

## **Paleoecology of the Large Mammalian Fauna from the Irrawaddy Formation, Myanmar**

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### **Abstract**

The mammal species composition and abundance are analyzed based mainly on the 206 dental specimens which were collected from the three localities such as Kyauksaungsan, Tebingan, and Kyitsonbwe in Magway Region, central Myanmar. The 24 species of large mammalian fauna: 8 proboscideans, 12 artiodactyls, 3 perissodactyls and one carnivore were recognized in these dental specimens. The interpretation of the paleoecological conditions for the Mio-Pleistocene faunal assemblages of the Irrawaddy Formation are elaborated in the present study. The Neogene paleoecological patterns of the Irrawaddy Formation in Myanmar suggest a shift from open woodland with drier conditions to closer forest habitats with more humid conditions during late Middle Miocene to Early Pleistocene.

**Key words:** Large mammals, Irrawaddy Formation, Neogene paleoecological patterns, Early Pleistocene pattern

### **Introduction**

The Irrawaddy Formation (Middle Miocene to Early Pleistocene) in Myanmar, composed of various deposits of a fluvial palaeoenvironment, is famous for preserving fossil remains of a land mammal fauna including proboscideans, rhinos, suids, hippos, giraffids, bovids, and equids (Lydekker, 1876; Pilgrim, 1906, 1926; Colbert 1938, 1943; Osborn, 1942; Moe Nyunt, 1987). Recent collection has yielded more fossils and completed with a large amount of specimens comprising many remains of mammalian dentition (Thaung Htike *et al.*, 2005, 2007; Takai *et al.*, 2006; Chavasseau *et al.*, 2006, 2010; Chit Sein *et al.*, 2006, 2009; Chit Sein & Tin Thein, 2008, 2009). The specimens herein described were collected from three rich fossil localities such as Kyauksaungsan, Tebingan, and Kyitsonbwe in the Magway Region of central Myanmar (Figure 1).

The paleoecological conditions for the fauna of the Irrawaddy Formation are poorly known. Moe Nyunt (1987) described the general ecological characters of the Pleistocene fauna of the upper part of the Irrawaddy Formation, the Plateau Gravel and the Red Earth from the Seikpyu area. However, the paleoecological conditions for the dominant Mio-Pliocene faunas of the Irrawaddy Formation have not been studied so far, because of an insufficient number of specimens. Thus, interpretation of the paleoecological conditions for the Mio-Pleistocene faunal assemblages of the Irrawaddy Formation are elaborated in the present study.

Body size is a useful predictor of species adaptations, because it is correlated with many aspects of life history, ecology, and behaviour (Morgan *et al.*, 1995). Moreover, tooth morphology and body size provide strong clues to dietary preference among the mammalian groups (Gunnell *et al.*, 1995). In the present study, the mammalian community structure from the Middle Miocene to the Early Pleistocene is reconstructed based on the characteristics of taxonomic composition, species diversity and abundance, and besides on body size distribution and dental morphology.

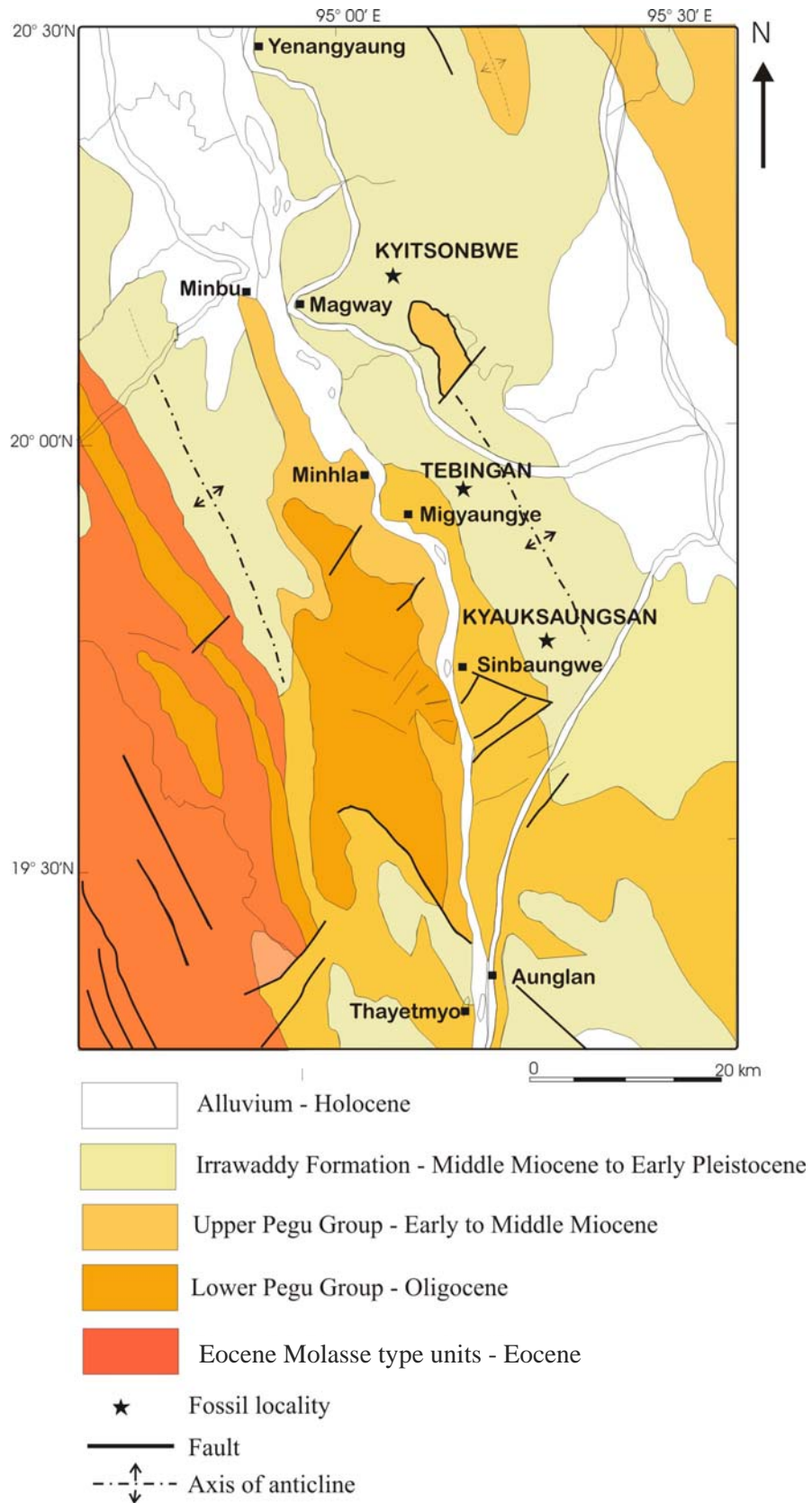


Figure 1 Regional geological map of the three fossil localities (modified after Geological Map of Myanmar, 1977; 1: 1,000,000 scale)

### **Aim of Study**

The present work is aimed to study the dental morphology, faunal composition, species diversity and calculation of body weight of the large mammalian faunas from the Irrawaddy Formation in order to reconstruct the paleoecological conditions of those faunas in the past.

### **General Geology**

The sediments of the Irrawaddy Formation are widely exposed in all three localities (Figure 1). The considerable amount of the fossil specimens was collected from these sediments of the Irrawaddy Formation. It is mainly composed of fluvial channel sediments associated with over bank deposits. This formation consists mainly of light grey to yellowish brown, medium-to thick-bedded, coarse-grained, gritty, and loosely consolidated sandstones with intercalated siltstones and light grey claystone or mudstone.

The rocks of the lower part of this formation is characterized by more arenaceous, false bedded, massive, ferruginous sandstones intercalated with silty clay. Vertebrate fossils are relatively rare.

The upper part is characterized by loose, poor to moderately sorted, coarse-grained sandstones and conglomerates, with large cross stratification and large amount of sandstone nodules. Fossil woods and concretions are also abundant. It yields abundant vertebrate fossils.

### **Materials**

A total of 293 fossil remains of large mammals were collected from the sediments of Irrawaddy Formation in three localities. Among them, 206 fossil teeth remains of large mammals are analyzed in this study. The studied material includes 24 mammalian species: eight proboscidean species (two genera belonging to one family), 12 artiodactyl species (eight genera belonging to four families), three perissodactyl species (three genera belonging to two families), and one carnivore species (Table 1).

### **Method of Study**

The body mass of the mammal species is estimated to compare extant and fossil communities (Legendre, 1986, 1989). Body mass estimates for the mammal species of the Irrawaddy Formation are based mainly on dental measurements, because teeth are abundant in the fossil record and they are more definitely identified at species level than postcranial elements. Morgan *et al.* (1995) pointed out that although tooth-based body mass estimates are problematic to use as discussed by Gould (1975), Smith (1984), Damuth (1990), Fortelius (1990), and Janis (1990), nevertheless, the major trends in body-size distributions within a community based on dental measurements are generally robust.

Table 1 List of mammals found in the Irrawaddy Formation of the here described compared to the mammal assemblage of the Siwalik Group in Indo-Pakistan (Siwalik, China and Europe data cited in Colbert 1935; Pilgrim, 1937, 1939; Heissig, 1972; Pickford 1988; Made, 1999; and Tassy, 1983).

Taxa	Middle Miocene	Late Miocene	Pliocene - Pleistocene		
	SIWALIK GROUP OF INDO-PAKISTAN REGION				
	Lower	Middle		Upper	
	Chinji	Nagri	Dhok Pathan	Tatrot	Pinjor
<b>PROBOSCIDEA</b>					
Stegodontidae					
			+		
					+
			+		
			+		
					+
<b>ARTIODACTYLA</b>					
Suidae					
			+	+	
			+		
		+			
Hippopotamidae					
				+	+
Bovidae					
		+	+		
	+				
			+		
	+				
			+		
Giraffidae					
		+	+		
<b>PERISSODACTYLA</b>					
Rhinocerotidae					
	+	+	+		
					+
Chalicotheriidae					
	+	+			
<b>CARNIVORA</b>					
Amphicyonidae					
	+				

\* the age from the locality of Lufeng and Yunnan, China; \*\* the age from the locality of Europe

The estimated values are based on the surface area of M<sub>1</sub>, because of the availability of specimens and the emphasis on this estimator in previous studies (Legendre, 1986, 1989; Damuth, 1990; Morgan *et al.*, 1995; Tsubamoto *et al.*, 2005). In Table 1, the body mass of the

mammal species of the Irrawaddy Formation is calculated by using the equation and parameters of Legendre (1986). However, the estimated mean body masses for the suid *Tetraconodon magnus* and the rhino *Brachypotherium perimense* were taken from Morgan *et al.* (1995), because of the lack of  $M_1$ . Some species such as the stegodontids *Stegolophodon* sp. A, *Stegolophodon* sp. B, *Stegodon elephantoides*, *Stegodon insignis*, *Stegodon* sp.; the giraffid *Hydaspitherium megacephalum*, the hippopotamid *Hexaprotodon* cf. *sivalensis* and the suid cf. *Sivachoerus* sp. are not included in the body mass estimation, because no  $M_1$  are recorded of these species and their body masses have never been estimated. However, at least it can be concluded from their teeth sizes that these species were very large-sized mammals (> 250 kg). The absence of medium-sized (500 g to 8 kg) and small-sized mammals (< 500 g) is due to sampling bias of the surface-prospecting performed to obtain the fossils for the present study.

The mammal species composition and abundance were recorded based mainly on the dental specimens. The taxonomic faunal composition is given in the number of species per family (Figure 2). The species abundance is calculated based on the number of specimens in each family as shown in pie charts (Figure 3).

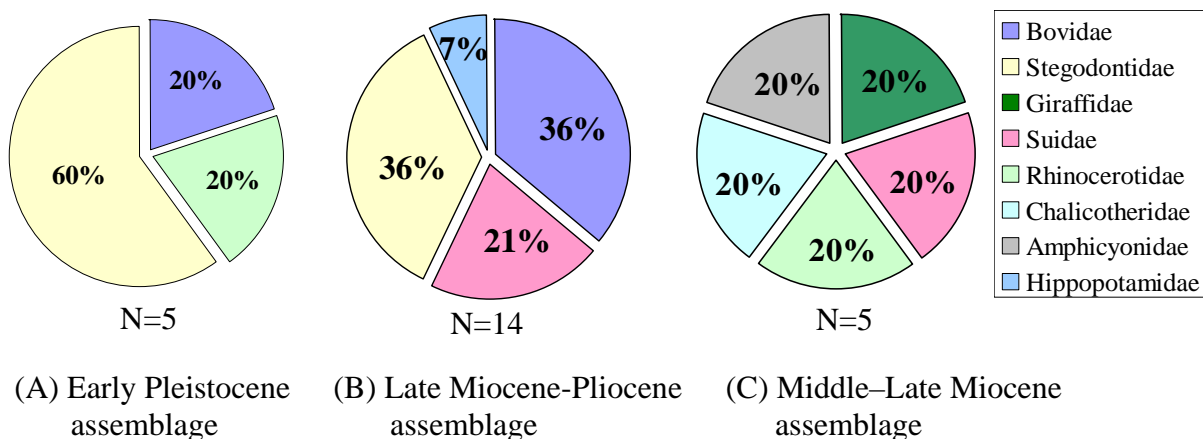


Figure 2 Taxonomic compositions of the three assemblages of the Irrawaddy Formation (based on the number of species)

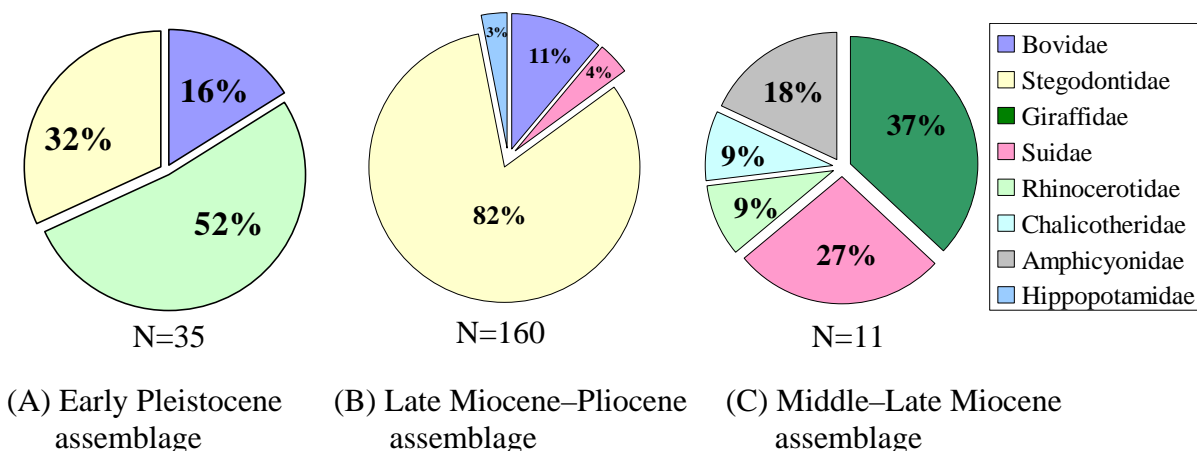


Figure 3 Taxonomic abundance of the three assemblages of the Irrawaddy Formation (based on the number of fossil specimens)

## Results

The mammalian fauna of Irrawaddy Formation include 24 species: 8 proboscideans, 12 artiodactyls, 3 perissodactyls and one carnivore (Table 1). Based on biostratigraphy and species composition, three time-related assemblages are distinguished in this study (Figure 2 & 3).

In the Middle to Late Miocene assemblage, there are five species of five families (Figure 2, A) and the diversification in each family is similar. However, the giraffid is the most abundant element, and the suids and the carnivores are common, but others are rare in terms of collection size (Figure 3, A).

In the Late Miocene to Pliocene assemblage, 14 species of four families are recorded (Figure 2, B). The faunal diversity is similar to the abundance of specimens. The stegodontids are the most diverse taxa as well as the most abundant elements in this assemblage (Figure 3, B). Bovids are common, but suids and hippopotamids are rare.

In the Early Pleistocene assemblage, five species of three families are recorded (Figure 2, C). Stegodontids are the most diverse taxon in this assemblage, but rhinocerotids are the most abundant element in the specimen collection size (Figure 3, C).

According to the body mass estimation, the Middle to Late Miocene fauna of Irrawaddy Formation is composed of very large-sized (>250 kg) species (Table 2). In the Late Miocene to Pliocene assemblage, the fauna of the Irrawaddy Formation are mostly large-sized species (>100 kg) except the suids *Propotamochoerus hysudricus* and *Propotamochoerus wui* (<100 kg) (Table 2). In the Early Pleistocene assemblage of the Irrawaddy Formation three *Stegodon* species and *Rhinoceros sivalensis* are represented, which are very large-sized animals (>1000 Kg).

Table 2 Estimated mean body weights of the mammals of the Irrawaddian fauna. They are calculated by using the equation and parameters of Legendre (1986) on the mean  $M_1$  area of each mammal.

Rank	Taxa	L	W	area	Slope (a)	Intercept (Ln b)	Ln Y	Ln X	Body Weight (kg)
1	<i>Stegolophodon stegodontoides</i>	148.44	81.48	12094.89	1.54	3.12	9.40	17.58	42842
2	<i>Stegolophodon cf. stegodontoides</i>	128.38	75.66	9713.23	1.54	3.12	9.18	17.24	30577
3	<i>Stegolophodon cf. latidens</i>	106.8	53.3	5692.44	1.54	3.12	8.65	16.41	13442
4	<i>Rhinoceros sivalensis</i>	45.7	30.8	1407.56	1.56	3.27	7.25	14.61	2203
5	<i>Brachypotherium peremense</i>	-	-	-	-	-	-	14.50	1983
6	<i>Tetraconodon magnus</i>	-	-	-	-	-	-	13.10	489
7	<i>Amphicyon major</i>	32.44	18.55	601.76	1.92	0.71	6.40	13.01	447
8	<i>Chalicotherium salinum</i>	25.3	14.5	366.85	1.56	3.27	5.90	12.50	269
9	<i>Plesiaddax simplex</i>	19.37	13.60	263.43	1.56	3.27	5.57	11.98	160
10	<i>Selenoportax vexillarius</i>	20.39	12.83	261.60	1.56	3.27	5.57	11.97	159
11	<i>Tragoportax cf. amalthea</i>	18.90	13.08	247.21	1.56	3.27	5.51	11.89	145
12	<i>Selenoportax sp.</i>	19.70	12.11	238.57	1.56	3.27	5.47	11.83	137
13	<i>Tragoportax cf. rugosifrons</i>	18.75	11.73	219.94	1.56	3.27	5.39	11.70	121
14	<i>Propotamochoerus hysudricus</i>	13.36	12.16	162.46	1.56	3.27	5.09	11.23	75
15	<i>Propotamochoerus wui</i>	14.0	10.5	147.00	1.56	3.27	4.99	11.07	64

## Discussion

### Middle to Late Miocene paleoecology

The composition of this assemblage is smaller in species diversity and specimen number than the Late Miocene to Pliocene assemblage [Figures 2(B); 3(A)]. The absence of stegodontids possessing brachyodont teeth and the smaller mammals in the Middle to Late Miocene assemblage might indicate the humid woodland habitats with an abundance of low-quality vegetation.

All mammal species of this assemblage are very large-sized (>250 kg) (Table 2). These sized species are most numerous in woodland to grassland habitats, with an abundance of low-quality vegetation in the modern faunas (Morgan *et al.*, 1995; Legendre, 1989). The tetraconodont suids correspond with the suoid size class 4 (201 – 1000 kg) of Fortelius *et al.* (1996). This size class contains forms from woodland to grassland mosaic habitats, which are more open than the habitats of the smaller sized *Propotamochoerus*.

The teeth of the suid *Tetraconodon* sp. cf. *magnus* show a combination of thick enamel and conical premolars with hyaenalike macrowear, which might indicate the cracking of hard food items such as hard-shelled seeds. It was an important component of the diet of *Tetraconodon* species (Fortelius *et al.*, 1996).

The milk tooth of *Brachypotherium perimense* is broad and bunolophodont, which indicates a diet of soft plants. It had a hippo like mode of life with certain percentage of reed grasses in the diet (Heissig, 1999a).

The lower molar of *Chalicotherium salinum* is lophodont comprising two crescents. The chalicotheres are leaf eating animal and they have been slow moving, partly bipedal, partly quadrupedal woodland dwellers (Heissig, 1999b).

Therefore, this assemblage indicates woodland habitats which were more open than the habitats of the Late Miocene to Pliocene assemblage.

### Late Miocene to Pliocene paleoecology

The Late Miocene to Pliocene assemblage is composed of much more specimens and is more diverse in species than the Middle to Late Miocene assemblage (Figure 2, B). The presence of great number of bovids as well as the absence of cervids and tragulids indicate a community adapted to open and dry conditions (Koufos, 2006). The *Tragoportax* cf. *amalthea* and *Tragoportax* cf. *rugosifrons* are the large forms (Table 2) which might have lived in a moderately humid to very humid habitat with open to closed woodlands (Spassov & Geraads, 2004).

However, the most abundant taxa are *Stegolophodon* species, which exhibit brachyodont cheek teeth with thick enamel and relatively few cementums. The molar brachyodonty in stegodonts indicates an adaptation to browsing or mixed feeding in forested environs (Janis, 1986). Moreover, the fauna have brachyodont teeth, which are adapted to a diet of soft plants, such as buds, young leaves, and fruits, suggesting that their habitats were not open lands but a forested/ woodland environment (Tsubamoto *et al.*, 2005).

The estimated body masses of *Propotamochoerus "hysudricus"* and *Propotamochoerus wui* are comparable with the suoid size class 2 (21 – 80 kg) of Fortelius *et al.* (1996). They stated that the extant suoids of this smaller size class contain a mixture of forms like larger peccaries and the bush pig, but all of them do not inhabit open environments, and some are exclusively forest animals (Fortelius *et al.*, 1996). Moreover,

*Propotamochoerus* has a dental morphology with high point cusps. This dentition is comparable to certain cercopithecoid primates and tragulids, which are adapted to the forest (Fortelius *et al.*, 1996). This might indicate a similar diet for *Propotamochoerus* found in forests.

The hippopotamid, *Hexaprotodon* cf. *sivalensis*, indicates a semi-aquatic habitat. Most of the representatives of this assemblage are large-sized mammals (>250 kg) (Table 2). The large number of these large-sized species indicates certain humidity (Morgan *et al.*, 1995).

According to the above mentioned facts, the habitats of the Late Miocene to Pliocene assemblage of the Irrawaddy Formation can be interpreted to have been a mosaic of diverse vegetation types, including forest, humid/ subhumid woodland, a large river and neighbouring semi-aquatic areas to accommodate the diversity of the inferred diets.

### **Early Pleistocene paleoecology**

The Early Pleistocene assemblage of the Irrawaddy Formation consists mainly of stegodontids [Figure 3(C), 2(C)] and rhinocerotids. These are very large-sized mammals (>1000 kg) (Table 2).

The *Stegodon* species have brachyodont cheek teeth which are adapted to a forested environment (see above). These stegodontid and rhinocerotid species might have flourished in a thick forest as modern Asian elephants and rhinoceroses.

Therefore, the paleoenvironment of the Early Pleistocene is suggested as thick forested humid habitats.

### **Conclusion**

A total of 293 remains of fossil large mammals were collected from the sediments of Irrawaddy Formation in three localities such as Kyauksaungsan, Tebingan, and Kyitsonbwe in Magway Region, central Myanmar. The mammal species composition and abundance were analyzed based mainly on the 206 dental specimens. 24 species of mammalian fauna: 8 proboscids, 12 artiodactyls, 3 perissodactyls and one carnivore are identified from these dental specimens. The mammalian community structure from the Miocene to Pleistocene is reconstructed based on the characteristics of taxonomic composition, species diversity and abundance, body size distribution and dental morphology in the present study.

Conclusively the Neogene paleoecological patterns of the Irrawaddy Formation in Myanmar suggest a shift from open woodland with drier conditions to closer forest habitats with more humid conditions during late Middle Miocene to Early Pleistocene. This interpretation is supported by the hypothesis of Morgan *et al.* (1995) and Gunnell *et al.* (1995) in which Miocene to Pliocene mammalian fauna of the Siwalik Group from northern Pakistan suggested that a shift from open woodland to Savannah scrub by the body-size structure and trophic structure and composition. The Early Pleistocene pattern suggested as thick forested humid habitats. However, there has been no interpretation as a comparison between Myanmar and Indo-Pakistan, and other areas so far. It would be necessary to find more mammalian fossils, especially middle and small-sized mammals to get more complete interpretation in the future.



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