Stable isotope analysis of the tooth enamel of Chaingzauk mammalian fauna (late Neogene, Myanmar) and its implication to paleoenvironment and paleogeography

Zin-Maung-Maung-Thein [a,*], Masanaru Takai [b], Hikaru Uno [c], Jonathan G. Wynn [d], Naoko Egi [b], Takehisa Tsubamoto [e], Thaung-Htike [f], Aung-Naing-Soe [g], Maung-Maung [h], Takeshi Nishimura [b], Minoru Yoneda [c]

[a] Mandalay University, 73rd Road, Mandalay, Myanmar
[b] Primate Research Institute, Kyoto University, Inuyama, Aichi 484-8506, Japan
[c] University of Tokyo, Kashiwa, Chiba 277-8562, Japan
[d] University of South Florida, 4202 E Fowler Ave, Tampa, FL 33620, USA
[e] Center for Paleobiological Research, Hayashibara Biochemical Laboratories, Inc., Okayama 700-0907, Japan
[f] Shwebo Degree Collage, Shwebo, Myanmar
[g] Sittwe University, Sittwe, Myanmar
[h] Hinthada University, Hinthada, Myanmar

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ABSTRACT

The tooth enamel of a mammalian fauna from the uppermost Miocene/lower Pliocene Irrawaddy sediments at Chaingzauk, west-central Myanmar were analyzed using stable carbon and oxygen isotopes. The $\delta^{13}C$ values of porcupines, tragulids, rhinocerotids, suids and proboscideans show that these mammals preferentially consumed C_3 plants in a wooded environment, whereas the $\delta^{13}C$ values of bovids and hippopotamids indicate that they were grassland-adapted grazers to mixed feeders. In contrast to the thorn scrub, grassland and shrubland vegetation of present-day central Myanmar, stable carbon isotope results of the Chaingzauk fauna suggest a presence of wooded environment in the Chaingzauk area at that time. Present-day arid conditions are likely to have been caused by the uplift of the Indo-Burman Ranges due to the Himalayan Orogeny during the late Miocene to Pliocene, resulting in a rainshadow effect in central Myanmar. Furthermore, southward marine regression due to the rapid influx of sediments from the Indo-Burman Ranges, Eastern Himalayan Ranges and Sino-Burman Ranges into the Central Myanmar Basin in the Miocene to Pliocene might have played an important role in the aridification of this region since the lower Pliocene.

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1. Introduction

The Neogene Irrawaddy sediments are widely distributed along the Ayeyarwady (Irrawaddy) and Chindwin Rivers in central Myanmar (Fig. 1), and yield a variety of fossils such as silicified wood, molluscs, and terrestrial and aquatic vertebrates. Mammalian fossils from these sediments have been documented since the late 19th Century (e.g. Lydekker, 1876) and have been biostratigraphically correlated with those from the Siwalik Group of the Indian Subcontinent (Bender, 1983; Colbert, 1938, 1943; Pilgrim, 1939).

The stable isotopic evidence from paleosols and fossil teeth on the Indian Subcontinent indicate that many C_3 plant-dominant forests were replaced by C_4 grasslands between 8 Ma and 6 Ma, corresponding to the global floral turnover (Cerling et al., 1993; Quade and Cerling, 1995; Quade et al., 1992), and *Sivapithecus*, a large hominoid, became extinct presumably due to the fragmentation of forests (Nelson, 2007). Such floral transitions also probably occurred in Southeast Asia due to the effect of an enhanced monsoon since the Miocene. For example, the environment of the late Middle Eocene of central Myanmar was warm and humid with tropical forests near the sea (Tsubamoto et al., 2005). The abundance of silicified fossil wood like Dipterocarpaceae (Prakash, 1973) and remains of forest dwelling mammals from the early Neogene sediments of Myanmar suggest the persistence of tropical rainforests in the early Neogene. However, present day central Myanmar is relatively arid with little forest cover, and is the driest region in Southeast Asia, receiving between 600 and 1000 mm of annual rainfall with a dry season lasting for about eight months (Kress et al., 2003). Accordingly, it is expected that there was a large shift in the paleoenvironment from relatively humid conditions to the present day arid conditions during the late Neogene in central Myanmar. In
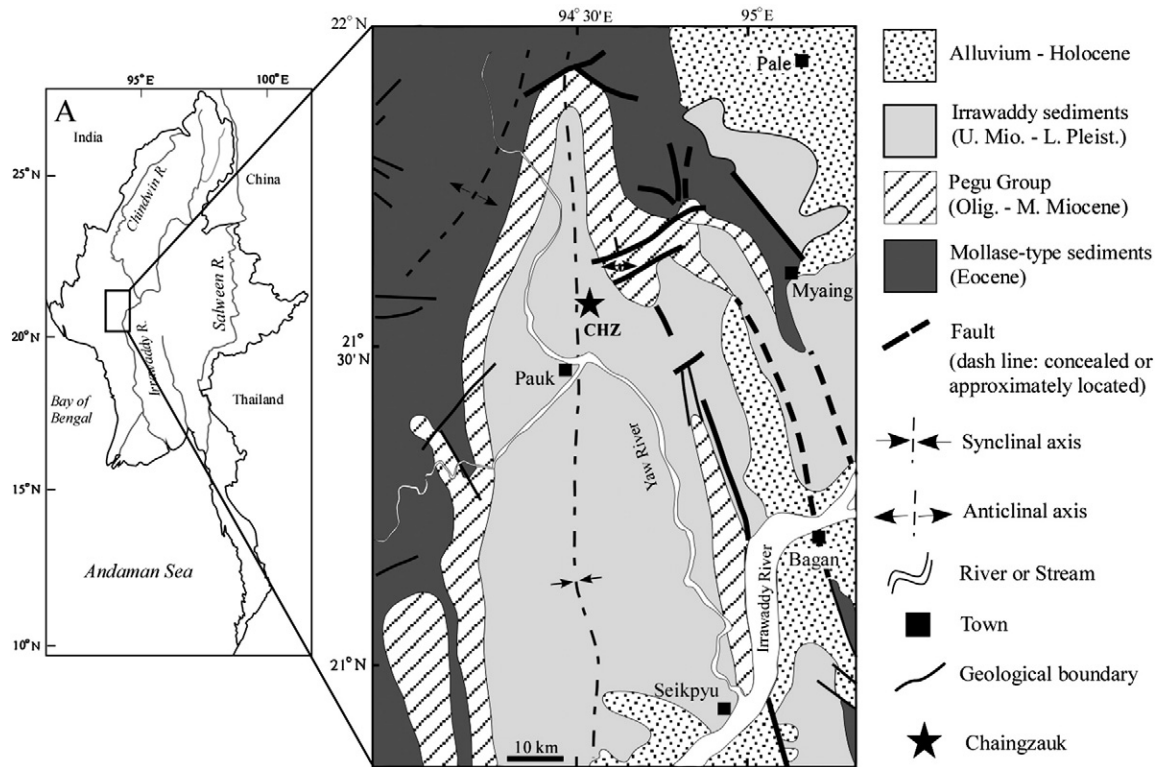
Fig. 1. A, Geographic position of Chaingzauk area, Pauk township, central Myanmar and its geological map (after the Geological Map of Burma; Earth Sciences Research Division, 1977).

spite of these expected climatic changes in Southeast Asia, precise paleoenvironmental analyses using stable isotopes in this region have not yet been well documented.

In this article, we explore the paleoenvironmental change in Southeast Asia during the late Neogene in relation to the Himalayan Orogeny and the formation of the monsoon, using stable carbon and oxygen isotope analyses of tooth enamel of the fossil mammals discovered in the Irrawaddy sediments at the Chaingzauk area, in the western part of central Myanmar. Then, we reconstruct the paleoenvironment of the Chaingzauk fauna. Finally, we discuss the environmental change from the humid conditions at the Miocene/Pliocene boundary to the relatively dry conditions in central Myanmar, on the basis of the geological and paleogeographical context.

2. Geological and paleontological setting

2.1. Geological background

The Neogene Irrawaddy sediments (= Fossil wood Group: Theobald 1869; = Irrawaddian Series: Noetling, 1900; = Irrawaddy Formation: Aung Khin and Kyaw Win, 1969; = Irrawaddy Group: Bender, 1983) are mainly composed of the fluviatile sediments derived from the Indo-Burman Ranges, Eastern Himalayas and Sino-Burman Ranges. Its thickness has been estimated to be 2000 to 3000 m (Bender, 1983; Wandrey, 2006). These sediments unconformably overlie the predominantly marine deposits of the Oligocene to Miocene Pegu Group, and are overlain by the middle Pleistocene to Holocene Terrace Deposits (Aung Khin and Kyaw Win, 1969; Stamp, 1922).

The Irrawaddy sediments are traditionally subdivided into the "Lower Irrawaddy" and "Upper Irrawaddy" based on the lithological and palaeontological criteria (Bender, 1983; Colbert, 1938; Stamp, 1922). The Lower Irrawaddy is correlated with the Dhok Pathan Formation of the Siwalik Group, suggesting a late Miocene to early Pliocene age, based on the vertebrate fossils. On the other hand, the Upper Irrawaddy has conventionally been referred to the Early Pleistocene (Bender, 1983; Colbert, 1938, 1943). The Upper Irrawaddy

fauna shows close resemblance to the Tatrot and Pinjor Faunas of the Indian subcontinent, suggesting the extension of its geological age to the Pliocene. Note: Although the Pliocene–Pleistocene boundary has recently been redefined to 2.59 Ma (IUGS, 2009), the Pliocene and Pleistocene here refer to the former boundary age (1.8 Ma) to avoid misrepresenting previous work on correlations with the Siwalik Fauna.

The Lower Irrawaddy sediments in the Chaingzauk area are exposed near the north–south trending axis of the Salin Syncline in the western part of central Myanmar (Fig. 1). In the syncline, the Late Miocene to Early Pleistocene massive sandstone and gravels of the Irrawaddy sediments are exposed in the central part, while the Eocene to Miocene deposits outcrop in the eastern and western flanks (Trevena et al., 1991). The sediments of the syncline are thick, estimated as more than 9000 m in thickness, containing lithic sandstones that alternate with the transgressive shallow marine shales (Trevena et al., 1991). Sedimentary facies and paleocurrent studies indicate that north and south prograding tidal deltas and associated Proto-Ayeyarwady River deposited sediments in this syncline (Rodolfo, 1975; Stamp, 1922; Trevena et al., 1991).

The fossil-bearing Irrawaddy sediments at Chaingzauk cover about 16 km^2 and are dominated by pebbly sandstone, weakly consolidated sandstone and siltstone with clay intercalation. Trough cross stratification, as well as parallel laminations, are observed in sandstone horizons. The vertebrate fossils were mostly recovered from pebbly sandstone horizons. In the columnar section of one of the fossil bearing localities, the lower part of the sequence is dominated by silt and fine-grained sandstone with lamination and trough stratification, whereas the upper part is dominated by pebbly sandstone, suggesting deposition in a fluvial environment with moderately strong energy conditions (Reading, 1996) (Fig. 2).

2.2. Geological age of the Chaingzauk mammalian fauna

Cotter (1938) first reported the remains of ungulates from Chaingzauk area and suggested its correlation with the Tatrot Fauna
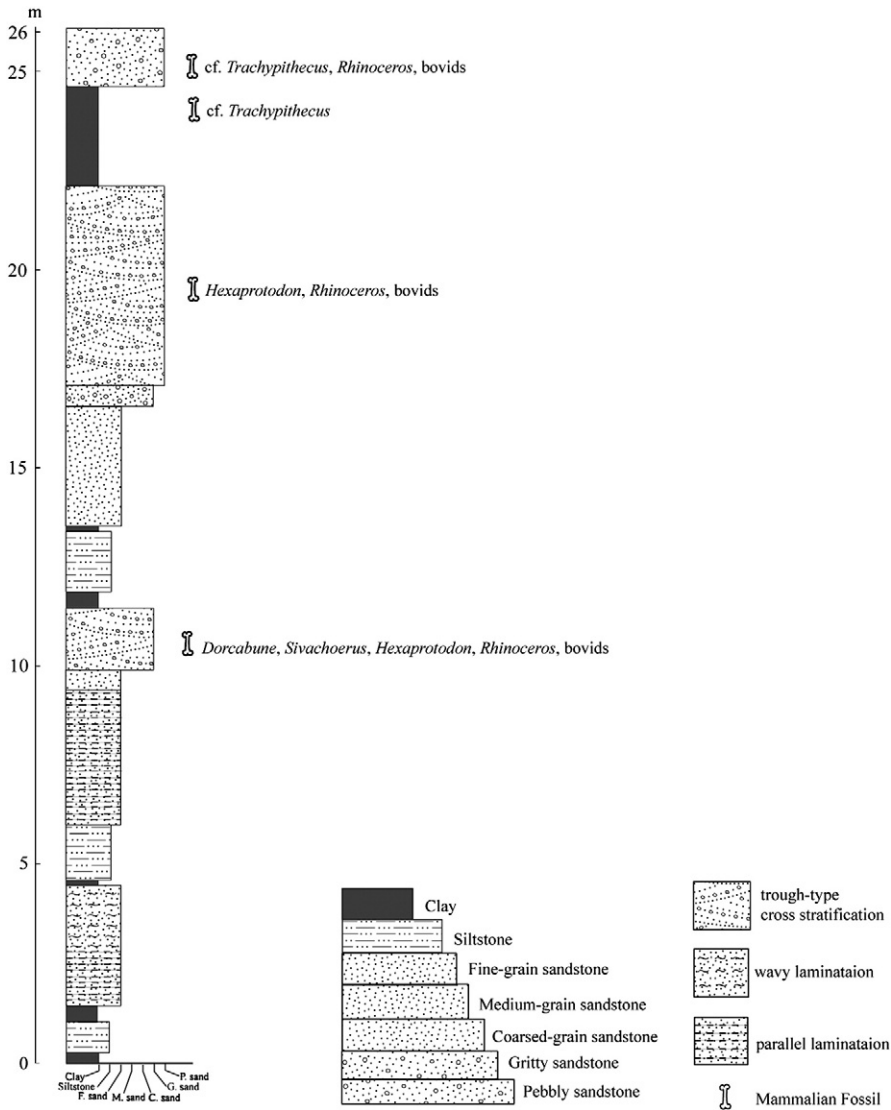
Fig. 2. Columnar section of the fossil-bearing Irrawaddy sediments at Chaingzauk.

of the upper Siwalik Group. Pilgrim (1939) also described a bovid, *Tragoportax* cf. *islami* from same area, suggesting its correlation with the Dhok Patan Fauna. However, there was no paleontological expedition in this area after these preliminary reports until the Myanmar–Japan Joint Fossil Expedition Team (collaboration between the Primate Research Institute, Kyoto University, Japan and the Government of Myanmar) began paleontological research at Chaingzauk in 2003. This effort has since recovered more than 1200 fossil specimens by surface collection.

The Chaingzauk fauna consists of colobine monkeys, porcupines, carnivores, tragulids, boars, bovids, hippopotamuses, anthracotheres and elephants representing 15 genera of mammals (Table 1). Among the Chaingzauk mammals, the presence of the hippopotamid *Hexaprotodon* suggests that the geological age of the Chaingzauk is not older than 6 Ma because they are suggested to have first dispersed into Asia around 6.3 Ma from Africa, and *Hex. sivalensis* appeared in the Indian Subcontinent about 6 Ma (Van Der Made, 1999; Barry et al., 2002; Badgley et al., 2008). The occurrence of the large-sized suid *Sivachoerus*, which is assumed to have migrated into South and Southeast Asia in the latest Miocene (Pickford, 1988), also constrains the lower biostrati-graphical range of the Chaingzauk fauna from ~6 to ~5 Ma. On the other hand, the occurrence of the suid *Propotamochoerus hysudricus* suggests an older geological age correlation because this clade was distributed in Siwalik of northern Pakistan from 12.2 to 6.5 Ma (Badgley et al., 2008).

However, it survived until the latest Miocene (~6 Ma) in the Ertemte Fauna of Inner Mongolia (Li et al., 1984) and the Early Pliocene in Europe (Hünermann, 1999), constraining the upper biostratigraphical range

Table 1
List of mammalian fossils from the Irrawaddy sediments at Chaingzauk area.

Primate	Hippopotamidae
Cercopithecidae	*Hexaprotodon sivalensis*
Cf. *Trachypithecus sp.*	*Hexaprotodon iravaticus*
Rodentia	Suidae
Hystricidae	*Sivachoerus prior*
Hystrix sp.	*Propotamocheorus hysudricus*
Carnivora	Bovidae
Ursidae	Cf. *Tragoportax sp.*
Agriotherium sp.	Cf. *Selenoportax vexillaris*
Hyaenidae	Cf. *Selenoportax lydekkeri*
Cf. *Ictitherium sp.*	**Perissodactyla**
Artiodactyla	Rhinocerotidae
Anthracotheriidae	*Rhinoceros sp.*
Merycopotamus dissimilis	**Proboscidea**
Gen. et. sp. indet	Stegodontidae
Tragulidae	*Stegodon sp.*
Dorcatherium sp.	Gomphotheriidae
Dorcabune Cf. *anthracotherioides*	*Sinomastodon sp.*

of the Chaingzauk fauna to around 5 to 4 Ma. Likewise, the occurrence of tragulids, *Dorcatherium* and *Dorcabune*, also constrains the upper biostratigraphical range of Chaingzauk fauna to ~6 Ma because they were distributed from 14 to 6 Ma on the Indian Subcontinent (Badgley et al., 2008) and in the Late Miocene of China (Lucas, 2001; Rössner, 2007).

3. Application of stable isotopes in paleoenvironmental analysis

3.1. Carbon isotopes

Stable carbon isotope analysis of extant and extinct herbivores shows that the carbon isotope composition of body tissues reflects the composition of vegetation consumed (DeNiro and Epstein, 1978; van der Merwe and Vogel, 1978; van der Merwe, 1982; Lee-Thorp and van der Merwe, 1987; Lee-Thorp et al., 1989; Quade et al., 1995; Cerling et al., 2003a,b; Nelson, 2003). The carbon isotopic composition ($\delta^{13}C_{sample-VPDB} = ([^{13}C/^{12}C]_{sample}/[^{13}C/^{12}C]_{VPDB} - 1) \times 1000‰$) is informative of the diet and habitat of animals due to the differences in rates of ^{13}C and ^{12}C assimilation between plants, which are transferred to the body tissues of fauna feeding on them (DeNiro and Epstein, 1978). Particularly, tooth enamel of herbivores has been used to reconstruct paleodiet, habitats, and climate change because it is less susceptible to diagenesis than bone (Cerling et al., 1997a,b; Lee-Thorp et al., 1989).

Terrestrial plants use three types of metabolic pathways to fix CO_2 from the atmosphere: the C_3 photosynthesis pathway (the Calvin Cycle); the C_4 photosynthesis pathway (Hatch–Slack cycle) and the CAM (Crassulacean Acid Metabolism) pathway (Ehleringer et al., 1991; Bender, 1971). C_3 plants, which include most trees, shrubs, and high-altitude or high-latitude grasses, utilize the RuBisCO enzyme in the C_3 photosynthetic pathway to fix CO_2, forming three-carbon sugars. C_4 plants, which include tropical grasses and sedges, have an additional preliminary step that uses PEP carboxylase in meso-phyll cells to fix CO_2 resulting in a four-carbon acid, which is then transferred to bundle sheath cells, decarboxylated, and the CO_2 then fixed in a second step using RuBisCO (Farquhar et al., 1989). This physiological adaptation increases the CO_2 assimilation efficiency, and as a byproduct, the water use efficiency of C_4 plants is greater than that of C_3 plants. CAM plants, which include xeric-adapted desert succulents such as cacti, carry out carbon assimilation at night via the C_4 pathway; the CO_2 fixed is stored as four-carbon acids to be released during the day and fixed via C_3 pathway when the plant's stomata can be closed to conserve water (O'Leary, 1988).

Because of their different physiology, the C_3 and C_4 photosynthetic pathways exhibit different $\delta^{13}C$ values with most C_3 plants ranging from about $-22‰$ to $-35‰$, whereas most C_4 plants fall between $-10‰$ and $-15‰$ (Bender, 1971; Vogel, 1980). On the other hand, CAM plants yield $\delta^{13}C$ values between $-10‰$ and $-20‰$, partially overlapping with the range of C_4 plants (O'Leary, 1988). In this study, CAM plants were disregarded because such desert-adapted plants were unlikely to be observed in the vegetation types of the Miocene/Pliocene Chaingzauk flora.

The isotopic distinction between C_3 and C_4 plants allows the discrimination of browsing versus grazing diet in the isotopic composition of tooth enamel carbonate. Enamel bioapatite reflects the carbon isotopic composition of the plants consumed, with enrichment of ^{13}C due to metabolic processes and equilibrium constraints. The enrichment factor between the ingested plants and the enamel apatite ranges from 12 to 14‰ due to the different digestive system of herbivores (ruminant vs. nonruminant; Lee-Thorp and van der Merwe, 1987; Lee-Thorp et al., 1989; Cerling and Harris, 1999; Passey et al., 2005). The enrichment factor for all taxa analyzed in the present study is assumed to be 14‰, as suggested by Cerling and Harris (1999) in an extensive analysis of ungulates. Therefore, $\delta^{13}C$ values of enamel ranging from $-20‰$ to $-7‰$ represents browsing

C_3 plants. In contrast, a $\delta^{13}C$ value of $-1‰$ to 4‰, indicates grassland-adapted C_4 grazers. Intermediate $\delta^{13}C$ values between C_3 and C_4 plant eaters represent mixed feeding on both C_3 and C_4 plants (Cerling, 1997; Cerling and Harris, 1999; Kohn and Cerling, 2003). However, $\delta^{13}C$ values for extant herbivores are more ^{13}C-depleted by approx-imately 1.5‰ than for fossil mammals due to the atmospheric $^{12}CO_2$ enrichment during the industrial revolution (Cerling et al., 1997a,b; Passey et al., 2002). Therefore, $\delta^{13}C$ values between $-21‰$ and $-8‰$ reflect a C_3 diet, whereas values between $-2‰$ and 3‰ indicate a C_4 diet when interpreting the paleoenvironment (Cerling and Harris, 1999; Cerling et al., 2003a, b). The herbivores that fed in closed canopy forests are expected to have lower $\delta^{13}C$ values compared to those feeding in more open environments because of the recycling of CO_2 on the forest floor and low light intensities at ground level, resulting in low $\delta^{13}C$ values in plants (Cerling et al., 2004; van der Merwe and Medina, 1991). For the present analysis, $\delta^{13}C$ values of tooth enamel from ungulates more negative than $-14‰$ are considered to represent sub-canopy browsing in multi-tiered, closed canopy forests, $-14‰$ to $-12‰$ for browsing in forest, $-12‰$ to $-8‰$ for browsing in woodlands, and $-8‰$ to 3‰ for the mixed feeding and/or grazing in more open habitats (Cerling et al., 1997a,b, 2004; Kohn et al., 2005).

3.2. Oxygen isotopes

The stable oxygen isotopic composition of tooth enamel ($\delta^{18}O_{sample-VPDB} = ([^{18}O/^{16}O]_{sample}/[^{18}O/^{16}O]_{VPDB} - 1) \times 1000‰$) in mammals is useful in reconstructing the diet and habitat preferences as well as seasonality (Fricke and O'Neil, 1996; Longinelli, 1984). The $\delta^{18}O$ values of tooth enamel or body water is controlled by the oxygen isotopic composition of ingested water, which is related to precipitation, latitude, altitude, aridity and evaporative processes, physiological and behavioral water conservation factors as well as metabolic processes (Kohn, 1996; Kohn et al., 1996; Luz and Kolodony, 1985; Luz et al., 1984).

Paleoenvironmental interpretation derived from $\delta^{18}O$ values is not simple as with the carbon isotopic composition because of the complexity of oxygen flux in mammals. There are several principles that can be applicable for interpreting the $\delta^{18}O$ variation: the $\delta^{18}O$ values for mammals that frequently drink water depend on rainwater $\delta^{18}O$ values, whereas drought-tolerant animals usually have relatively higher $\delta^{18}O$ values (Ayliffe and Chivas, 1990; Kohn et al., 1996; Levin et al., 2006). Thus aquatic or semi-aquatic mammals such as hippopotami generally have lower $\delta^{18}O$ values than associated terrestrial mammals (Bocherens et al., 1996; Cerling et al., 2003b; Clementz et al., 2008); grassland-adapted grazers may generally yield more enriched $\delta^{18}O$ values than forest dwelling browsers (Bocherens et al., 1996; Sternberg et al., 1989); and carnivores are depleted in ^{18}O relative to herbivores (Sponheimer and Lee-Thorp, 2001).

3.3. Serial carbon and oxygen isotope analysis

The $\delta^{18}O$ value of ingested water is controlled by local precipita-tion and water resources, and is potentially modified by evaporative effects (Longinelli, 1984). The variation in oxygen isotopic composi-tion has been attributed to environmental temperature changes, leading to the enrichment of ^{18}O in warmer conditions and depletion of ^{18}O in cooler conditions (Bryant et al., 1996). Thus, higher $\delta^{18}O$ values indicate summer and lower $\delta^{18}O$ values indicate winter in temperate regions. In the tropics, where environmental temperatures remain above 20 °C, the "amount effect" is dominant, whereby lower $\delta^{18}O$ values indicate periods of increased rainfall compared to higher values during dry periods (Dansgaard, 1964; Feranec and MacFadden, 2000; Higgins and MacFadden, 2004). Some herbivorous mammals such as horses, bison, and rhinocerotids have high-crowned teeth. These teeth preserve an isotopic record of a certain time span because

Table 2
Stable carbon and oxygen isotopic values of Chaingzauk mammals.

NMMP-KU	Family	Taxa	Tooth	δ¹³C (V-PDB)	δ¹⁸O (V-PDB)
IR0822	Hystricidae	*Hystrix*	P/4	−12.7	−7.3
IR0542	Ursidae	*Agriotherium*	M/3	−3.6	−8.2
IR1308	Tragulidae	*Dorcabune*	M/2	−9.7	−6.3
IR1306	Antharocotheriidae	*Merycopotamus*	P4/	−1.1	−6.4
IR0797	Hippopotamidae	*H. iravaticus*	M/2	−1.7	−7.8
IR0802	Hippopotamidae	*H. sivalensis*[a]	M3/	−0.4	−6.0
IR0803	Hippopotamidae	*H. iravaticus*[a]	Canine	−1.2	−6.6
IR0806	Hippopotamidae	*H. iravaticus*[a]	M3/	−1.2	−6.6
IR0807	Hippopotamidae	*H. sivalensis*	P4/	−1.0	−6.3
IR0815	Hippopotamidae	*Hexaprotodon*[a]	Canine	0.7	−6.7
IR1332	Hippopotamidae	*Hexaprotodon*[a]	M/3	2.5	−6.2
IR1124	Hippopotamidae	*Hexaprotodon*	Canine	2.7	−7.5
IR1125	Hippopotamidae	*Hexaprotodon*	M/3	0.8	−8.4
IR1126	Hippopotamidae	*Hexaprotodon*	M2/	−6.2	−9.9
IR1128	Hippopotamidae	*H. iravaticus*	M/3	0.2	−8.9
IR1129	Hippopotamidae	*Hexaprotodon*	M/3	0.9	−8.1
IR1268	Hippopotamidae	*Hexaprotodon*	P/4	0.6	−5.8
IR1273	Hippopotamidae	*Hexaprotodon*	Canine	2.2	−7.8
IR1310	Hippopotamidae	*H. sivalensis*	M/3	2.1	−7.5
IR1333	Hippopotamidae	*Hexaprotodon*	M/3	1.7	−7.5
IR0805	Suidae	*Sivachoerus*	M/3	−10.4	−6.9
IR0553	Suidae	*Sivachoerus*	M3/	−12.1	−5.1
IR0812	Suidae	*Sivachoerus*	M/2	−13.8	−3.6
IR0813	Suidae	*Sivachoerus*[a]	M/3	−10.4	−6.6
IR0814	Suidae	*Sivachoerus*	M/3	−12.3	−8.1
IR0804	Suidae	*Propotamochoerus*	M/2	−12.0	−7.4
IR0816	Suidae	*Propotamochoerus*	M/2	−10.0	−7.0
IR1458	Suidae	*Propotamochoerus*	M/3	−10.4	−6.4
IR0819	Bovidae	Cf. *Tragopartax*	M/3	−2.7	−4.1
IR1104	Bovidae	Cf. *Tragopartax*	M/3	−6.1	−4.3
IR0809	Bovidae	cf. *S. vexillaris*	M/3	−2.7	−3.9
IR0811	Bovidae	cf. *S. vexillaris*	M/3	−0.7	−1.9
IR0823	Bovidae	cf. *S. vexillaris*	M/3	1.9	−2.7
IR0824	Bovidae	cf. *S. vexillaris*	M/3	0.9	−4.1
IR0827	Bovidae	cf. *S. vexillaris*	M/2	−1.8	−4.3
IR1094	Bovidae	cf. *S. vexillaris*	M/3	1.0	−6.0
IR1170	Bovidae	cf. *S. vexillaris*	M/1	−0.7	−3.7
IR0808	Bovidae	cf. *S. lydekkeri*	M/2	0.2	−2.4
IR0817	Bovidae	cf. *S. lydekkeri*	M/3	−2.9	−2.6
IR0818	Bovidae	cf. *S. lydekkeri*	M/3	−2.1	−2.3
IR0828	Bovidae	cf. *S. lydekkeri*	M/3	−3.5	−5.0
IR0826	Bovidae	cf. *S. lydekkeri*	M/3	−4.0	−5.6
IR0825	Bovidae	cf. *S. lydekkeri*	P/4	−1.4	−4.9
IR1194	Bovidae	cf. *S. lydekkeri*	M/3	−8.1	−3.6
IR1105	Bovidae	cf. *S. lydekkeri*	M/1	−5.2	−5.7
IR1204	Bovidae	cf. *S. lydekkeri*	M/3	−1.2	−3.4
IR1092	Bovidae	cf. *S. lydekkeri*	M/3	−0.5	−5.6
IR0294	Rhinocerotidae	*Rhinoceros*	Molar fragment	−11.9	−3.3
IR0820	Rhinocerotidae	*Rhinoceros*	M/3	−12.8	−5.5
IR0991	Rhinocerotidae	*Rhinoceros*	Molar fragment	−12.3	−5.4
IR1133	Rhinocerotidae	*Rhinoceros*	M/1	−13.8	−3.3
IR1134	Rhinocerotidae	*Rhinoceros*	P3/	−14.0	−4.4
IR1135	Rhinocerotidae	*Rhinoceros*[a]	M3/	−12.0	−6.2
IR1136	Rhinocerotidae	*Rhinoceros*	P2/	−12.7	−5.5
IR 1138	Rhinocerotidae	*Rhinoceros*	M/1	−13.3	−3.7
IR1139	Rhinocerotidae	*Rhinoceros*	P/3	−12.8	−5.3
IR1140	Rhinocerotidae	*Rhinoceros*	P2/	−13.2	−5.6
IR1260	Rhinocerotidae	*Rhinoceros*	P/3	−12.5	−7.3
IR1335	Rhinocerotidae	*Rhinoceros*[a]	Molar fragment	−12.0	−6.3
IR0800	Proboscidea	*Stegodon*[a]	Molar fragment	−11.7	−7.3
IR0821	Proboscidea	*Stegodon*	Molar fragment	−9.9	−7.5
IR1143	Proboscidea	*Stegodon*	Molar fragment	−10.6	−6.5
IR1144	Proboscidea	*Stegodon*	Molar fragment	−12.6	−7.9
IR1150	Proboscidea	*Stegodon*[a]	Molar fragment	−12.1	−7.6

Table 2 (continued)

NMMP-KU	Family	Taxa	Tooth	δ¹³C (V-PDB)	δ¹⁸O (V-PDB)
IR1152	Proboscidea	*Stegodon*	Molar fragment	−6.6	−7.0
IR1159	Proboscidea	*Stegodon*	Molar fragment	−11.6	−6.5
IR1151	Proboscidea	*Stegodon*	Molar fragment	−5.4	−4.8
IR1153	Proboscidea	*Stegodon*[a]	Molar fragment	−10.7	−9.2
IR1157	Proboscidea	*Stegodon*	Molar fragment	−9.0	−6.6
IR1158	Proboscidea	*Stegodon*	Molar fragment	−9.3	−6.9
IR1161	Proboscidea	*Stegodon*	Molar fragment	−7.0	−8.4
IR1162	Proboscidea	*Stegodon*	Molar fragment	−10.2	−6.2
IR0544	Proboscidea	*Sinomastodon*[a]	M/3	−10.9	−6.8

V-PDB: Vienna-Pee Dee Belemnite.
NMMP-KU-IR: National Museum of Myanmar Paleontology-Kyoto University (Japan)-Irrawaddy.
[a] Average value (samples were taken from more than one region of the tooth).

their teeth mineralize from the top (oldest) to the base (youngest) over a period of time, usually between 1 and 2 years (Feranec and MacFadden, 2000; Kohn et al., 1998; Sharp and Cerling, 1998). Therefore, the serial δ¹⁸O values along the growth line of unworn teeth of a mammal can reflect the seasonal variation during ontogeny.

The serial δ¹³C values along the growth line of a tooth are informative of seasonal differences in foraging, depending on the availability of C_3/C_4 plants and temporal partitioning of food resources (Feranec and MacFadden, 2000; Sharp and Cerling, 1998). Moreover, serial δ¹³C values of C_3 plant browsers are also useful for tracing water use in plants (Ehleringer et al., 1986; Ehleringer, 1991).

4. Materials and methods

A total of 73 bulk samples and 52 serial samples from 12 genera of mammals were analyzed (Table 2). Samples were mainly collected from the late erupting teeth (e.g. third molars) in order to avoid the effect of additional fractionation during the weaning period. The enamel (~10–20 mg) was removed from the tooth using a diamond tipped rotary drill. The bulk samples were taken from one region of each tooth perpendicular to the growth axis. Tooth samples of *Hexaprotodon*, *Sivachoerus*, *Stegodon* and *Sinomastodon* were taken from more than one region of each tooth to obtain the mean values of δ¹³C and δ¹⁸O for the whole tooth. The serial samples were collected from the teeth by cutting parallel grooves at intervals of 3 to 5 mm, perpendicular to the growth axis of the tooth. This sampling interval was intended to overcome the attenuation of a primary time-series of body water isotopic composition as reflected in tooth enamel (Passey and Cerling, 2002).

The enamel powder was pretreated with 2.5% sodium hypochlorite (NaOCl) for 12 h, followed by 1 M acetic acid (pH: 3.8) for six hours to remove organics and secondary carbonates (method of Koch, 1997; Lee-Thorp et al., 1989; Lee-Thorp and van der Merwe, 1991a,b). Samples were centrifuged at a high speed and rinsed in distilled water to neutral pH before proceeding with the next solution. Samples were then freeze-dried for a maximum of 48 h. Isotopic composition of treated samples was measured on a Gasbench II coupled to a Finnigan Delta V Mass Spectrometer at the University of South Florida. The CO_2 samples were run in continuous flow mode after reaction with 103% phosphoric acid (100% H_3PO_4 with excess P_2O_5) at 25 °C for 24 h (McCrea, 1950). Seven replicate samples of Carrara Marble (an internal standard which has been assigned a value of δ¹³C = +2.01‰, δ¹⁸O = −1.79‰, based on analysis with respect to
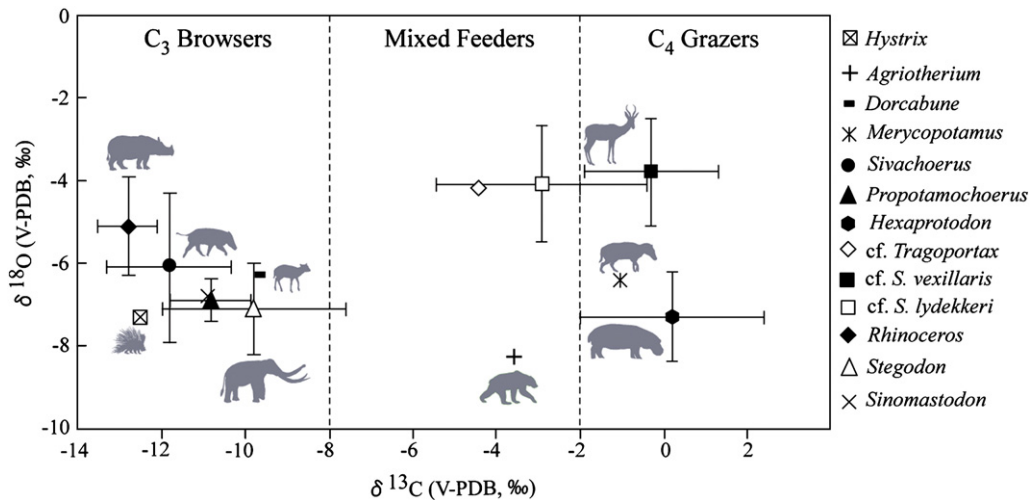
Fig. 3. δ^{13}C and δ^{18}O values in tooth enamel of Chaingzauk mammals. Symbols represent the mean values and error bars indicate one standard deviation.

NBS-19, $\delta^{13}C = +1.95‰$, $\delta^{18}O = -2.20‰$) and NBS-18 carbonatite ($\delta^{13}C = -5.04‰$, $\delta^{18}O = -23.05‰$, NIST, 1992) were analyzed in each run of 60 samples. Standard deviation of replicate analyses for both isotope values was <0.15‰. Stable isotope data were reported in the conventional delta (δ) notation for carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) relative to V-PDB (Vienna-Pee Dee Belemnite, i.e., PDB expressed in terms of NBS-19): $\delta = [(R_{sample}/R_{standard}) - 1] \times 1000‰$, where R denotes $^{13}C/^{12}C$ or $^{18}O/^{16}O$. The statistical analyses were carried out using SPSS (SPSS 13.0, 2004).

5. Bulk carbon and oxygen isotopes results and interpretations

5.1. General results

The stable carbon isotope values ($\delta^{13}C$) of Chaingzauk mammals fall between −14.0‰ and 2.6‰, for a range of 16.6‰ (Fig. 3; Table 2). The $\delta^{13}C$ values of porcupines (*Hystrix*), tragulids (*Dorcabune*), rhinocerotids (*Rhinoceros*), suids (*Propotamochoerus* and *Sivachoerus*) and elephants (*Stegodon* and *Sinomastodon*) show that they preferred C_3 plants in wooded environments, whereas those of bovids (cf. *Tragoportax* and cf. *Selenoportax*), athracotheres (*Merycopotamus*) and hippopotamids (*Hexaprotodon*) indicate that they were grassland-adapted grazers to mixed feeders. The $\delta^{13}C$ values of Chaingzauk C_3 browsers are not lower than −14‰ and are distinct from $\delta^{13}C$ values of herbivores living in closed canopy forests (Cerling et al., 2004; Kohn et al., 2005). The co-existence of mixed feeders and grassland-adapted grazers also supports the notion that Chaingzauk mammals inhabited the transitional environment between woodlands and grasslands.

The $\delta^{18}O$ values Chaingzauk mammals range between −9.9‰ and −1.9‰, for a range of 8‰ and a mean of −5.9‰. These values are lower than those of Siwalik mammals from ca. 9 Ma (−9.2‰ to 0.7‰ for a range of −9.9 and a mean of −4.5‰: n = 54) and from ca. 8 Ma (−8‰ to 3.5‰ for a range of mean of −2.7‰: n = 48; Nelson, 2007). The low $\delta^{18}O$ values of Chaingzauk mammals may reflect the intensity of monsoons and accordingly, they probably lived in more humid environments than are present today. On the other hand, the low $\delta^{18}O$ values of Chaingzauk mammals may be explained by distillation effect of meteoric water during transport over continents (Sharp, 2007) because air masses from the Andaman and Bangle Seas passed through the rising Indo-Burman Ranges in west and south west, more and more precipitation cycles occurred, and the $\delta^{18}O$ of vapors and condensate become progressively more ^{18}O-depleted farther from the ocean source.

There are significant differences in $\delta^{13}C$ and $\delta^{18}O$ values between taxa, suggesting they inhabited different ecological niches. The bovids shows significantly higher $\delta^{18}O$ values than the co-existing open-adapted grazer, *Hexaprotodon*, (Mann–Whitney pairwise comparisons and ANOVA, p = <0.05) indicating that they have different habitat preferences. Furthermore, *Rhinoceros* had significantly lower $\delta^{13}C$ values than other forest/woodland dwelling browsers (*Propotamochoerus* and *Stegodon*) and mixed feeder to C_4 grazers (*Tragoportax, Selenoportax,* and *Hexaprotodon*) (Mann–Whitney pairwise comparisons and ANOVA, p = <0.05). These carbon and oxygen isotopic results confirm that true dietary signals are reflected in the isotopic composition of fossil teeth because diagenetic alteration would have led to isotopic homogeneity rather than clustering by taxa.

5.2. Hystricidae

The extant porcupine, *Hystrix*, mainly feeds on roots, tubers, bark and fallen fruit (Nowak, 1991). The water storage organs of plants (roots and tubers) are more depleted in ^{18}O than carbohydrates in leaves (Yakir, 1992) and the fruit water is depleted in ^{18}O compared to leaf water (Dunbar and Wilson, 1983). Thus, the selective feeding behavior on the ^{18}O-depleted parts of plants may explains the relatively low $\delta^{18}O$ value (−7.3‰) of a large *Hystrix* from Chaingzauk. Likewise, the depleted $\delta^{13}C$ value (−12.6‰) of this animal suggest that it fed on the fallen fruit as well as parts of trees such as roots and tubers on the forest/woodland floor.

5.3. Ursidae

The extinct bear, *Agriotherium*, has conventionally been assumed to have been a carnivore which preyed on large terrestrial mammals (Kurtén, 1967). The $\delta^{13}C$ value of Chaingzauk *Agriotherim* (−3.6‰) suggests that its diet consisted of mixed feeding on C_4 and C_3 plants, or animals that consumed both C_3 and C_4 plants. Sponheimer and Lee-Thorp (2001) suggested that carnivores have relatively low $\delta^{18}O$ values compared with herbivores, probably due to several factors: they drink water more frequently than herbivores; liquid water that they ingest from their prey is less enriched in ^{18}O than water in plant foods, and proteins from meat are relatively depleted in ^{18}O compared to carbohydrates. The $\delta^{18}O$ value found for *Agriotherium* (−8.2‰) was one of the most depleted values in the Chaingzauk fauna, suggesting that it was a faunivore and consumed fewer plant materials.

5.4. Tragulidae

The extant tragulids are nocturnal and feed on various kinds of food, such as grasses, leaves and fruits that have fallen on the forest

floor (Nowak, 1991). The $\delta^{13}C$ value ($-9.7‰$) of *Dorcabune* from Chaingzauk indicates that it browsed C_3 plants in woodlands. This value falls in the range of *D. nagrii* ($-11.1‰$ to $-9.6‰$) from the early Late Miocene of northern Pakistan (Nelson, 2003). The Chaingzauk *Dorcabune* had a relatively depleted $\delta^{18}O$ value ($-6.3‰$), like other forest/woodland dwelling browsers, consistent with its preference for a forest/woodland habitat.

5.5. Suidae

The $\delta^{13}C$ values of Chaingzauk *Propotamochoerus* ranged between $-12.0‰$ and $-10.0‰$ (n = 3), suggesting that it inhabited forests/woodlands. The microwear analysis of *P. hysudricus* from late Miocene of Siwalik suggests that it was omnivorous and depended on both fallen fruit and foliage, when fruit was not available, and its diet is most similar to that of the extant bush pig, *Potamochoerus porcus*, and the giant forest hog, *Hylochoerus meinertzhangeni* (Nelson, 2003, 2007). Likewise, the mean $\delta^{13}C$ values of Chaingzauk *Propotamochoerus* ($-10.8‰$) are comparable to those of *Potamochoerus porcus* ($-9.4‰$: n = 17), suggesting that it had a varied diet in wooded habitats (Harris and Cerling, 2002; Nelson, 2003).

The coexisting large sized suid, *Sivachoerus*, was distinct in its extremely large third molars with a complex talon/talonid. The enlargement of third molars in Suidae has been considered an adaptation to a more abrasive diet (Cerling et al., 2005; Harris and Cerling, 2002). However, *S. prior* showed slightly lower $\delta^{13}C$ values ($-13.8‰$ to $-12.4‰$) than those of its coexisting species, *Propotamochoerus hysudricus*. The low $\delta^{13}C$ values of *S. prior* are closely comparable to those of extant bush pigs (Harris and Cerling, 2002).

The $\delta^{18}O$ values of Chaingzauk suids were relatively low which can be attributed to their feeding on fallen fruit, roots and tubers on the forest/woodland floor, and which are depleted in ^{18}O compared to leaf water (Dunbar and Wilson, 1983; Yakir, 1992). The water-dependent behavior of suids (Harris and Cerling, 2002) would also account for the low $\delta^{18}O$ values.

5.6. Hippopotamidae

The $\delta^{13}C$ values of the extant common hippopotamus *Hippopotamus amphibus* show that it mainly consumes C_4 grasses in an open environment, and also that it feeds on considerable amounts of C_3 plants in closed to moderately open environments (Boisserie et al., 2005). The $\delta^{13}C$ values of Chaingzauk hippopotamid, *Hexaprotodon*, ranged from $-1.7‰$ to $2.7‰$ (n = 13), except for one taken from an isolated M2 ($-6.2‰$), suggesting that it mainly consumed C_4 grasses as well as some C_3 plants. Therefore, this taxon was likely to be an inhabitant of a moderately open to open environment.

The $\delta^{18}O$ values of extant hippopotamids from several localities in Africa were consistently lower than those of associated fauna (Bocherens et al., 1996; Kohn et al., 1996; Levin et al., 2006). Likewise, the Chaingzauk *Hexaprotodon* showed lower mean $\delta^{18}O$ values ($-7.3 \pm 1.1‰$, n = 16) compared to co-occurring ungulates ($-5.4 \pm 1.7‰$, n = 53), indicating that it had a hippoecomorph like that of its extant relatives. These depleted $\delta^{18}O$ values are attributable to the semi-aquatic behavior that leads to reduced evaporative loss of ^{16}O-enriched water from the body, nocturnal foraging that leads to reduced evaporative water loss across the skin and consumption of plant water than had not experienced ^{18}O-enrichment due to transpiration, or the unique physiology of hippopotamids (Bocherens et al., 1996).

5.7. Anthracotheriidae

Conventionally, anthracotheres are assumed to be mainly semi aquatic mammals like extant hippopotamids according to their morphological similarities (Lihoreau and Ducrocq, 2007). The $\delta^{13}C$

value of Chaingzauk anthracothere, *Merycopotamus*, ($-1.1‰$) suggests that its diet consisted of mainly C_4 plants in grasslands. However, this taxon shows low $\delta^{18}O$ values ($-6.4‰$) in contrast with the other grassland-adapted grazers which usually show relatively higher $\delta^{18}O$ values than forest-dwelling browsers. Thus, it can be generally assumed that that it had a similar habitat preference like hippopotamids. The anthracotheres from the early Late Miocene of northern Pakistan also show low $\delta^{18}O$ values ($-7.2‰$ to $-5.8‰$; Nelson, 2003). But the $\delta^{13}C$ value ($-11.5‰$ to $-8.5‰$) of Siwalik anthracotheres suggest that they are forest/woodland adapted browsers (Nelson, 2007).

5.8. Rhinocerotidae

The $\delta^{13}C$ values of Chaingzauk rhinocerotids ($-14.0‰$ to $-11.9‰$: n = 12) reveal that they browsed on C_3 plants in the forest/woodland. Unfortunately, there is no isotope data on the extant Asian rhinoceros in the wild. Nevertheless, the $\delta^{13}C$ values of Chaingzauk rhinocerotids suggests that they had a more similar habitat preference to extant browsers *Rhinoceros sondaicus* and *Diceros sumatresis* than grazer/mixed feeder *R. unicornis* (Nowak, 1991).

The Chaingzauk rhinocerotids yielded relatively high $\delta^{18}O$ values compared to other browsers such as *Stegodon*, *Propotamochoerus* and *Sinomastodon*. Forest/woodland dwelling browsers and semi-aquatic mammals are usually expected to have relatively depleted $\delta^{18}O$ values because they generally have lower metabolic rates than grazers (less massive than browsers such as elephants, rhinoceros and hippopotamids), feed mostly on well-shaded vegetation and frequently drink water from less evaporated sources (Bocherens et al., 1996). However, selective feeding on evaporated leaves versus unselective feeding on leaves, stems, roots and fruit may have an influence on the $\delta^{18}O$ among browsers (Kohn, 1996; Kohn et al., 1996), suggesting that Chaingzauk rhinocerotids browsed leaves in relatively open habitats like woodland rather than closed canopy forests.

5.9. Bovidae

The $\delta^{13}C$ values for bovids from Chaingzauk range from $-8.1‰$ to $1.9‰$, indicating that they depended on a variety of foods from C_3 to C_4 plants. The small bovid cf. *Tragoportax* shows mixed feeding on C_3 and C_4 plants ($-6.2‰$ to $-2.7‰$), whereas the medium sized cf. *Selenoportax vexillaris* was an obligate grazer ($-2.7‰$ to $1.9‰$). The wide range of $\delta^{13}C$ values for the large sized bovid, cf. *S. lydekkeri* ($-8.1‰$ to $0.1‰$), suggests that it consumed both C_3 and C_4 plants.

It is generally assumed that C_4 grazers tend to have enriched ^{18}O compared to C_3 browsers because C_4 plants remain active in warm, dry conditions, causing more evaporation across the leaf surface (Bocherens et al., 1996; Sternberg et al., 1984). Likewise, $\delta^{18}O$ values of Chaingzauk bovids are higher than those of other coexisting mammals. These relatively high values can be attributed to the feeding behavior of bovids that graze on foliage from open, irradiated portion of the vegetation, which is enriched in ^{18}O during transpiration (Sternberg et al., 1989).

5.10. Stegodontidae and Mastodontidae

It had been presumed that proboscideans adapted to a C_4-dominated diet from 7 to 1 Ma in Asia and Africa, coinciding with the worldwide spread of C_4 vegetation (although all extant elephants are mainly C_3 plants consumers; Cerling et al., 1999) The $\delta^{13}C$ values of *Stegodon* and *Sinomastodon* from Chaingzauk ranges from $-12.6‰$ to $-5.4‰$ (n = 15), indicating that it mainly consumed C_3 plants as well as mixed C_3 and C_4 plants. Thus, Chaingzauk proboscideans generally retained their primitive feeding style even though grasslands were present. The $\delta^{18}O$ values of these proboscideans were relatively
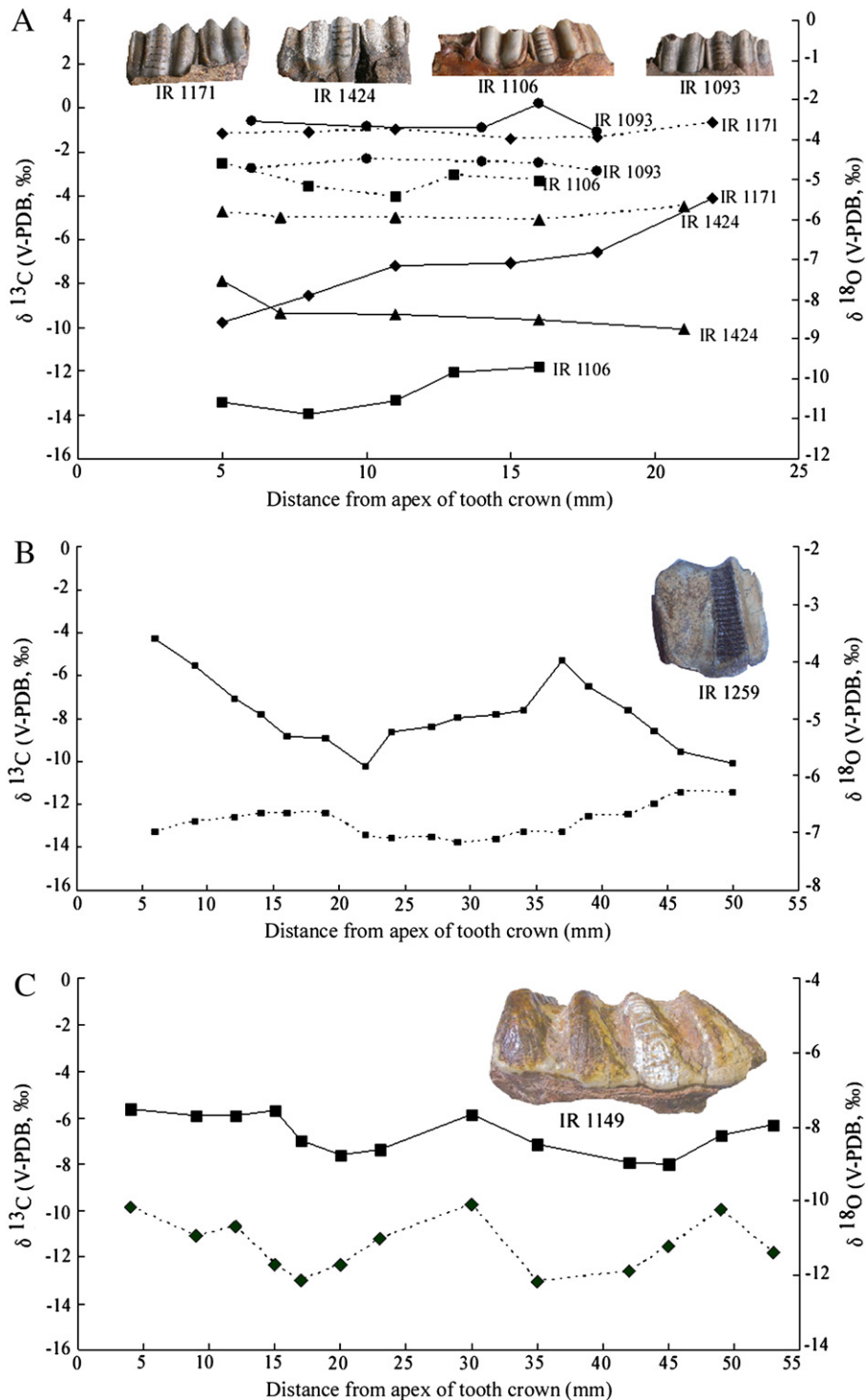
Fig. 4. Serial δ13C and δ18O values of Chaingzauk mammals. A, cf. *Selenoportax*; B, *Rhinoceros*; C, *Stegodon*. Dashed lines represent carbon isotopic values and solid lines indicate oxygen isotopic values.

depleted (−9.2‰ to −4.8‰, n = 15) which is likely due to the consumption of parts of plants such as stems, fruit, roots and leaves, obligate drinking and water-dependent behaviors of elephants.

6. Serial carbon and oxygen isotope results and interpretations

The serial oxygen isotope analyses of bovid teeth (M3 molars) showed seasonal cycles throughout half of the year (Fig. 4A). However, the serial δ18O values of IR1093, IR1424 and IR1106 yielded

relatively little variation less than 1.5‰ among individual serial samples, whereas those of IR1171 showed a considerable fluctuation (−6.6‰ to −3.5‰) with the low δ18O values (wet season), followed by the high δ18O values (dry season). The serial δ13C values of bovids shows little variation suggesting that they mainly grazed on C_4 plants without significant seasonal shift in diet (Fig. 4A).

The molars of rhinocerotids are usually mineralize over two years (Goddard, 1970), and accordingly, the serial samples from fossil rhinocerotids have a potential to reflect the seasonal cycles

representing more than one year. The serial $\delta^{18}O$ values IR1259 (M2) range from -5.9 ‰ to -4.0 ‰, showing two dry season peaks and one rainy season trough (Fig. 4B). The serial $\delta^{13}C$ values show that it was obligate browser without seasonal dietary shifts. The fluctuations of $\delta^{13}C$ values (-13.8 ‰ to -11.5 ‰) was likely caused by the variations in water stress of C_3 plants consumed because plants close their stomata to conserve water, reducing CO_2 intake and enriching the $\delta^{13}C$ of C_3 plant tissue (Ehleringer et al., 1986; Ehleringer et al., 1991; Fig. 4B).

The serial $\delta^{18}O$ value of *Stegodon* molar (IR1149) shows three dry season peaks with two wet season troughs, suggesting that the tooth had mineralized more than two years. The $\delta^{18}O$ values range from -7.9 ‰ to -5.9 ‰, indicating that this animal experienced a considerable seasonal variation. The serial $\delta^{13}C$ values vary from -12.2 ‰ to -10.1 ‰, suggesting that it was an obligate browser (Fig. 4C). The fluctuation of $\delta^{13}C$ values indicates it consumed water-stressed C_3 plants as coexisting rhinocerotids did.

7. Discussion

The carbon isotopic values of Chaingzauk mammals suggest that they lived in a wide range of habitats from woodlands to grasslands rather than multi-tiered, closed canopy forests. The serial oxygen isotope sampling of *Rhinoceros*, *Stegondon* and *Selenoportax* showed the variation in $\delta^{18}O$ values from tooth crowns to tooth bases, suggesting that a seasonal pattern of wet and dry cycles existed at the Miocene/Pliocene boundary of central Myanmar. Thus, the Chaingzauk mammals might have experienced a seasonal variation under the influence of the monsoon which had developed since 10.7 Ma in Asia (Dettman et al., 2001). The fluctuation of serial $\delta^{13}C$ values of *Rhinoceros* and *Stegodon* also suggest that they consumed the C_3 plants that periodically experienced water stress in a seasonal environment.

Carbon isotopic analysis from the fossil tooth enamel of ungulates around the world suggest a large scale vegetation shift occurred during the late Miocene to early Pliocene, when C_4 biomass began to expand globally (Cerling, 1997; Cerling et al., 1997a,b). The transition from C_3 to C_4 plants first took place in low latitude regions and spread outward to the mid-latitudes (Cerling, 1997). In East Africa (3°S to 5°N), the transition was complete by 8 to 7.5 Ma (Cerling et al.,1997b). In the Siwalik of northern Pakistan (31°–32°N), the transition was slightly more gradual and occurred between 8 and 6 Ma (Cerling et al., 1997b; Quade et al., 1992). The present study also indicates that grasslands had already expanded by the latest Miocene of Myanmar, which is located at relatively lower latitudes than northern Pakistan.

On the other hand, the pattern of the floral transitions in the Neogene of Myanmar is probably different from the Siwaliks of northern Pakistan despite faunal similarities between the two regions. For example, obligate browsers such as a suid (*Propotamochoerus*) and the tragulids (*Dorcatherium* and *Dorcabune*) were assumed to have become extinct due to the fragmentation of forest around 6 Ma in northern Pakistan (Badgley et al., 2008; Barry et al., 2002). However, the remains of these animals were usually recovered together with those of hippopotamids, which first appeared in South Asia around 6 Ma (Badgley et al., 2008; Barry et al., 2002), at Chaingzauk as well as in other Pliocene to early Pleistocene fossil localities in Myanmar (Thaung-Htike et al., 2006; Tsubamoto et al., 2006; Zin-Maung-Maung-Thein et al., 2008, 2010). This suggests that these forest/woodland dwelling browsers probably survived in Chaingzauk as well as at other parts of central Myanmar until the end of the Pliocene. Moreover, the existence of other forest/woodland dwelling animals, such as leaf eating monkeys (colobinae), rhinocerotids and porcupines, also indicates the abundance of forested/wooded habitats.

Carbon isotopic evidence has indicated that fossil proboscideans from Africa and Southern Asia around 7 to 1 Ma favored C_4 plants, except the brachyodont *Deinotherium*, in contrast to their extant relatives who mainly browse on C_3 plants (Cerling et al., 1999). The adaptive shift of diet from C_3 to C_4 plants in proboscideans coincides with the worldwide spread of C_4 vegetation, and corresponds with an
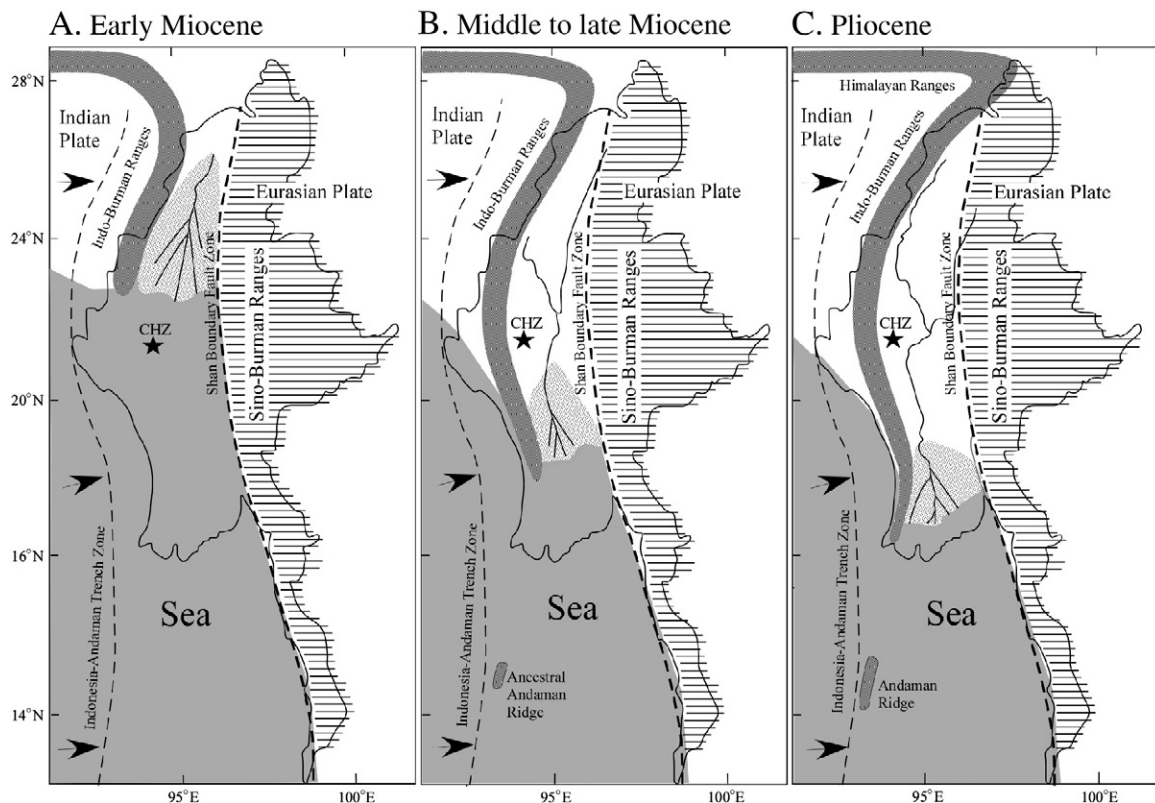

Fig. 5. Simplified Neogene paleogeography of central Myanmar Basin (illustrated after Aung Khing and Kyaw Win, 1969; Rodolfo, 1975; Wandrey, 2006).

increase in size and hypsodonty of proboscidean cheek teeth, which is considered to have been an adaptation to the newly available food (Cerling, 1997: Cerling et al., 1999). However, the δ^{13}C values of Chaingzauk proboscideans show that their main diet was C$_3$ plants, suggesting that they retained their primitive feeding style even though grasslands were present at Chaingzauk. Therefore, it is very likely that C$_3$ plants occurred in sufficient amounts to be able to support the survival of abundant forest/woodland dwelling browsers at Chaingzauk.

At present, central Myanmar is a semi-arid zone with an annual precipitation of 600 to 1000 mm and its mean temperature is about 30 °C (Bender, 1983). In contrast, carbon isotopic results of Chaingzauk mammals suggest that a considerable extent of wooded habitats was present at the Miocene/Pliocene boundary of Myanmar. According to the vegetation type, depending on the temperature versus precipitation model of Whittaker (1970), an annual precipitation between 500 and 900 mm favors the formation of thorn scrubs and grasses (savannah) and greater than 900 mm prefer the formation of thorn forest and tropical seasonal forest (mean temperature: >18 °C). Thus, the presence of woodlands at the Miocene/Pliocene boundary of Myanmar imply that central Myanmar might, at that time, have received an annual precipitation of more than 1000 mm.

The arid conditions in central Myanmar is usually attributed to the rain shadow effect of the Indo-Burman Ranges (1500 to 4000 m), which hamper the passage of summer monsoon humid winds from the west and southwest into central Myanmar (Chhibber, 1934). In contrast, western and southern parts of Myanmar annually receive 3000 to 4000 mm of rainfall and are covered with tropical rainforests (Kress et al., 2003). The Indo-Burman Ranges are a southern branch of the Himalayan–Tibetan Plateau which was significantly uplifted between 10 and 8 Ma due to the collision of the Indian Plate and Eurasian Plate (Dettman et al., 2001; Harrison et al., 1992). The terminal folding phase of the Indo-Burman Ranges, caused by the Himalayan Orogeny, is assumed to have occurred in the latest Miocene to Pliocene (Allen et al., 2008; Brunnschweiler, 1974). The carbon isotopic composition of Chaingzauk mammals indicate the absence of close canopy forests at the Chaingzauk, and are more conformable with the transitional environment that includes both woodlands and grasslands. This indicates that the rain shadow effect of the Indo-Burman Ranges might have had a gradual effect on the environment of central Myanmar since the Early Pliocene, although the woodlands were still existed to a considerable extent.

The other factor in the aridification in the central Myanmar might be related to its paleogeographic position. In the Early Miocene, marine conditions prevailed in most areas of central Myanmar, and the shoreline likely lay around 22°N (Fig. 5A). Throughout the Miocene, terrestrial sediments derived from the rapidly rising Indo-Burman and Himalayan Ranges, and the Sino-Bruman Ranges, which was a stable land block since the latest Cretaceous, gradually filled the central Myanmar Basin. In the Late Miocene, the shoreline receded southward, and estuarine/brackish condition might have prevailed as far as 18°N (Fig. 5B). During the latest Miocene to Pliocene, the terminal folding phase of Indo-Burman Ranges rapidly filled the basin to become an area of terrestrial sedimentation (Fig. 5C). Thus, central Myanmar was located closer to the shoreline than it is today in the Miocene/Pliocene boundary, probably inducing relatively humid conditions, preferable for the forest/woodland adapted mammals.

8. Conclusion

The uppermost Miocene/lower Pliocene Irrawaddy sediments at Chaingzauk area of central Myanmar yield a variety of mammals (primates, rodents, carnivores, rhinocerotids, bovids, hippopotamids, tragulids, anthracotheres, boars and elephants). The paleoenvironmental analysis of Chaingzauk fauna using stable carbon and oxygen isotope composition of tooth enamel indicated that the Chaingzauk mammals

inhabited a transitional environment between woodland and grassland. The considerable amount of C$_4$ plants in the diet of bovids and hippopotami indicates that grasslands had already expanded by the latest Miocene of Myanmar. The existence of forest/woodland dwelling animals, such as porcupines, leaf eating monkeys (colobinae), suids, rhinocerotids and elephants suggest the abundance of forested/wooded vegetation in Chaingzauk as well as at other parts of central Myanmar until the end of the Pliocene. Present-day arid conditions have likely been caused by the uplift of the Indo-Burman Ranges due to the Himalayan Orogeny during the late Miocene/Pliocene, resulting in the rain shadow effect in central Myanmar and also have been perhaps caused by the marine regression to the south in central Myanmar due to the rapid influx of sediments related to orogenic activity.

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