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<th>A revision of Tetraconodon (Mammalia, Artiodactyla, Suidae) from the Miocene of Myanmar and description of a new species.</th>
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<td>Author</td>
<td>Dr. Thaung Htike</td>
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A revision of *Tetraconodon* (Mammalia, Artiodactyla, Suidae) from the Miocene of Myanmar and description of a new species

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Abstract. We describe five new dento-gnathic specimens of *Tetraconodon*, a genus of Miocene tetraconodontine suid (Mammalia, Artiodactyla), discovered in Myanmar (= Burma). In Myanmar, we recognized three distinct species of *Tetraconodon* (*T. minor*, *T. intermedius* and *T. malensis* sp. nov.) and one specifically undetermined specimen, which is here named *Tetraconodon* sp. cf. *T. intermedius*. The new species, *T. malensis*, has characteristics of *Tetraconodon*, such as extremely enlarged P3₄/₃₄ and simple and relatively small M₃. It is distinct from the other *Tetraconodon* species in being much smaller, suggesting that it is the most primitive known *Tetraconodon* species. The dental size and characteristics of *T. malensis* suggest that *Tetraconodon* was derived during the late middle Miocene from the early middle Miocene *Conohyus sindensis*, which was discovered in the Siwalik Group of Indo-Pakistan and Nepal and has also been found in the middle Miocene deposits of Thailand, or a close relative. The discovery of the most primitive form in Myanmar suggests that *Tetraconodon* may have originated in Myanmar.

Key words: Mammalia, Miocene, Myanmar, new species, Suidae, *Tetraconodon*

Introduction

*Tetraconodon* Falconer, 1868 is one of the tetraconodontine suid (pig) genera that existed in the Miocene of Indo-Pakistan and Myanmar (= Burma) (Pilgrim, 1910a, 1926, 1927; Colbert, 1935b; Pickford, 1988; Made, 1999). Among the tetraconodontine suids, *Tetraconodon* is characterized by its extremely enlarged P3₄ −/₃₄ (Pilgrim, 1926; Made, 1999). In Myanmar, only one species, *Tetraconodon minor*, was previously reported from the basal part of the Irrawaddy Beds (Pilgrim, 1910a, 1927).

In this paper, we describe five new dento-gnathic specimens of *Tetraconodon* collected from several localities in Myanmar, and establish a new species for part of the collection. Four of the five specimens are housed in the National Museum of Myanmar, and one was discovered by our recent paleontology expedition.

The precise geologic ages of these localities have been unclear, but the occurrence of *Tetraconodon* suggests a middle to late Miocene correlation for them (Made, 1999; Pickford, 1988).

Abbreviations

NMM = National Museum, Yangon, Myanmar; NMMP-KU-IR = National Museum, Myanmar, Paleontology–Kyoto University–Irrawaddy (stored in the National Museum, Yangon); GSI = Geological Survey of India, Kolkata, India; GSP = Geology Survey of Pakistan; AMNH = American Museum of Natural History, BMNH = British Museum of Natural History, TF = Thai Fossil; Kpg = Gyatpyegyi (= Kyatpyegyi) fossil locality (southwest of Male village, Sagaing Division, central Myanmar).
Materials and methods

All new fossil materials were collected in central Myanmar (Figure 1). They are now stored in the National Museum of Myanmar.

Dental terminology and method of measurement are shown in Figure 2. We mainly follow Made (1996), Hünermann (1968), Wilkinson (1976) and Pickford (1986) for dental terminology, and Made (1996) for dental measurement method. All measurements were taking using digital calipers. Dental measurements of the new Tetraconodon specimens and other correlated tetraconodont specimens are shown in Table 1, 2 and 3.

We choose the length of lower M1 for the diagnoses of Tetraconodon species because M1 have been considered to express less size variation from individual to individual than other teeth, and mandibular fragments with lower cheek teeth are more recovered than maxillary fragments with upper cheek teeth in general. We used the mean dental measurements of Propotamochoreus wui (Made and Han, 1994) (Lufeng, China), which is recovered from the upper Miocene deposits of the same East Asian regions that yield Tetraconodon, to compare dental measurement ratios.

Systematic paleontology

Family Suidae Gray, 1821
Subfamily Tetraconodontinae Lydekker, 1876

Diagnosis.—Small to gigantic Suidae with enlarged P3<sub>3-4</sub> and reduced P1<sub>2</sub>-1. Detail diagnosis was described in Pickford (1988).

Genus Tetraconodon Falconer, 1868

Type species.—Tetraconodon magnum Falconer, 1868 (including Tetraconodon mirabilis Pilgrim, 1926).

Other included species.—Tetraconodon minor Pilgrim, 1910a; Tetraconodon intermedius Made, 1999; Tetraconodon malensis sp. nov.

Diagnosis.—Differs from the other tetraconodontine genera in having extremely enlarged P3-4<sub>3-4</sub>, simple and relatively small M3<sub>3</sub>, and thick and highly wrinkled enamel in P3-4<sub>3-4</sub>, and less wrinkled enamel in M1<sub>1-3</sub>.
**Tetraconodon minor** Pilgrim, 1910a

*Figure 3*

*Tetraconodon minor* Pilgrim, 1910a, p. 67; Pilgrim, 1910b, p. 202; Pilgrim, 1926 (in part), p. 160–163, pl. 14, fig. 1; Matthew, 1929, p. 459; Colbert, 1935b; Colbert, 1938; Made, 1999.

**Type locality.**—Yenangyaung, central Myanmar (Pilgrim, 1910a).

**Type horizon and age.**—Lowermost part of the Irrawaddy Formation (= Irrawaddy Beds) (Aung-Khin and Kyaw-Win, 1969), Nagri Formation (Siwalik Group) equivalent, early late Miocene (Pilgrim, 1910a; Colbert, 1938; Made, 1999).

**New material.**—NMM AN-1, a right mandibular fragment with P$_4$-M$_2$ (the meaning of “AN” is unknown); NMM-KU-IR 0107, a left P$_3$.

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**Table 1.** Upper dental measurements (mm) of *Tetraconodon cf. intermedius* (NMMP-KU-IR 0225) and *T. intermedius* (GSI B 675) and mean measurements of *Propotamochoerus wui* (Made and Han, 1994). Abbreviations: L = mesiodistal length; W = buccolingual width; W$_1$ = first lobe width; W$_2$ = second lobe width; W$_3$ = third lobe width of M$^3$; * = estimate.

<table>
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<th>Taxa</th>
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<th>M$^1$</th>
<th>M$^2$</th>
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<td>W</td>
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<td>49.4</td>
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<td><em>P. wui</em> Made &amp; Han (1994) mean 7–28 spec.</td>
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<td>10.1</td>
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<td>12.1</td>
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**Figure 2.** Dental terminology and measuring method of tetraconodontine teeth. All are occlusal views of right cheek teeth. Abbreviations: BL = base line; L = mesiodistal length; W = buccolingual width; W$_1$ = first lobe width; W$_2$ = second lobe width; W$_3$ = third lobe width of M$^3$. 

**Figure 3.** Dental terminology and measuring method of tetraconodontine teeth. All are occlusal views of right cheek teeth. Abbreviations: BL = base line; L = mesiodistal length; W = buccolingual width; W$_1$ = first lobe width; W$_2$ = second lobe width; W$_3$ = third lobe width of M$^3$. 

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**Tetraconodon minor** Pilgrim, 1910a

*Figure 3*

*Tetraconodon minor* Pilgrim, 1910a, p. 67; Pilgrim, 1910b, p. 202; Pilgrim, 1926 (in part), p. 17–19, pl. 2, fig. 12; Pilgrim, 1927, p. 160–163, pl. 14, fig. 1; Matthew, 1929, p. 459; Colbert, 1935b; Colbert, 1938; Made, 1999.

**Lectotype.**—GSI B677, a left mandibular fragment with P$_3$–4.
Table 2. P4 and M1 measurements (mm) of the *Tetraconodon* and Asian *Conohyus* which are used in Figure 8 A. Tooth measurements for the Indian and Thai specimens are taken from Colbert (1935), Pickford (1988), Ducrocq et al. (1997) and Pickford and Gupta (2001). Abbreviations: L = mesiodistal length; W = greatest buccolingual width.

<table>
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Table 3. Lower dental measurements (mm) of the new *Tetraconodon* specimens and mean measurements of *Propotamochoerus wui* (Made and Han, 1994). Abbreviations: L = mesiodistal length; W1 = first lobe width; W2 = second lobe width; W3 = third lobe width of M3; * = estimate.

<table>
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<th>Taxa</th>
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<th>M2</th>
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<td>W1</td>
<td>W2</td>
<td>L</td>
<td>W1</td>
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<td>29.2</td>
<td>37.4</td>
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<td><em>T. minor</em></td>
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<td>37.3</td>
<td>25.0*</td>
<td>27.0*</td>
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Figure 3. *Tetraconodon minor* Pilgrim. A–B, NMM AN-1, a right mandibular fragment with P3-M2: A, occlusal view; B, lingual view. C–E, NMM KU-IR 0107, a right P3: C, occlusal view; D, lingual view; E, buccal view.
Localities of the new material.—The locality of NMM AN-1 is near Mingin City (Figure 1), northwest of Mandalay, central Myanmar, but the exact locality is unknown. The locality of NMMP-KU-IR 0107 is unknown.

Diagnosis.—Small *Tetraconodon*. M1 length is about 23 mm.

Description and comments.—The present material shows *Tetraconodon* features in having extremely large P3 and P4, thick and highly wrinkled enamel in the last two premolars, distinct anterior cingulum in molars, and distinct furchen (Figure 2) on the four main cusps of the molars. Because of their size and morphology, they are referable to *T. minor*, which previously was the only *Tetraconodon* species reported from Myanmar.

*Tetraconodon intermedius* Made, 1999

Figure 4

*Tetraconodon mirabilis* Pilgrim, 1926 (in part), p. 16, pl. 3, fig. 4. 

Revised diagnosis.—Medium-sized *Tetraconodon*. M1 length is about 27 mm.

Holotype.—GSI B675, a fragmentary skull with right and left P3-M3.

Type locality.—Unknown exact locality (Jammu, Pakistan).

Type horizon and age.—Dhok Pathan or upper Nagri Formation equivalent, late Miocene.

New material.—NMM 839/80, a left mandibular fragment with P4-M3.

Locality of the new material.—The locality of NMM 839/80 is near Male Village (Figure 1), Sagaing Division, central Myanmar, but the exact locality is unknown.

Description.—The cheek teeth show typical bunodont suid morphology, and are smaller than the type of *T. magnus* and larger than the type of *T. minor*. The mandible is robust and is broken at the anterior part of P4 and also at the posterior of M1. The base of the mandible is also broken and it is impossible to measure the thickness. The cheek teeth enamel is very thick and fairly wrinkled.

P4 is relatively enlarged and rugose. The crown is heavily worn, so that the protoconid and metaconid cannot be clearly observed. But the metaconid is close to the distal part of the protoconid. The hypoconulid is distinct and is located on the most distal part of the crown. The anterior prestylid and precristid are distinct.

M1-2 are nearly rectangular in occlusal view and are narrower and shorter than P4. The first lobe is longer and wider than the second lobe. Each cusp of the M1 is worn along the entire length of the tooth. So, the two cusps for each lobe blend in such a way that the details of the cusp configuration are unclear (Figure 4). M1 < M2.

M2 has four inflated main cusps (protoconid, metaconid, hypoconid and entoconid) arranged into two distinct lobes with rounded corners separated from each other by a well-developed median valley. The furchen are indistinct. A distinct anterior cingulum protrudes at the mesiobuccal corner of the crown. The protopreconulid, hypopreconulid and pentaconid are well developed. The pentaconulid is almost worn away.

M3 is elongated and narrower distally than mesially. Furchen are not so distinct. The morphology of the two anterior lobes is the same in M1-2. The third lobe (“talonid” of suids) is relatively simple compared to other advanced suids. The pentapreconulid is well developed and is nearly the same size as the hypopreconulid. The pentaconid is very distinct. A distinct small accessory cuspule is present at the mesiolingual part of the pentaconid. The pentaeconoconulid is tiny. The first lobe width of M3 is narrower than the second lobe width of M2.

Comments.—Made (1999) established a new species, *Tetraconodon intermedius*, based on a maxillary fragment with premolars and molars (GSI B 675) that was previously assigned to *T. magnus*. However, the lower dentition of this species was unknown. The present lower dentition (NMM 839/80) has M1 with a mesiodistal length of 26.5 mm, and in dental size and morphology matches the upper dentition of *T. intermedius*.

*Tetraconodon* sp. cf. *T. intermedius* Made, 1999

Figure 5

Material.—NMMP-KU-IR 0225, a right maxillary fragment with P3-M3.

Locality.—The Chaungsong area, about 25 km south of Pauk City (Figure 1), central Myanmar.

Description.—The preserved cheek teeth are bunodont with thick enamel. The enamel of P3-4 is more heavily wrinkled than that of M1-3.

P3 is longer than wide and is nearly triangular in occlusal view. The paracone is the largest cusp located at the center of the crown. The precrista is distinct. The metacone is almost fused with the paracone and is located distally to it. The anterior and posterior cingula are almost continuous and surround the crown, but their lingual and mesiobuccal parts are weakly
developed, while the mesiolingual and distolingual parts are strongly developed.

$P^4$ is much wider than long and is buccally longer than lingually. It has three main cusps, the paracone, metacone and protocone. The paracone and metacone are almost fused, and are separated from the protocone by a deep protofossa. It also has distinct anterior and posterior cingula, which are nearly continuous and surround the crown, but the lingual and buccal parts are weakly developed and its mesial and distal parts are strongly developed.

$M^1$-2 are nearly rectangular in occlusal view. They have four main inflated cusps, the paracone, protocone, metacone and hypocone. The hypopreconule and pentapreconule are distinct. The protopreconule is weak. The pentacune is absent. The medium valley is deep. The distolinguinal root is incipiently bifurcated. The anterior and buccal cingula are distinct. $M^1 < M^2$.

$M^3$ is buccolingually narrower and mesiodistally longer than $M^2$ and has a minute third lobe ("talon" of suids). The anterior two lobes are very similar in morphology to those of $M^{1-2}$, and differ from the latter in having a small minor cuspule at the lingual side of the medium valley and in lacking a buccal cingulum. The pentacune is small but distinct. A small minor cuspule exists at the mesiolingual base of the hypocone.

*Comments.*—NMMP-KU-IR 0225 shows the typical large $P^{3-4}$ dimensions of *Tetraconodon*, distinctly different from *Sivachoerus*, which has much smaller $P^{3-4}$. Its $M^1$ length is about 26.7 mm and is very similar to that of the medium-sized *Tetraconodon* species, *T. intermedius*. However, the dimensions of its $P^{3-4}$ and $M^3$ are somewhat smaller than those of *T. intermedius* (Figure 6). This difference may be due to individual variation, but alternatively might suggest a specific separation.

*Tetraconodon malensis* sp. nov.

*Holotype and only known specimen.*—NMM Kpg-1, a right mandibular fragment with $P_4$-$M_3$.

*Type locality.*—The Gyatpyegyi fossil locality (22°58.44′N; 95°54.59′E), about 12 km southwest of Male Village (Figure 1), Sagaing Division, central Myanmar.

![Figure 4](image-url)
Figure 5. *Tetraconodon* sp. cf. *T. intermedius* Made, NMMP-KU-IR 0225, a right maxillary fragment with P$^3$-M$^3$: A, occlusal view (stereo pair); B, buccal view; C, lingual view.
Etymology.—Named after Male Village, which is the village nearest to the type locality.

Diagnosis.—Small species of Tetraconodon. M1 length is about 14 mm.

Description.—The teeth are bunodont and brachydont. The tooth enamel is very thick and weakly wrinkled. P4 is larger in size and taller than M1 and is wider in its distal part than in its mesial one. It has a large protoconid, smaller hypoconid, and much smaller prestylid. The presence or absence of the metaconid is unclear due to wear. The inflated protoconid is located at the center of the crown. A distinct precristid is present. Distal to the hypoconid, short and small grooves are formed on the buccal and lingual sides. M1 < M2. M3 is labiolingually narrower than M2. The trigonid is wider than the talonid. Furchen are indistinct. M2 has an additional large distal cusp, the pentaconid (Figure 7); therefore, it is mesiodistally longer than M2. The pentaconid is well developed, and is nearly the same as the hypopreconulid in size. Small accessory cusplets are present in the anterior lingual part of the pentaconid. There is a small pentaectocynulid.

Comparison and discussion.—The lower dento-gnathic material, NMM Kpg-1, has nearly the same dental size as a very primitive tetraconodontine species, Conohyus sindiensis (Lydekker, 1884). However, it has extremely enlarged P4, simple and relatively small M3, and thick enamel in P4-M3, all of which makes it referable to the genus Tetraconodon; it differs from Conohyus and other tetraconodontines in having relatively much larger P4 (Figure 8A). Therefore, NMM Kpg-1 is attributed to the genus Tetraconodon. It is much smaller than the other species of Tetraconodon (Figure 8B). In conclusion, we established a new species Tetraconodon malensis for NMM Kpg-1.

Discussion

Most of the fossil materials of Tetraconodon as well as other tetraconodontines have been found in the Siwalik Group of Indo-Pakistan, so that the evolutionary history of Tetraconodon had been based mainly on these fossils (Pilgrim, 1926; Pickford, 1988; Made, 1999). Pilgrim (1926) concluded that Tetraconodon was probably derived from the oldest known Asian tetraconodontine, Conohyus sindiensis, from the lower middle Miocene (Kamlial or lower Chinji) of the Siwalik Group of Indo-Pakistan and Nepal; this species also occurs from the middle Miocene deposits of Thailand.

Previously, the smallest and the geochronologically oldest species Tetraconodon minor had been considered to be the most primitive Tetraconodon (Pilgrim, 1926; Colbert, 1935a; Made, 1999). However, T. minor is about three times larger than Conohyus sindiensis, and a large morphometric gap existed between them.

When compared with Asian Conohyus, the newly discovered Tetraconodon malensis is similar in M1 dimensions to Conohyus sindiensis and smaller than C. indicus (Lydekker, 1884) and C. thailandicus (Duchrocq et al., 1997). But the relative size of the enlarged
P₄ with respect to M₁ and the relatively small M₃ of *T. malensis* differ from the situation of *C. sindiensis*, in which P₄ is relatively small with respect to M₁ and M₃ is relatively large (Figure 8A). When compared with *C. indicus* and *C. thailandicus*, *T. malensis* shows in terms of relative dimensions a large P₄ with respect to M₁, and a small M₁ (Figure 8A). The relatively enlarged P₄ is one of the important characters distinguishing *Tetraconodon* from *Conohyus* and other tetraconodontines (Pilgrim, 1926; Made, 1999). According to this character, *T. malensis* belongs to *Tetraconodon* rather than *Conohyus*.

Pickford and Gupta (2001) revised *Conohyus thailandicus*, making it a junior synonym of *C. indicus*. When comparing the relative proportions of P₄ and M₁ of Asian *Conohyus* and *Tetraconodon*, we see that the P₄ of *C. thailandicus* is relatively large in proportion to M₁ and is clearly separate from *C. indicus* and *C. sindiensis* (Figure 8A). This indicates that the dental morphology of *C. thailandicus* differs from *C. indicus*, and we suggest that identifying *C. thailandicus* as a synonym of *C. indicus* is not appropriate.

Pickford (1988) and Made (1999) wrote that, in tetraconodontine suids, the younger the geological age, the larger the tooth size. Therefore, the small tooth size of *Tetraconodon malensis* (Figure 8B) indicates that it would be more primitive and older geologically than *T. minor* (basal late Miocene).

The discovery of the smallest known specimen of *Tetraconodon, T. malensis* in Myanmar, which has nearly the same M₁ size as *C. sindiensis* (Pilgrim, 1926; Made, 1999). Pilgrim (1926) stated that *Tetraconodon* is distinguished from *C. sindiensis* by the still greater enlargement of the lower premolars together with increase in tooth size. How-

Figure 7. *Tetraconodon malensis* sp. nov., NMM Kpg-1, a right mandibular fragment with P₄-M₃: A, occlusal view (stereo pair); B, lingual view; C, buccal view.
ever, the discovery of *T. malensis* suggests that *C. sindiensis* evolved into *Tetraconodon* by first changing the enlargement of the posterior premolars, and late increasing overall tooth size and proportion within the last two premolars and M1 (Figure 8A) in younger species. Therefore, the discovery of *T. malensis* fills the morphometric gap between *C. sindiensis* and previously described *Tetraconodon* species.

*T. malensis* is considered to be derived from the early middle Miocene *C. sindiensis*, and is probably the ancestor of the basal late Miocene *T. minor*. Therefore, the most probable correlation of *T. malensis* based on the morphological evolutionary stage within tetraconodontine suids suggests a late middle Miocene age, which is intermediate in geological age between *C. sindiensis* and *T. minor*.

Although the geologic age of the Gyatpyegyi fossil locality, where *T. malensis* was found was previously unknown, the evolutionary position of *T. malensis* suggests an upper middle Miocene date.

**Concluding remarks**

In Myanmar, three distinct species of *Tetraconodon* are recognized: *T. minor*, *T. intermedius* and the new species, *T. malensis*. *Tetraconodon malensis* is morphologically the most primitive of them. It is also similar in dental size to, but different in morphology from the early middle Miocene *Conohyus sindiensis* from the Siwalik Group of Indo-Pakistan and Nepal and the middle Miocene deposits of Thailand. The genus *Tetraconodon* was probably derived from *C. sindiensis* or a close relative during the late middle Miocene. The discovery of the most primitive *Tetraconodon* in Myanmar suggests the possibility that the genus originated in Myanmar.

**Acknowledgments**

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