paracone basal diameter relatively larger than the metacone diameter" (character 12 in Egi *et al.* 2005: table 5). However, the relative height or size of these cusps on the only preserved holotype M1 cannot be estimated. In the dentition of the holotype, left and right M1 and right M2 are

Table 2. — Measurements (in mm) of the lower dentition of *Kyawdawia lupina* Egi *et al.*, 2005. Abbreviations: **L**, maximum length; **Ltrigo**, maximum trigonid length; **Wtrigo**, trigonid width; **Wtal**, talonid width; **Ht proto**, protoconid height. Measurements of Egi *et al.* (2005) are based on NMMP-KU 1661 (holotype) and NMMP-KU 1288; number in parentheses is the sample size if greater than 1.

		Bhn-2000	**Pkg-1050**	**Pkg-1051**	**Egi *et al*. (2005)**
m2	L			14.2	17.6
	Ltrigo			8.0	9.6
	Wtrigo			7.7	8.6
	Wtal		7.5	7.7	7.5
	Ltal/Ltrigo			0.78	0.83
	L/Wtrigo			1.87	2.04
	Ht proto			11.0	
m3	L	13.6	15.0		18.4-20.3 (2)
	Ltrigo	8.2	8.4		10.3-12.5 (2)
	Wtrigo	7.4	8.9		9.1-11.0 (2)
	Wtal	6.0			7.2-8.3 (2)
	Ltal/Ltrigo	0.66	0.79		0.62-0.79 (2)
	L/Wtrigo	1.84	1.68		1.85-2.02 (2)

far too heavily worn and/or damaged for a precise measurement of height and basal diameter, with the paracone being even more damaged than the metacone on the M2; the left M2 is well preserved and displays the metacone slightly longer than the paracone. The upper molars (M1 and M2) described here (NMM Bhn-1040, NMM Tdg-800, NMM Kmi-500) show that the height of the two cusps is roughly similar and that the metacone is more elongated than the paracone, which mainly results from the distal development of the postmetacrista on the former. The basal diameter of the paracone is rather lesser than that of the metacone on M1 and M2 in *Kyawdawia lupina*. The relative height and size of the paracone and metacone of M1-2 is therefore similar to that stated in *Paratritemnodon* and *Masrasector*, *contra* Egi et al. (2005). The heavy wear and/or poor preservation obscure other details on the upper molars of the holotype such as the presence or absence of the conules in M1 and M2. Egi *et al.* (2005) state that the paraconule is "indistinct or absent" on M1 and that the metaconule is "present only on M2" in the holotype (characters 20 and 23 respectively; Egi *et al.* 2005), which is exactly the same as in *Masrasector*. While from our observations, the molars on the holotype are much too worn or too damaged for determining whether the conules are present or absent. The M1 and M2 described here have small but distinct conules, the paraconule being larger than the metaconule. Character states are therefore not confirmed for both teeth, *Kyawdawia* having the primitive state for the two characters. In *Paratritemnodon*, Kumar (1992) mentions a paraconule on M1 and M2, and a tiny metaconule only on M2 (*contra* Egi *et al.* 2005); *Masrasector* also has distinct conules at least on M1 (Crochet *et al.* 1990), which contrasts with the definition of the character states for this genus in Egi *et al.* (2005). Unfortunately, there are no published data for upper teeth of *Masrasector* from the Fayum.

The lower dentitions referred to here agree with the previous description of *K. lupina*. Thus, as in the holotype, the m2 of NMM Pkg-1051 has a metaconid very reduced and smaller than the paraconid, and a paraconid and protoconid subequal in length. Such a reduction of the metaconid is known in *Paratritemnodon*, *Masrasector*, *Kyawdawia* and distinguishes the m2 described here from that of *Yarshea cruenta*. However, it is known from a couple of other proposed proviverrines, e.g., *Alienetherium* Lange-Badré, 1981, *Eurotherium* Polly & Lange-Badré, 1993, *Prodissopsalis* Matthes, 1952, and *Matthodon* Lange-Badré & Haubold, 1990 (Morlo & Habersetzer 1999), and, thus cannot easily be used as a diagnostic feature. In addition, in NMM

Pkg-1051, the length of the m2 trigonid relative to the height of the m2 protoconid, which equals 0.72, corresponds to that found in the genera of the so-called "Afro-Asian proviverrines" (see Egi *et al.* 2005; Fig. 4A); this character cannot be measured in the holotype. Finally, like in the holotype of *K. lupina*, the labial cingulid is continuous and present on the whole labial side in NMM Pkg-1051. The main difference observable on the lower dentition between the holotype and the new material is the relative greater width of the talonid of m2. It is subequal to the trigonid width in NMM Pkg-1051 while the talonid is clearly narrower than the trigonid in the holotype of *Kyawdawia lupina*, based on measurements in Egi *et al.* (2005). On m2, however, the talonid is wider than in m3 and it is less triangular in occlusal shape in both the holotype and in NMM Pkg-1051. Proviverrine taxa in which the m2-talonid width is subequal or greater than its trigonid width are numerous and present on all continents, e.g., *Arfia*, *Proviverra*, *Lesmesodon*, *Proviverroides*, *Allopterodon* Ginsburg *in* Ginsburg *et al.*, 1977, *Cynohyaenodon trux* Van Valen, 1965 (but not *Cynohyaenodon cayluxi* Filhol, 1873, the only species of the genus Egi *et al.* 2005 included into their analysis), *Metasinopa* Osborn, 1909 or *Anasinopa* Savage, 1965. This character cannot be used to establish a clade *Masrasector-Paratritemnodon-Kyawdawia* even if *Allopterodon*, *Cynohyaenodon*, *Proviverra*, and *Lesmesodon* (all are closely related to each other) are much smaller than *Kyawdawia* and display, e.g., completely separate paracone and metacone and a shorter metastyle on M1, and an unreduced m2 metaconid (which is reduced in *Cynohyaenodon cayluxi* and *Cynohyaenodon ruetimeyeri* (Depéret, 1917)) (Morlo & Habersetzer 1999). *Metasinopa* and *Anasinopa* differ by lacking the complete labial cingulid on m3, which is diagnostic of the suggested clade *Masrasector-Paratritemnodon-Kyawdawia*, and by having a less mesiolingually projected protocone on M1-2 and a narrower talonid with a lower entoconid crest on m3. Moreover, both genera (and *Buhakia*) are now included in Hyainailourinae (Morlo *et al.* 2007) as was their close relative *Dissopsalis* already (Polly 1996). The morphology of the m3 of NMM Bhn-2000 and NMM Pkg-1050 is very similar to that of the m3 of the hypodigm specimens of *Kyawdawia lupina*. The proportion of the trigonid compared to the total length (Ltrigo/L) and the proportion of the tooth (L/Wtrigo) are exactly the same (Table 2). In contrast, the talonid/trigonid proportion in NMM-Bhn 2000 and NMM-Pkg 1050 is much different from that in *Yarshea cruenta*. An additional difference is that the labial cingulid is restricted to the paraconid in the latter, while it is extended distally in *K. lupina* and in NMM Bhn-2000 and NMM Pkg-1050. The talonid of m3 is shorter than the trigonid, with a talonid/trigonid length proportion greater than 0.5, as in diverse North American proviverrines like *Arfia*, *Prototomus*, *Proviverroides*, and partly *Sinopa* Leidy, 1871, European *Allopterodon*, *Proviverra*, *Lesmesodon*, but not *Cynohyaenodon* (only very occasionally in *C. trux*; MM unpublished data), and *Masrasector* (Egi *et al.* 2005). The talonid of m3 is distinctly narrower than its trigonid (like in nearly all proviverrines). The m2 and m3 of this new material share the absence of distinction between the hypoconulid and the entoconid and the presence of a notch separating the hypoconid and the hypoconulid with African and Asian proviverrines. However, these characters are typical as well for the "North American" proviverrines (see Morlo & Gunnell 2003). It could serve as an argument that African and Asian, but not European proviverrines, root in taxa related to *Prototomus* or *Arfia* rather than those close to *Proviverra*.

Hyaenodontidae sp. indet.

REFERRED MATERIAL. — From Thamingyauk: NMM Tmk-500 (isolated subcomplete right M3, Fig. 2L, M).

DISTRIBUTION AND AGE. — Pondaung Formation, Myanmar (see Fig. 1); late middle Eocene.

DESCRIPTION

The tooth is complete except for the mesiolabial corner. It is large and transversely elongated. The parastylar wing, which develops transversely, is broken, but it is likely to be short. The paracone is slightly larger than the metacone, which is located roughly distally to it. Both cusps are separated by an open V-shaped valley continuing by a small notch,

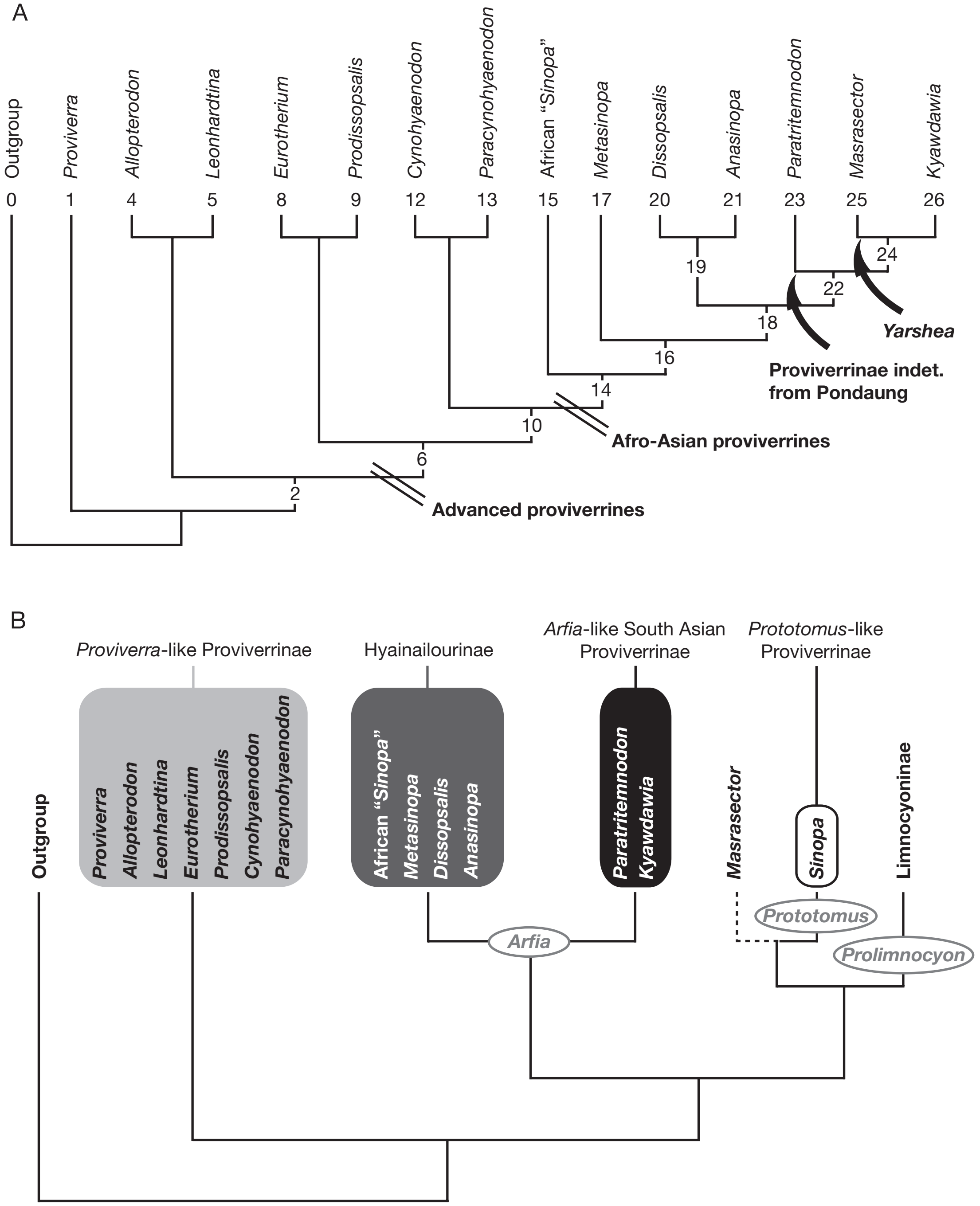

FIG. 4. — Comparison between the cladogram obtained by Egi *et al*. (2005) (**A**) and that proposed here (**B**). The position of *Arfia*, *Prototomus*, and *Prolimnocyon* as ancestor of *Arfia*-like South Asian proviverrine-Hyainailourinae, *Prototomus*-like Proviverrinae, and Limnocyoninae, respectively, illustrate the current status of these genera. Dotted line represents imprecise relationships of *Masrasector*. See text for explanation.

and they are lingually flanked by a small conule. The metaconule is transversely more elongated than the paraconule, and it is located on the distal rim of the tooth, just lingual to the metacone from which it is separated by a small notch. The paraconule is located on the mesial rim of the preprotocrista. The trigon basin is wide and deep, especially distally. The protocone is a large, triangular transversely-developed cusp. The cingulum is poorly developed mesially to the paracone-paraconule and around the protocone; it is slightly more developed labially and on the parastylar shelf; it is completely absent at the level of the metacone-metaconule.

Measurements: M3 L = 9.5; W = 18.7.

COMPARISONS AND DISCUSSION

Although there is a great size difference between NMM Tmk-500 and NMM Tdg-801 (assigned here to *K. lupina*, see above) it is less than to the holotype of *K. lupina*. The great size of NMM Tmk-500 may therefore be insignificant. In addition to the size, however, proportional and morphological differences indicate that this specimen probably represents a different species. Compared to *K. lupina*, NMM Tmk-500 has a less reduced metacone compared to the paracone and, more or less correlatively, a lesser fusion between the bases of these cusps. It also possesses a shorter parastyle, and a greater length, resulting in part from a less reduced and more distally prominent metacone and from a more open angle (at the parastylar extremity) between the transverse mesial and the distolabial faces. Only the size is a significant difference of NMM Tmk-500 to *Yarshea cruenta* and Proviverrinae indet. from Pondaung. The distinction is even greater with *Paratritemnodon*. Besides a much larger size, NMM Tmk-500 differs in lacking a distal cingulum and in the retention of a metaconule, well developed metacone and protocone, and a postmetacrista.

Because we would need more material and a better knowledge of the morphological variations in these Asian creodonts, we refrain from naming this isolated tooth though it possibly represents a new species. If so, it would reveal an even richer creodont fauna from Pondaung than previously thought and would further support the significance of Pondaung in the evolution of the Creodonta in Asia.

CONCLUSIONS

Besides the already given discussion on character states used in the matrix of the phylogenetic analysis performed by Egi *et al.* (2005) some other remarks on the included taxa are necessary to understand the relevance of this analysis.

1) Egi *et al.* (2005) included *Cynohyaenodon*, but it is unclear which of the three known species they coded. Character states imply coding of its most evolved species, *C. cayluxi*, only. This species is the presumed descendent of the most plesiomorphic species of the genus, *C. trux* from the late middle Eocene of Egerkingen and Geiseltal (Lange-Badré & Haubold 1990). Coding the most plesiomorphic instead of the most apomorphic species would probably change placement of *Cynohyaenodon* from a member of "advanced proviverrines" to a position close to *Allopterodon*, because *C. trux* differs only slightly from *Allopterodon torvidus*, especially in the lower dentition (Lange-Badré & Haubold 1990).

2) European proviverrines are clearly defined by their tricuspid talonids and in having p1 double-rooted in plesiomorphic species (e.g., Morlo & Habersetzer 1999; Morlo & Gunnell 2003). Even apomorphic, hypercarnivorous members reveal this structure in at least m1 (e.g., *Paracynohyaenodon*, *Prodissopsalis*, *Matthodon*). The character is not included in the analysis of Egi *et al.* (2005). If European "*Proviverra*-like" proviverrines are considered to form a separate clade rooting in a single ancestor different from that of other "proviverrines", the supposed clade "advanced proviverrines" in the cladogram of Egi *et al.* (2005) collapses and turns out to be not natural (Fig. 4).

3) With the description of *Buhakia*, Morlo *et al.* (2007) corroborated the removal of *Dissopsalis* from Proviverrinae to Hyainailourinae (Polly 1996) including the close relatives of *Dissopsalis*, *Anasinopa* and *Metasinopa*. Considering these taxa to belong to hyainailourines, a subfamily maybe rooting in *Arfia* (Polly 1996), removes them from "Afro-Asian proviverrines" (see Fig. 4A) of Egi *et al.* (2005) and leaves *Masrasector* as the only possible African proviverrine related to the Pondaung taxa.

4) Among the characters defining "Afro-Asian proviverrines" (p1 shorter than it is high, metaco-

nid of m2 less than half as high as protoconid and paraconid, metaconid of m2 smaller than paraconid) the last two are not independent (and thus should not be separate characters). Even more important is that, by exclusion of *Dissopsalis*, *Anasinopa*, and *Metasinopa*, those characters become homoplastic. Moreover, other, not included proviverrine taxa share these characters as well, e.g., the European *Matthodon* and, especially, the North American *Tritemnodon* (*sensu* Morlo & Habersetzer 1999), which also shares its talonid structure with the so-called "Afro-Asian proviverrines". With good reason, thus, the genus was said to be the most similar taxon to *Paratritemnodon* (Ranga Rao 1973), the supposed sister-taxon of *Kyawdawia* after Egi *et al.* (2005). Because the character combination is homoplastic and not unique to African and Asian proviverrines it cannot be used to unite them until autapomorphies have been identified.

5) *Masrasector* differs in several respects from the Pondaung taxa and *Paratritemnodon*: its p3 is very low and blunt, p4 is not much larger than m1 and not standing in a crowded position to the first molar, m1-2 have a much smaller length/width ratio, m2 has an entoconid, m1-3 have the metaconids being less reduced and placed mesiolingually rather than distolabially of the protoconid, and m3 is not larger than m2. Especially relative tooth sizes are not coded in the analysis of Egi *et al.* (2005), which is why *Masrasector* shows up as being closely related to the South Asian taxa in their cladogram (Fig. 4A). However, the character combination of small length/width ratio of m1 with the low, blunt p3 and a relatively short p4 separates *Masrasector* from every other proviverrine. Removing it from the South Asian proviverrine clade due to its singular morphology leaves "Afro-Asian proviverrines" formed by South Asian taxa only, and thus drops the suggested relationship between African and Asian proviverrines. Due to its uniqueness, the relationships of *Masrasector* remain completely unresolved for the moment (see Fig. 4B).

6) *Arfia* is the only genus generally placed into Proviverrinae that is present in the Eocene of North America, Europe, and Asia (Gingerich 1989; Smith & Smith 2001; Lavrov & Lopatin 2004). It shares several characters with the so-called Afro-Asian proviverrines (see above). Moreover, the genus was regarded as the ancestor of hyainailourines (Polly 1996), which may play an important role in the supposed Eocene connection between Asia and Africa supported by the suggested hyainailourine *Orienspterodon dahkoensis* from Pondaung (even if the European *Francotherium* may represent the oldest hyainailourine record). For unknown reasons, *Arfia* was not included in the analysis by Egi *et al.* (2005). Inclusion of the genus may change the position of the Pondaung taxa to *Paratritemnodon*, to the *Prototomus*-like proviverrines, and to limnocyonines, because it suggests the existence of a proviverrine clade which represents the sister-group of Hyainailourinae (Fig. 4).

As a consequence of all these points we feel the resulting tree of Egi *et al.* (2005) being not well supported especially concerning the supposed clades of "advanced proviverrines" and "Afro-Asian proviverrines" (and their respective members). Performing an alternative phylogenetic analysis, however, is far beyond the scope of this paper because it would necessitate a re-evaluation of used characters and an evaluation of critical characters missing in the analysis of Egi *et al.* (2005), e.g., talonid morphology. Moreover, it would be crucial to: 1) include several other taxa, especially *Arfia*, *Tritemnodon*, *Matthodon, Prototomus*, and also *Sinopa*, the first Asian member of which was recently discovered (Schaal *et al.* in press); 2) exclude taxa now identified as hyainailourines (*Dissopsalis*, *Anasinopa*, *Metasinopa*); and 3) assess possible ancestor-descendent relationships by a stratocladistic analysis (Fisher 1994), especially in *Cynohyaenodon* and for *Arfia* vs. *Prototomus* as possible ancestors of larger clades. The result of such an enhanced analysis may shed much better light on the implied Afro-Asian paleobiogeographic connection in the Eocene.

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