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Discovery of *Propotamochoerus* (Artiodactyla, Suidae) from the Neogene of Myanmar

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Abstract

Dento-gnathic specimens of *Propotamochoerus* (Mammalia, Artiodactyla, Suidae) were discovered from the upper Miocene and lower Pliocene of the Irrawaddy Group, central Myanmar. These specimens were identified as *Propotamochoerus hysudricus* and *Propotamochoerus* sp. cf. *P. hysudricus*. The discovery of *P.* cf. *hysudricus* from the lower Pliocene indicates a younger stratigraphic position of this genus. Small size of the premolars in the lower Pliocene specimens possibly suggests an intermediate stage of dental evolution for this form.

Introduction

Neogene fossil localities of central Myanmar are mainly distributed with the fresh water deposits of the Irrawaddy Beds (= Irrawaddy Formation, Aung Khin and Kyaw Win, 1969; = Irrawaddy Group, Bender, 1983). The Irrawaddy deposits are divided into the lower and upper parts as the deposits yielding two distinct faunas, the upper Miocene to Pliocene fauna from the lower part and the lower Pleistocene fauna from the upper part (Stamp, 1922; Colbert, 1938; Bender, 1983). The Irrawaddy deposits are rich in mammalian fossils that are correlated with those of the Middle and Upper Siwalik Group of Indo-Pakistan, which are upper Miocene to lower Pleistocene (Lydekker, 1876; Pilgrim, 1910, 1926; Colbert, 1938, 1943). However, the mammalian faunas of the Irrawaddy Beds are still poorly studied.

Concerning suids, the genera from the lower part of the Irrawaddy deposits have been described as *Tetraconodon* and *Sivachoerus* (Pilgrim, 1910, 1926; Thaung-Htike *et al.*, 2005), and that from the upper part has been described as *Potamochoerus* (Colbert, 1943).

Recently, we discovered new dento-gnathic specimens of a fossil suid from Central Myanmar. All specimens except two were discovered during the recent paleontological

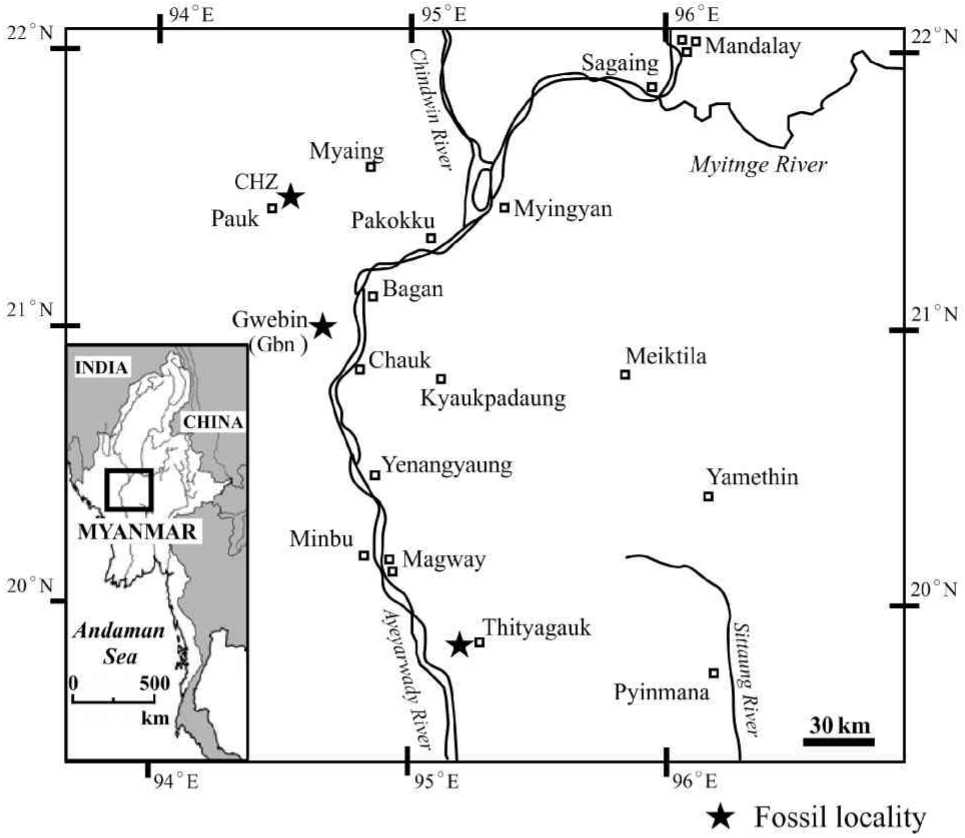

Figure 1. Geographical map showing the fossil localities of *Propotamochoerus* in central Myanmar.

expeditions by the Primate Research Institute, Kyoto University in the 2001 to 2003 field seasons. The remaining two specimens are housed in the Geology Museum of the Magway University, Myanmar. We studied these suid specimens, and identified these as the genus *Propotamochoerus*.

In this paper, we report the *Propotamochoerus* specimens of Myanmar, and discuss the age of the recovered horizon that yielded them. This is the first discovery of *Propotamochoerus* from the Irrawaddy Group and from the upper Miocene of Myanmar.

Abbreviations

NMMP-KU-IR, National Museum - Myanmar - Paleontology - Kyoto University - Irrawaddy (stored in the National Museum, Yangon, Myanmar, and in the Department of Geology, University of Yangon, Yangon, Myanmar); MGW = Magway (stored in the Geology Museum, Magway University, Magway); GSI= Geological Survey of India, Kolkata, India.

Stratigraphic position

Detailed stratigraphic studies of the Irrawaddy Group have been provided by many researchers (Aung Khin and Kyaw Win, 1969; Bender, 1983; Moe Nyunt, 1987; Chit- Sein *et al.*, 2006 = this volume). The specimens described here were recovered from three areas.

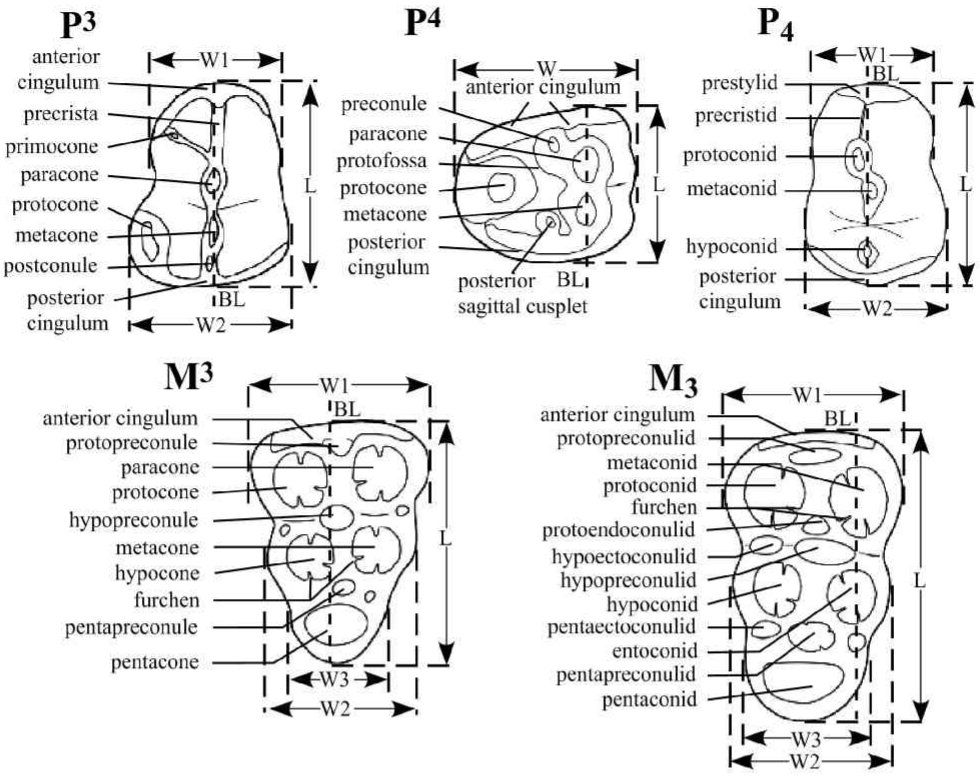

Figure 2. Dental terminology and measurement of propotamochoerine-type suid teeth. A.. are left cheek teeth. Abbreviations: BL = base line; L = length; W = maximum width; W1 = width of the first lobe; W2 = width of the second lobe; W3 = width of the third lobe in M3/3.

The Chaingzauk fossil locality (CHZ) is near Chaingzauk Village, Pauk Township, Magway Division, Central Myanmar, the Gwebin fossil locality (Gbn) is near Gwebin Village, Seikpyu Township, Magway Division, and a locality near the Thityagauk Township, Magway Division. These localities are located in the lower part of the Irrawaddy Group of Central Myanmar (Figure 1; see the discussion below).

Systematic paleontology

Dental terminology and measurement methods are described in Figure 2. Dental measurements of the new specimens are shown in Tables 1 and 2.

Order Artiodactyla Owen, 1848

Family Suidae Gray, 1821

Subfamily Suinae Gray, 1821

Genus *Propotamochoerus* Pilgrim, 1925

Type species.—Propotamochoerus hysudricus Stehlin, 1899.

Other included species.—Propotamochoerus palaeochoerus Kaup, 1833; *Propotamochoerus hyotherioides* Schlosser, 1903; *Propotamochoerus provincialis* Gervais,

1859; *Propotamochoerus parvulus* Chang, 1974; *Propotamochoerus wui* Made and Han, 1994.

Diagnosis.—The height of the protoconid (main cusp) much taller than that of the other cusps in P_4. The metaconid disto-lingually close to the protoconid in P_4. Third molar with simple talonid. Detailed diagnoses were described in Pilgrim (1925), Pickford (1988), and Made and Moyà-Solà (1989).

Propotamochoerus hysudricus Stehlin, 1899

Figures 3 and 4

Lectotype.—GSI B 30, a right mandibular ramus with P_3-M_3, illustrated by Lydekker (1884: pl. VIII, figures 3a).

Type locality.—Potwar Plateau, Pakistan.

Type horizon and age.—Middle Siwalik, Dhok Pathan Formation, late Miocene (Pilgrim, 1926; Colbert, 1935; Pickford, 1988).

Diagnosis.—Medium-sized *Propotamochoerus* (i.e., M_1 length is about 14.5 to 18.5 mm) with little or no diastema in the upper and lower cheek tooth rows. Detailed diagnoses was described in Pilgrim (1926) and Pickford (1988).

New materials.—NMMP-KU-IR 0190, a right mandibular fragment with a root of P_2, well-preserved P_3-M_2, and a mesial half of M_3; MGW 0003, a right maxillary fragment with P^3-M^3; MGW 0004, a left mandibular fragment with roots of P_2 and P_3, and well-preserved P^4-M^3.

Localities of the new materials.—NMMP-KU-IR 0190 was discovered from CHZ 15 (21°32'6.0"N, 94°31'4.2"E), about 1.6 km south of Chaingzauk Village, which is about 9.5 km northeast of Pauk City, Magway Division, Central Myanmar (Figure 1). MGW 0003 and 0004 were recovered near Thityagauk City, Magway Division, but the exact locality is unknown.

Horizon of the new materials.—Lower part of the Irrawaddy Group, probably equivalent of the Dhok Pathan Formation of the Middle Siwalik Group, which is upper Miocene.

Description of the new materials.—The cheek teeth show typical bunodont suid morphology, and are smaller than the type specimens of *Propotamochoerus palaeochoerus*, *P. hyotherioides*, and *P. provincialis*, and larger than the type specimens of *P. parvulus* and *P. wui*. NMMP-KU-IR 0190, the mandible from Chaingzauk, is larger in M_1 size but smaller in M_2 and M_3 than MGW 0004, the mandible from Thityagauk (Figures 3 and 4, Table 1). The maxillary and mandibular fragments from Thityagauk (MGW 0003 and 0004) probably belong to the same individual. The mean height of the mandible at the mesial of M_1 is 35 mm. The alveolus of P_1 can be seen in NMMP-KU-IR 0190. The mandibular symphysis reaches back to the rear of P_2 (Figure 3D). Distinct mandible foramens can be seen below the buccal of P_2, P_3 and P_4 (Figures 3F, 4B).

Widths of the first and second lobes (W1 and W2) are nearly same in P_3. The distinct

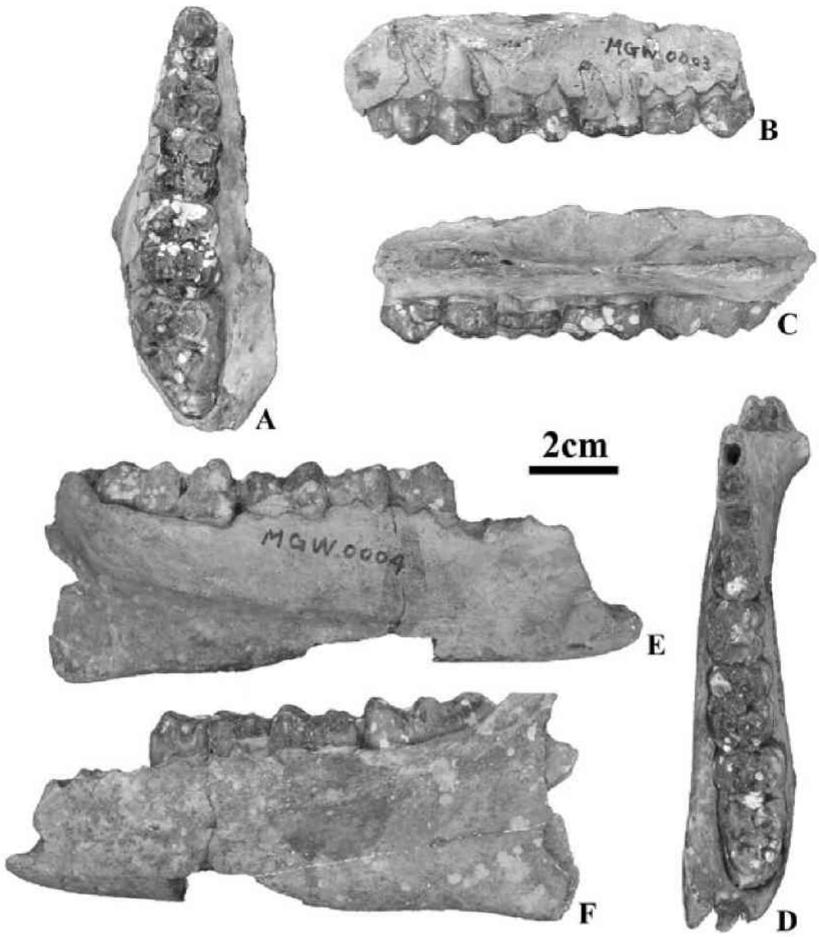

Figure 3. Cheek teeth of *Propotamochoerus hysudricus* from Thityagauk locality. **A-C**, MGW 0003, a right maxillary fragment with P^3-M^3: **A**, occlusal view; **B**, buccal view; **C**, lingual view. **D-F**, MGW 0004, a left mandibular fragment with roots of P_2 and P_3, and well-preserved P_4-M_3: **D**, occlusal view; **E**, buccal view; **F**, lingual view.

protoconid is the highest among the cusps and appears as the main cusp. Small but distinct metaconid is closely located behind the protoconid. The hypoconid is low and distinct. The prestylid is low and has only one third of the height of the protoconid. The precristid is sharp and distinct.

The fourth lower premolar (P_4) is wider but shorter than the third (P_3), and it is more molarised. The second lobe is wider than the first lobe in P_4. The metaconid migrated lingually but not far from the protoconid. The height of the prestylid increases, so that it approximately as tall as the half of the protoconid. The hypoconid of P_4 becomes taller than that of P_3. The posterior cingulum is expanded both in buccally and lingually. Between the metaconid and hypoconid, short and small grooves are formed in the buccal and lingual sides.

Outlines of M_1 and M_2 are identical, being nearly rectangular in occlusal view. In the present specimens, M_1 is heavily worn, and detail morphology can only be seen in M_2. There are four main cusps (protoconid, metaconid, hypoconid and entoconid) with shallow and distinct furchen. The second lobe is slightly wider than the first (W2>W1). The anterior

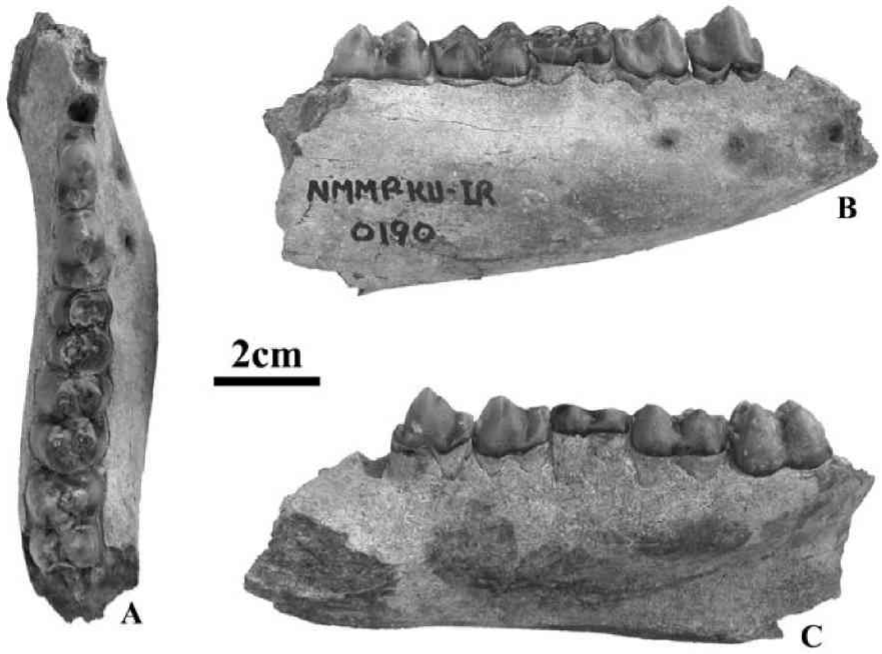

Figure 4. *Propotamochoerus hysudricus* from Chaingzauk locality, NMMP-KU-IR 0190, a right mandibular fragment with a root of P_2, well-preserved P_3-M_2, and mesial half of M_3: **A**, occlusal view; **B**, buccal view; **C**, lingual view.

cingulum is small but distinct. The protopreconulid, protoendoconulid, hypoectoconulid and pentapreconulid are small and weakly developed. The hypopreconulid and pentaconid are distinct. Size of the M_1 is distinctly smaller than M_2 (M_1<M_2).

The third lower molar (M_3) is larger than M_2 both in length and width. It is elongated, and the distal width is narrower than the mesial. Cusp morphology of the first and second lobes in M_3 is same as those in M_2. The third lobe is simple with a large and distinct pentaconid. The pentapreconulid is distinct and nearly same in size as the hypopreconulid. The distinct small accessory cuspules are present at the mesiolingual part of the pentaconid. The pentaectoconulid is tiny.

In P^3, the mesiodistal length is longer than the buccolingual width, and the width increases distally. It consists of a centrally placed, tall, and inflated paracone. The precrista is very distinct. The anterior and posterior cingula are well developed. The distinct protocone is at the mesiolingual extension of the posterior cingulum. The metacone is located behind the paracone, and they are separated by shallow grooves both in buccal and lingual sides. The primocone and postconule are tiny but distinct.

In P^4, the buccolingual width is much longer than the mesiodistal length. The fourth upper premolar (P^4) is larger and more molarised than P^3. It consists of two buccal cusps, paracone and metacone, and one lingual cusp, protocone. There are distinct and beaded anterior and posterior cingula. The preconule is small but distinct. At the lingual part of the metacone, a posterior sagittal cusplet appears in the deep protofossa.

The first and second upper molars (M^1 and M^2) have four main cusps (paracone,

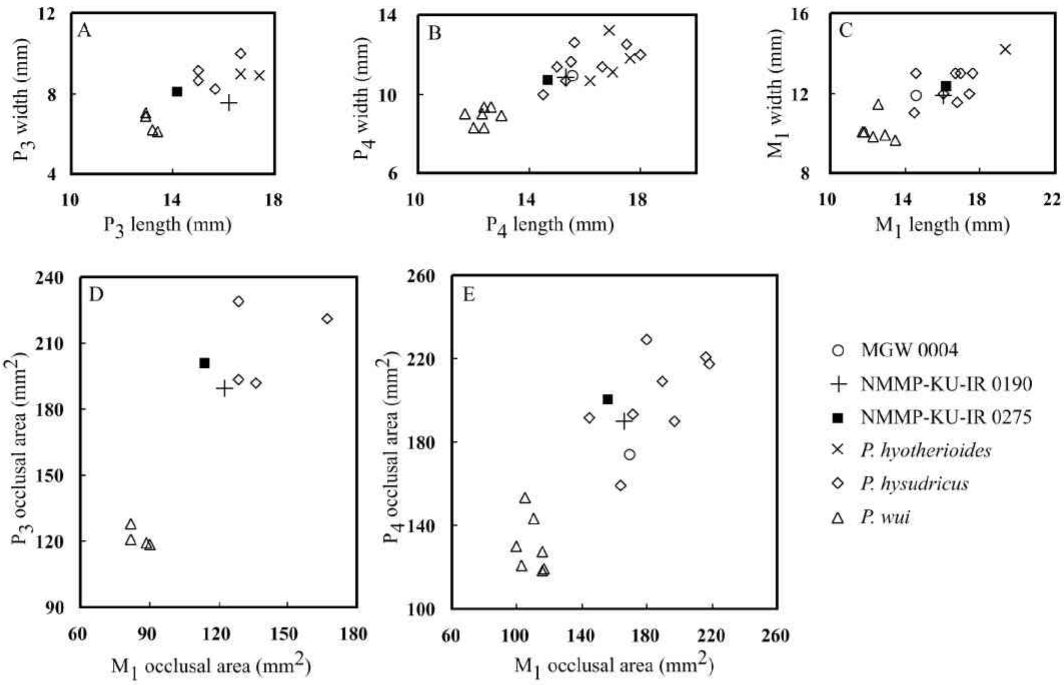

Figure 5. Bivariate plots for the dental measurements of the Siwalik *Propotamochoerus hysudricus* and Chinese *P. wui*, together with the Irrawaddy *Propotamochoerus* specimens. **A-C**, width on length: **A**, P_3; **B**, P_4; **C**, M_1. **D-E**, occlusal areas of lower premolars on that of M_1: **D**, P_3 on M_1; **E**, P_4 on M_1. The dental measurements were adopted from Pickford (1988) for the Siwalik specimens and from Made and Han (1994) for the Yunnan specimens.

protocone, metacone and hypocone). The protopreconule is fused to the anterior cingulum. The furchen are shallow but distinct. The second lobe is slightly wider than the first. The enamel is relatively thick compared to other suines such as *Sus*. The hypopreconule and pentacone are large and distinct. The pentapreconule is indistinct. Small minor cuspules appear in both side of the medium valley which lies between the first and second lobes. The posterior cingulum is distinct and beaded. Size of the M^1 is distinctly smaller than M^2 (M^1<M^2).

The third upper molar (M^3) is larger than M^2, and it narrows distally. The cusps of the anterior two lobes are similar in morphology to with those of M^{1-2}. The pentacone appears as a simple and distinct third lobe (talon of suids). The pentapreconule is distinct. There are small minor cuspules at the mesio-buccal side of the pentacone.

Comments.—These two mandibular and one maxillary fragments show typical *Propotamochoerus* features: presence of P_1, the protoconid becoming tall relative to the hypoconid and prestylid in P_4, the metaconid distolingually not too separated from the protoconid in P_4, presence of the median cusplet in the protofossa of P^4, and a simple talonid in M_3. Because of their size and morphology of the cheek teeth, they are referable to *P. hysudricus* of the Middle Siwalik of Indo-Pakistan (Figure 5).

Propotamochoerus sp. cf. *P. hysudricus* Stehlin, 1899

Figure 6

Materials.—NMMP-KU-IR 0275, a left mandibular fragment with P_3-M_2; NMMP-KU-

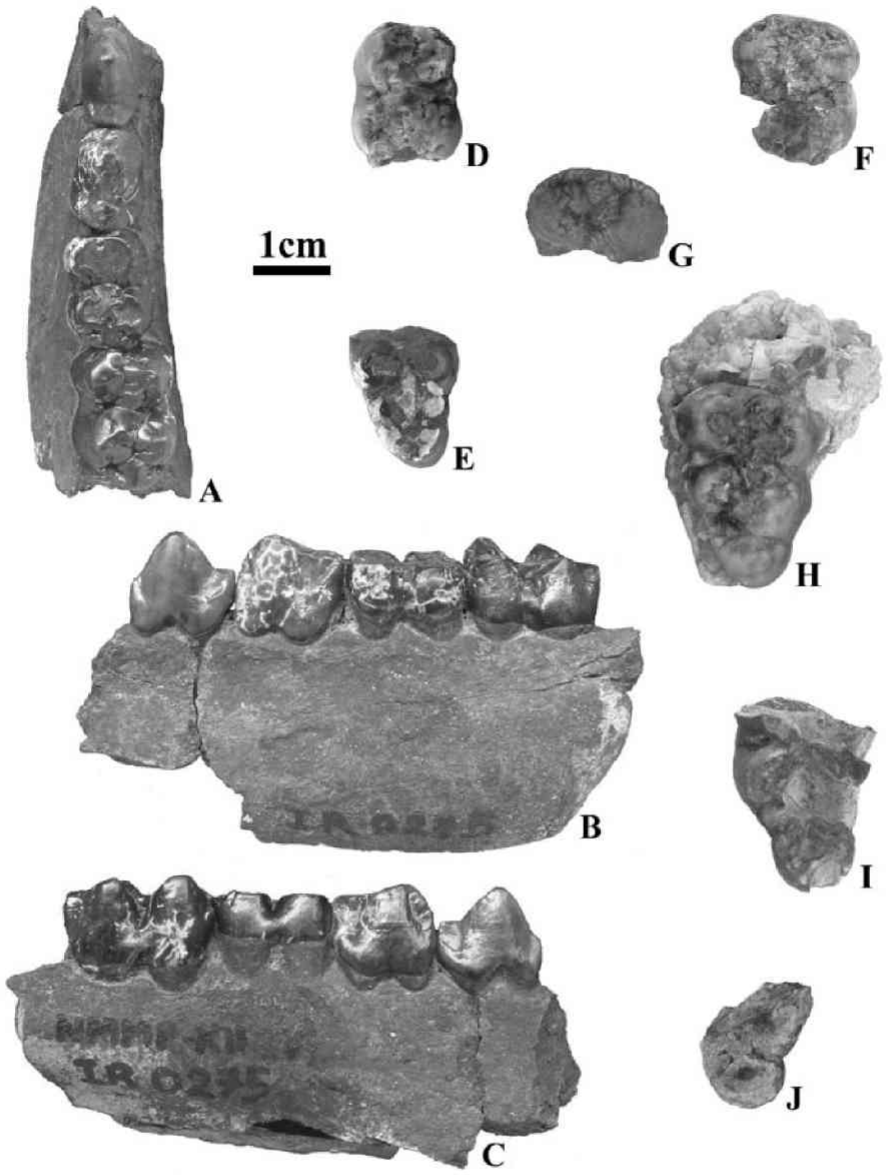

Figure 6. *Propotamochoerus* sp. cf. *P. hysudricus* from the Gwebin localities. **A-C**, NMMP-KU-IR 0275, a left mandibular fragment with P_3-M_2: **A**, occlusal view; **B**, buccal view; **C**, lingual view. **D**, NMMP-KU-IR 0082, a right M_2, occlusal view. **E**, NMMP-KU-IR 0005, a fragment of right M_3 with the second and third lobes, occlusal view. **F**, NMMP-KU-IR 0081, a right M^2, occlusal view. **G**, NMMP-KU-IR 0232, a mesial fragment of right M^3 with the first lobe, occlusal view. **H**, NMMP-KU-IR 0054, a right maxillary fragment with distal fragment of M^2, and M^3, occlusal view. **I**, NMMP-KU-IR 0250, a distal fragment of right M^3 with a distal half of the first lobe, occlusal view. **J**, NMMP-KU-IR 0083, a fragment of right M^3 with the third lobe, occlusal view.

IR 0082, a right M_2; NMMP-KU-IR 0005, a fragment of right M_3 with the second and third lobes; NMMP-KU-IR 0081, a right M^2 ; NMMP-KU-IR 0054, a right maxillary fragment with distal fragment of M^2, and M^3;NMMP-KU-IR 0232, a mesial fragment of right M^3 with the first lobe; NMMP-KU-IR 0250, a distal fragment of right M^3 with distal half of the first lobe; NMMP-KU-IR 0083, a fragment of right M^3 with the third lobe.

Locality.—NMMP-KU-IR 0250 is from Gbn 2 (20°59'42.0"N, 94°42'15.0"E) and the other materials are from Gbn 1 (20°58'31.2"N; 94°41'27.0"E), near Gwebin Village, Seikpyu

Table 1. Dental measurements (in mm) of *Propotamochoerus hysudricus* from Thityagauk and Chaingzauk localities. Abbreviations: L= length; W1= width of the first lobe; W2 = width of the second lobe; W3= width of third lobe in $M^3/_3$; * = estimate.

specimen	P^3			P^4			M^1			M^2			M^3			
	L	W1	W2	L		W	L	W1	W2	L	W1	W2	L	W1	W2	W3
MGW 0003	15.3	9.6	11.4	12.9	-	14.6	15.6	14.9	15.2	21.7	17.9	18.6	29.5	20.1	18.6	11.2

specimen	P_3			P_4			M_1			M_2			M_3			
	L	W1	W2	L	W1	W2	L	W1	W2	L	W1	W2	L	W1	W2	W3
MGW 0004	16.2*	-	-	15.6	9.3	10.9	14.7	10.8	11.8	20.5	14.6	15.1	32.5	16.9	15.4	13.1
NMMP-KU-IR 0190	16.2	7.2	7.57	15.3	9.3	10.9	16.0	11.4	11.8	19.7	14.3	14.4	-	15.4	14.1	-

Table 2. Dental measurements (in mm) of *Propotamochoerus* sp. cf. *P. hysudricus* from the Gwebin localities. Abbreviations: see Table 1.

specimen	P^3			P^4			M^1			M^2			M^3			
	L	W1	W2	L		W	L	W1	W2	L	W1	W2	L	W1	W2	W3
NMMP-KU-IR 0054	-	-	-	-	-	-	-	-	-	-	-	-	30.0	20.8	18.0	11.4
NMMP-KU-IR 0081	-	-	-	-	-	-	-	-	-	21.4	18.2	>17.0	-	-	-	-
NMMP-KU-IR 0083	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11.1
NMMP-KU-IR 0232	-	-	-	-	-	-	-	-	-	-	-	-	-	19.8*	-	-
NMMP-KU-IR 0250	-	-	-	-	-	-	-	-	-	-	-	-	-	-	17.5*	10.9

specimen	P_3			P_4			M_1			M_2			M_3			
	L	W1	W2	L	W1	W2	L	W1	W2	L	W1	W2	L	W1	W2	W3
NMMP-KU-IR 0005	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15.0	11.0
NMMP-KU-IR 0082	-	-	-	-	-	-	-	-	-	20.8*	15.4*	16.3	-	-	-	-
NMMP-KU-IR 0275	14.2	7.14	8.06	14.7	9.4	10.6	16.3	11.7	12.3	20.8	14.7	15.6	-	-	-	-

Township, Magway Division, Central Myanmar (Figure 1).

Description.—All the specimens are isolated teeth with the exception of NMMP-KU-IR 0275, which consists of a mandibular fragment with P_3-M_2. The basal part of this mandible is broken. Although it is impossible to measure the complete height of the mandible, its height below the mesial of M_1 is greater than 30 mm.

The morphology of the cheek teeth is nearly identical to that of *Propotamochoerus hysudricus*. It differs from *P. hysudricus* by its relatively smaller posterior premolars, especially P_3, and a short P_3 relative to P_4 in mesiodistal length.

Comments.—The materials of *Propotamochoerus* sp. cf. *P. hysudricus* from Gwebin, especially in the mandibular fragment with P_3-M_2, show the morphology of typical propotamochoerine-type suids (Pickford, 1993; = dicoriphochoerine-type suid of Made and Moyà-Solà, 1989): the protoconid becomes very tall relative to the hypoconid and prestylid in P_4; the metaconid is distolingually not too separated from the protoconid in P_4; simple talon and talonid are in the third molars. The premolars of the present materials, especially for P_3, are relatively small compared to those of *Propotamochoerus* species (Figures 5A, B, D and E), and size of the premolars relative to the first molars rather resembles those of *Potamochoerus* and *Sus*. However, the tall protoconid with closely located metaconid

in the P_4 of *Potamochoerus* cf. *P. hysudricus* is a typical propotamochoerine-type suid characteristic that has been used to differentiate the genus from *Sus* (Stehlin, 1899: page 147, figure III). The present specimens are clearly smaller than that of any extinct and extant species of *Potamochoerus*, and size of the M_1 is more similar to that of *P. hysudricus* than other *Propotamochoerus* species (Figure 5C). Consequently, we identified these suid dentognathic materials discovered from the Gwebin under the name of *Propotamochoerus* sp. cf. *P. hysudricus*.

Discussion

The fossil materials of the extinct genus *Propotamochoerus* have been well recorded from the upper Miocene to lower Pliocene of Asia and Europe (Lydekker, 1884; Pilgrim, 1926; Pearson, 1928; Colbert, 1935; Made and Han, 1994; Fortelius *et al.*, 1996). According to Pickford (1988) and Fortelius *et al.* (1996), the *Propotamochoerus*-group arose in South Asia from a hyotherine suid around 11 Ma, and migrated westward into Southwestern Asia (Arabian peninsular) and Europe.

Propotamochoerus palaeochoerus and *P. provincialis* have been discovered from Europe (Fortelius *et al.*, 1996). In the comparisons of species mean values, cheek teeth dimensions of *P. palaeochoerus* and *P. provincialis* are 104 % and 110 % greater than those of *P. hysudricus*, respectively, characterizing their large size (Made and Han, 1994). *Propotamochoerus wui*, *P. parvulus*, and *P. hyotherioides* have been discovered from Asia, mainly from China (Pearson, 1928; Chang, 1974; Made and Han, 1994). Pickford and Liu (2001) regarded *P. wui* as a junior synonym of *P. parvulus* because of their similarity in dental size. Cheek teeth dimensions of *P. wui* are only 78 % of those of the *P. hysudricus* (Made and Han, 1994). Cheek teeth dimensions of *P. hyotherioides* are 107 % greater than those of *P. hysudricus*. This species was suggested as an ancestor of *P. provincialis* (Made and Han, 1994).

Among the *Propotamochoerus* species, *P. hysudricus* was firstly described from the Potwar Plateau of Indo-Pakistan (Lydekker, 1884; Stehlin, 1899; Pilgrim, 1926; Colbert, 1935). This species has been recovered from the Middle Siwalik Group, the upper part of the Nagri Formation and the Dhok Pathan Formation, suggesting its occurrence from an interval of 10.2 to 6.8 Ma in the upper Miocene (Barry *et al.*, 2002). It was also discovered from the late Miocene of Abu Dhabi, U.A.E., in the Arabian Peninsula (Bishop and Hill, 1999), and was recorded from Yunnan, China (Liu and Ji, 2004). The specimen from China is slightly larger (M_1 length is 19.3 mm) than that from Siwalik, and its age was suggested likely to be of the Pliocene (Liu and Ji, 2004).

Because *Propotamochoerus hysudricus* was previously only known from the late Miocene, with the exception of the Pliocene of China, the discovery of this species from the lower part of the Irrawaddy deposits suggests the late Miocene or early Pliocene equivalent of the age of the localities. The Thityagauk locality is in a southern extension of the Tebingan locality where *Tetraconodon* sp. cf. *T. magnus* was discovered (Chit-Sein *et al.*, 2006=this

volume), and the late Miocene equivalent as its age is unquestionable. The specimen of *Propotamochoerus hysudricus* from Chaingzauk was discovered together with *Sivachoerus prior*, which is a member of the early Pliocene part of the Siwalik fauna (Pilgrim, 1926; Pickford, 1988; Made, 1999). Moreover, the M_1 of the Chaingzauk specimen is larger than that of Thityagauk specimen (see Table 1), and this may suggest that the Chaingzauk mandible is more derived than Thityagauk mandible because size increase can be observed as a derived characteristics in evolution of many suid lineages. Thus, we suggest that the age of the Chaingzauk locality is younger than that of the Thityagauk locality and that the possible age of the Chaingzauk locality is the uppermost Miocene or the lowermost Pliocene.

The *Propotamochoerus* sp. cf. *P. hysudricus* specimens from the Gwebin localities show the dental characteristic of *Propotamochoerus*, and resemble *P. hysudricus* in M_1 size. However, their premolars are relatively smaller than those of *P. hysudricus*, suggesting that it is probably in a more derived stage of *P. hysudricus*. The age of the Gwebin localities were suggested as an early Pleistocene equivalent (Moe Nyunt, 1987), placing the localities in the upper part of the Irrawaddy Group. However, *Propotamochoerus* has not been discovered from deposits younger than the early Pliocene. It is reasonable to consider that the Gbn 1 and Gbn 2 localities of Gwebin has an age of early Pliocene equivalent and are stratigraphically located in the lower part of the Irrawaddy Formation.

The earliest record of *Propotamochoerus hysudricus* from the Siwalik is earlier than that from Myanmar, which is the early late Miocene, and the fossil record in China has been suggested to be the Pliocene. Thus, it can be suggested that *P. hysudricus* spread from the Siwalik to the eastern region during the late Miocene, was present in Myanmar during the late Miocene to early Pliocene, and reached China region in the Pliocene. The relatively small premolars of *Propotamochoerus* sp. cf. *P. hysudricus* from Myanmar suggests an intermediate stage of dental morphology during evolution of *Propotamochoerus*.

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