New Materials of *Tetraconodon malensis* (Mammalia, Artiodactyla, Suidae) from the Middle Miocene of Central Myanmar

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Abstract

In this study, we report the additional dental specimens of *Tetraconodon malensis* (Artiodactyla, Suidae) discovered near Nwegwe Village, Chaung-U Township, Sagaing Division, central Myanmar. The well preserved maxillary and mandibular fragments of *T. malensis*, firstly recorded from the basal part of the Khabo Formation (Middle Miocene) provide new dental characteristics of this species: large P_3 with salient buccal and lingual walls; longer and wider P_3 relative to P_4; extremely large P^3 and P^4; longer but not wider P^3 relative to P^4; minute M^3 with indistinct talon; well developed buccal cingulum in upper molars. The additional dental characteristics of *T. malensis* elucidates the taxonomic status of this species among tetraconodont suids, suggesting that *T. malensis* may have originated in Myanmar and was derived from *Conohyus sindiensis* of Indian Subcontinent during the Early Miocene.

Key words: Middle Miocene, new materials, taxonomic status, *Tetraconodon malensis*

Introduction

The fossil suids of Myanmar have been known since the earlier part of 19th Century (Clift, 1828). Most of the Myanmar suids were described or mentioned by Colbert (1938, 1943) and Pilgrim (1910a, 1926, 1927a). Among their descriptions, *Tetraconodon minor* Pilgrim 1910a is a well known species which has been collected from the earliest Late Miocene of Myanmar.

Recently, new species of *Tetraconodon*, *T. malensis*, *T. irramedius* and *T. irramagnus* were described from the Miocene of Myanmar (Thaung-Htike *et al.* 2005, 2007). *Tetraconodon* has been suggested that it was originated in Myanmar by the first appearance of smallest and most primitive *T. malensis*, which evolved from the probable ancestor *Conohyus sindiensis* during the late Middle Miocene (Thaung-Htike *et al.*, 2005). However, Chavasseau *et al.* (2006) relocated the holotype of *T. malensis*

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under the name *Conohyus thailandicus*, which has been described from the Middle Miocene of Thailand (Ducrocq *et al.*, 1997).

During our recent paleontological works, well preserved dentognathic specimens of *Tetraconodon malensis* were discovered near Nwegwe Village, Chaung-U Township, Sagaing Division, central Myanmar. That discovery prompted us to reevaluate the age and phylogenetic status of *T. malensis.*

Abbreviations

NMM, National Museum, Yangon, Myanmar; MUDG–V, Mandalay University, Department of Geology–Vertebrate; YUDG, University of Yangon, Department of Geology; P, premolar; M, molar.

Geologic setting

The additional dental specimens of *Tetraconodon malensis* are recovered from the Khabo Formation (= Khabo Sandstone, Myint Thein, 1966) crop out near Nwegwe and Thanbinkan Villages, Chaung-U Township (Figure 1). According to Win Myint (1986), The Khabo Formation overlies the Moza Formation, and is unconformably overlain by the Irrawaddy Formation in that area. It is about 997m thick, and characterized by mostly sandstone, which is light grey to buff in color, less indurated, fine- to medium-grained, large-scale planar and trough type current beddings with a few shale partings in features. The brackish environment is suggested for the beds in that area. Win Myint (1986) described the Late Miocene equivalent for the Khabo Formation. However, a lot of Middle Miocene mammalian fossils have been recently discovered from the Khabo Formation, and suggested that the Middle Miocene equivalent for those strata.

Materials and Methods

The additional specimens of *Tetraconodon malensis* are now stored at the Department of Geology, University of Yangon (Yangon, Myanmar) and Department of Geology, University of Mandalay (Mandalay, Myanmar). Dental terminology and measurement method used are according to Thaung-Htike *et al.* (2005). Dental measurements of some Myanmar specimens and other correlated foreign suid specimens were adopted from Pilgrim (1926), Pickford (1988) and Made (1999). The length of first molar

have been considered to express less size variation and chosen for the diagnoses of tetracondont suids to compare the body size differences. The dental measurements of the present specimens are listed in Table 1 and 2

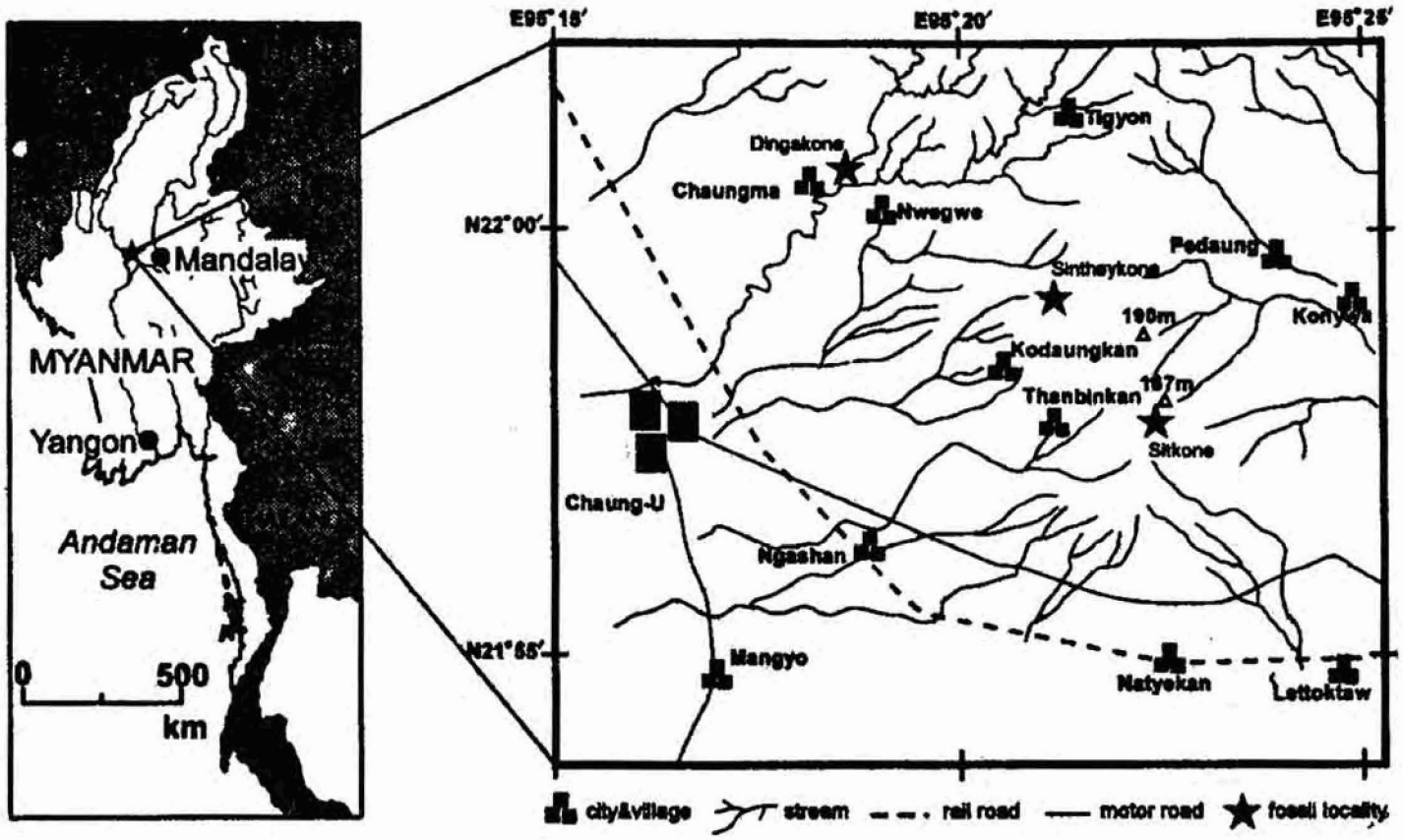

Figure 1. Fossil localities near Nwegwe and Thanbinkan Villages, Chaung-U Township, Sagaing Division, central Myanmar.

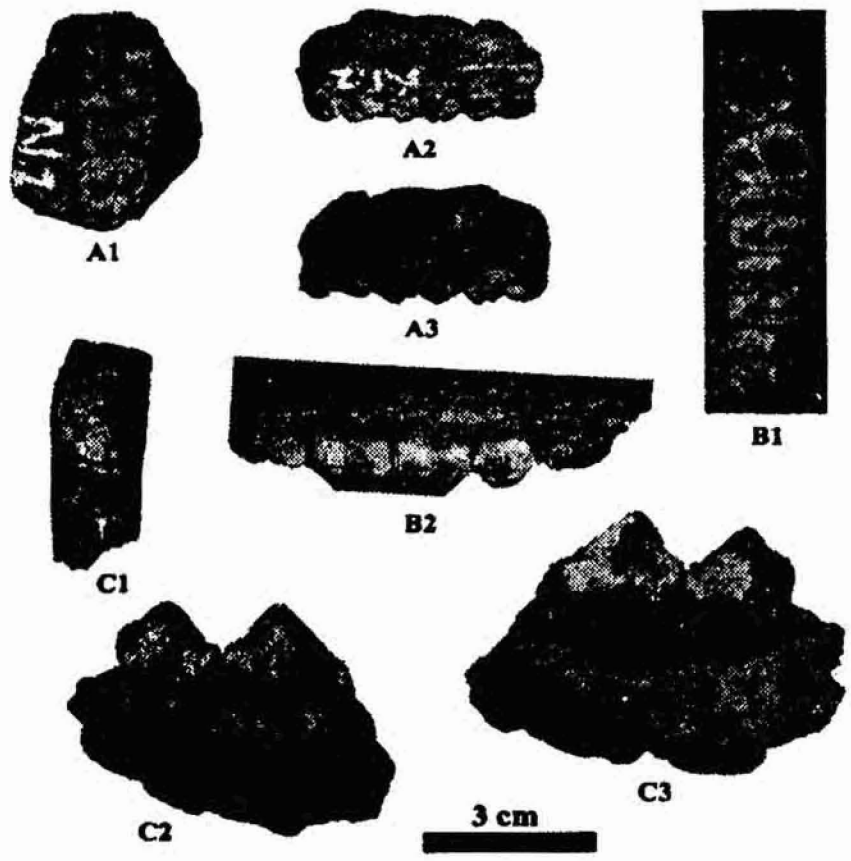

Figure 2. *Tetraconodon malensis*. A, YUDG-N 1, left maxillary fragment with M^{1-3}: A1, occlusal view; A2. lingual view; A3. buccal view. B, YUDG-N 2, left maxillary fragment with P^3-M^3: B1, occlusal view; B2. lingual view. C, MUDG-V 1029, left mandibular fragment with P_{3-4}: C1, occlusal view; C2. lingual view; C3. buccal view.

Systematic paleontology

Order Artiodactyla Owen, 1848

Family Suidae Gray, 1821

Subfamily Tetraconodontinae Lydekker, 1876

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* Thaung-Htike *et al.*, 2005; *Tetraconodon irramagnus* Thaung-Htike *et al.*, 2007; *Tetraconodon irramedius* Thaung-Htike *et al.*, 2007.

Emended diagnosis.—Differs from other tetraconodontini 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 $M^{1-3}/_{1-3}$. M^3 is always smaller in width than M^2.

Tetraconodon malensis Thaung-Htike *et al.*, 2005 Figure 2

Tetraconodon malensis Thaung-Htike *et al.*, 2005, fig. 7.

Conohyus thailandicus, Chavasseau *et al.*, 2006, fig. 4.

Lectotype.—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, Sagaing Division, central Myanmar.

Horizon and age of type locality.—Upper part of Freshwater Pegu Beds, Middle Miocene.

Emended dental diagnosis. —Smallest species of *Tetraconodon*. M_1 length is about 14 mm. P^3 and P^4 are extremely large relative to M^1. P^3 is longer but not wider than P^4. M^3 is minute, having indistinct pentacone (talon). Strong buccal cingula are distinguished in upper molars. P_3 is large, having salient buccal and lingual walls, and longer, wider and higher than P_4.

New materials.—YUDG-N 1, left maxillary fragment with M^{1-3}; YUDG-N 2, left maxillary fragment with P^3-M^3; MUDG-V 1029, left mandibular fragment with P_{3-4} (see Figure 2).

Locality of new materials.—In museum descriptions, all new materials were recovered from near Nwegwe Village, Chaung-U Township, Sagaing Division (Figure 1) but exact locality is open to question.

Horizon and age of new materials.—Khabo Formation, Middle Miocene.

Associated fauna.—All these specimens were rediscovered from the museum collections, however, following mammalian fauna were discovered together from the same locality: *Dorcatherium* sp. (small), *Prodeinotherium* sp., *Choerolophodon corrugatus*, cf. *Hemimeryx* sp., cf. *Anthracotherium* sp., *Brachypotherium* sp., cf. *Gaindartherium* sp., indet. trilophodont gomphothere.

Description.—P^3-M^3 and P_3 were firstly discovered for this species. Although the base of the mandible in the present material is broken, the remaining mandibular corpus shows formerly deep mandibular relative to size of the cheek teeth. The cheek teeth are bunodont and brachyodont. The tooth enamel is very thick and weakly wrinkled.

P_3 is very similar to but distinctly larger than P_4. They are conical and rugose, and wider in their distal part than in their mesial one. A large protoconid, smaller hypoconid and much smaller prestylid are distinct. Metaconid is indistinct. An 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 labial and lingual sides. Both of P_3 and P_4 are unworn, and crown height at the buccal of P_3 is 25.66 mm and buccal of P_4 has 20.14 mm. The wrinkled enamel in P_3 is more distinct than that of P_4.

P^3 is narrower but longer than P^4. The occlusal surface of P^3 is so damage that its morphology is not observable. It is rugose, longer than wide and nearly triangular in occlusal view. Disto-lingual heel is distinct. Posterior cingulum is distinct.

P^4 is wider than long and is buccally longer than lingually. Only paracone and protocone can be traced, and they are separated by a deep protofossa. Metacone is indistinct. The anterior and posterior cingula are well developed.

M^{1-2} are nearly squared in occlusal view having four inflated main cusps (paracone, protocone, metacone and hypocone) arranged in two distinct lobes with rounded corners, which are separated by a distinct medium valley. Hypopreconule and protopreconule are also distinct.

Furchen are indistinct. The anterior lobe is longer and wider than the posterior. The anterior, posterior and buccal cingula are very distinct and connect each others. The pentacone is absent. $M^1 < M^2$.

Anterior width of M^3 is smaller than the posterior width of M^2. M^3 is buccolingually narrower and mesiodistally longer than M^2. It is slightly narrower to the distal. The first and second lobes are similar in morphology to those of M^{1-2}. Talon is small and pentacone can not be traced.

Comparison—Present specimens have large $P^{3-4}/_{3-4}$ and small M^3, which is a typical morphology of *Tetraconodon*. *T. malensis* is similar to *Conohyus sindiensis* in having distinctly longer and higher crown for P_3 relative to P_4, but differ in having wider P_3 relative to P_4 and smaller M^3. Very minute and indistinct talon for M^3 in present specimens is a distinct character of all Myanmar *Tetraconodon*.

Chavasseau *et al.* (2006) correlated the lectotype of *Tetraconodon malensis* to *Conohyus thailandicus* of Thailand. Thaung-Htike *et al.* (2005) described that *T. malensis* is clearly distinguished from *C. thailandicus* by its larger in relative size (especially in width) of P_4 with respect to that of M_1 and narrower M_3. Newly discovered materials for *T. malensis* show extremely large P_3 relative to P_4 (Figure 3). The unworn crown height of P_3 (21 mm; Pickford and Gupta, 2001) in *C. thailandicus* is distinctly lower than that of the present material of *T. malensis* (25.66 mm). In P_3 and P_4 of *C. thailandicus*, a very slight cingulid occurs around the whole crown (Ducrocq *et al.*, 1997), which is not present in well preserved P_{3-4} of *T. malensis*. Moreover, the talon with pentacone of M^3 is large and distinct in *C. thailandicus* (Ducrocq *et al.*, 1997), whereas the talon in M^3 of *T. malensis* is as small as in other *Tetraconodon* of Myanmar. The above mentioned characters for the present specimens of *T. malensis* suggest that the present specimens are not *Conohyus* but *Tetraconodon*.

Discussion

Until recent years, *Tetraconodon minor* Pilgrim, 1910a, had been considered the smallest, the geochronologically oldest and the most primitive species of *Tetraconodon* (Pilgrim, 1926; Colbert, 1935b; Made 1999). It has been discovered only from the earliest Late Miocene of Myanmar. Pilgrim (1926) concluded that *Tetraconodon* probably evolved from the oldest known Asian tetraconodontine, *Conohyus sindiensis* Lydekker, 1878, from the lower Middle Miocene (Kamlial to Chinji) of the

Siwalik Group. However, *T. minor* is about three times larger than *C. sindiensis*, and a large morphological gap is existed between them.

Recently, Thaung-Htike *et al.* (2005) described *Tetraconodon malensis*, new species of small *Tetraconodon*, from the Middle Miocene Freshwater Pegu Beds of Myanmar. Compared to Asian *Conohyus*, *T. malensis* resembles *C. sindiensis* in M_1 dimensions and is smaller than *C. indicus* Lydekker, 1884, and *C. thailandicus* Ducrocq *et al.*, 1997. But the relative size of the enlarged 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 (see Thaung-Htike *et al.*, 2005; fig. 8A). When compared with *C. indicus* and *C. thailandicus*, *T. malensis* has extremely large P_4 and small M_1 (see Thaung-Htike *et al.*, 2005; fig. 8A), which is one of the important characters distinguishing *Tetraconodon* from *Conohyus* and other tetraconodontine (Pilgrim, 1926; Made 1999). When reevaluating Myanmar *Tetraconodon* (*T. irramagnus*, *T. irramedius*, *T. minor* and *T. malensis*) all of the Myanmar species are similar in the following character: the relative sizes of the last two premolars with respect to the first molar. It can be seen that the relative dental sizes of the Myanmar species are situated on the same trend of size enlargement (see Thaung-Htike *et al.*, 2007, fig. 3). Additionally, newly discovered upper dentition of *T. malensis* also characterizes the same trend of dental size enlargement with other Myanmar *Tetraconodon*, which is distinctly apart from the size enlargement of Siwalik species (*T. intermedius*) (Figure 4).

If, as Pilgrim (1926) considered, *Conohyus sindiensis* is an ancestor of *Tetraconodon*. In *Conohyus-Tetraconodon* lineage, enlargement of the posterior premolars occurred first and overall tooth size increased later (Thaung-Htike *et al.*, 2005). Pickford (1988) and Made (1999) suggested that size increasing is an evolutionary trend in *Tetraconodon*. Therefore, the small tooth-sized *T. malensis* would be more primitive and older chronologically than *T. minor*. Considering *T. malensis* as a derived form of *C. sindiensis* (Middle Miocene) and as an ancestor of *T. minor* (basal Late Miocene) suggested a late Middle Miocene for *T. malensis* which is an intermediate in geological age between *C. sindiensis* and *T. minor* (Thaung-Htike *et al.*, 2005).

As mentioned in the above, Chavasseau *et al.*, (2006) placed the lectotype of *T. malensis* for junior synonym of *C. thailandicus* of Thailand.

Although they said the Myanmar specimen had larger P_4 than Thailand specimen, they did not discuss on the enlargement of P_4 in Myanmar specimen. In the newly discovered additional specimens of *T. malensis*, well-preserved P_3 is distinctly larger than P_3 of *C. thailandicus* (Figure 3), and, M^3 has an indistinct talon, both of which are definitive feature of *Tetraconodon* not *Conohyus*.

Table 1. Upper dental measurements (mm) of the new *Tetraconodon malensis* specimens. Abbreviations: L = mesiodistal length; W1= first lobe width, W2 = second lobe width.

Taxa	Spec. no.	P^3		P^4		M^1			M^2			M^3		
		L	W	L	W	L	W1	W2	L	W1	W2	L	W1	W2
Tetraconodon malensis	YUDG-N 1					14.1	15.2	14.3	14.5	16.5	14.7	16.2	15.3	12.4
Tetraconodon malensis	YUDG-N 2	20.4	15.1	13.5	17.9	13.8	14.1	14.1	14.8	15.5	14.2	16.7	14.3	12.8

Table 2. Lower dental measurements (mm) of the new *Tetraconodon malensis* specimen. Abbreviations see in the above.

Taxa	Spec. no.	P_3			P_4			M_1		
		L	W1	W2	L	W1	W2	L	W1	W2
Tetraconodon malensis	MUDG-V 1029	25.2	15.3	17.9	19.3	13.6	16.8	-	11.8	-

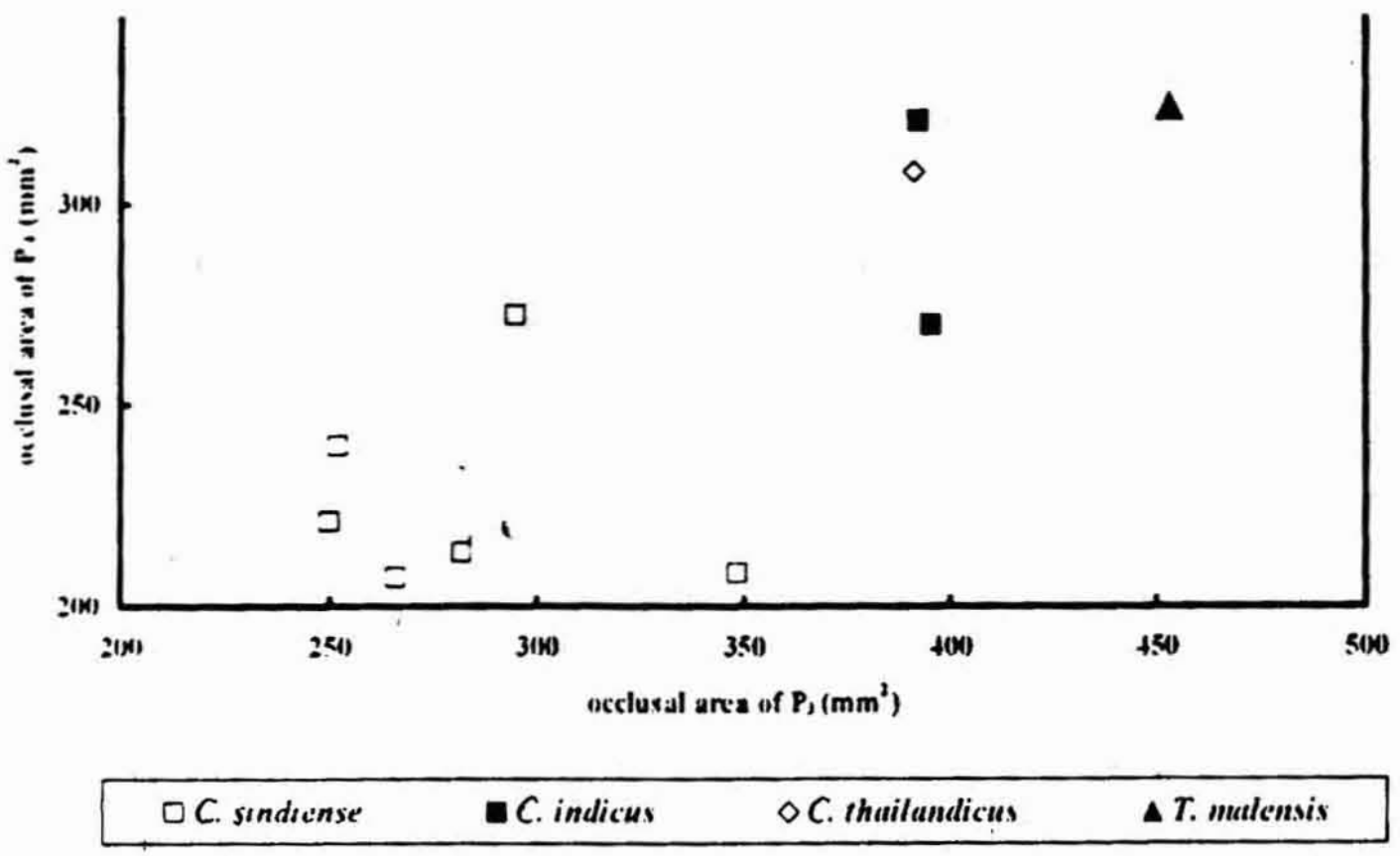

Figure 3. Dental comparison of the occlusal areas of P_3 vs P_4 between *Tetraconodon malensis* and Asian *Conohyus*.

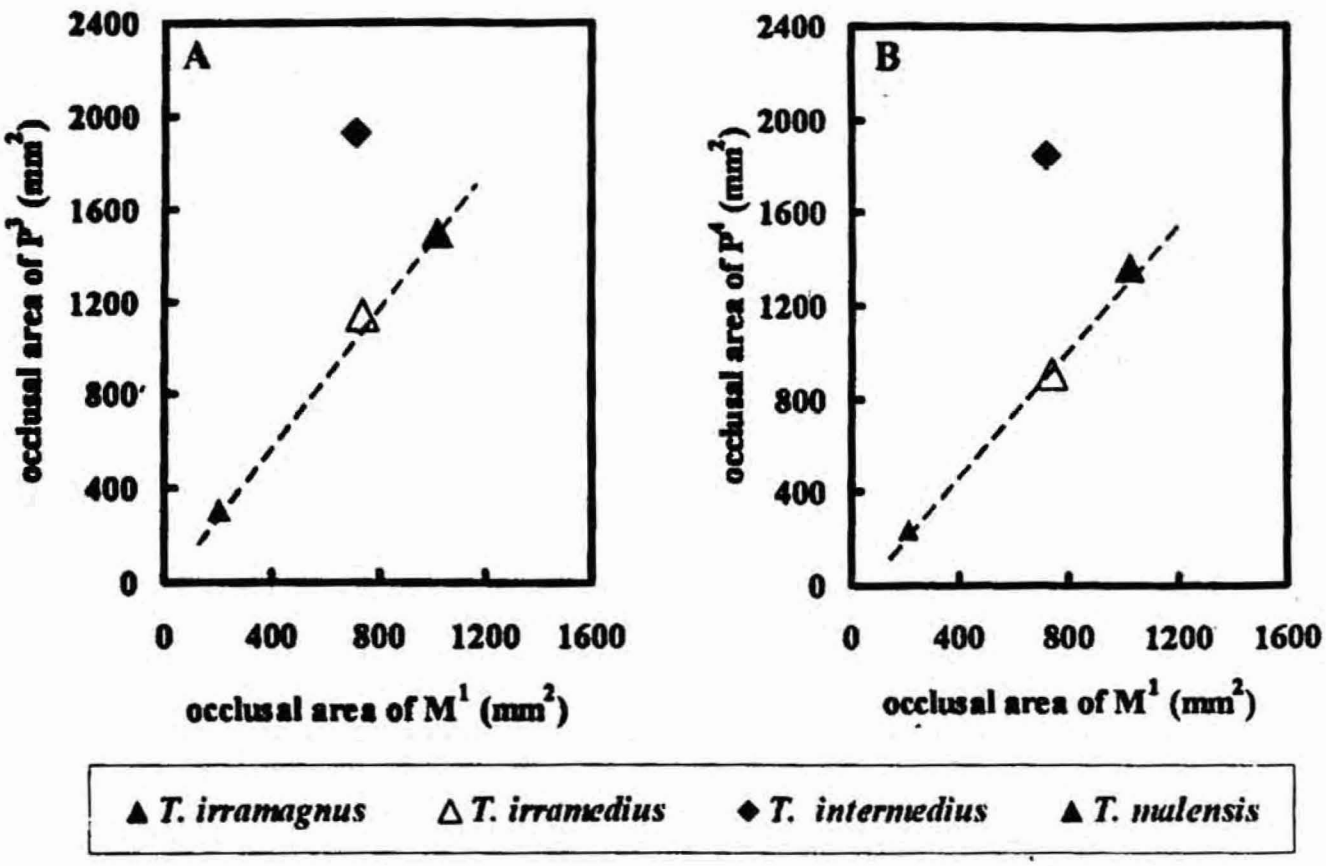

Figure 4. Bivariate plots for the dental measurements of *Tetraconodon* specimens from Siwalik and Myanmar. **A**, occlusal areas of P^3 on that of M^1; **B**, occlusal areas of P^4 on that of M^1.

Origin of *Tetraconodon*

According to Pickford (1988) and Made (1999), in *Tetraconodon* lineage, the small form indicates the primitive condition and suggests that chronologically older than the large form. Thaung-Htike *et al.* (2005) suggested the late Middle Miocene for the probable age of *T. malensis*. New dental materials of *T. malensis* from the Thanbinkan-Nwegwe area is associated with the typical Middle Miocene fauna, *Prodeinotherium* sp. and *Choerolophodon corrugatus*. *Prodeinotherium* sp. has been discovered from the Kamlial and Chinji Formations, the basal Middle Miocene of Lower Siwalik (Dehm, 1963; Harris, 1973) and *Choerolophodon corrugatus* has been discovered from the Lower and Middle Siwalik. The coexistence of these two fossil elephants suggested that the Middle Miocene age for Thanbinkan-Nwegwe area (Takai *et al.*, 2006), and the discovery of *Prodeinotherium* sp. suggests the early Middle Miocene rather than the late Middle Miocene.

The first appearance of *Conohyus sindiensis*, the probable ancestor of *Tetraconodon*, in Siwalik is the latest Early Miocene or early Middle Miocene (Pickford, 1988; Made, 1999). Barry *et al.* (2002) introduced 14.0 Ma, which is early Middle Miocene, for the first appearance of *C. sindiensis*

in northern Pakistan by the evidence of radiometric and paleomagnetic dating. In their description, the first appearance of *C. sindiensis* is identical to that of *Deinotherium* spp., the appearance of which in Siwalik is later than *Prodeinotherium* sp. Therefore, the co-occurrence of *T. malensis* and *Prodeinotherium* sp. suggests that *T. malensis* likely appeared in the early Middle Miocene which is older than the previous estimated level of *T. malensis*, the late Middle Miocene (Thaung-Htike *et al.*, 2005). Early Middle Miocene equivalent for *T. malensis* suggests that *Tetraconodon* evolved from *C. sindiensis* during the early Middle Miocene or both of *Tetraconodon* and *C. sindiensis* evolved from a common ancestor during the latest Early Miocene.

Conclusion

In Myanmar, four distinct species of *Tetraconodon*, *T. irramagnus*, *T. irramedius*, *T. minor* and *T. malensis* are recognized. Newly discovered additional dental specimens of *T. malensis* strongly elucidate the taxonomic status of this species, which is a definitive *Tetraconodon* not *Conohyus*. The first discovery of *T. malensis* and its associated mammalian fauna from the Khabo Formation near Chaung-U Township suggest that the Middle Miocene equivalent rather than the Late Miocene for the Khabo Formation. New geochronological evidence for the *T. malensis*, the early Middle Miocene, suggests that *Tetraconodon* might be originated in Myanmar and evolved from *C. sindiensis* during the early Middle Miocene or both of *Tetraconodon* and *C. sindiensis* evolved from a common ancestor during the latest Early Miocene.

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