CHAPTER 4

Discussion and Interpretation

The characteristics of microwear features were observed by using a light microscope and scanning electron microscope. The number of pit and scratch of each species is variable. The paleodiet and evolution of Miocene Proboscidea is discussed.

4.1 The paleodiet of the Miocene Proboscidea in Thailand

Miocene proboscideans were divided into three groups based on the molar evolution and relative age dating; early Middle Miocene proboscidean including *Stegolophodon nasaiensis*; Middle Miocene proboscideans including *Stegolophodon* cf. *latidens*, cf. *Protanancus macinnesi* and *Prodeinotherium pentapotamiae*; and late Middle Miocene proboscideans including *Stegolophodon* cf. *stegodontoides* and *Tetralophodon* cf. *xiaolongtanensis* (Thasod, 2007). However, the results from the microwear analysis may suggest the different age of the previous study as discussed below.

Two aspects of microwear analyses: quantitative analyses (e.g., scratch and pit counts) and qualitative analyses (e.g., size and shape of microwear features) are used for interpretation the paleodiet of the Miocene proboscidean. The two species that exhibited the same microwear number may not consume the same type of food, as they have different size of microwear features. Thus, microwear counts reflect the frequency of the consumed material and microwear features reveal the specific types of such material.

The dietary of Miocene proboscideans were classified into 3 groups.

1) Browser

Stegolophodon nasaiensis and *Prodeinotherium pentapotamiae* were classified into the same dietary category, browser. However, hypercoarse scratches observed from the *P. pentapotamiae* implied that this species consumed coarser material than *S. nasaiensis*.

All of the four samples of *S. nasaiensis* from Ban Na Sai coal mine exhibited the eating behaviour of browsing. The samples of NS-01a and NS-01b are from the same individual and are observed on the same molar at the second and fourth loph, respectively. The number of scratch and pit are not much different from each other. This may be implied that microwear number are not significantly different within the same molar. Meanwhile, the number of pit observed in M4732a1 (second molar) is obviously different from M4732a2 (third molar) despite both of them are from the same individual. The latter show doubly higher in the number of pit than the former with nearly no difference in the number of scratches. The position of microwear observation should be included in the consideration. Pretrite which is the main area of food mastication is more prone to have a higher microwear number than posttrite. M4732a1 was examined on the posttrite side and M4732a2 was examined on the pretrite side. Understanding the microwear variation within the same or different molar help explain the relationship of the number of microwear and the position examined. Generally, elephants do not replace their molars in a vertical manner as most mammals do, rather in a horizontal progression. When the elephants become older, newer and bigger teeth are developing from behind and slowly moving forward. As a result, the number of microwear is decreasing from the anterior to the posterior loph and denser on the pretrite than on the posttrite (Todd *et al*., 2007).

Microwear features observed from both light microscope and scanning electron microscope showed all of the varieties of pits, including small, large and puncture, whereas the features of scratches include fine and coarse. It is not uncommon to find the small and large pit. Puncture pits are the indicator of hard-object consumption, especially hard seed. All of the four samples of *S. nasaiensis* show the presence of puncture pits with the characteristic of very dark areas in the center due to low reflectivity and sharp edge around the rim. Puncture pit is deeper than large pit and always appear dark under light microscope.

Seeds were the primary cause of all kinds of pits as reported by Semprebon *et al*. (2004). The diameter of pits depended on the variety of seeds. There were two possible explanations for the presence of pits. First, *Stegolophodon nasaiensis* might consume and swallow the whole seeds through the gut with a minute amount of food mastication. The diameter of pits tended to be small and puncture pits might be caused by exogenous

particles (e.g., soil particles). In this process, the seeds passed through the alimentary organs with no digestion and this species might not intently consume such seeds. Second, *Stegolophodon nasaiensis* might be the seed consumers. In this case, seeds were selectively consumed and grind until they became powder in order to be absorbed by the alimentary organs. This process required a large amount of force and pit diameter tended to be large.

The number of scratch and pit observed from the two samples of *Prodeinotherium pentapotamiae* from Tha Chang sand pits also ensure the feeding habit of browsing. The microwear number of browsers is represented by more pits and fewer scratches. The two samples barely differ from each other in terms of microwear number despite they were examined on different positions. The fourth premolar of KHO yields the same microwear number as in the third molar of RIN15. The mastication functionality which controls the grinding and shearing process is different from scpecies to species. The study of Todd *et al.* (2007) which observed the microwear variation of extant proboscideans including *Loxodonta africana* and *Elephas maximus* may not apply for *P. pentapotamiae*. The two living species have the molar morphology of the modern elephant, lophodonty. *P. pentapotamiae* posseses typical bunolophodont molar. In general, the masticatory mechanism between lophodont and bunolophodont impact the different pattern of microwear.

The scratch width is obviously coarse, with the hypercoarse scratch being nearly two times wider than coarse scratch. The pit shape include small and puncture. Hypercoarse scratch is the indicator of high silica phytolith consumption such as C_4 grasses. Hypercoarse scratches were found in both KHO and RIN15.

The results indicate that there is an obvious difference in scratch texture between *S. nasaiensis* and *P. pentapotamiae* despite both were classified into the same browsing domain. Scratch texture could identify the specific type of graminacee or vegetables, which contain different amount of phytolithes. Scratch texture was evaluated on a scale from 1 to 5, as follows: 1 = fine, 2 = mixture of fine and coarse, 3 = coarse, 4 = mixture of coarse and hypercoarse, and 5 = hypercoarse (Semprebon *et al.*, 2004). Thus, *S. nasaiensis* has the scratch texture value of 2 and *P. pentapotamiae* has the scratch texture value of 4.

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The pollen evidence from the fossil locality of *P. pentapotamiae*, Tha Chang sand pits, indicated the forest dominated by the genus Syzygium and Poaceae (Sepulchre *et al.*, 2010). Syzygium is the genus of flowering plant and comprises about 2000 species. One of them is very well-known as Java plum. Poaceae is a genus of grasses distributed mainly in tropical to warm-temperate areas of the world. Tha Chang sand pits show the highest percentage of Poaceae assemblage, clearly suggesting widespread grasslands at the regional scale. While selectively eating woody plants, *P. pentapotamiae* had the available grasses as their alternative resource, as seen from the presence of hypercoarse scratches.

Both *S. nasaiensis* and *P. pentapotamiae* show the molar morphology of bunolophodont, typified by the simple cusps and lophs. The cusps and lophs are spacely situated and could simply be distinguished. Browsers usually have the bunolophodont molar morphology.

1) Mixed-feeder

Another mixed-feeder comparison is the scratch width of *Stegolophodon* cf. *latidens* and *Tetralophodon* cf. *xiaolongtanensis*. These two species exhibited small pits, but *T.* cf. *xiaolongtanensis* showed broad scratch width variation from fine to coarse. Thus, it is probably that *T.* cf. *xiaolongtanensis* was well adapted to a wide range of food types.

The four samples of *S.* cf. *latidens* analyzed from Mae Moh coal mine indicate exclusively mixed-feeding diet. Mixed-feeders that change their diet seasonally or occasionally have an average percentage of pits and scratches between browsers and grazers. All of the samples showed the percentage of pits higher than scratches, especially MMEL-6 (73%). The percentage of the scratch range from 27-38% and the percentage of pit range from 62-73%. High percentage of pits indicate the leaf-dominated diet. The samples of MMEL-3, MMEL-5 and MMEL-6 are fragmented molar with unknown dental orientation. The direction of the anterior and posterior could only be identified by the presence of their talons or talonids. The comparison of microwear percentage between each sample, on different examined position, should be omitted to avoid confusion. The complete lower left molar of M4733f shows the scratch and pit number of 13 and 21, respectively. Inasmuch as the microwear number of

M4733f are quite similar to those observed in MMEL-3, MMEL-5 and MMEL-6, the microwear results of these four samples could be grouped in the same category.

The scratch texture of *S*. cf. *latidens* composed mainly of coarse scratch (with only the exception of M4733f which had fine scratch). The overall scratch texture evaluation of all samples is 3, according to Semprebon *et al*., 2004. Small pits were found on the teeth of all samples. Puncture pits were found on the enamel surface of MMEL-5, suggesting a close association with hard-object feeder.

The four samples of *T*. cf. *xiaolongtanensis* from Chiang Muan coal mine show that this species has average scratch and pit result consistent with mixed-feeder. The percentage of the scratch range from 36-48% and the percentage of pit range from 52-64%. The second loph or lophid of second molar was used in the analysis whenever possible. When those specified molars were unavailable or exhibited postmortem damage that obscured microwear, the first or third molar or even the fragmented molar was substituted to maximize sample sizes. Microwear counting was examined on the second molar (CMn2 and CMn5), third molar (CMn6) and fragmented molar (CMn7). Although microwear were observed at different positions, the microwear number of these four samples is relatively equal to each other.

T. cf. *xiaolongtanensis* tended to have surfaces dominated by scratches of varying width from fine to coarse. The scratch texture is 2 (mixture of fine and coarse scratch). The pit size is totally small with the absence of puncture pit.

Although both *S*. cf. *latidens* and *T*. cf. *xiaolongtanensis* were classified into the same mixed-feeding category, there were some difference in term of microwear features between two of them. Low magnification light microscopy documented higher pit frequencies on the enamel surfaces of *S*. cf. *latidens*. This, combined with the presence of puncture pits, suggested a leaf-dominated mixed-feeding for *S*. cf. *latidens*. The scratch texture value of *S*. cf. *latidens* (3) is coarser than those of *T*. cf. *xiaolongtanensis* (2). This may imply that the diet of *S*. cf. *latidens* composed of higher phytolith content than those of *T*. cf. *xiaolongtanensis*. The high phytolith content usually occur in seeds and leaves of silicon-accumulating plants.

The pollen evidence from Mae Moh coal mine show higher percentage of pollen of Pteridophyte and Rubiaceae than those of Chiang Muan coal mine (Sepulchre *et al*. 2010). Pteridophytes is the genus comprises mainly of fern, horse tail, club mosses,

spike mosses and quillwort. Rubiaceae is a genus of the tropical plants, such as coffee. These two genera of woody plants could lead *S*. cf. *latidens* to be leaf-dominated mixed-feeders. It is clear that *S*. cf. *latidens* have a higher percentage of pit than *T*. cf. *xiaolongtanensis*. The outstanding pollen evidence shows that Fabaceae, commonly known as bean family, may contribute in the diet of *T*. cf. *xiaolongtanensis* (Sepulchre *et al*., 2010).

Both *S*. cf. *latidens* and *T*. cf. *xiaolongtanensis* have molar morphology in the transition between bunolophodont and lophodont, which corresponding to the mixed-feeding diet, between browsers and grazers.

2) Grazer

Although the microwear results placed *Stegolophodon* cf. *stegodontoides* and cf. *Pronancus macinnesi* into the same grazing morphospace, the latter exhibited very wide scratches, hypercoarse scratches. cf. *Protanancus macinnesi* may consume C_4 grasses, whereas *Stegolophodon* cf. *stegodontoides* may consume regular grasses or C_3 plants.

A clear difference is evident in microwear patterning between the two species, with *S*. cf. *stegodontoides* characterized by only fine to coarse scratches and small pits, and those of cf. *P*. *macinnesi* by an enamel surface comprised largely of hypercoarse scratches and puncture pit. Hypercoarse scratches found in cf. *P*. *macinnesi* are associated with the ingestion of higher levels of abrasives. It is not clear from these results, whether the presence of hypercoarse scratches can be the indicator of C_4 grasses or soil and grit particles (Semprebon *et al*., 2004).

Pollen evidence from the fossil localities of these two species, Tha Chang sand pits, surprisingly show the highest percentage of Poaceae (Sepulchre *et al*., 2010). There is no doubt that the diet of these two proboscideans included mostly grasses.

Both *S*. cf. *stegodontoides* and cf. *P*. *macinnesi* show the molar morphology of bunodont. The cusps and lophs were arranged in a parallel manner as is usually seen in living elephants. It could be implied that the enamel ridges were optimized to increase the shearing surface of grass mastication in grazers.

Stegolophodon is the genus that could adapt themselves to a wide range of resource availabilities from browsers to grazers during Miocene.

The microwear results of *Stegolophodon* lineage showed broad dietary variability. The dietary trend varied from browsers in *Stegolophodon nasaiensis* which

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emerged from the early Middle Miocene is the most primitive species of the *Stegolophodon* lineage, to mixed-feeders in *Stegolophodon* cf. *latidens* which exhibited more advanced form having larger molar and more transverse loph(id)s, and finally to grazers in *Stegolophodon* cf. *stegodontoides*, the most advanced form of the lineage which showed the highest number of loph(id)s.

Microwear pattern is taxon independent. It depends chiefly on the available resources at the time the proboscideans lived. The same species may have different microwear results (Semprebon *et al.*, 2004).

4.2 The possibilities of niche separation between cf. *Protanancus macinnesi* and *Prodeinotherium pentapotamiae*

According to the samples of cf. *Protanancus macinnesi* and *P. pentapotamiae* were collected from unknown stratigraphy in Tha Chang sand pit. The previous study suggested these two species may live during the Middle Miocene (ref). The evidences from the dental microwear could be implied comparative ages of these fossils.

Since both cf. *Protanancus macinnesi* and *Prodeinotherium pentapotamiae* co-occurred at the same locality during Middle Miocene, they probably avoid competition by selecting different available resources. cf. *Protanancus macinnesi* might be specialized in grazing and *Prodeinotherium pentapotamiae* might be specialized in browsing. The significant dental microwear differences between species clarifies the feeding habits of these extinct proboscideans and their ecological segregation to avoid direct competition (Calandra *et al.*, 2008).

The microwear results could identify the age of *Prodeinotherium pentapotamiae* and cf. *Protanancus macinnesi*, more specifically. According, the dental morphology and the dental microwear of *Stegolophodon* linear, *S. nasaiensis*, *S.latidens*, *S.stegodontoides* can be used for comparative age because they have the stratigraphic record.

The microwear features observed in *Prodeinotherium pentapotamiae* are similar to those of *Stegolophodon nasaiensis,* browser. These two species may the early Middle Miocene species. However, the microwear features observed in cf. *Protanancus macinnesi* are similar to *Stegolophodon* cf. *stegodontoides*, grazer. These two species may live in the late Middle Miocene. That means cf. *Protananacus macinnesi* may be

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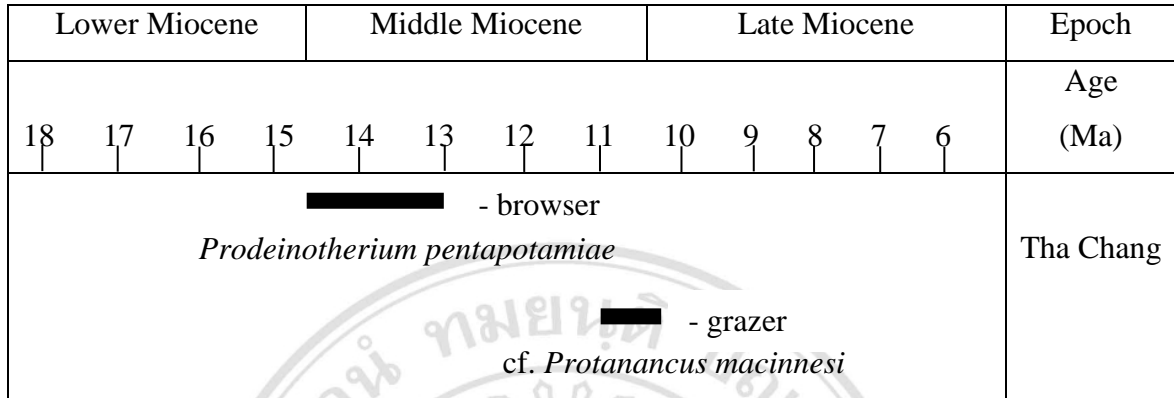younger than *Prodeinotherium pentapotamiae* and lived at the time when grassland dominated (Fig 4.1).

Lower Miocene				Middle Miocene				Late Miocene				Epoch
												Age (Ma)
18	17	16	15	14	13	12	11	10	9	8	7 6	
			▬▬▬▬ - browser *Prodeinotherium pentapotamiae*									Tha Chang
						▬▬ - grazer cf. *Protanancus macinnesi*						

Fig. 4.1 Proposed age specification of *Prodeinotherium pentapotamiae* and cf. *Protanancus macinnesi* from microwear results.

4.3 Paleoecology implication

The study of dental microwear could be suggested that Miocene paleoclimate consists of the greenhouse world and the icehouse world. The greenhouse world start from Early Miocene until the beginning of Middle Miocene (Zachos *et al*., 2008). The climate is considered to be hot and humid, thus the woody plants flourished (Hoorn *et al*., 2000). *Stegolophodon nasaiensis* probably browse the widespread woody plants at this time. In constrast, the icehouse world start from the beginning of Middle Miocene to Pliestocene (Zachos *et al*., 2001). The global climate is considered to be cool and arid, thus the grassland dominated the ecosystem (Hoorn *et al*., 2000). *Stegolophodon* cf. *latidens* and *Tetralophodon* cf. *xiaolongtanensis* were found to be mixed-feeders, which correspond to the time they lived in Middle Miocene, between the browsers and grazers. The grazers including *Stegolopodon* cf. *stegodontoides* and cf. *Protanancus macinnesi* lived during late Middle Miocene, when grassland flourished at this time.

Browsers usually live in closed areas such as forests and woodlands. Grazers inhabit more open patches and mixed-feeders occupy a variety of environments (Calandra *et al*., 2010). The grassland, especially C_4-grass, were increasing throughout the Miocene, which correspond to the transition from browsers to mixed-feeders and finally to grazers of Miocene proboscideans.

4.4 Microwear orientation

The angle of microwear orientation reflects the jaw movement of each species (Fig. 4.2). There are two obvious conclusion of microwear orientation within Miocene proboscideans.

First, the average angles of microwear orientation are reducing within the genus of *Stegolophodon*, from *Stegolophodon nasaiensis* (113°), *Stegolophodon* cf. *latidens* (90°) and *Stegolophodon* cf. *stegodontoides* (80°).

Second, the average angles of microwear orientation tend to decrease from browsers (*S. nasaiensis* and *Prodeinotherium pentapotamiae*), mixed-feeders (*S.* cf. *latidens* and *Tetralophodon* cf. *xiaolongtanensis*) and grazers (*S.* cf. *stegodontoides* and cf. *Protanancus macinnesi*), respectively.

Pits were created by the vertical jaw movement and the attrition of upper and lower molars, whereas scratches were created by the transverse jaw movement and the abrasion between molars and food particles. The evolution of jaw movement within the genus *Steglophodon* could be predicted from the angles of microwear orientation. In *S. nasaiensis*, the angle is widest (113°), suggesting the jaw movement dominated by buccal and lingual direction. The angle becomes narrower in *S.* cf. *latidens* (90°) and *S.* cf. *stegodontoides* (80°), respectively, suggesting the jaw movement dominated by the anterior and posterior direction. The jaw movement during chewing of proboscideans have evolved from the side to side direction to the forward and backward direction, as seen in the living elephants. This may be because the forward and backward direction increased the surface of mastication and lead to the effective food comminution as the enamel ridges act as two rasps grating upon one another. The trend of the angle observed from browsers, mixed-feeder and grazers also confirm that the jaw movement changed from buccal - lingual direction to anterior - posterior direction. The main diet of grazers composed mostly of grasses which required more energy to masticate than those of browsers. Thus, the effective jaw movement should be anterior – posterior direction, rather than buccal – lingual direction.
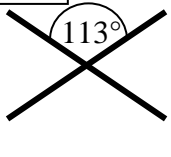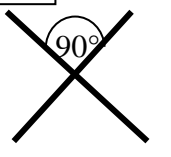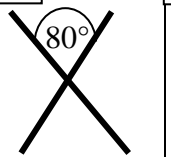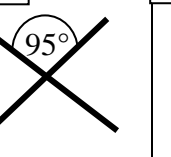
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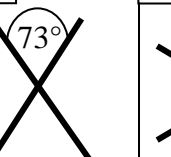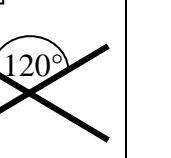| A.	B.	C.	D.	E.	F.
113°	90°	80°	95°	73°	120°
browser	mixed-feeder	grazer	mixed-feeder	grazer	browser

Fig. 4.2 The simple average angle of microwear orientation of each species. A = *Stegolophodon nasaiensis* (113°): B = *Stegolophodon* cf. *latidens* (90°): C = *Stegolophodon* cf. *stegodontoides* (80°): D = *Tetralophodon* cf. *xiaolongtanensis* (95°): E = cf. *Protanancus macinnesi* (73°): F = *Prodeinotherium pentapotamiae* (120°).