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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 P_4 and simple and relatively small M_3. 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 sindiensis*, 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 $P^{3-4}/_{3-4}$ (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).

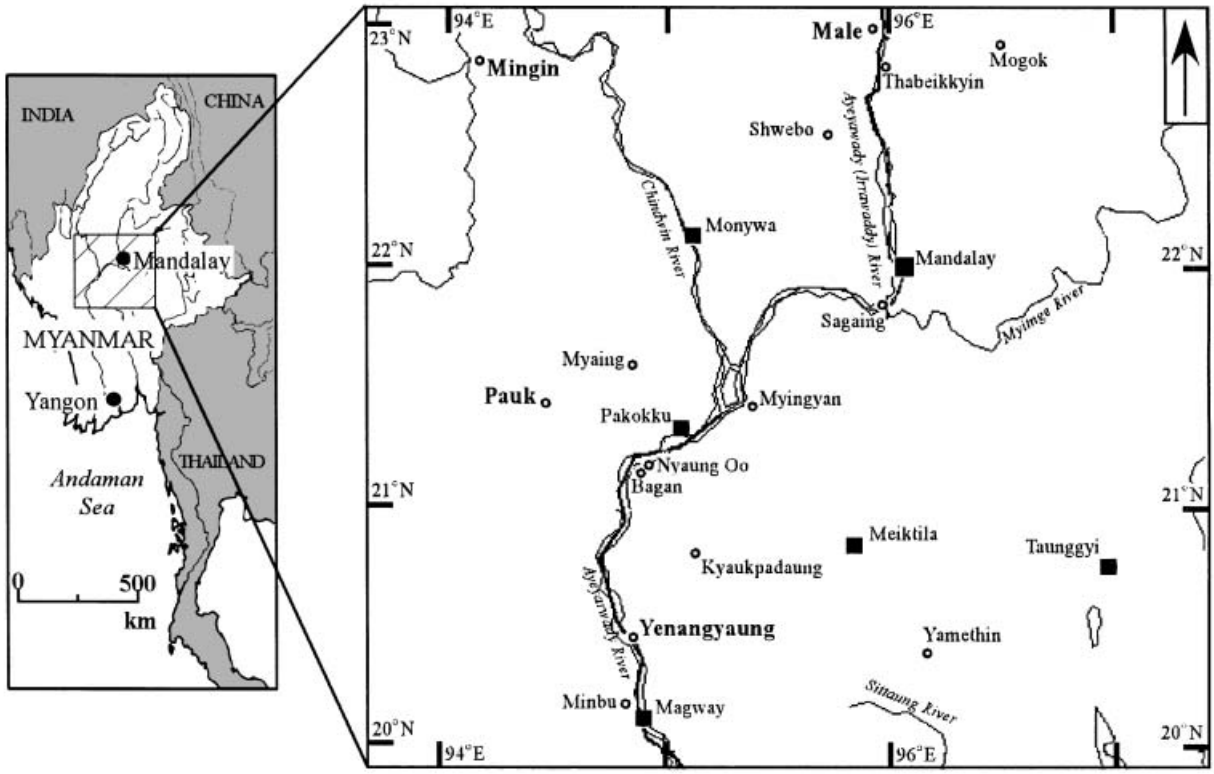

Figure 1. Map of central Myanmar.

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 we 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 M_1 for the diagnoses of *Tetraconodon* species because M_1 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 *Propotamochoerus 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 $P^{3-4}/_{3-4}$ and reduced $P^{1-2}/_{1-2}$. 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 $P^{3-4}/_{3-4}$, simple and relatively small $M^3/_3$, and thick and highly wrinkled enamel in $P^{3-4}/_{3-4}$, and less wrinkled enamel in $M^{1-3}/_{1-3}$.

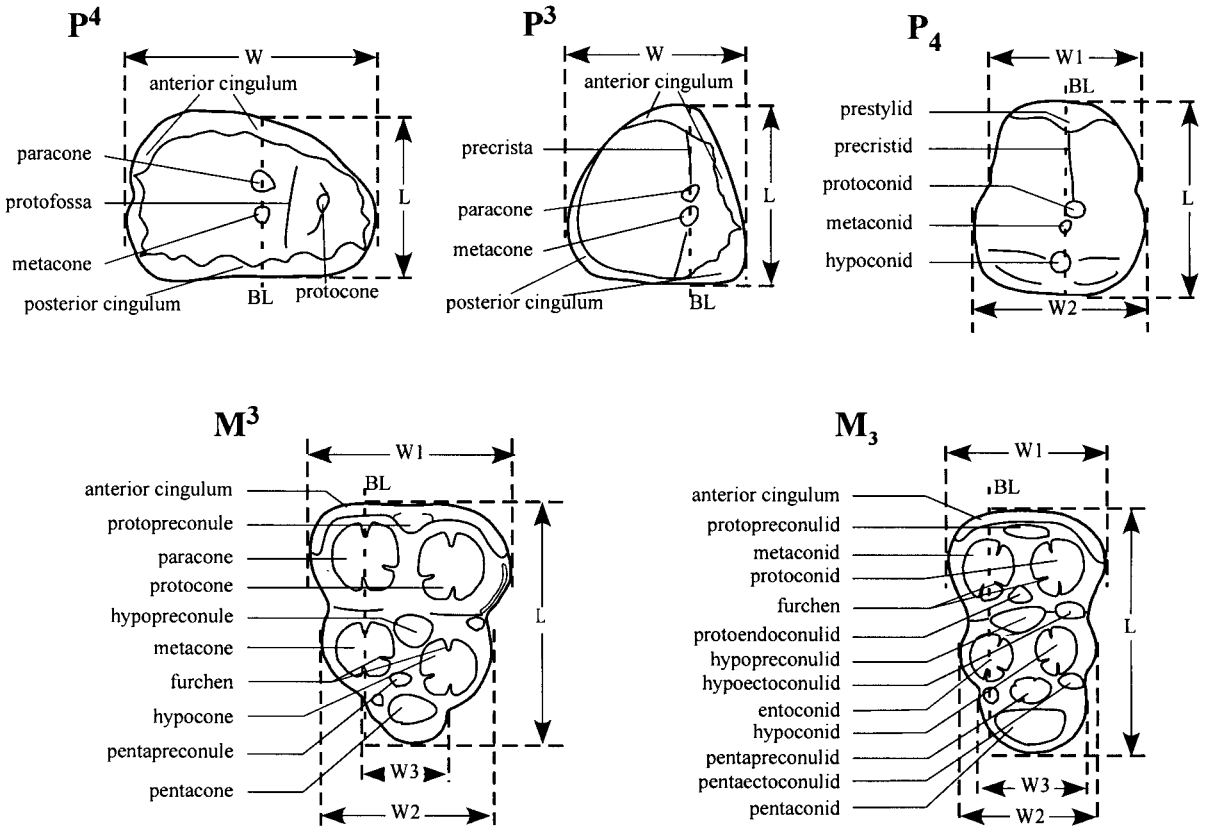

Figure 2. Dental terminology and measuring method of tetraconodontine teeth. All are occlusal views of right cheek teeth. Abbreviations: BL = base line; L = mesiodistal length; W = buccolingual width; W1 = first lobe width; W2 = second lobe width; W3 = third lobe width of $M^3/_3$.

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; W1 = first lobe width; W2 = second lobe width; W3 = third lobe width of M^3; * = estimate.

		P^3		P^4		M^1			M^2			M^3			
Taxa	Specimen	L	W	L	W	L	W1	W2	L	W1	W2	L	W1	W2	W3
T. cf. *intermedius*	NMMP-KU-IR 0225	33.4	34.1	24.4	37.2	26.7	27.7	25.2	30.6	32.6	29.1	33.3	26.8	22.9	12.1
T. intermedius	GSI B 675	46.5	41.4	37.4	49.4	26*	27.5		31.1	35.8*		43*	32*		
P. wui Made & Han (1994)	mean 7–28 spec.	10.8	10.1	9.7	12.1	13.6	12.1	12.3	17.2	15.9	15.6	24.1	17.4	14.9	8

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, p. 230; Colbert, 1938, p. 408.

Sivachoerus giganteus, Falconer and Cautley. Pilgrim, 1926, p. 21, pl. 3, fig. 2.

Lectotype.—GSI B677, a left mandibular fragment with P_{3-4}.

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); NMMP-KU-IR 0107, a left P_3.

Table 2. P_4 and M_1 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.

		P_4		M_1	
Taxa	Specimen	L	W	L	W
C. indicus	GSI B 710	16.6	11.8	16.6	12.6
C. indicus	Pickford & Gupta (2001)	17.2	15.7	17.3	13.0
C. thailandicus	TF 2577	19.5	15.8	14.5	13.3
C. sindiense	GSP 12587	17.0	16.0	15.0	13.5
C. sindiense	GSI B 773	16.0	13.0	15.3	12.0
C. sindiense	GSI B 537	14.4	14.4	13.4	11.5
C. sindiense	AMNH 19386	16.0	15.0	14.0	12.5
C. sindiense	BMNH M 12757	14.4	14.9	13.6	11.5
T. magnus	GSI B 71	53.4	56.4	31.1	28.7
T. intermedius	NMM 839/80	37.7	37.4	26.5	25.8
T. minor	GSI B 771	34.6	31.1	24.0	20.4
T. minor	NMM AN-1	30.8	29.3	23.3	22.0
T. malensis	NMM KPG-1	18.2	16.5	13.9	12.2

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 M_3; * = estimate.

		P_3			P_4			M_1			M_2			M_3			
Taxa	Specimen	L	W1	W2	L	W1	W2	L	W1	W2	L	W1	W2	L	W1	W2	W3
T. intermedius	NMM 839/80				37.7	29.2	37.4	26.5	25.8	25.1	31.6	30.4	28.8	43.8	28.0	24.7	18.7
T. minor	NMMP-KU-IR 0107	37.3	25.0*	27.0*													
T. minor	NMM AN-1				30.8	24.8	29.3	23.3	22.0	20.1	26.3	24.4	22.3				
T. malensis	NMM Kpg-1				18.2	14.9	16.5	13.9	12.2	12.0	16.7	14.2	12.7	20.1	12.5	10.3	8.5
P. wui (Made & Han, 1994)	mean 13–28 spec.	13.1	5.9	6.5	12.6	7.9	8.7	13.3	9.3	9.8	17.1	12.6	13.2	25.9	14.0	12.9	9.7

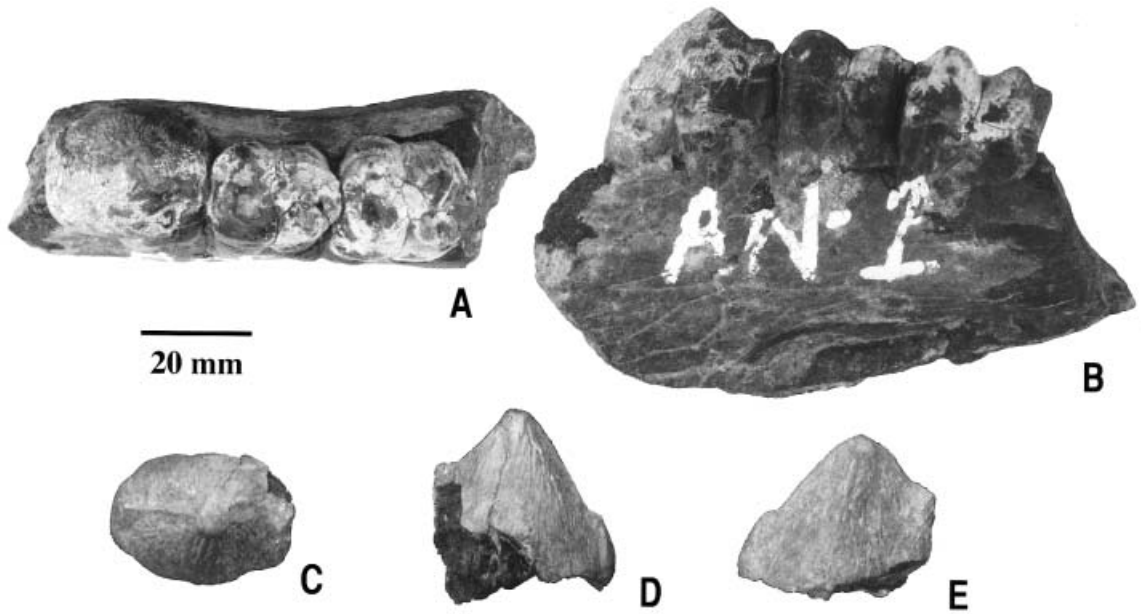

Figure 3. *Tetraconodon minor* Pilgrim. **A–B**, NMM AN-1, a right mandibular fragment with P_4-M_2: A, occlusal view; B, lingual view. **C–E**, NMMP-KU-IR 0107, a right P_3: C, occlusal view; D, lingual view; E, buccal view.

Locality 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*. M_1 length is about 23 mm.

Description and comments.—The present material shows *Tetraconodon* features in having extremely large P_3 and P_4, 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.
Tetraconodon cf. *mirabilis* Pilgrim, 1926, p. 16–17, pls. 4, 6.
Tetraconodon intermedius Made, 1999, p. 203–205.

Revised diagnosis.—Medium-sized *Tetraconodon*. M_1 length is about 27 mm.

Holotype.—GSI B675, a fragmentary skull with right and left P^3-M^3.

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 P_4-M_3.

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 P_4 and also at the posterior of M_3. 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.

P_4 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.

$M_{1–2}$ are nearly rectangular in occlusal view and are narrower and shorter than P_4. The first lobe is longer and wider than the second lobe. Each cusp of the M_1 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). $M_1 < M_2$.

M_2 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 pentapreconulid is almost worn away.

M_3 is elongated and narrower distally than mesially. Furchen are not so distinct. The morphology of the two anterior lobes is the same in $M_{1–2}$. 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 pentaectoconulid is tiny. The first lobe width of M_3 is narrower than the second lobe width of M_2.

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 M_1 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 P^3-M^3.

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 $P^{3–4}$ is more heavily wrinkled than that of $M^{1–3}$.

P^3 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

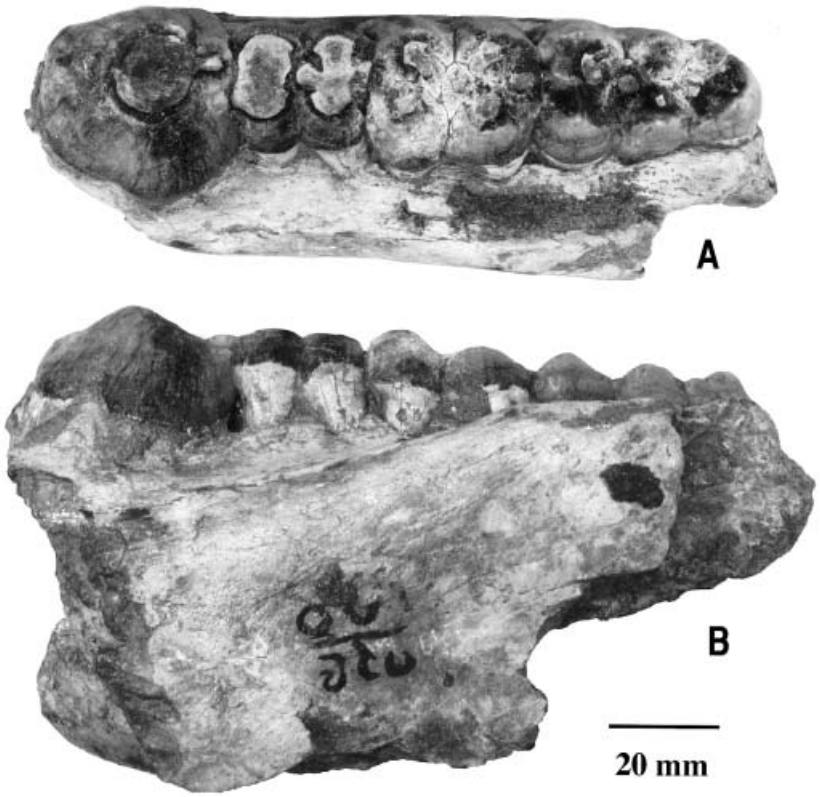

Figure 4. *Tetraconodon intermedius* Made, NMM 839/80, a left mandibular fragment with P_4-M_3: **A**, occlusal view; **B**, buccal view.

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 pentacone is absent. The medium valley is deep. The distolingual root is incipiently bifurcate. 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 pentacone 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.

Figure 7

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.

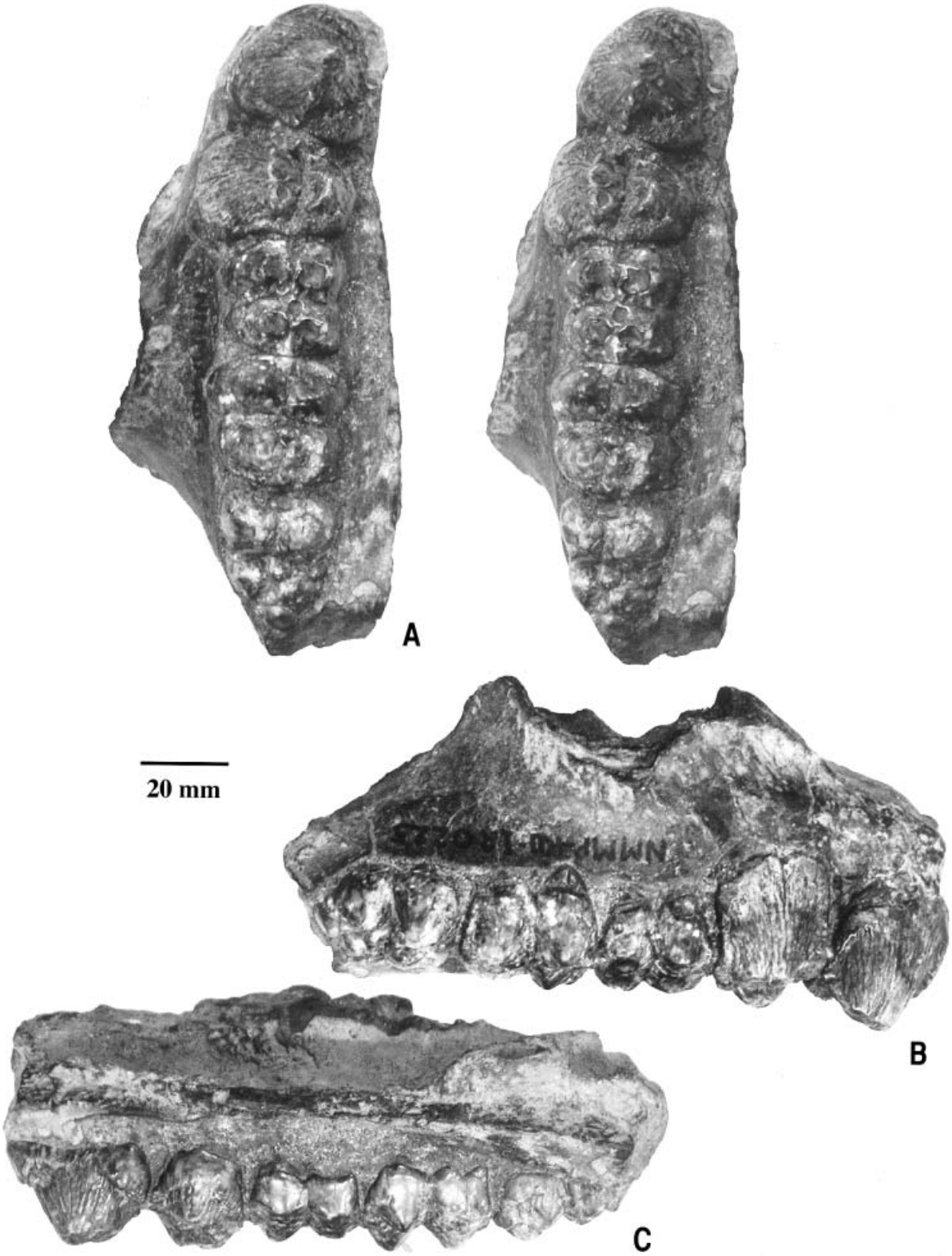

Figure 5. *Tetraconodon* sp. cf. *T. intermedius* Made, NMMP-KU-IR 0225, a right maxillary fragment with P^3-M^3: **A**, occlusal view (stereo pair); **B**, buccal view; **C**, lingual view.

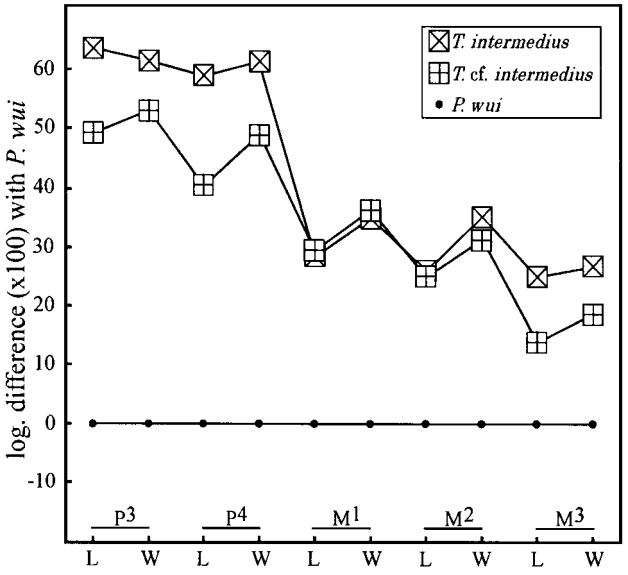

Figure 6. Dental ratio diagram of *Tetraconodon intermedius* (GSI B 675) and *T.* cf. *intermedius* (NMMP-KU-IR 0225). The log difference (×100) of their tooth size with the mean tooth measurements of *Propotamochoerus wui* (Made and Han, 1994) indicates that size ratios in P^3, P^4 and M^3 are clearly different relative to M^1 and M^2 size ratios. Comparative measurements are described in Table 1. L = mesiodistal length; W = greatest buccolingual width.

Etymology.—Named after Male Village, which is the village nearest to the type locality.

Diagnosis.—Small species of *Tetraconodon*. M_1 length is about 14 mm.

Description.—The teeth are bunodont and brachyodont. The tooth enamel is very thick and weakly wrinkled.

P_4 is larger in size and taller than M_1 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.

M_{1-2} are nearly rectangular in occlusal view with four main cusps (protoconid, metaconid, hypoconid and entoconid) arranged in two distinct lobes with rounded corners, which are separated by a distinct medium valley. Furchen are indistinct. The anterior lobe is longer and wider than the posterior. The anterior cingulum is distinct and protrudes near the middle of the anterior lobe in the buccal surface. The mesiobuccal face of the anterior lobe of M_1 is crushed, and the cingulum can be seen only on the mesial face. The hypopreconulid and pentaconid are distinct. The protopreconulid is weakly developed, and the pentapreconulid is worn flat. The hypoectoconulid is small. $M_1 < M_2$.

M_3 is labiolingually narrower than M_2. The trigonid is wider than the talonid. Furchen are indistinct. M_3 has an additional large distal cusp, the pentaconid (Figure 7); therefore, it is mesiodistally longer than M_2. The pentapreconulid 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 pentaectoconulid.

Comparison and discussion.—The lower dentognathic 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 P_4, simple and relatively small M_3, and thick enamel in P_4-M_3, all of which makes it referable to the genus *Tetraconodon*; it differs from *Conohyus* and other tetraconodontines in having relatively much larger P_4 (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 M_1 dimensions to *Conohyus sindiensis* and smaller than *C. indicus* (Lydekker, 1884) and *C. thailandicus* (Ducrocq *et al.*, 1997). But the relative size of the enlarged

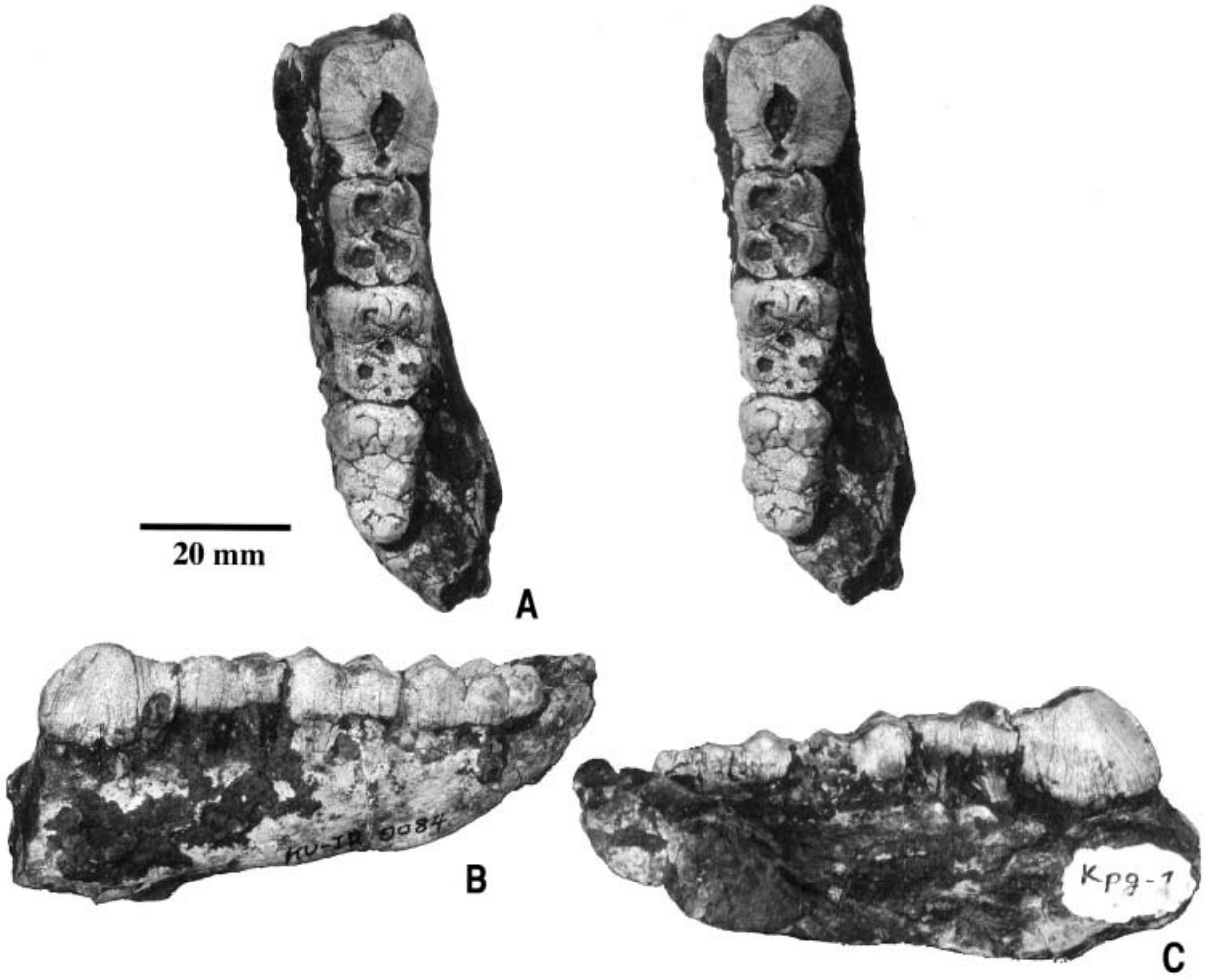

Figure 7. *Tetraconodon malensis* sp. nov., NMM Kpg-1, a right mandibular fragment with P_4-M_3: **A**, occlusal view (stereo pair); **B**, lingual view; **C**, buccal view.

P_4 with respect to M_1 and the relatively small M_3 of *T. malensis* differ from the situation of *C. sindiensis*, in which P_4 is relatively small with respect to M_1 and M_3 is relatively large (Figure 8A). When compared with *C. indicus* and *C. thailandicus*, *T. malensis* shows in terms of relative dimensions a large P_4 with respect to M_1, and a small M_1 (Figure 8A). The relatively enlarged P_4 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 P_4 and M_1 of Asian *Conohyus* and *Tetraconodon*, we see that the P_4 of *C. thailandicus* is relatively large in proportion to M_1 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 M_1 size as *C. sindiensis*, supports the hypothesis that *Tetraconodon* was derived from *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-

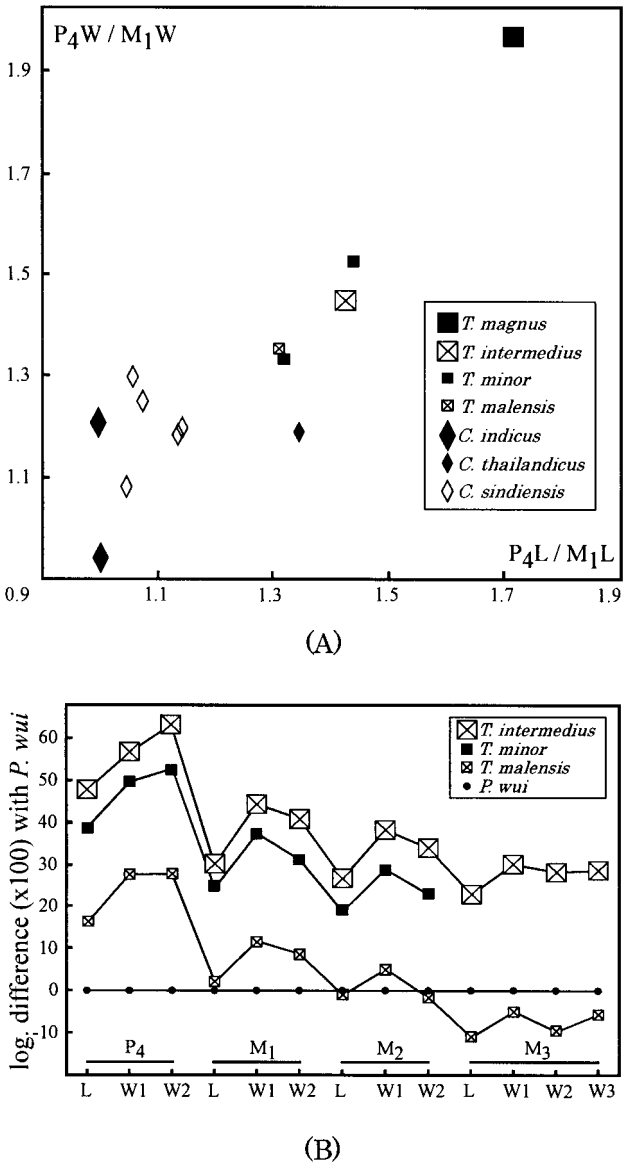

Figure 8. **A**. Bivariate plots within width and length of P_4 relative to width and length of M_1 for *Tetraconodon* and Asian *Conohyus*. Comparative tooth measurements are described in Table 2. L = mesiodistal length; W = greatest buccolingual width. **B**. Dental ratio diagram of three *Tetraconodon* species (*T. malensis*, *T. minor* and *T. intermedius*) from Myanmar. The log difference (×100) of their tooth size with the mean tooth measurements of *Propotamochoerus wui* (Made and Han, 1994) indicates that their tooth size ratio patterns are nearly identical, and *T. malensis* differ from the other two species only by being smaller in size. Comparative measurements are described in Table 3.

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 M_1 (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.

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