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# Paleoecological Evolution of the Fossil Suidae (Mammalia, Artiodactyla) in Neogene of Central Myanmar

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## Abstract

In this work, the dental morphology the Neogene fossil Suidae of central Myanmar are analyzed, and the paleoecological evolution of the Neogene fossil suids are discussed. Morphological evolution of the third molar in suids has been considered an adaptation to more abrasive diet, that is from a browsing to grazing diets. In Myanmar, three distinct types of diet, predominant frugivore (Middle to Late Miocene), frugivore to hyperbrowser or folivore (Late Miocene to Early Pliocene) and predominant folivore (Middle Pliocene to Early Pleistocene), have been distinguished in the dental characteristics of suid fossils. The pattern of faunal transition in Neogene suids strongly suggests a critical floral change at the Late Miocene in Myanmar. The coexisted appearance of *Propotamochoerus* with *Sivachoerus* suggesting that the C3-C4 floral transition accompanying the last faunal turnover may have occurred to bring wide spreading of C4 plants in the Early Pliocene of Myanmar, later than that in Late Miocene of Siwalik of Indo-Pakistan.

Key Words: Neogene, Paleoecological evolution, Suidae

## Introduction

Suidae is one of the most widely known Cenozoic fossil artiodactyls in Asia. At present, the earliest known fossil suid is recorded from the Late Eocene of Krabi Basin, Thailand, Southeast Asia (Ducrocq *et al.*, 1998). Fossil materials of Suidae have been discovered from the Neogene deposits of Myanmar. In the early 20th Century, there were some descriptions on suid materials of Myanmar but few detail systematic descriptions and discussions (Pilgrim, 1910a, 1910b, 1926, 1927; Matthew, 1929; Colbert, 1935, 1938, 1943; Cotter, 1938). These descriptions were done based on very few specimens, most of which are so poorly preserved that it is too inadequate for us to discuss their phylogeny and paleobiogeography. Recently, some genera of Myanmar Suidae have been revised within these years (Chit Sein *et al.*, 2009; Thaung Htike, 2008; Thaung-Htike *et al.*, 2005, 2006, 2007, 2008, 2010, 2014)

In Myanmar, the fossil materials of Suidae are recovered throughout the Neogene but relatively rare compared to other artiodactyls such as Bovidae and Hippopotamidae. Most suid genera of Myanmar can be correlated with those of Siwalik. The chronology of the Myanmar suids has been estimated mostly by comparing with their occurrences in Siwalik. Within these years, some new materials of Myanmar Suidae were discovered together with some well known mammalian fossils, which are not contemporaneous in Siwalik. It suggests that the first and last appearances of some Myanmar taxa may not be identical with those of the Siwalik taxa.

Three subfamilies, seven genera and at least 12 species of fossil Suidae have been identified from the Neogene sediments of Myanmar. In this study, well-preserved dentognathic materials of the fossil suids of Myanmar, most of them were discovered from the known horizons of Neogene deposits during the recent paleontological works, are studied, and it investigate the paleoecological evolution of the Neogene fossil suids are discussed.

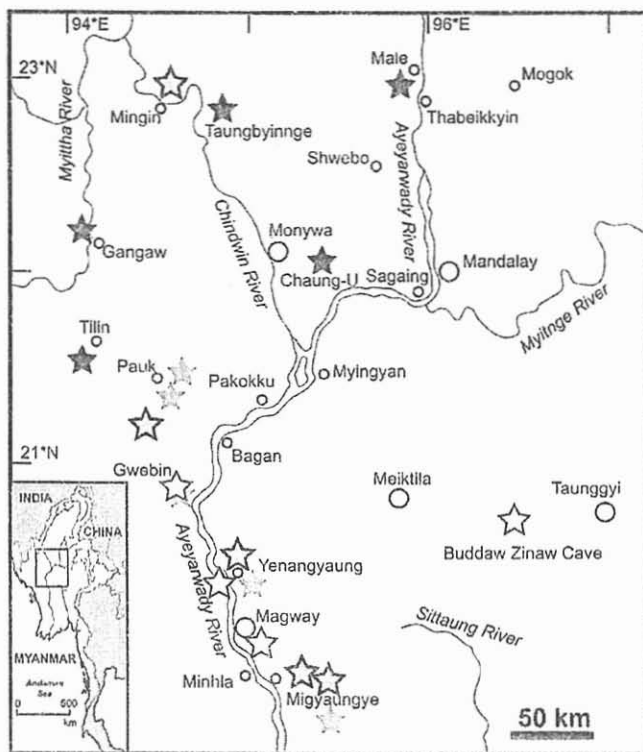
## Materials and methods

Recently discovered dentognathic materials of Myanmar suids have been studied in this work (Table 1). All new fossil materials were collected in central Myanmar (Figure 1). They are now stored at the National Museum (Yangon, Myanmar), Department of Geology,

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University of Yangon (Yangon, Myanmar), Department of Geology, Mandalay University (Mandalay, Myanmar), Department of Geology, Magway University (Magway, Myanmar), and the Sagaing Buddha Museum, Sagaing, Myanmar. Dental terminology and measurement method used are according to Thaug-Htike *et al.* (2006) (Figure 2).

The length of lower first molar has been used to compare the body size differences because  $M_1$  is usually considered to express less size variation than other teeth, and mandibular fragments with lower cheek teeth are discovered more frequently than maxillary ones in general. Moreover  $M_1$  length has been used to correlate to the body size by many workers (Legendre, 1986, 1989; Bown *et al.*, 1994; Damuth, 1999; Tsubamoto *et al.*, 2002, 2003).



#### Suid fossil localities

- |                            |                            |
|----------------------------|----------------------------|
| ★ M. Miocene localities    | ★ L. L. Miocene - Pliocene |
| ☆ E. L. Miocene localities | ☆ Pleistocene              |

Figure (1) Neogene suid fossil localities in central Myanmar.

### Results

#### Occurrence and paleobiogeography of the fossil Suidae of Myanmar

In Myanmar, the first occurrence of fossil Suidae is introduced by *Listriodon* and *Tetraconodon* during the Middle Miocene. The origin of Listriodontinae is unknown, but the oldest record of Listriodontinae in Asia is in the Early Miocene of Bugti, Pakistan. Later

members of the subfamily are found in Europe and China, suggesting that the early listriodontines evolved somewhere south of the Himalayas (Made, 1996). In Siwalik, *Listriodon pentapotamiae* has been discovered from the Middle Miocene Chinji Formation. *Listriodon* has also been discovered from the late Middle Miocene in the southern part of China. The discovery of *Listriodon pentapotamiae* in Myanmar was reported by Pilgrim (1927). The associated fauna of Gomphotheriidae suggested the Middle Miocene occurrence. Although some trilophodont gomphotheres are contemporaneous with *Prodeinotherium* sp. in Thanbinkan area, there is no record for *Listriodon* from that area. The locality of *Listriodon* is in the northern part of central Myanmar, near the border of India, suggesting that Myanmar species might be an easternmost distribution of Siwalik species, during its dispersal from Siwalik to southern China.

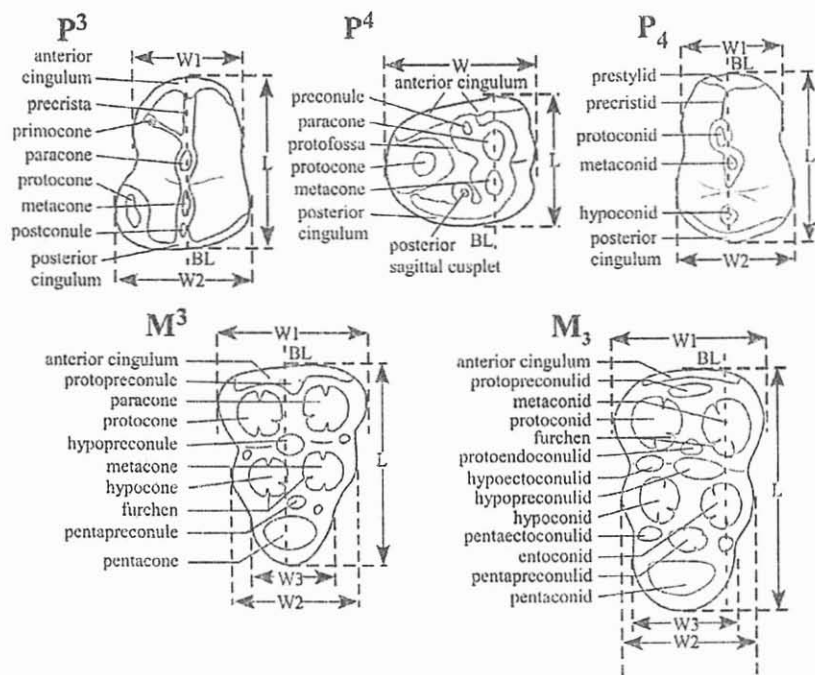


Figure (2) Dental terminology and measurement method of suid teeth.

All are left cheek teeth. Abbreviations: BL = base line; L = length; W = maximum width; W<sub>1</sub> = width of the first lobe; W<sub>2</sub> = width of the second lobe; W<sub>3</sub> = width of the third lobe in M<sup>3</sup>/<sub>3</sub> (upper and lower third molar).

The first appearance of *Tetraconodon* in Myanmar is associated with *Prodeinotherium* sp. and *Choerolophodon corrugatus*, suggesting the early Middle Miocene. The last occurrence of *Tetraconodon* in central Myanmar is from the basal strata of Irrawaddy Formation which is characterized by the co-occurrence with *Hipparion* sp. The arrival of an ancient horse, *Hipparion*, in the Indian Subcontinent from North America has recently been considered 11.1 Ma (Pickford & Liu, 2001). The occurrence of *Hipparion* in Myanmar is only from the basal part of Irrawaddy Formation, slightly above the "Red Beds" in Yenangyaung. In Siwalik, the Last appearance of *Tetraconodon*, *T. magnus*, has been suggested 9.3 Ma, early Late Miocene

(Barry et al., 2002). Large *Tetraconodon* of Siwalik and Myanmar may have become extinct during the early Late Miocene, after the first appearance of *Propotamochoerus* sp. In Myanmar, both the smallest and largest suids are *Tetraconodon*, and up to 5 species have been discovered between a relatively short period (the early Middle Miocene and early Late Miocene), suggesting that Myanmar was the most suitable environment for *Tetraconodon* during the late Middle Miocene and earliest Late Miocene.

The earliest Late Miocene time in Myanmar is also associated with the occurrence of *Parachleuastochoerus* sp., which was discovered also from the basal Irrawaddy deposits. The occurrence of *Parachleuastochoerus* sp. in Myanmar is contemporaneous with early Late Miocene *T. minor*, suggesting that *Parachleuastochoerus* sp. is also a member of the early Late Miocene fauna. In Asia, *Parachleuastochoerus sinensis* has been recorded from early Late Miocene of southern China and northern Thailand (Pickford & Liu, 2001; Pickford et al., 2004). The Dental size of *Parachleuastochoerus sinensis* is slightly larger than that of Myanmar *Parachleuastochoerus* sp. The oldest record of *Parachleuastochoerus* in the world is from the latest Middle Miocene (Made, 1999) in Europe, suggesting a probable migration of this genus from Europe to Asia (Pickford, 2001). Because of smaller size in Myanmar species compared to southern China and Thailand species, *Parachleuastochoerus* sp. of Myanmar might be an "intermediate" form of *Parachleuastochoerus*, which may have migrated from Europe to southern China and Thailand.

The first appearance of *Propotamochoerus* sp. in Myanmar is associated with the Late Miocene forms of China and Siwalik, *Propotamochoerus wui* and *P. hysudricus* (Chit Sein et al., 2009; Thaug Htike et al., 2006). However *P. wui* has not been recorded from Siwalik, suggesting that Myanmar species is the western extremity of the distribution of *P. wui*. In Myanmar, *P. hysudricus* is also contemporaneous with Pliocene tetraconodont, *Sivachoerus prior*. These two taxa are not associated in Siwalik fauna of northern Pakistan (Barry et al., 1982, 2002). *P. hysudricus* has been recorded from the Pliocene deposit of southern China, suggesting that *P. hysudricus* eastwardly spread from Siwalik during the late Miocene, appeared in Myanmar during the late Miocene, and reached China in the Pliocene.

*Sivachoerus* is contemporaneous with *Propotamochoerus hysudricus* in early Pliocene and cf. *Sus* sp. in the Middle to Late Pliocene. It is a typical Pliocene faunal member of Siwalik, and has been suggested as an immigrant from Africa. The first appearance of this species in Myanmar is not earlier than the Pliocene, suggesting that *Sivachoerus* migrated into Myanmar via Siwalik during Pliocene.

In Siwalik, *Sus*-like suid has been recorded from the Pliocene (Pickford, 1988) and it might be an immigrant form of Europe. In Myanmar, *Sus*-like species, cf. *Sus* sp., is recorded from the upper part of Irrawaddy deposit associate with Pliocene hippos, *Hexaprotodon iravaticus* and *Hex. sivalensis*. It suggests that the late Pliocene appearance of *Sus*-like suids in Myanmar can be correlated with that in Siwalik.

In the Pleistocene, *Potamochoerus* sp. widely occurred in Siwalik and China contemporaneously with *Sus* sp. In Myanmar, it is also associated with *Sus* sp. cf. *S. scrofa* suggesting that *Potamochoerus* widely spread in South Asia and northern part of Southeast Asia during the Pleistocene.

Nowadays, only single species, *Sus scrofa*, is distributed in Myanmar. The occurrences of that species in the Recent cave deposits suggest that present day wild boar appeared in Myanmar since the prehistoric times.

Table (1) Dental measurements (mm) of the Myanmar suid specimens. \* = estimate.

Taxa	Spec. no.	References	P <sup>3</sup>		P <sup>4</sup>		M <sup>1</sup>			M <sup>2</sup>			M <sup>3</sup>			
			L	W	L	W	L	W1	W2	L	W1	W2	L	W1	W2	W3
<i>Tetraodon iramagnus</i>	YUDG-Mge 089	-	39.1	38.2	29.0	47.1	31.6	32.2	30.2*	35.9	37.1	35.9	-	34.2	-	-
<i>Tetraodon iramagnus</i>	YUDG-Mge 091	-	-	-	-	-	-	-	-	35.2	37.0	34.4	39.0	34.3	28.2	17.2
<i>Tetraodon iramedius</i>	NMMP-KU-IR 0225	-	33.4	34.1	24.4	37.2	26.7	27.7	25.2	30.6	32.6	29.1	33.3	26.8	22.9	12.1
<i>Tetraodon malensis</i>	YUDG-N 1	-	-	-	-	-	14.1	15.2	14.3	14.5	16.5	14.7	16.2	15.3	12.4	-
<i>Tetraodon malensis</i>	YUDG-N 2	-	20.4	15.1	13.5	17.9	13.8	14.1	14.1	14.5	15.5	14.2	16.7	14.3	12.8	-
<i>Sivachorus prior</i>	NMMP-KU-IR 0328	-	-	-	-	-	-	-	-	-	-	-	43.1	30.3	26.7	18.4
<i>Sivachorus prior</i>	NMMP-KU-IR 0553	-	-	-	-	-	-	-	-	-	-	-	43.4	33.0	28.5	19.5
<i>Sivachorus prior</i>	NMMP-KU-IR 0329	-	-	-	-	-	-	-	-	31.6	27.8	27.4	-	-	-	-
<i>Parachleuastochoerus</i> sp.	NMM SU-6	NMMP-KU-IR 0094	16.8	13.6	13.5	15.4	-	-	-	-	-	-	-	-	-	-
<i>Parachleuastochoerus</i> sp.	NMM SU-8	NMMP-KU-IR 0096	-	-	13.6	15.3	-	-	-	-	-	-	-	-	-	-
<i>Parachleuastochoerus</i> sp.	NMM SU-5	NMMP-KU-IR 0093	-	-	-	-	-	-	-	20.2	19.7	19.0	-	-	-	-
<i>Parachleuastochoerus</i> sp.	NMM SU-7	NMMP-KU-IR 0095	-	-	-	-	-	-	-	20.4	19.8	19.0	-	-	-	-
<i>Propotamochoerus hysudricus</i>	NMMP-KU-IR 0552	-	-	-	12.5	14.7	16.1	14.3	14.9	-	-	-	-	-	-	-
<i>Propotamochoerus hysudricus</i>	MGW 0003	-	15.3	11.4	12.9	14.6	15.6	14.9	15.2	21.7	17.9	18.6	29.5	20.1	18.6	11.2

Taxa	Spec. no.	References	P <sub>2</sub>		P <sub>3</sub>		P <sub>4</sub>			M <sub>1</sub>			M <sub>2</sub>			M <sub>3</sub>				
			L	W	L	W1	W2	L	W1	W2	L	W1	W2	L	W1	W2	L	W1	W2	W3
<i>Tetraodon iramagnus</i>	YUDG-Mge 090	-	-	-	-	-	-	42.7	32.3	36.7	32.0*	27.8*	26.8*	-	-	-	-	-	-	
<i>Tetraodon iramedius</i>	NMM 839/80	-	-	-	-	-	-	37.7	29.2	37.4	26.5	25.8	25.1	31.6	30.4	28.8	43.8	28.0	24.7	18.7
<i>Tetraodon minor</i>	NMM AN 1	-	-	-	-	-	-	30.8	24.8	29.3	23.3	22.0	20.1	26.3	24.4	22.3	-	-	-	-
<i>Tetraodon minor</i>	SBM-V-46	-	-	-	36.6	21.9	29.2	29.3	25.0	32.9	-	22.6	-	-	-	-	-	-	-	-
<i>Tetraodon malensis</i>	NMM Kpg 1	-	-	-	-	-	-	18.2	14.9	16.5	13.9	12.2	12.0	16.7	14.2	12.7	20.1	12.5	10.3	8.5
<i>Tetraodon malensis</i>	MUDG-V 1029	-	-	-	25.2	15.3	17.9	19.3	13.6	16.8	-	11.8	-	-	-	-	-	-	-	-
<i>Tetraodon</i> sp. nov.	MUDG-V 1102	-	-	-	27.1	17.03*	24.0	24.0	19.1	23.1	18.2	16.9	16.1	20.3	18.1	17.0	27.7	17.8	14.8	9.1
<i>Sivachorus prior</i>	NMMP-KU-IR 0361	-	18*	-	32.0	18.9	24.5	24.1	21.1	23.9	24.5	19.3	18.0	31.1	25.8	25.4	48.5	30.8	27.9	19.8
<i>Sivachorus prior</i>	NMMP-KU-IR 0140	-	12.3	8.6	28.1	16.2	22.8	27.8	18.4	23.2	23.0	19.3	19.1	30.2	23.4	22.3	55.4	30.9	27.3	22.7
<i>Sivachorus prior</i>	YUDG-KPN 2	-	19.2	10.1	32*	18*	23*	27.5	20.8	25.4	24.7	19.8	19.1	-	-	-	-	-	-	-
<i>Sivachorus prior</i>	NMM NKE-2	NMMP-KU-IR 0085	-	-	-	-	-	27*	18*	22*	23.7	19.3	19.8	-	22.1	-	-	-	-	-
<i>Propotamochoerus hysudricus</i>	MGW 0004	-	-	-	16.2*	-	-	15.6	9.3	10.9	14.7	10.8	11.8	20.5	14.6	15.1	32.5	16.9	15.4	13.1
<i>Propotamochoerus hysudricus</i>	NMMP-KU-IR 0190	-	-	-	16.2	7.2	7.6	15.3	9.3	10.9	16.0	11.4	11.8	19.7	14.3	14.4	-	15.4	14.1	-
<i>Propotamochoerus hysudricus</i>	NMM SU 1	NMMP-KU-IR 0089	-	-	-	-	-	-	-	-	-	-	-	20.4	15.9	15.0	29.0	16.5	13.7	10.3
<i>Propotamochoerus wui</i>	NMMP-KU-IR 0413	-	-	-	-	-	-	-	-	-	-	-	-	19.0	13.9	13.3	27.3	15.5	13.2	10.0
<i>Parachleuastochoerus</i> sp.	NMM SU-4	NMMP-KU-IR 0092	10.2*	5.6*	18.7	6.7	8.7	19.3	10.3	12.4	-	-	-	-	-	-	-	-	-	-
<i>Parachleuastochoerus</i> sp.	NMM SU-3	NMMP-KU-IR 0091	10.7*	6.3*	18.4	-	7.3	17.7	10.2	11.3	-	-	-	-	-	-	-	-	-	-
<i>Parachleuastochoerus</i> sp.	NMM SU-2	NMMP-KU-IR 0090	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Parachleuastochoerus</i> sp.	MUDG-V 1101	-	-	-	-	-	-	-	-	-	-	-	-	19*	14.5*	14*	28.5	14.7	13.3	11.5
<i>cl. Sus</i> sp.	NMMP-KU-IR 0275	-	-	-	14.2	7.1	8.1	14.7	9.4	10.6	16.3	11.7	12.3	20.8	14.7	15.6	-	-	-	-



## Discussion

### Paleoecology of Myanmar suids

Suid fossils are discovered throughout the Neogene of Myanmar, and the appearances and extinctions of the varied forms principally depend on their dietary adaptations to the habitat ecology. Living suids, archetypal omnivores, show varied diets from predominantly frugivorous to predominantly folivorous (Fortelius *et al.*, 1996). The suid genera found from the Neogene of Myanmar, except for *Parachleuastochoerus*, also existed in the Neogene of Siwalik, and their diets of the Siwalik forms have been studied by the radioisotopic and dental microware analyses (e.g., Nelson, 2003).

*Listriodon*, a Middle Miocene form in Myanmar, is a distinct folivore for closed forest habitat. The large incisors and the lophodont molar with absent of hypsodonty in *Listriodon* strongly suggested that this animal ate herb, not grass (Made, 1996).

*Tetraconodon*, another form from the Middle to early Late Miocene of Myanmar, shows the ecological conditions permitting its frugivorous diet. This genus is considered to have mainly fed on fruit fallen from the uppermost canopy with less dependence on drinking water even in open habitat (Nelson, 2003). *Tetraconodon* is distinct for its combination of thick enamel and conical figure in the last two premolars. Its dental wear pattern is argued to present evidence that this animal has predominantly cracked the hard food items, such as seed (Fortelius *et al.*, 1996). The five species of *Tetraconodon* from Myanmar show a great variation in dental size (see Table 1). Body size changes in varied lineages of mammals are believed to depend on contemporary climatic change, survival competition within the same or against the different lineages, and varied predation pressures (Morgan *et al.*, 1995). A factor of climatic changes more reasonably accounts for the size variation in Myanmar species of *Tetraconodon*, because their co-existing fauna provide little evidence for the competition on food webs and habitats and for the presence of putative predators against this genus. The Middle to Late Miocene is well known for the era of long-term global cooling caused by a major expansion and permanent establishment of the East Antarctic Ice Sheet, which led strong glacial events driving the paleoclimatic evolution (Westerhold *et al.*, 2005). The climatic changes probably entailed the changes in composition in body size of the Siwalik fauna, from the Middle to Late Miocene (Morgan *et al.*, 1995). Increase in body size in *Tetraconodon* species is distinct in the Late Miocene from 108 to 648 kg, rather than in the Middle Miocene from 46 to 108 kg, in Myanmar. It is probably correlated with a size enlargement in the Late Miocene fauna of Siwalik (Morgan *et al.*, 1995). Myanmar *Tetraconodon* ranges between Class 2 (21 – 80 kg) to Class 4 (201 – 1000 kg) in body size (Thaung Htike, 2008), according to the criteria by Fortelius *et al.*, (1996), and this fact suggests closed forest to woodland-grassland mosaic habitats for them. However, despite such an enlargement in body size in this lineage, the largest *Tetraconodon magnus* maintained their frugivorous diet in the forest habitat in Siwalik (Nelson, 2003). Thus, their unchanged frugivorous diet strongly suggests that despite their large body size the Myanmar *Tetraconodon* were associated with the exclusive forest environment.

*Parachleuastochoerus*, a small-sized tetraconodont, appeared in a short term of the early Late Miocene of Myanmar. It occurred in Europe during the early Late Miocene and dispersed to southern China and northern Thailand in Late Miocene (Pickford & Liu, 2001; Pickford *et al.*, 2004). The occurrence of *Parachleuastochoerus* in Myanmar strongly suggests that (Myanmar was a way for the dispersion). According to Fortelius *et al.* (1996), *Parachleuastochoerus* is an inhabitant of forest with drier conditions.

*Propotamochoerus*, including Siwalik form (*P. hysudricus*) and southern China form (*P. wui*), appeared in the latest Miocene in Myanmar, later than Siwalik and China, suggesting it invaded from these areas into Myanmar in the Late Miocene. The paleodiet and habitat of *P. hysudricus* has been well studied. This suid is principally an omnivore in the open forest habitat and predominantly frugivorous hyperbrowser. Later *Propotamochoerus* gradually changed to prefer a fruit/foilage combination diet and finally to be a predominantly folivore in more open habitat since dietary fruit resources had decreased (Nelson, 2003). Although *P. hysudricus* was discovered only from the Late Miocene (6.51 – 10.2 Ma) in Siwalik, it was discovered up to the Early Pliocene in Myanmar. It suggests that the ecological transition in Myanmar is delayed compared to those in Siwalik.

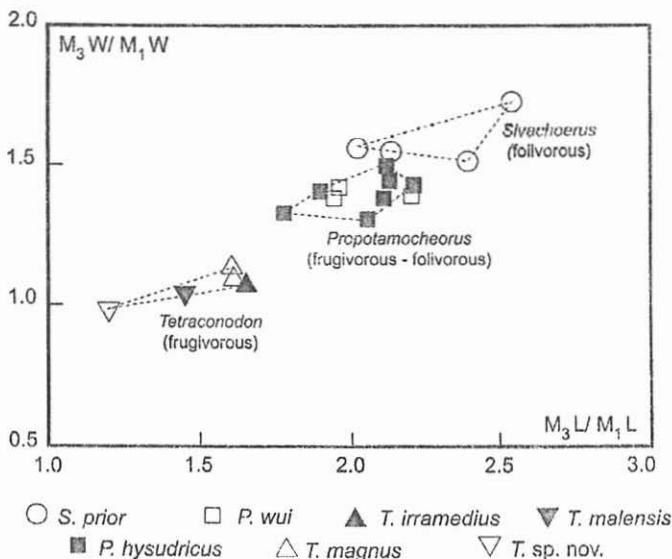


Figure (3) Size proportion of lower third molar relative to lower first molar indicating three different diet groups of Neogene suids.

*Sivachoerus prior* is a Pliocene immigrant tetraconodont into Myanmar. This form is distinct in its extremely large third molar with complex talon/talonid. The same species was discovered from the Pliocene of the Middle Siwalik, and both Myanmar and Siwalik forms are considered to have arisen from *Nyanzachoerus*, the Late Miocene of Africa (Pickford, 1989). The dental size and morphology of *S. prior* is similar to those of *N. syrticus*, an earliest species of this genus (Thaung Htike *et al.*, 2010). The changes in the third molar length and radioisotopic results for *Nyanzachoerus* species indicate that this genus changes from a folivore to grazer accompanied with increasing of third molars length (Cerling *et al.*, 2005). Large  $M_3^2/3$  with complex talon/talonid of *S. prior* is similar in morphology to that of primitive forms of *Nyanzachoerus*, suggesting that they were probably a predominantly folivore in open forest habitat rather than a grazer.

The species like extant forms of wild boar, cf. *Sus* sp., was recorded in the Middle Pliocene of Myanmar. This species is more similar in dental size and morphology to *Sus* rather than *Propotamochoerus*. Extant wild boars are opportunistic omnivores whose diet is largely



determined by the relative availability of any types of foods, although they depend on energy-rich plant materials as a major component of the diet. They are distinct forest inhabitants.

*Potamochoerus* existed in the Pleistocene of Myanmar and this genus is still extant in Africa. The present *Potamochoerus* in Africa is believed to be an immigrant from Asia in the Middle Pliocene. It is closed forest inhabitants and favors fruits and rootles plants (frugivore/hyperbrowser).

*Sus*, another Pleistocene suid, is folivorous and still survives in forests of present Myanmar.

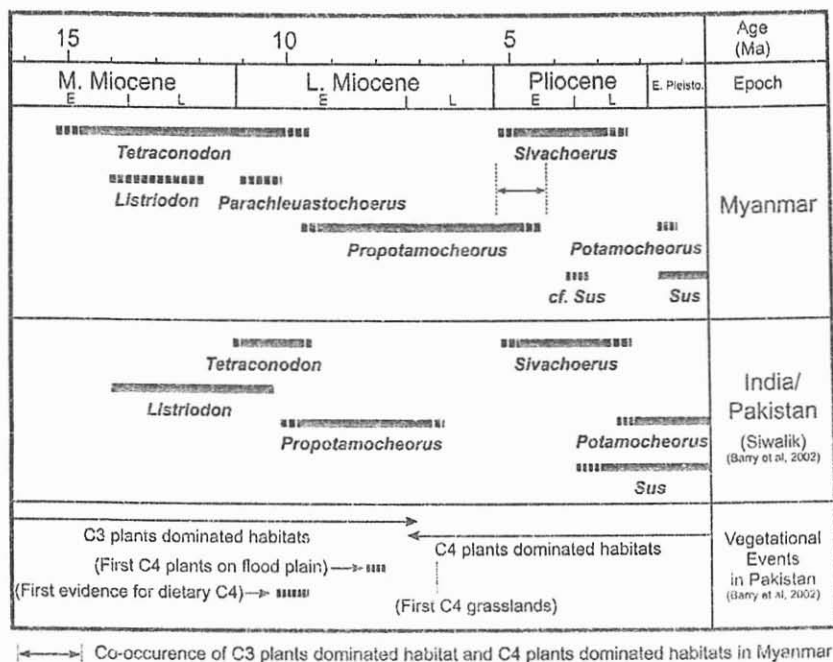


Figure (4) Comparison of the appearance and extinction periods of the suid genera between Siwalik and Myanmar together with the vegetational events in Siwalik of Northern Pakistan.

#### Paleoecological evolution of the fossil suid in Myanmar

Evolution of the third molar in the Suidae has been considered an adaptation to more abrasive diet, i.e. from a browsing to grazing diet (Cerling *et al.*, 2005). The present study on the dental morphology identified three distinct types of diets in Myanmar suids (Figure 3): (1) predominant frugivore with the relatively smallest  $M^3/3$ , such as *Tetraconodon*; (2) frugivore to hyperbrowser/folivore which the intermediate size  $M^3/3$ , such as *Propotamochoerus*; and (3) predominant folivore within the largest  $M^3/3$ , such as *Sivachoerus*.

It presumed that, the predominantly grazer suids would have existed in Myanmar, because it existed in the Pliocene of Siwalik, such as *Hippohyus*, and has survived since the Pliocene of Africa, such as *Notochoerus* and *Phacochoerus*. These Siwalik and African grazers are very distinct in their extremely long and hypsodont third molars and prefer an open habitat like savannahs. The diet of suids essentially relies on their environment, and the chronological

change of their diet likely indicates the environmental change in Myanmar. Suids from the Middle Miocene to early Late Miocene of Myanmar, such as *Listriodon*, *Tetraconodon* and *Parachleuastochoerus*, have relatively smaller third molars, suggesting closed forest inhabitants. Next groups from the latest Miocene, *Propotamochoerus* spp., are more open forest inhabitants compared to the genera from the Middle Miocene and their diet varies from frugivorous to folivorous. The third group, Pliocene *Sivachoerus* has large and complex third molars, suggesting it is a predominantly folivorous in open forest habitats (Figure 4). Thus, the paleontological records of Myanmar suids suggest that the predominantly frugivorous forest dwellers gradually became extinct and the folivorous, open habitat species alternatively appeared in the early Late Miocene. In the Pliocene, it was replaced by predominantly folivorous species in more open habitats. After the Pleistocene, hyperbrowser/frugivore species in closed forest habitats have exclusively survived in Myanmar.

### Floral transition patterns in the Neogene of Myanmar

The Late Miocene to early Pliocene period is distinct for the global cooling and aridification which led a global terrestrial ecology change. A world where plants used C3 photosynthesis was almost exclusively replaced by one where C4 photosynthesis was a major component (Cerling *et al.*, 1997). Such an abrupt change inevitably press terrestrial mammals for a major change in their food resources, bring the faunal turnover where most browsers consuming C3 plants (shrub and herb) were replaced by grazers feeding mainly C4 plant diet. The floral transition from C3 to C4 was demonstrated by using radioisotopic analysis and accompanying faunal turnover was recorded, in the Miocene of Siwalik, northern Pakistan (Barry *et al.*, 2002).

The land mammalian fauna in the Neogene of Myanmar has been considered to be similar to those of Siwalik of India/Pakistan rather than those of southern China and northern Thailand. The paleoecological evolution in Myanmar fauna was therefore, examined in the comparisons with the Siwalik fauna, in the most ways. The diet of suids and hippos strongly relies on their environment, so the chronological differences in their diet indicate the ecological transitions in their habitats. Information on the paleohabitats allows us to reconstruct the paleoenvironmental changes in Myanmar, based on precise knowledge concerning those in Siwalik.

The present studies identified three distinct suid taxa in Myanmar, which are in part different from those in Siwalik as for the appearance and extinction periods, diets, and habitats. The pattern of faunal transition in the suids strongly suggests a critical floral change at the late Miocene in Myanmar. The predominantly frugivorous *Tetraconodon* disappeared in the Early Late Miocene of Myanmar and Siwalik, and the first evidence of C4 plant was recorded in that period of Siwalik (Barry *et al.*, 2002). *Propotamochoerus hysudricus* in Siwalik and Myanmar probably appeared before the extinction of *Tetraconodon*, suggesting the C3-C4 floral transition occurred in the period of their coexisting. The extinction of *P. hysudricus* was contemporaneous with the wide spreading of C4 grass in the latest Miocene of Siwalik (Nelson, 2003). In Myanmar, this species survived until the Early Pliocene to have coexisted together with *Sivachoerus prior*, suggesting that the C3-C4 floral transition accompanying the last faunal turnover may have occurred to bring wide spreading of C4 plants in the Early Pliocene of Myanmar, later than in the Late Miocene of Siwalik.

*Hippohyus*, a typical grazer, was not recorded in Myanmar, while it existed contemporaneously with *Sivachoerus* and disappearing *Propotamochoerus* in the latest Miocene and Pliocene of Siwalik. It appeared at the beginning of C4 grassland expansion in Siwalik, so this genus has been used as evidence for grassland environment (Pickford, 1988). If there were expanded grassland in the latest Miocene and Pliocene of Myanmar, *Hippohyus*

might have entered into this area earlier than *Sivachoerus*, who prefers more open land. Thus, Myanmar was probably covered by the more open forests preferred by *Sivachoerus* rather than grassland in the Pliocene.

Large mammals, such as *Potamochoerus* and *Hexaprotodon palaeindicus*, disappeared at the end of Early Pleistocene in Southeast Asia, including Myanmar. The mega fauna extinction is probably accounted for not only by a single floral factor but more likely by a combination of human activity and climatic factors (Louys *et al.*, 2007). Finally, only *Sus scrofa*, a small-sized closed forest inhabitant, survives at the present day in the forest of Myanmar, as a member of the pre-Pleistocene to present fauna.

### Conclusion

Three subfamilies, seven genera, and at least 12 species of fossil Suidae have been discovered from the Neogene of Myanmar, *Listriodon pentapotamiae* (Middle Miocene), five species of *Tetraconodon* (Middle to early Late Miocene), *Parachleuastochoerus* sp. (early Late Miocene), two species of *Propotamochoerus* (Late Miocene - Early Pliocene), *Sivachoerus prior* (Pliocene), cf. *Sus* sp. (Middle to Late Pliocene) and *Potamochoerus* sp. (Pleistocene) *Sus scrofa* (Recent). The paleontological record from the suids fossils of Myanmar indicates that the predominantly frugivorous forest dwellers became extinct and the first folivorous open habitat species has appeared in the early Late Miocene. The occurrence of *Propotamochoerus* and even of *Sivachoerus* in Myanmar suggests that the last faunal turnover for the extinction of C3-C4 floral transition period species in Myanmar may have been the Early Pliocene, which is not earlier than the Late Miocene of Siwalik in northern Pakistan. Although the faunal transition in Myanmar suids is very similar in sequence to those in Siwalik, transition period for C3 to C4 dominated habitats in Myanmar is later than that in Siwalik. It suggested that the closed forest habitat have relatively maintained until the Early Pliocene and the beginning of the aridification was delayed in Myanmar compared to Siwalik.

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