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Neogene mammalian fauna in Myanmar

Masanaru Takai[1], Haruo Saegusa[2], Thaung-Htike[1], Zin-Maung-Maung-Thein[1]

[1] *Primate Research Institute, Kyoto University, Inuyama 484-8506, Japan*
[2] *Institute of Natural and Environmental Sciences, University of Hyogo, Sanda 669-1546, Japan*

Abstract

In this paper, we review the Neogene mammalian fossils from the Pegu and Irrawaddy beds of Myanmar, comparing them with the contemporaneous mammalian faunas of south Asia (India and Pakistan) and east Asia (China). Although fossil specimens discovered in Myanmar so far are scarce, preliminary analysis of their faunal composition suggests greater similarity of the Myanmar fauna to the south Asian fauna than to the east Asian fauna until the Pliocene. The faunal interchange between Myanmar and east Asia (southern China) seems to have increased after the Pleistocene.

Introduction

Since the 19th century, many mammalian fossils have been reported from the Neogene sediments of Myanmar (e.g., Falconer, 1868). Much fossil material was collected by the paleontological expedition led by Dr Barnum Brown of the American Museum of Natural History in 1923, and was described by Colbert (1938). However, most of these specimens were of large mammals, such as elephants or herbivorous ungulates, and the locality data and/or geological ages of most specimens are inadequate for modern paleontological study.

Since 1998, the Myanmar–Japan Joint Expedition Team has continued paleontological work in central Myanmar, especially at the latest middle Eocene Pondaung Formation and the late Miocene to early Pleistocene Irrawaddy beds, primarily with the intention of finding primate fossils (Figure 1).

The Irrawaddy beds are usually correlated with the Siwalik Group in Indo–Pakistan, the thickness of which is estimated to be 2,000–5,000 m (Bender, 1983), and the Irrawaddy mammalian fauna is very similar to the Siwalik fauna (Figure 2). The geological age of the Siwalik Group in northern Pakistan is now considered to be about 18.3–1.5 Ma (Barry *et al.*, 2002; Nelson, 2003). It has traditionally been divided into three parts: the Lower, Middle, and Upper Siwaliks (Barry *et al.*, 2002; Nelson, 2003). According to recent comprehensive work by the Harvard University team in the Potwar Plateau in northern Pakistan, the Lower Siwalik (18.3–11.2 Ma) consists of the Kamlial (or Murree) and Chinji Formations, the

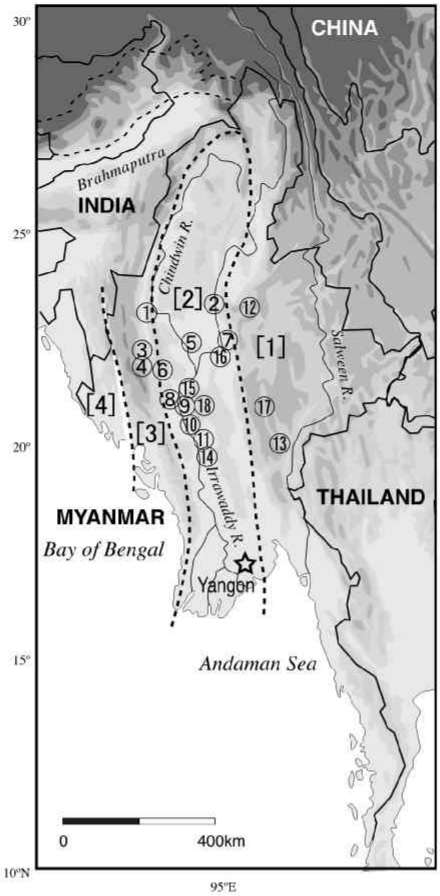

Figure 1. Index map of Myanmar, indicating four major geological regions and the fossil localities of the "Freshwater Pegu," Irrawaddy, and Post Irrawaddy faunas. [1] Eastern Highland (= Sino-Burman Ranges); [2] Central Tertiary Basin (CTB) (= Central Tertiary Belt or Inner Burman Tertiary Basin); [3] Western Ranges (= Indo-Burman Ranges); [4] Rakhine Coastal Plain (= Arakan Coastal Area). 1, Mingin (Lower Irrawaddy); 2, Malé (Upper Pegu and Lower Irrawaddy); 3, Gangaw (Lower and Upper Irrawaddy); 4, Tilin (Lower and Upper Irrawaddy); 5, Thanbinkan, Nwegwe (Upper Pegu and Lower Irrawaddy); 6, Pauk (Lower Irrawaddy); 7, Sagaing (Lower and Upper Irrawaddy); 8, Gwebin (Lower and Upper Irrawaddy); 9, Chauk (Lower and Upper Irrawaddy); 10, Yenangyaung (Lower and Upper Irrawaddy); 11, Tebingan, Thityagauk (Lower and Upper? Irrawaddy); 12, Mogok Caves (Pleistocene); 13, Moebye Cave (Pleistocene); 14, Sinbaungwe (Lower and Upper Irrawaddy); 15, Nyaung Oo (middle Pleistocene Terrace deposits); 16, Tado Oo (Upper Pegu); 17, Buddawzinaw Cave (Pleistocene Cave deposits); 18, Singu (Pleistocene Terrace deposits).

Middle Siwalik (11.2–3.5 Ma) consists of the Nagri and Dhok Pathan Formations, and the Upper Siwalik (3.5–1.5 Ma) is the Soan (or Samwal) Formation (or the Tatrot Formation) (Barry, 1995; Barry *et al.*, 1995; Nelson, 2003).

Many researchers have studied the faunal turnover in the Siwalik fauna (e.g., Barry, 1995; Barry *et al.*, 2002; Nelson, 2003). According to these studies, there seems to have been two major faunal turnovers at 13.5–13.0 Ma and 8.5–8.0 Ma, and one minor turnover at 7.3–7.0 Ma. There was also a floral transition from C3-plants-dominant forest conditions to a C4-plants-dominant open environment at about 8–7 Ma (Quade *et al.*, 1989; Quade and Cerling, 1995; Cerling *et al.*, 1997). Although it is uncertain whether the faunal and floral transitions that occurred in northern Pakistan occurred in the Neogene of Myanmar, such a comparison would provide valuable information for the paleoenvironmental analysis of the Irrawaddy fauna.

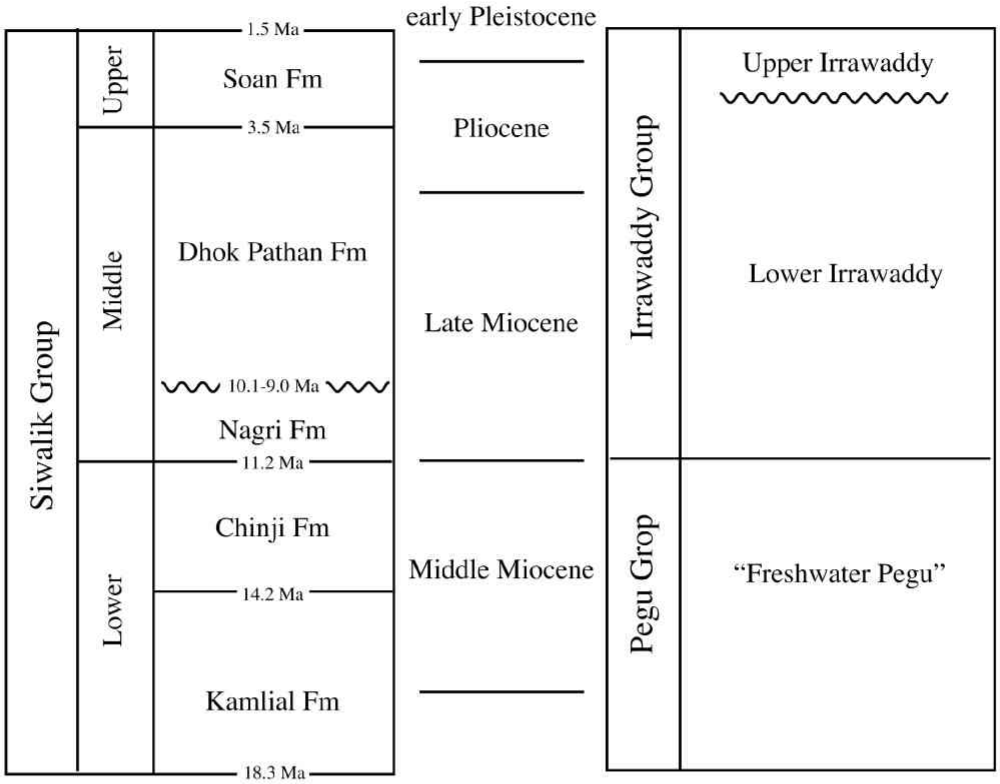

Figure 2. Correlations of the Neogene sediments of Myanmar and Siwaliks.

At present, unfortunately, most of the Neogene mammalian fossils collected in Myanmar are fragmentary and their locality names are often unreliable, so the available data are still far from the level required to construct a paleontological framework. In this paper, we review the previously discovered mammalian fossil specimens from the Neogene sediments in Myanmar and their locality data. We also attempt a preliminary analysis of the Neogene fauna in Myanmar, comparing it with the paleontological data for contemporaneous faunas in south Asia (Siwaliks and Bugti) and east Asia (China) (Figure 3).

Geological Setting

Geologically, Myanmar can be subdivided into four north–south trending regions (Figure 1): [1] Eastern Highlands (= Sino-Burman Ranges), which consist of Shan Plateau and Tanintharyi Ranges; [2] Central Tertiary Basin (CTB; = Central Tertiary Belt or Inner Burman Tertiary Basin); [3] Western Ranges (= Indo–Burman Ranges), which consist of the Rakhine, Chin, and Naga Ranges; [4] Rakhine Coastal Plain (= Arakan Coastal Area) (see Stamp, 1922; Chhibber, 1934; Bender, 1983; Kyi Khin and Myitta, 1999).

Neogene freshwater sediments, which yield many mammalian fossils, are only distributed in the CTB and mainly consist of two sedimentary units: the Freshwater Pegu Beds (= freshwater sediments of the Pegu Group, Oligocene through to middle Miocene) and Irrawaddy sediments (= Irrawaddy Group, late Miocene through to early Pleistocene).

The Pegu Group (Oligocene to middle Miocene) and its equivalents in Myanmar are

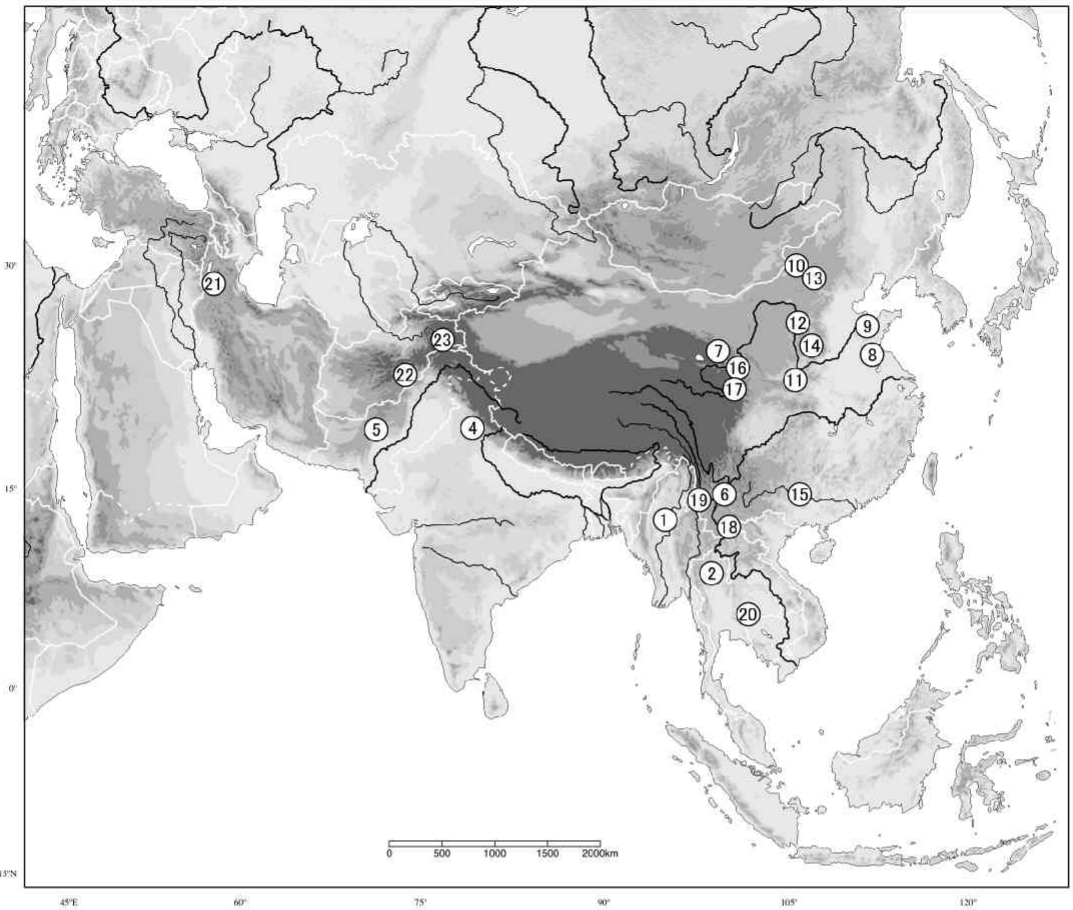

Figure 3. Index map of Eurasia, indicating the Neogene fossil localities mentioned in the text. 1, Myanmar localities; 2, northern Thailand localities; 3, Potwar (Pakistan); 4, Pinjor (India); 5, Bugti (Pakistan); 6, Lufeng & Yuanmou (Yunnan Province); 7, Xiejia (Qinghai Province); 8, Sihong (Jiangsu Province); 9, Shangwan (Shandong Province); 10, Tun-gur (Inner Mongolia); 11, Bahe (Shaanxi Province); 12, Baode (Shangxi Province); 13, Ertemte (Inner Mongolia); 14, Yushe (Shangxi Province); 15, Liuchang (Guangxi Province); 16, Tongxin (Ningxia Hui Autonomous Region); 17, Wudu (Gangsu Province); 18, Keiyuan (Yunnan Province); 19, Baoshan (Yunnan Province); 20, Khorat (Thailand); 21, Maragheh (Iran); 22, Molayan (Afghanistan); 23, Kuruk-Say (Tajikistan).

characterized by marine sediments in the south and are mainly continental in the north, where their transition boundary occurs in the area between latitudes 20–22° N (Stamp, 1922; Aung Khin and Kyaw Win, 1969; Bender, 1983). There are various stratigraphic names for the freshwater sediments of the Pegu Group: the Freshwater Pegu beds (Stamp, 1922; Colbert, 1938), the Freshwater Formation of the Pegu Group (Aung Khin and Kyaw Win, 1969), and the Khabo Formation (= Khabo Sandstone) for the upper part of the middle Miocene equivalent of the Pegu Group (Myint Thein, 1966; Kyi Khin and Myitta, 1999). In this paper, we tentatively use the term "Freshwater Pegu beds" for the Oligocene to middle Miocene freshwater sediments of Myanmar.

The Irrawaddy sediments were originally described as the "Irrawaddy beds" or "Irrawaddy series" (e.g., Pilgrim, 1910b; Colbert, 1935b), and are now called the "Irrawaddy Formation" mainly by Myanmar researchers (e.g., Aung Khin and Kyaw Win, 1969; Kyi Khin and Myitta, 1999) or the "Irrawaddy Group" by others (e.g., Bender, 1983). Considering the long time span from the late Miocene to the early Pleistocene, the Irrawaddy sediments

Figure 4. Right mandible with M_2 and M_3 of *Brachypotherium*.

probably correspond to a group, rather than to a formation, by modern stratigraphic criteria. In this paper, we tentatively use the term "Irrawaddy sediments" or "Irrawaddy beds".

The Freshwater Pegu beds and Irrawaddy sediments are distributed widely along the Irrawaddy River (= Ayeyarwady River) and Chindwin River in the CTB. The estimated thickness of the Irrawaddy sediments is more than 2,000 m (Bender, 1983), and they are traditionally divided into two parts, the Lower Irrawaddy (upper Miocene through to the Pliocene) and Upper Irrawaddy (early Pleistocene) (e.g., Colbert, 1938, 1943). However, the stratigraphy of the Freshwater Pegu beds and Irrawaddy sediments is not yet clearly determined and there are no data on the absolute ages based on radioisotopes or paleomagnetism.

"Freshwater Pegu" Fauna (Table 1A)

To date, only three orders (Perissodactyla, Artiodactyla, and Proboscidea), seven families (Deinotheriidae, Gomphotheriidae, Amynodontidae, Rhinocerotidae, Suidae, Anthracotheriidae, and Tragulidae), and 12 genera of mammals have been reported from the Freshwater Pegu and its equivalent beds (Table 1A). Most of these mammals seem to be survivors of archaic Oligocene forms.

Perissodactyla:

Four genera, *Cadurcotherium* (Amynodontidae), *Brachypotherium*, *Diceratherium*, and *Aceratherium* (Rhinocerotidae), have been discovered.

Cadurcotherium was collected from the northwest of Myaing, Magway Division, central Myanmar, but there is no figure of the specimen in the description papers (Pilgrim, 1910b; Stamp, 1922; Colbert, 1938). *Cadurcotherium* was originally discovered in the Lower Siwalik, but the description of the specimen is far from adequate (Pilgrim, 1910a). *Cadurcotherium* is the last survivor of the amynodontids, the primitive rhinoceros, retaining hypsodont teeth (Wall, 1989). They have been discovered in the Oligocene sediments of Europe and also in the Oligocene of the Bugti Hills, southern Pakistan (Welcomme *et al.*, 1999, 2001). *Brachypotherium* is a large, hornless, hippopotamus-like aquatic rhinoceros

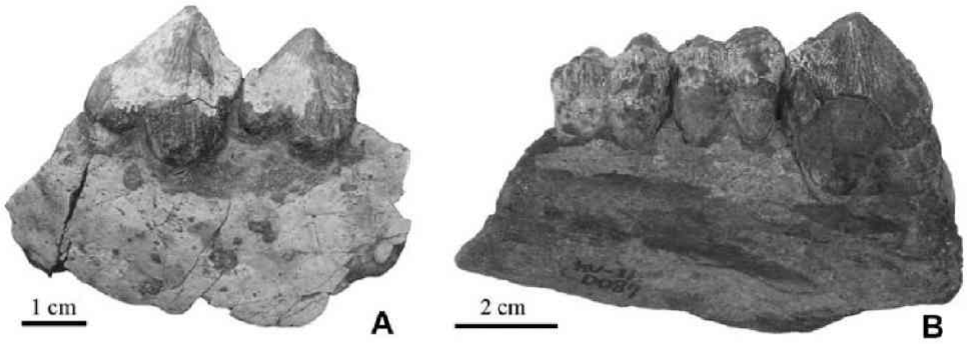

Figure 5. Left mandibular fragment with P_{3-4} cf. *Conohyus indicus* (a) and right mandibular fragment with P_4-M_2 of *Tetraconodon* (b).

with hypsodont teeth (Figure 4), distributed in Eurasia and Africa during the late Oligocene through to the Miocene. In Myanmar, it has been discovered in the Freshwater Pegu deposits near Thanbinkan village in Chaung-U, Sagaing Division. It has also been discovered in the early Miocene of the Bugti Hills, Pakistan (Welcomme and Ginsburg, 1997; Welcomme *et al.*, 2001), and from the Lower and Middle Siwaliks (Barry, 1995). In China, it has been reported from early Miocene localities, such as Xiejia (Qinghai Province), Shanwang (Shandong Province), and Puzhen (Jiangshu Province) (Li *et al.*, 1984; Qiu, 1990). *Brachypotherium* has also been discovered in the Lower Irrawaddy sediments.

In contrast, *Diceratherium*, a paired-horned rhinoceros, seems to have originated in North America and invaded Eurasia during the early Miocene (Prothero *et al.*, 1989). It has been discovered in the late Oligocene through to the middle Miocene of North America, from the early Miocene of western Europe, and from the Oligocene of Bugti, Pakistan (Welcomme *et al.*, 2001). In Myanmar, it has been reported from the Maw gravels in Gangaw, Magway Division, together with *Aceratherium*, a hornless rhinoceros, *Tetrabelodon* (Gomphotheriidae), *Deinotherium* (Deinotheriidae), and *Hemimeryx* and *Anthracotherium* (Anthracotheriidae) (Cotter, 1938). It has been suggested that the lower Maw beds correspond to the Freshwater Pegu beds.

Artiodactyla:

Seven genera of three families (Suidae, Anthracotheriidae, and Tragulidae) have so far been described from the middle Miocene Freshwater Pegu beds.

Among the Suidae, *Listriodon* (Listriodontinae) (Cotter, 1938), and *Conohyus* and *Tetraconodon* (Tetraconodontinae) (Thaung-Htike *et al.*, 2005) have been discovered. Listriodontine suids inhabited Africa and Eurasia during the Miocene. According to Made (1996), *Listriodon* seems to have evolved from *Bunolistriodon* in the early middle Miocene, about 13.8 Ma. *Listriodon* has been discovered in the middle Miocene of Bugti (Welcomme *et al.*, 2001) and in the Lower to Middle Siwaliks (Pilgrim, 1926; Barry, 1995). In China, it has been reported from middle Miocene localities at Lengshuigou (Shaanxi Province) and

Table 1. List of mammalian fauna of the "Freshwater Pegu"

"Freshwater Pegu" Fauna

ARTIODACTYLA
- Suidae
  - Tetraconodontinae
    - cf. *Conohyus* sp.
    - *Tetraconodon malensis*
    - *Tetraconodon* sp. indet.
  - Listriodontinae
    - *Listriodon* sp.
- Anthracotheriidae
  - *Anthracotherium* sp.
  - *Hemimeryx* sp.
  - *Telmatodon* sp.
- Tragulidae
  - *Dorcatherium* sp.

PERISSODACTYLA
- Rhinocerotidae
  - *Aceratherium perimense*
  - *Diceratherium naricum*
  - *Brachypotherium* sp.
- Amynodontidae
  - *Cadurcotherium* sp.

PROBOSCIDEA
- Deinotheriidae
  - *Prodeinotherium* sp.
- Gomphotheriidae
  - *Choerolophodon corrugatus*
  - gen. et sp. indet.

Tung-gur (Inner Mongolia) (Li *et al.*, 1984; Qiu, 1990).

Of the two tetraconodontines, *Conohyus* (Figure 5A) and *Tetraconodon* (Figure 5B), the former is more primitive morphologically, and was discovered in the Lower and Middle Siwaliks (Pilgrim, 1926; Colbert, 1935a; Pickford and Gupta, 2001) and in the middle Miocene of northern Thailand (Ducrocq *et al.*, 1997), whereas the latter is considered more derived and has been collected from the Middle and Upper Siwaliks (Pickford, 1988). In Myanmar, cf. *Conohyus* has been found near Chaung-U, Sagaing Division. The middle Miocene *Tetraconodon* is reported only from Myanmar (Thaung-Htike *et al.*, 2005), and this genus seems to have derived from *Conohyus* in Myanmar as early as the late middle Miocene.

Three genera of Anthracotheriidae (*Anthracotherium*, *Hemimeryx*, and *Telmatodon*) have been reported to date (Pilgrim, 1910b; Colbert, 1938). *Anthracotherium* and *Hemimeryx* have been discovered in the lower and middle Miocene of Bugti (Pickford, 1987) and in the Lower and Middle Siwaliks (Barry, 1995). Pilgrim (1910b) reported an isolated lower molar of *Telmatodon* collected at Maingyaung, near Pakokku, but there is no figure of the specimen.

Telmatodon has also been discovered in the upper Oligocene/lower Miocene of Bugti (Pickford, 1987) and from the Chinji Formation of the Lower Siwaliks. These anthracotherids were widely distributed in south Asia during the early Miocene, but there is no fossil record from the contemporaneous sediments in China, probably because there was no adequate environment for aquatic anthracotheres in the inland areas of China.

Dorcatherium (Tragulidae) was a small ruminant that preferred relatively humid and forested conditions (Agustí and Antón, 2002). It has been discovered in the early to late Miocene sediments of Africa, Europe, and eastern Asia, suggesting a faunal interchange between Africa and Eurasia during the early Miocene. In Myanmar, it has been discovered in Yenangyaung, Magway Division (Pilgrim, 1910b; Colbert, 1938). In south Asia, many *Dorcatherium* specimens have been discovered in the Lower through to the Upper Siwaliks (Pickford *et al.*, 2000), whereas in China, it has been collected only from the lower Miocene of Sihong (Jiangsu Province) (Li *et al.*, 1984).

Proboscidea:

Although it has generally been believed that no proboscidean fossils have been reported from the Freshwater Pegu, Cotter (1938) reported "*Dinotherium*" from the Maw gravels in Gangaw (Magway Division), which has now been correlated with the middle Miocene Freshwater Pegu (Bender, 1983). Recently, we observed the proboscidean fossil specimens collected from the Freshwater Pegu and its equivalent sediments in Myanmar, and identified three taxonomic groups (*Prodeinotherium* sp., *Choerolophodon corrugatus*, and a trilophodont gomphothere).

The dental specimens of *Prodeinotherium* sp. (Figure 6A) are very similar in size to those of *Prodeinotherium pentapotaminae*, which was found in the Lower Siwaliks (the Kamlial and Chinji Formations) (Dehm, 1963; Harris, 1973). Although *Prodeinotherium* and *Deinotherium* are apparently distinguishable on their cranial and postcranial morphologies (Harris, 1973; Huttunen, 2002), it is rather difficult to distinguish them only by their dental characters. Harris (1973) proposed that *Prodeinotherium* differs from *Deinotherium* in some features of the molars, such as the degree of development of the postmetaloph ornamentation in M^{2-3}. However, Huttunen (2002) insists that the individual variation in these dental features is very great and that the only definitive criterion between them is their size. Here, we treat the deinotheriids from the Freshwater Pegu as *Prodeinotherium* sp., because it is so difficult to differentiate *Prodeinotherium* discovered in the Old World (Europe, Africa, and Asia) at the species level that many researchers have treated them as conspecific (Harris, 1976; Huttunen, 2002).

Choerolophodon is a relatively primitive Elephantoidea known from the early to late Miocene of Africa, Europe, and western/southern Asia (Tassy, 1989). Pickford (2001) subdivided the early, primitive member of the genus into a different genus, *Afrochoerodon*, which is now widely accepted by many researchers. However, the reclassification of

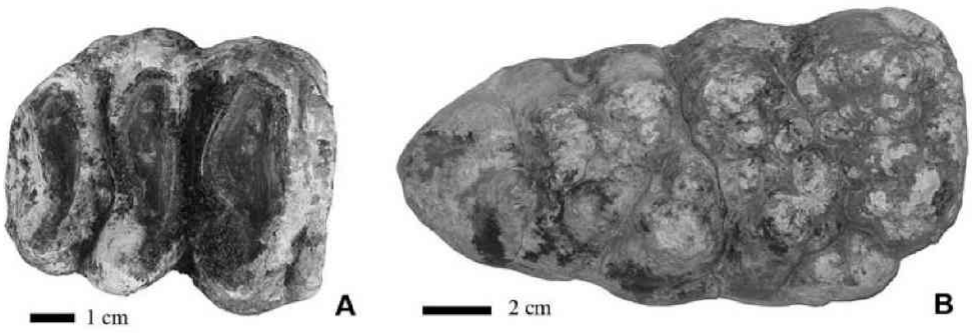

Figure 6. Right M_1 of *Prodeinotherium* (**A**) and an isolate lower? molar of *Choerolophodon* (**B**).

Choerolophodon and *Afrochoerodon* still seems far from resolved (Sanders and Miller, 2002). *Choerolophodon corrugatus* is a relatively derived member of the genus, and was discovered in the Lower and Middle Siwaliks. The Myanmar specimen (M^3, Figure 6b) is very similar to the Siwalik specimen of *C. corrugatus* in both size and morphology (Tassy, 1983), so it has been identified as the same species. Tobien *et al.* (1986) and Guan (1996) have reviewed the fossil record of *Choerolophodon*, but at least some of the specimens are apparently *Sinomastodon* (Chen, 1999) and others are unlikely to be *Choerolophodon*. The discovery of *Choerolophodon* in the Freshwater Pegu is the easternmost fossil recorded so far.

Some dental materials (P^4, M^1, M^2) of the trilophodont gomphothere have been found in the Freshwater Pegu at Thanginkin, Chaung-U Township (Sagaing Division). No definitive dental characters can be observed in this specimen, so it is impossible to identify it at a more detailed taxonomic rank. Additional specimens, such as well-preserved incisors, would be useful in determining the genus and species of this animal.

On the Eurasian continent, the oldest fossil record of Elephantoidea is a fragment of an incisor collected from the late Oligocene Chitarwata Formation in the Bugti Hills, Pakistan (Antoine *et al.*, 2003). The coexistence of *Choerolophodon corrugatus* and *Prodeinotherium* sp. and the fact that the elephantoideans from the Freshwater Pegu are apparently more derived than the Bugti forms indicate a middle Miocene age for the Freshwater Pegu.

Thus, the Pegu mammalian fauna is similar to contemporaneous southern Asian faunas, such as those of the Lower and Middle Siwaliks and Bugti. In contrast, some large aquatic animals, such as anthracotheres and the *Brachypotherium* rhinoceros, have not been discovered in the contemporaneous sediments of China, suggesting differences in the ecological environments of southern Asia and the inland areas of China.

Irrawaddy Fauna (Table 1B-C)

The Irrawaddy sediments are usually divided into the lower and upper parts based on the mammalian fauna: the Lower Irrawaddy is late Miocene through to Pliocene and the Upper Irrawaddy is early Pleistocene (Stamp, 1922; Colbert, 1938). To date, four mammalian orders (Carnivora, Proboscidea, Perissodactyla, and Artiodactyla) including 14 families have been discovered; however, these contain no small mammals, such as rodents, lagomorphs,

or insectivores, so it is impossible to make detailed comparisons with the contemporaneous faunas of southern or eastern Asia. Here, we draw preliminary faunal comparisons based on large to medium-sized mammalian genera.

Carnivora:

The only carnivorous mammal collected from the Lower Irrawaddy near Magway, Magway District, is *Amphicyon* (Amphicyonoidae) (Figure 7). *Amphicyon* is a "cosmopolitan" animal, which inhabited a vast area of the northern hemisphere from the late Oligocene through to the late Miocene. In Asia, it has been reported from the lower to middle Miocene of Bugti (Welcomme *et al.*, 2001), from the Lower and Middle Siwaliks (Barry, 1995), from the late Miocene Tung-gur Fauna (Inner Mongolia), and from the middle to late Miocene beds of Yunnan Province, China (Li *et al.*, 1984; Qiu, 1990; He, 1997).

Proboscidea:

In addition to the two proboscidean families, Stegodontidae and Elephantidae, which were reported from the Irrawaddy sediments (Clift, 1828; Falconer and Cautley, 1846; Colbert, 1938; Colbert 1943), Gomphotheriidae was confirmed in the fossil specimens housed at the National Museum of Myanmar. Here, we first review the fossil taxa of Stegodontidae and Elephantidae, both known since the 20th century, and then add some new findings.

Stegolophodon latidens and *Stegodon elephantoides* (Stegodontidae) are among the mammalian fossils first described from the Irrawaddy sediments, and are the type specimens of these two genera (Osborn, 1942; Hopwood, 1935). Clift (1828) described two Irrawaddian proboscideans, *Mastodon latidens* and *Mastodon elephantoides*. However, Falconer and Cautley (1846) recognized only *Mastodon latidens* and renamed *Mastodon elephantoides Elephas clifti*, regarding the former name as *nomen nudum*. Falconer and Cautley (1846) thought that *M. elephantoides* should be included in the genus *Elephas* and that Clift (1828) had incorrectly used the figure of *M. elephantoides* to represent *Mastodon latidens*. Falconer and Cautley (1846) categorized *Elephas clifti* in the subgenus *Stegodon*, together with *Elephas insignis, E. ganesa,* and *E. bombifrons* from the Siwaliks. Thus, *Stegodon clifti* was widely used instead of *Mastodon elephantoides* until the 1930s. Osborn (1942) reviewed the Stegodontoidea and Elephantoidea in his monographic tome, and revived *elephantoides* as the specific name, regarding the discussion of Falconer and Cautley (1846) as inadequate. Now, all the relatively primitive stegodons from the Irrawaddy sediments of Myanmar are called *Stegodon elephantoides*. Meanwhile, the lectotypes of *Stegolophodon latidens* and *Stegodon elephantoides* were indicated by Colbert (1938). Osborn (1929) founded the subspecies *Stegodon insignis birmanicus* for the relatively derived stegodon fossils collected from the Upper Irrawaddy sediments.

Mastodon latidens was moved to the genus *Stegolophodon*, which was founded by Schlesinger (1917). *Hypselephas hysudricus* from the Upper Irrawaddy sediments was

Table 2. List of mammalian fauna of the Lower Irrawaddy (**A**) and Upper Irrawaddy (**B**) faunas.

A. Lower Irrawaddy Fauna

CARNIVORA
- Amphicyonidae
  - *Amphicyon* sp. indet.

ARTIODACTYLA
- Suidae
  - Tetraconodontinae
    - *Tetraconodon minor*
    - *Tetraconodon* cf. *magnus*
    - *Tetraconodon* cf. *intermedius*
    - *Sivachoerus prior*
    - *Parachleuastochoerus* sp. indet.
  - Suinae
    - *Propotamochoerus hysudricus*
- Anthracotheriidae
  - *Merycopotamus dissimilis*
- Hippopotamidae
  - *Hexaprotodon iravaticus*
  - *Hexaprotodon sivalensis*
- Giraffidae
  - *Hydaspitherium birmanicum*
  - *Vishnutherium iravaticum*
- Bovidae
  - *Pachyportax latidens*
  - *Proleptobos birmanicum*
  - *Hemibos* sp.

PERISSODACTYLA
- Equidae
  - *Hipparion antelopinum*
- Rhinocerotidae
  - *Aceratherium lydekkeri*
  - *Brachypotheium* sp.

PROBOSCIDEA
- Stegodontidae
  - *Stegolophodon latidens*
  - *Stegolophodon stegodontoides* (large)
  - *Stegodon* sp. indet. (most primitive)
  - *Stegodon elephantoides* (primitive)
- Gomphotheriidae
  - *Sinomastodon* sp.

B. Upper Irrawaddy Fauna

ARTIODACTYLA
- Suidae
  - *Potamochoerus* sp.
- Anthracotheriidae
  - *Merycopotamus dissimilis*
- Hippopotamidae
  - *Hexaprotodon iravaticus*
  - *Hexaprotodon palaeindicus*
- Tragulidae
  - *Dorcabune* sp.
- Cervidae
  - *Cervus* sp.
- Bovidae
  - Bovinae
    - *Proleptobos birmanicus*
    - *Hemibos triquetricornis*
    - *Bos* cf. *sondaicus*
  - ?Boselapini
    - gen. et sp. indet.
  - Caprinae
    - *Capricornis* cf. *sumatrensis*
    - gen. et sp. indet.
  - Antilopinae
    - ?*Gazella* sp.
  - ?Hippotraginae
    - gen. et sp. indet.

PERISSODACTYLA
- Equidae
  - *Equus yunnanensis*
- Chalicotheriidae
  - cf. *Nestoritherium* sp.
- Rhinocerotidae
  - *Rhinoceros sivalensis*
  - *Rhinoceros sondaicus*

PROBOSCIDEA
- Stegodontidae
  - *Stegodon insignis birmanicus* (derived)
  - *Stegodon* sp. indet. (most derived)
- Elephantidae
  - *Elephas* (= *Hypselephas*) *hysudricus*

described by Colbert (1938, 1943), but it is now considered by most researchers to be a junior synonym of *Elephas*. Since the 1940s, there have been few paleontological studies of proboscidean fossils from the Irrawaddy sediments. However, Tassy (1983) noted the possible variations in size of the Irrawaddian specimens, all of which have been referred to *Stegolophodon latidens*. Our preliminary observation of the proboscidean fossils also supports the view of Tassy (1983). The lectotype of *Stegolophodon latidens*, which was assigned by Colbert (1938), is relatively small, whereas most *Stegolophodon* specimens

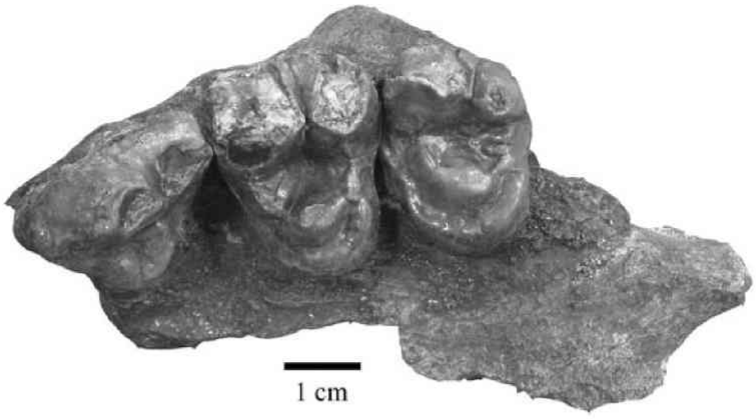

Figure 7. Left maxilla with P^4-M^2 of *Amphicyon* sp.

collected from the Irrawaddy sediments are much larger than the lectotype. The size difference between them probably greatly exceeds the individual variation within the same species of elephants. Moreover, most of the large *Stegolophodon* specimens from the Irrawaddy sediments are identified as *Stegolophodon stegodontoides* (or its close relatives), which is found in the Siwaliks. There seems to be two species in Irrawaddian *Stegolophodon*, representing earlier and later forms.

It is widely accepted that there are two species of *Stegodon* from the Irrawaddy sediments, the relatively primitive *Stegodon elephantoides* and the relatively derived *Stegodon insignis birmanicus* (Figure 8B-C). In addition to these two species, we recently identified another two forms among the fossil specimens housed at the National Museum in Yangon. One specimen is more primitive than *Stegodon elephantoides*, and similar to the specimen collected from a late Miocene locality (Tha Chang) in Thailand (Saegusa *et al.*, 2005), whereas the other, the locality of which is unfortunately unknown, is more derived than *Stegodon insignis birmanicus*. Therefore, there are at least four types of *Stegodon* forms, probably representing different evolutionary stages of this genus. The classification of the *Stegodon* fossils of Myanmar would be useful for the Neogene biostratigraphy not only of Myanmar but also of Southeast Asia.

In this paper, we first report two forms of Gomphotheriidae from the Irrawaddy sediments: one is *Sinomastodon* sp. and the other is probably a new genus and species of gomphothere. The specimen of *Sinomastodon* sp. is a maxillopalatine bone preserving the intermediate molars, housed at the National Museum in Yangon (Figure 8A). *Sinomastodon* is a gomphothere known from the latest Miocene through to the Pleistocene in China, and the oldest fossil record is reported from the Miocene/Pliocene boundary in Yushe locality, Shanxi Province, northern China (Tobien *et al.*, 1986; Flynn *et al.*, 1991, 1997; Saegusa *et al.*, 2005). The Irrawaddian *Sinomastodon* is more derived than those from Yushe, and seems more similar to the "moderately" derived forms, such as *S. yanyuanensis* (Zong, 1987) or *S. hanjiangensis* (Zong *et al.*, 1989). Although all the Chinese *Sinomastodon* have long been classified as *S. intermedius* (Teilhard and Trassaert, 1937; Tobien *et al.*, 1986), some derived

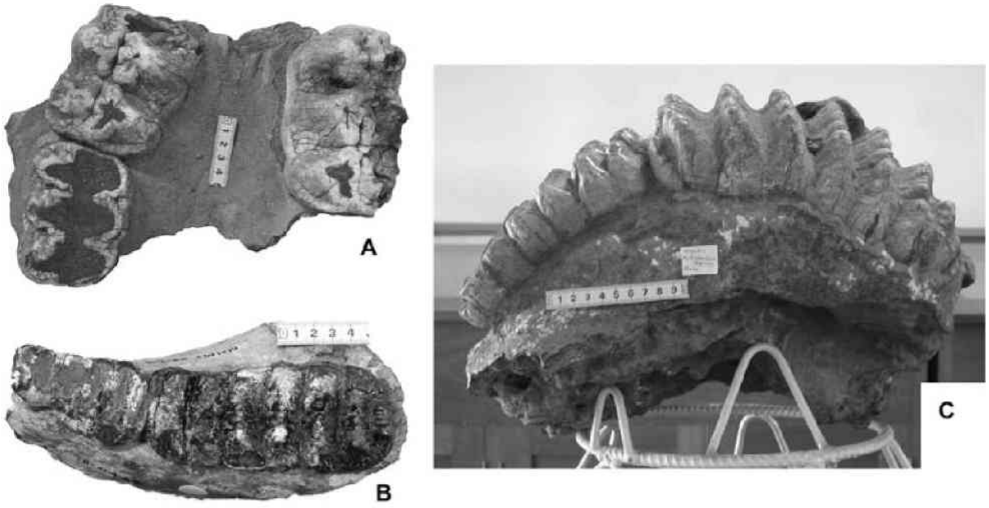

Figure 8. Palatine with left dP^4-M^1 and right M^1 of *Sinomastodon* (**A**), Left mandible with dP_4-M_1 of *Stegdon* (**B**), and maxilla with upper molars of *Stegodon* (**C**).

forms, such as *S. yanyuanensis* and *S. hanjiangensis*, are proposed from southern China. It is necessary to review these *Sinomastodon* forms based on many morphological characters, as Chen (1999) has done. On the other hand, the fossil materials of the new gomphothere are only known from two isolated molars. Further specimens are required for a more detailed description of this new form.

Thus, various kinds of proboscideans have been found in the Irrawaddy sediments, and their geological ages are probably distributed from the early late Miocene through to the early Pleistocene. More detailed descriptions and observations of the Irrawaddian fossils will contribute to the Neogene biostratigraphy of Myanmar.

Perissodactyla:

Three families and five genera, Equiidae (*Hipparion* and *Equus*), Rhinocerotidae (*Brachypotherium*, *Aceratherium*, and *Rhinoceros*), and Chalicotheriidae (cf. *Nestoritherium*) have been discovered in the Irrawaddy sediments.

Hipparion, a three-toed grazing horse, was collected from the Lower Irrawaddy, whereas *Equus* is from the Upper Irrawaddy. *Hipparion* originated in North America in the middle Miocene, and invaded the Old World. The first occurrences of *Hipparion* or its close relatives have been dated at about 11.5 Ma in Europe and 11–12 Ma in northern China (Bahe fauna, Shaanxi Province) (Kurtén, 1952; Li *et al.*, 1984; Qiu, 1990; Bernor *et al.*, 1990; MacFadden, 1992; Lucas, 2001). In south Asia, *Hipparion* fossils have been discovered in the Middle Siwaliks in Pakistan (Welcomme *et al.*, 1999; Barry *et al.*, 2002). Barry *et al.* (2002) estimated the first appearance of *Hipparion* in Siwalik at about 10.9 Ma. This appearance of *Hipparion* in south Asia slightly later than in Europe may indicate a biogeographic isolation of the Indian subcontinent in the middle Miocene (MacFadden, 1992). Nelson

(2003) estimates the beginning of their diet of C4 plants at about 8.7 Ma, using carbon radioisotope analysis of *Hipparion* teeth. This estimate could provide important information for determining the absolute age of the Irrawaddy sediments and an estimate of the C3–C4 plant transition in Myanmar. Unfortunately, however, the *Hipparion* specimens discovered in the Lower Irrawaddy so far comprise just three isolated teeth (Figure 9).

Like *Hipparion*, the monodactyl "real horse" *Equus* also originated in North America, probably in the Pliocene, and then migrated to the Old World via the Bering land bridge in the latest Pliocene (MacFadden, 1992). Many fossils have been reported from the Pleistocene in China and the Siwaliks. The *Equus* fossils discovered in the Upper Irrawaddy are regarded as the same species as *E. yunnanensis* from the Pleistocene deposits of Yunnan Province, southern China (e.g., Colbert, 1940) rather than as either of the two species, *E. sivalensis* or *E. namadicus*, from the Pinjor beds, Upper Siwalik (Falconer and Cautley, 1846; Colbert, 1935b). Based on the identification of *Equus* in the Irrawaddy beds, Colbert (1940) proposed a single *Equus* form that ranged through upper Myanmar and eastward into Yunnan in early Pleistocene times.

Of the Rhinocerotidae, *Brachypotherium* and *Aceratherium* have been discovered in the Lower Irrawaddy, and *Rhinoceros* has been collected from the Upper Irrawaddy. As already mentioned, *Brachypotherium* has also been discovered in the Pegu beds, suggesting a relatively long distribution from the middle to late Miocene in Myanmar. *Aceratherium* is a hornless aceratherine rhinoceros, retaining brachyodont teeth, which was widely distributed in Europe during the late Miocene. Although several previous researchers have reported *Aceratherium* from the Middle Siwalik and from the Upper Irrawaddy, (e.g., Pilgrim, 1910b; Stamp, 1922; Matthew, 1929; Colbert, 1938), it is now difficult to identify the original Irrawaddy specimen. Pilgrim (1910b) reported *Aceratherium* from the Bugti sediments, but there is no citation of *Aceratherium* in recent works (e.g., Welcomme and Ginsburg, 1997; Welcomme *et al.*, 2001). In China, an *Aceratherium* specimen has been reported from the late middle Miocene Shanwang Fauna of Shandong Province (Li *et al.*, 1984).

Rhinoceros discovered in the Irrawaddy belongs to the same genus as the living Asian one-horned rhinoceros, which inhabits the Indian subcontinent and Java (Figure 10). *Rhinoceros* is widely reported from the Pleistocene deposits of southern China (e.g., Yunnan Province), Indo–Pakistan, and Southeast Asia (Hooijer, 1946; Colbert and Hooiger, 1953; He, 1997; Tougard, 2001). In contrast, no fossil of *Dicerorhinus*, the Sumatran rhinoceros, has yet been reported from Myanmar, but has been reported from the upper Miocene of Bahe, Shaanxi Province (Li *et al.*, 1984; Lucas, 2001).

A possible chalicothere fossil was reported from the Lower Irrawaddy in the 19th century (Noetling, 1897a, b; Hooijer, 1951), but Colbert (1938) did not mention chalicotheres in his review of the fossil mammals of Myanmar. Recently, dental fragments referred to *Nestoritherium* were discovered in the Upper Irrawaddy sediments near Gwebin, Magway Division (Tsubamoto *et al.*, 2006). *Nestoritherium* has been reported from the early to middle

Figure 9. Left M^1 of *Hipparion*.

Figure 10. Right M^1 of *Rhinoceros*.

Pleistocene cave deposits of southern China (Colbert and Hooijer, 1953; Zong *et al.*, 1996; Lucas, 2001). It has also been discovered in the Upper Siwalik (Matthew, 1929; Colbert, 1935b), and *Chalicotherium*, a close relative of *Nestoritherium*, is well known from the early Miocene through to the early Pliocene sediments of Eurasia (e.g., McKenna and Bell, 1997; Agustí and Antón, 2002).

Artiodactyla:

Compared with those of other mammals, the fossil records of the artiodactyls of the Irrawaddy sediments are relatively abundant, suggesting their adaptive radiation in the later Neogene. To date, seven families (Suidae, Hippopotamidae, Anthracotheriidae, Tragulidae, Cervidae, Giraffidae, and Bovidae) and probably 18 genera have been reported from the Irrawaddy sediments. However, the identification of these taxa is not reliable, so their classification should be revised constantly to reflect new discoveries.

Two subfamilies of Suidae, Tetraconodontinae and Suinae, have been discovered. Three genera (*Sivachoerus*, *Tetraconodon*, and *Parachleuastochoerus*) of Tetraconodontinae have been found in the Lower Irrawaddy (Figure 11A-B; Thaung-Htike *et al.*, 2005). Three late Miocene species of *Tetraconodon* (*T. minor, T. intermedius*, and *T.* cf. *intermedius*) have been reported from central Myanmar (Pilgrim, 1910b; Thaung-Htike *et al.*, 2005). As already mentioned, *Tetraconodon* has also been discovered in the Freshwater Pegu beds, and from the Middle and Upper Siwaliks (Falconer, 1868; Colbert, 1938; Pickford, 1988; Thaung-Htike *et al.*, 2005). Compared with the Siwalik forms, *Tetraconodon* of Myanmar is more primitive, so Thaung-Htike *et al.* (2005) have presumed that *Tetraconodon* originated in Southeast Asia, such as in Myanmar, rather than in the India–Pakistan region. *Sivachoerus* has also been discovered in the Pliocene of the Middle and Upper Siwaliks (Pilgrim, 1926; Pickford, 1988; van der Made, 1999), but there is no fossil record from China, as is the case for *Tetraconodon*. In contrast, *Parachleuastochoerus* has been discovered in China (van der Made and Han, 1994; Pickford and Liu, 2001), but not in the Siwaliks.

Of the two genera (*Propotamochoerus* and *Potamochoerus*) of Suinae,

Propotamochoerus has been discovered in the Lower Irrawaddy (Figure 11C; Thaung-Htike *et al.*, 2006), whereas *Potamochoerus* has been discovered in the Upper Irrawaddy. *Propotamochoerus* has been collected from the Middle Siwaliks (Pickford, 1988; Barry, 1995; Barry *et al.*, 2002). In China, it has been reported from the upper Miocene Yuanmou Fauna, Yunnan Province, southern China (Pearson, 1928; van der Made and Han, 1994; He, 1997; Liu and Ji, 2004), and from the latest Miocene Ertemte fauna of Inner Mongolia, northern China (Li *et al.*, 1984), suggesting a wide distribution for this animal. *Propotamochoerus* is regarded as having originated in south Asia, expanding its distribution as far west as Europe (Pickford, 1988; Agustí and Antón, 2002).

Potamochoerus has been discovered in the Upper Siwalik (Barry, 1995; Barry *et al.*, 2002) and in the Pleistocene cave deposits of southern China (Han, 1987). The occurrence pattern of Suidae indicates that the Irrawaddy fauna was more similar to the Siwalik fauna than to the Chinese faunas until the Pliocene. The faunal interchange between southern Asia and eastern Asia (China) seems to have begun as early as the Pleistocene.

In south/southeast Asia, many fossil specimens of hippopotami, typical aquatic mammals, have been discovered, although there are no hippopotami in Asia today. All Asian fossil hippopotami are included in the genus *Hexaprotodon* of the family Hippopotamidae. Although the genus *Hexaprotodon* has been used for most of the fossil hippopotami discovered in the Old World for a long time, it is now restricted mostly to the Asian forms and one fossil species from North Africa (Boisserie, 2005). According to a recent cladistic analysis (Boisserie, 2005), the extant pygmy hippopotamus (or Liberian hippopotamus) of western Africa, which was once included in *Hexaprotodon*, belongs to an ancient, primitive lineage and has been reclassified as *Choeropsis*, with earlier generic nomenclature. In Myanmar, hippopotamus fossils have been discovered in the Lower and Upper Irrawaddy beds (Figure 12A; Thaung-Htike *et al.*, 2006). They were originally described as *Hippopotamus* by Falconer and Cautley (1846), but were revised as *Hexaprotodon* by later researchers (Matthew, 1929; Colbert, 1935a; Hooijer, 1950). Although hippopotamids are widely known from the upper Miocene to the upper Pleistocene of south and Southeastern Asia (Hooijer, 1950), there is no fossil record in China.

The family Anthracotheriidae is also considered to contain aquatic mammals and may be the ancestral group of the hippopotamids. *Merycopotamus dissimilis* (Anthracotheriidae) has been discovered in the Lower and Upper Irrawaddy sediments (Figure 12B; Pilgrim, 1910b; Colbert, 1938). It has also been discovered in the Lower and Middle Siwaliks, but there is no fossil record of *Hexaprotodon* in China. This phenomenon indicates that there was no adequate environment for large aquatic mammals such as hippopotamids and anthracotherids in inland China at the time.

Recently, the Myanmar–Japan Joint Expedition Team found a new tragulid artiodactyl, *Dorcabune*, in the Irrawaddy beds near Gwebin village, Magway Division (Tsubamoto *et al.*, 2006). Although it has been suggested that the Irrawaddy sediments of the Gwebin locality

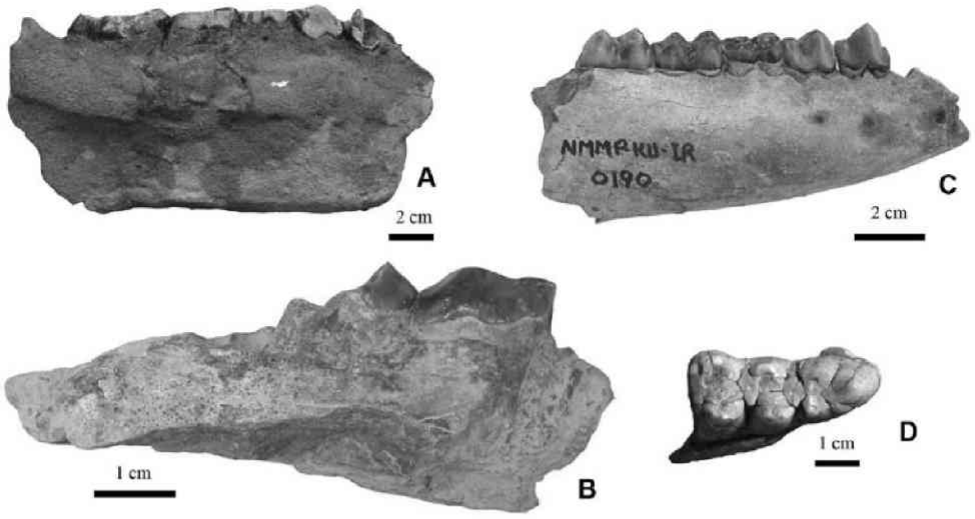

Figure 11. Right mandible with P_3-M_3 of *Sivachoerus* (**A**), Left mandibular fragment with P_3-P_4 of *Parachleuastochoerus* (**B**), right mandible with P_3-M_3 of *Propotamochoerus* (**C**), and an isolated right M_3 of *Sus scrofa* (**D**).

are equivalent to the Upper Irrawaddy (Moe Nyunt, 1987), Thaung-Htike *et al.* (2006) have correlated the Lower Irrawaddy with this locality. *Dorcabune* has been found in the Lower and Middle Siwaliks (Colbert, 1935b; Barry, 1995; Barry *et al.*, 2002), whereas in China, it is reported from the late Miocene of Yunnan (Lufeng and Yuanmou) and from the early Pleistocene of Guangxi (Liuchang) (Han, 1974; He, 1997; Lucas, 2001).

Cervus (Cervidae) is reported from the Upper Irrawaddy (Colbert, 1938). It is also reported from the Middle and Upper Siwaliks in south Asia, and is common after the middle Pleistocene in China.

The fossil specimens of Giraffidae from the Irrawaddy sediments are so fragmentary that their identification is not reliable. Two sivatheriine forms, *Hydaspitherium birmanicum* and *Vishnutherium iravaticum*, have been reported so far (Pilgrim, 1910b; Colbert, 1935b, 1938). Both *Hydaspitherium* and *Vishnutherium* have also been discovered in the Middle Siwaliks (Dhok Pathan Formation), whereas no sivatheriine has been reported from China. Giraffinae, another subfamily of Giraffidae, has been reported from the Siwaliks (Colbert, 1935b; Barry, 1995; Barry *et al.*, 2002) and from northern China (Li *et al.*, 1984; Qiu, 1990; He, 1997), but no fossils have been reported from the Irrawaddy beds.

Of the family Bovidae, three genera of Bovinae (*Pachyportax*, *Hemibos*, and *Proleptobos*) have been found in the Lower Irrawaddy (Figure 13A; Colbert, 1938). All these forms have also been found in the Upper Siwalik (Tatrot Zone) (Pilgrim, 1937), but no fossils have been reported from China. In contrast, four genera of Bovinae (*Hemibos*, *Proleptobos*, *Bos*, and boselaphinin), one genus of Antelopinae (*Gazella*?), and one genus of Caprinae (*Capricornis*) have been discovered in the Upper Irrawaddy (Figure 13B; Colbert, 1938). All these genera, except *Capricornis*, have also been found in the Siwaliks. *Bos*, *Gazella*, and *Capricornis* have been reported in China. Although both *Gazella* and *Bos* are commonly found in China, the former appeared in the late Miocene and the latter appeared only after the

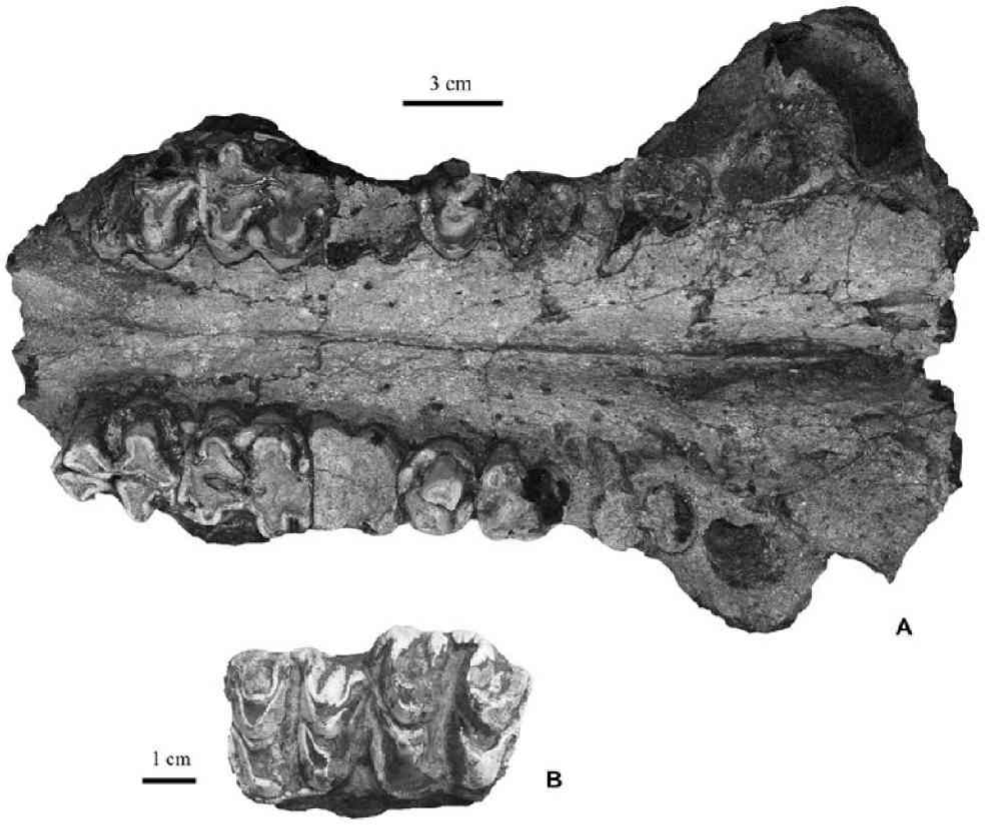

Figure 12. Occlusal view of cranial specimen with cheek teeth of *Hexaprotodon* (**A**) and left M^{1-2} of *Merycopotamus* (**B**).

Pleistocene (Handbook of Chinese Vertebrate Fossils Editorial Group, 1979; Li *et al.*, 1984; Lucas, 2001). *Capricornis*, the extant serow, is found in the middle Pleistocene and later in China (e.g., Colbert and Hooijer, 1953; Lucas, 2001).

Post-Irrawaddy fossils (Table 1D)

Most of the Post-Irrawaddy fossils have been collected from the middle to late Pleistocene terrace deposits in central Myanmar (Colbert, 1943) and from cave sediments on the Shan Plateau. Some fragmentary teeth of *Elephas hysudricus* have been reported from the terrace deposits of central Myanmar (Colbert, 1943). *Elephas hysudricus* is known from the late Pliocene through to the early Pleistocene of Siwalik, but its extinction date has not been specified exactly (Hussain *et al.*, 1992). A fossil specimen of *Stegodon* that is more derived than *Stegodon insignis birmanicus* may have been collected from the terrace deposits, because some gravels probably derived from the terrace sediments were attached to the specimen.

The most famous Post-Irrawaddian fossil assemblage is the middle Pleistocene assemblage collected at the Mogok cave, northern Mandalay Division. A nearly complete skull of the giant panda, *Ailuropoda* (= *Aeluropus*) *baconi* (Figure 14; Woodward, 1915; Colbert, 1938), many dental fragments of elephants (*Stegodon orientalis*, *Elephas* [=

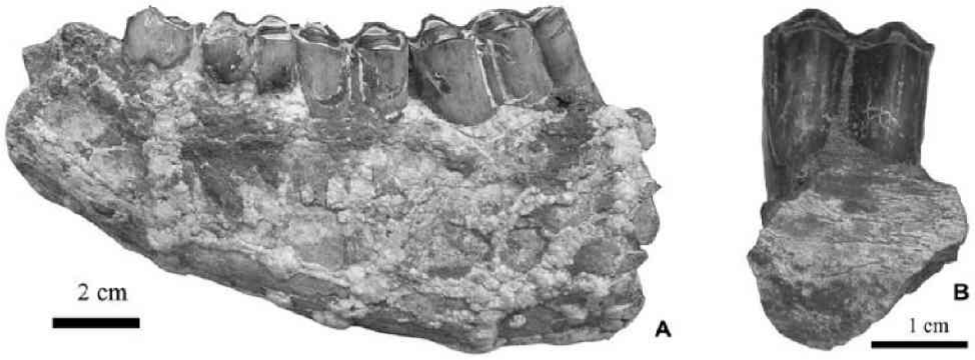

Figure 13. Left mandibular fragment with P_4-M_3 of *Hemibos* (**A**) and lower molar of *Capricornis* (**B**).

Palaeoloxodon] *namadicus*), and an isolated lower premolar of a porcupine (*Hystrix*) (Colbert, 1943) have been reported in published papers. *Stegodon orientalis* is in fact very similar to the *Stegodon* fossils discovered in the cave deposits of southern China. On the other hand, "*Palaeoloxodon namadicus*" does not have the morphological features of the genus *Palaeoloxodon* but resembles *Elephas maximus*, the extant Asian elephant. "*Palaeoloxodon namadicus*" from Myanmar should be a close relative of *Elephas maximus* or an early offshoot of this genus. "*Palaeoloxodon namadicus*" reported from the Pleistocene sediments of Southeast Asia (Mansuy, 1916; Patte, 1928) may also be confused with *Elephas maximus*, the origins of which are still unclear. A paleontological study of elephant fossils of the terrace and cave deposits of Myanmar is very important to any understanding of the origins of the extant Asian elephant, *Elephas*.

Although *Ailuropoda* today inhabits restricted mountain areas in southern China, such as Sichuan and Yunnan Provinces, their fossils are found in the Pleistocene (mostly cave) deposits of vast area of China, Viet Nam, and Thailand (e.g. Ciochon & Olsen, 1986; Pei, 1987; Tougard *et al.*, 1996; Lucas, 2001). *Ailuropoda* is also known as one of the most typical mammals characterizing the southern Chinese Pleistocene fauna, together with the stegodont proboscidean *Stegodon* (Lucas, 2001). This "*Ailuropoda–Stegodon* fauna" is also known in Southeast Asia and Indonesia. The discovery of fossil specimens of *Ailuropoda* and *Stegodon* in the Mogok cave also indicates the faunal similarity of the Pleistocene fauna of Myanmar to those faunas of Southeast Asia, including southern China and the Indonesian islands.

Fossil anthropoid primates expected from the Neogene of Myanmar

To date, no primate fossils have been found in the Neogene sediments of Myanmar. Considering the geographical and chronological situation in Myanmar, several primate taxa are expected in the Neogene of Myanmar, for instance in the Freshwater Pegu Group and Irrawaddy sediments.

In eastern Eurasia, three higher taxonomic groups of catarrhine primates have been discovered in Neogene sediments: Pliopithecoidea, Hominoidea, and Cercopithecoidea (e.g., Pope *et al.*, 2002; Jablonski, 2002; Takai, 2002). Of these, the pliopithecoids

Table 3. List of mammalian taxa of the Post-Irrawaddy faunas.

Post-Irrawaddy Fauna

RODENTIA
- Hystricidae
  - *Hystrix* sp.

CARNIVORA
- Ailuropodinae
  - *Ailuropoda baconi*

ARTIODACTYLA
- Suidae
  - *Sus scrofa*
- Cervidae
  - *Cervus* sp.
- Bovidae
  - Bovinae
    - *Bos* sp.
    - *Hemibos triquetricornis*
  - ?Antilopinae

PERISSODACTYLA
- Equidae
  - *Equus* sp.
- Rhinocerotidae
  - *Rhinoceros* sp.

PROBOSCIDEA
- Gomphotheriidae
  - *Sinomastodon* sp.
- Stegodontidae
  - *Stegodon orientalis*
- Elephantidae
  - *Elephas namadicus*
  - *Elephas* (= *Hypselephas*) *hysudricus*

probably appeared first in eastern/southern Asia, by the early Miocene. *Dionysopithecus* and *Platodontopithecus* have been found in the early to middle Miocene beds of Sihong, Jiangsu Province (Li, 1978; Li *et al.*, 1983; Gu and Lin, 1983; Harrison and Gu, 1999), and *Pliopithecus zhangxiangi* has been discovered in the middle Miocene of Tongxin, Ningxia Province. In southern China, *Laccopithecus* has been collected from the upper Miocene of Lufeng and Yuanmou, Yunnan Province (Wu and Pan, 1984, 1985; Badgley *et al.*, 1988; Pan, 1988, 1996). One mandibular specimen discovered in the upper Miocene of Wudu, Gansu Province (Xue and Delson, 1989), was originally described as "*Dryopithecus*" *wuduensis*, a member of the hominoids, but is now regarded as a member of the pliopithecids (Harrison, 2005). Some fragmentary pliopithecid fossils have also been discovered in south Asia: "*Pliopithecus krishnaii*" from the Dhok Pathan Formation, Haritalyangar, India (Chopra and Kaul, 1979; Chopra, 1983) and "*Dionysopithecus* sp" from the Kamlial Formation in Potwar, Pakistan (Bernor *et al.*, 1988; Barry *et al.*, 1986). These south Asian pliopithecids are fragmentary and unreliable specimens, but it is not improbable that pliopithecids will be

Figure 14. Left upper dentition of *Ailuropoda*. Modified from Woodward (1915).

discovered from the middle to late Miocene sediments of Southeast Asia, in places such as Myanmar and Thailand.

The second catarrhine newcomer to eastern Eurasia is the hominoidea. The first hominoid fossil recorded was *Sivapithecus* from the middle Siwaliks (e.g., Pilgrim, 1927; Pilbeam *et al.*, 1977; Kelly and Pilbeam, 1986; Ward and Brown, 1986; Cameron *et al.*, 1999; Nelson, 2003). A recently discovered *Khoratpithecus* from the middle to late Miocene of Thailand is believed to be the ancestral form or a close relative of the extant orangutan, *Pongo* (e.g., Chaimanee *et al.*, 2003, 2004). *Lufengpithecus* has been discovered in several late Miocene localities in Yunnan Province (Keiyuan, Lufeng, Baoshan, and Yuanmou) (e.g., Kelley and Etler, 1989; Takai *et al.*, 1998). *Gigantopithecus*, an extraordinary huge hominoid, was discovered in the upper Miocene of the Siwaliks (Simons and Chopra, 1969; Chopra, 1983; Patnaik and Cameron, 1997) and in Plio/Pleistocene cave deposits of southern China (e.g., Guangxi, Hubei, and Sichuan Provinces) (e.g., Pilgrim, 1915; Weidenreich, 1945; von Koenigswald, 1952; Pei and Woo, 1956; Pei, 1957; Wu, 1962; Simons and Chopra, 1969; Chang *et al.*, 1973; Hsu *et al.*, 1974; Chang *et al.*, 1975; Ciochon *et al.*, 1996). Thus, it is apparent that hominoids diversified in southern/eastern Asia during the later Miocene, so they are confidently expected to be found in later Miocene sediments in Myanmar.

The third catarrhine group, the cercopithecoids, the Old World monkeys, seem to have invaded eastern Asia in the latest Miocene, much later than the other two groups (Takai, 2002, 2005). Extant Old World monkeys are classified into two subfamilies, Cercopithecinae and Colobinae (or two families, Cercopithecidae and Colobidae). According to the fossil record, colobines probably began their adaptive radiation first on the Eurasian continent, as early as the late Miocene. The first fossil record of colobine monkeys in Asia is of *Mesopithecus*, discovered in the upper Miocene of Afghanistan (Molayan) and Iran (Maragehe) (Heintz *et al.*, 1981; de Mecqunnem, 1925). The second oldest colobine fossil is *Presbytis* (or *Semnopithecus*) *sivalensis*, from the upper Miocene of the Lower Siwalik (Barry, 1987).

The first fossil record of Cercopithecinae, the other cercopithecoid group, is the isolated teeth of *Macaca* from the latest Miocene beds of Yushe, Shangxi Province, northern China (Delson, 1996). In contrast to the colobine fossils from southern Asia, the oldest

Table 2. Comparisons of Neogene mamallian faunas of Myanmar, Siwalik, and China.

	Myanmar				China					Siwalik					
		Irrawaddy								Lower		Middle		Upper	
	Pegu?	Lower	Upper	Mogok cave	Yuanmou	Lufeng	Baode	Bahe	Tung-gur	Kamlial	Chinji	Nagri	Dhok Pathan	Tatrot	Pinjor
RODENTIA															
Hystricidae															
Hystrix				X							X		X		X
CARNIVORA															
Amphicyonide															
Amphicyon		X			X		X		X	X	X	X			
Ailuropodidae															
Ailuropoda				X											
PROBOSCIDEA															
Deinotheriidae															
Deinotherium	X									X	X	X	X		
Gomphotheriidae															
Gomphotherium	X				X	X	X		X	X	X	X	X		
Sinomastodon		X	X												
Elephantidae															
Stegolophodon		X	X								X	X	X	X	X
Stegodon			X	X	X		X						X	X	X
Elephas			X												X
PERISSODACTYLA															
Equidae															
Hipparion		X			X	X	X	X				X	X		
Equus			X												X
Chalicotheriidae															
Nestoritherium			X												X
Rhinocerotidae															
Diceratherium	X														
Brachypotherium	X	X									X	X	X		
Aceratherium		X									X	X	X		
Rhinoceros			X		X										X
Amynodontidae															
Cadrucotherium	X														
ARTIODACTYLA															
Suidae															
Tetraconodontinae															
Conohyus	X									X	X	X			
Tetraconodon	X	X										X	X		X
Sivachoerus		X											X	X	X
Parachleuastochoerus		X													
Listriodontinae															
Listriodon	X								X	X	X	X	X		
Suinae															
Propotamochoerus		X			X		X				X	X	X		
Potamochoerus			X												X
Sus			X		X		X					X	X	X	X
Hippopotamidae															
Hexaprotodon		X	X												
Anthracotheriidae															
Anthracotherium	X										X	X	X		
Hemimeryx	X										X	X	X		
Telmatodon	X										X				
Merycopotamus		X	X										X		X
Tragulidae															
Dorcatherium	X										X	X	X	X	
Do Çiabune			X		X	X					X	X	X		
Cervidae															
Cervinae															
Cervus			X		X		X						X		X
Giraffidae															
Sivatheriinae															
Vishnutherium		X											X		
Hydaspitherium		X											X		
Bovidae															
Antilopinae															
Gazella			X		X		X	X			X	X	X		
Caprinae															
Capricornis			X												
Bovinae															
Pachyportax		X													
Hemibos		X	X												X
Proleptobos		X	X										X		
Bos			X												X
Boselaphus			X										X		

cercopithecine fossil was discovered in a relatively northern region, about 37° N, suggesting that the early cercopithecines invaded eastern Eurasia through central Asia, a relatively high-latitude area, rather than through the southern piedmont of the Himalayan range (e.g., Takai, 2005). This "northern route" hypothesis has not yet been examined in detail.

It is highly likely that cercopithecoid fossils, such as those of macaques or colobines, will be discovered from the late Miocene through to the Pliocene sediments of Myanmar.

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