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# New species of large *Tetraconodon* (Mammalia, Artiodactyla, Suidae) from the late Miocene of Myanmar

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**Abstract.** We describe two new species of *Tetraconodon*, *T. irramagnus* sp. nov. and *T. irramedius* sp. nov., from the late Miocene of Myanmar recognized when reevaluating large *Tetraconodon* specimens. *Tetraconodon* had also been recovered from the late Miocene Siwalik sediments of India/Pakistan. However, in the Siwalik specimens, the dimensions of the last two premolars and the third molar with respect to those of the first molar are distinctly greater than those of the Myanmar specimens. In Myanmar species, the relative dental sizes are similar, and the most obvious interspecies distinctions are their dental size differences. Considering the variation in the relative sizes of the last two premolars and third molar with respect to the first molar among the Siwalik and Myanmar *Tetraconodon*, the enlargement of the last two premolars and the third molar could be regarded as a characteristic of the interspecies distinction.

**Key words:** Myanmar, new species, relative size, Siwalik, *Tetraconodon*

## Introduction

Neogene freshwater sediments yielding abundant mammalian fossils are widely distributed in central Myanmar. Most of the mammalian fossils recovered have been from the upper Miocene to lower Pleistocene Irrawaddy Group (Colbert, 1938; Bender, 1983). To date, four mammalian orders (Carnivora, Proboscidea, Perissodactyla, and Artiodactyla) have been described from the Irrawaddy sediments, and the fossil record of the artiodactyls is relatively abundant, comprising representatives of seven families (Takai *et al.*, 2006). Among the Artiodactyla, the genus *Tetraconodon* (Suidae) is distinguished by its extremely large  $P^{3-4}/_{3-4}$ , and it is presumed to have originated in Myanmar during the late middle Miocene (Thaung-Htike *et al.*, 2005). In *Tetraconodon*, dental size variation has been used to distinguish species, and two types, large and small, are recognized in Myanmar (Chit-Sein *et al.*, 2006).

Recently, three new large dentognathic specimens were described from central Myanmar (Chit-Sein *et al.*, 2006). These materials were correlated with *T. magnus* of the Middle Siwalik Group (India/Pakistan)

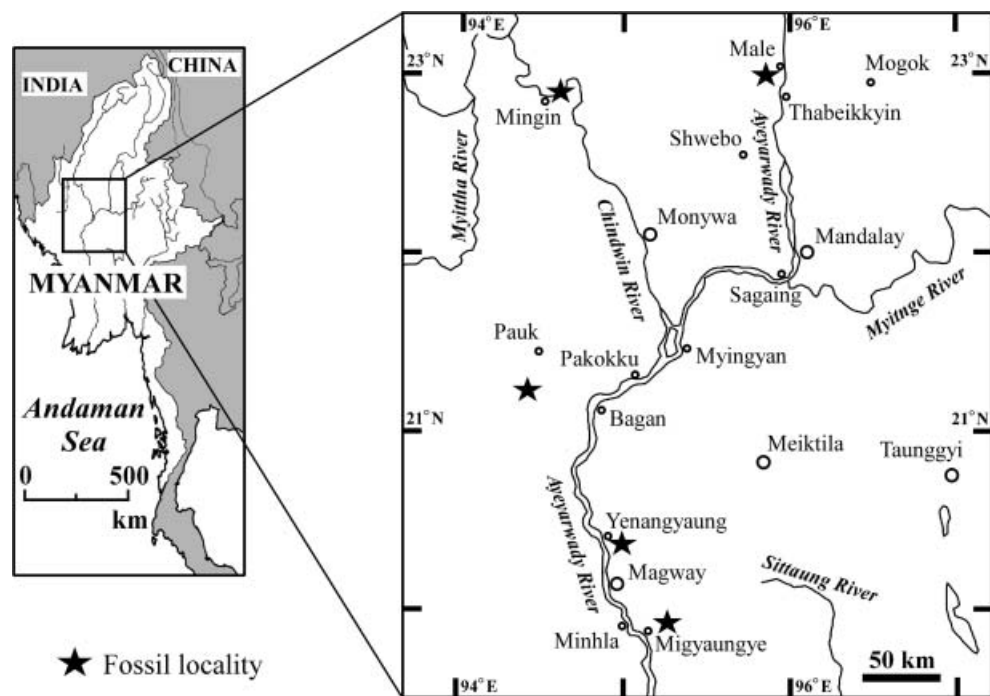
and described under the name *T. cf. magnus*. That discovery prompted us to reevaluate all *Tetraconodon* species, and we have reclassified the large *Tetraconodon* specimens from Myanmar, resulting in the description of two new species.

## Abbreviations

NMM, National Museum, Yangon, Myanmar; NMMP-KU-IR, National Museum, Myanmar, Paleontology-Kyoto University-Irrawaddy (stored at the National Museum, Yangon); GSI, Geological Survey of India, Kolkata, India; AMNH, American Museum of Natural History; YUDG-Mge, University of Yangon, Department of Geology-Migyaungye (name of the township, Magway Division, central Myanmar); Kpg, Gyatpyegyí (= Kyatpyegyí) fossil locality (southwest of Male village, Sagaing Division, central Myanmar).

## Materials and methods

All materials were collected in central Myanmar (Figure 1). They are now stored at the National Mu-



**Figure 1.** Map showing the fossil localities of *Tetraconodon* in central Myanmar.

**Table 1.** Upper dental measurements (mm) of *Tetraconodon irramedius* sp. nov. and *T. irramagnus* sp. nov. Abbreviations: L = mesiodistal length; W = buccolingual width; W1 = first lobe width; W2 = second lobe width; W3 = third lobe width of M<sup>3</sup>; \* = estimate.

Taxa	Specimen	P <sup>3</sup>		P <sup>4</sup>		M <sup>1</sup>			M <sup>2</sup>			M <sup>3</sup>			
		L	W	L	W	L	W1	W2	L	W1	W2	L	W1	W2	W3
<i>T. irramagnus</i>	YUDG-Mge 089	39.1	38.2	29.0	47.1	31.6	32.2	30.2*	35.9	37.1	35.9	—	34.2	—	—
<i>T. irramagnus</i>	YUDG-Mge 091	—	—	—	—	—	—	—	35.2	37.0	34.4	39.0	34.3	28.2	17.2
<i>T. irramedius</i>	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

seum (Yangon, Myanmar) and the Department of Geology, University of Yangon (Yangon, Myanmar). Dental terminology and measurement method used are according to Thaung-Htike *et al.* (2005). Dental measurements of the *Tetraconodon* specimens discussed here and other correlated *Tetraconodon* specimens are listed in Tables 1, 2, and 3.

**Systematic paleontology**

Order Artiodactyla Owen, 1848  
Family Suidae Gray, 1821  
Subfamily Tetraconodontinae Lydekker, 1876  
Genus *Tetraconodon* Falconer, 1868

*Tetraconodon irramagnus* sp. nov.

Figure 2

*Tetraconodon* sp. cf. *T. magnus*, Chit-Sein *et al.*, 2006, figs. 4 and 5.

*Holotype*.—YUDG-Mge 089, a right maxillary fragment with P<sup>3</sup>–M<sup>2</sup> and mesial half of M<sup>3</sup> (Figure 2A–2C) (Chit-Sein *et al.*, 2006, fig. 4).

*Paratype*.—YUDG-Mge 090, a left mandibular fragment with P<sub>4</sub>, and YUDG-Mge 091, a left maxillary fragment with M<sup>2–3</sup> (Figure 2D–2I) (Chit-Sein *et al.*, 2006, figs. 4 and 5).

*Type locality*.—West of Tebingan Village (19° 57' 51.1" N; 95° 08' 37.8" E), Migyaungye Township, Magway Division, central Myanmar.

*Type horizon and age*.—Basal part of the 'Irrawaddy Group', early late Miocene.

*Etymology*.—Irra-, the first four letters of the 'Irrawaddy Group', where the type specimen was discovered; -magnus, signifying the largest tooth size among *Tetraconodon* species of Myanmar.

*Diagnosis*.—A large species of *Tetraconodon*. The occlusal dimensions of the first molar are congruent

**Table 2.** Measurements of the P<sup>3</sup>, P<sup>4</sup>, M<sup>1</sup>, P<sub>4</sub> and M<sub>1</sub> of *Tetraconodon* which are used in Figure 4, and measurement of the M<sup>3</sup> of *T. magnus* which is used in the text. The measurement of the M<sup>3</sup> of *T. magnus* was modified and adopted from Falconer (1868), and other dental measurements were adopted from Colbert (1935), Pickford (1988), Thaung-Htike *et al.* (2005) and Chit-Sein *et al.* (2006). Abbreviations: L = mesiodistal length; W = greatest buccolingual width.

Taxa	Specimen	P <sup>3</sup>		P <sup>4</sup>		M <sup>1</sup>	
		L	W	L	W	L	W
<i>T. intermedius</i>	GSI B 675	46.5	41.4	37.4	49.4	26.0	27.5
Taxa	Specimen	M <sup>3</sup>					
		L	W				
<i>T. magnus</i>	Falconer (1868)	52.0	37.6				
Taxa	Specimen	P <sub>4</sub>		M <sub>1</sub>			
		L	W	L	W		
<i>T. magnus</i>	AMNH 9937	49.5	56.5	30	29		
<i>T. magnus</i>	GSI B 71	53.4	56.4	31.1	28.7		
<i>T. minor</i>	GSI B 771	34.6	31.1	24	20.4		
<i>T. minor</i>	NMM AN 1	30.8	29.3	23.3	22		
<i>T. malensis</i>	NMM Kpg-1	18.2	16.5	13.9	12.2		

**Table 3.** Lower dental measurements (mm) of *Tetraconodon irramedius* sp. nov. and *T. irramagnus* sp. nov. Abbreviations: L = mesiodistal length; W1 = first lobe width; W2 = second lobe width; W3 = third lobe width of M<sub>3</sub>; \* = estimate.

Taxa	Specimen	P <sub>4</sub>			M <sub>1</sub>			M <sub>2</sub>			M <sub>3</sub>			
		L	W1	W2	L	W1	W2	L	W1	W2	L	W1	W2	W3
<i>T. irramagnus</i>	YUDG-Mge 090	44.8	32.3	38.7	32.0*	27.8*	26.8*							
<i>T. irramedius</i>	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

with those of *T. magnus*, however, the dimensions of the last two premolars and third molar are distinctly smaller than those of *T. magnus*. The enamel wall and root at the distobuccal end of P<sup>4</sup> are more flared and larger than at the mesiobuccal end of P<sup>4</sup>. The paracone is located distally to the mesial margin of the distobuccal root of P<sup>4</sup>. The mesiodistal length of M<sub>1</sub> is about 32 mm.

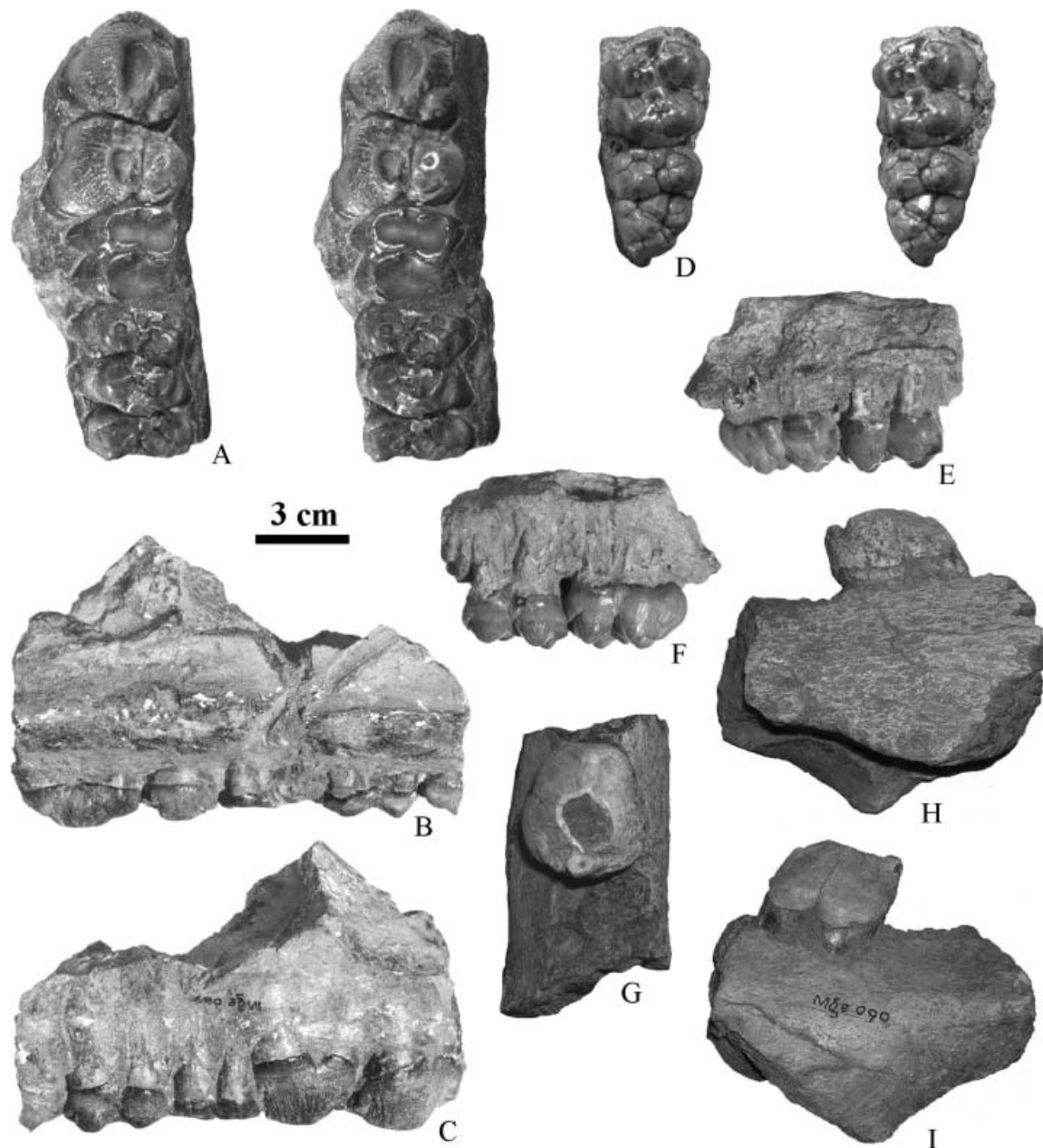
*Description.*—A detailed description for the dental morphology has been given by Chit-Sein *et al.* (2006), and the term *T. cf. magnus* was used in their description. We here redescribe only the distinct characters, and add some new morphology which was not described in Chit-Sein *et al.* (2006).

Three dentognathic specimens comprising maxillary and mandibular fragments with P<sup>3</sup>–M<sup>3</sup> and P<sub>4</sub>, are known. The cheek teeth show typical bunodont and brachyodont suid dental morphologies. The tooth enamel is very thick and highly wrinkled, which is distinct in P<sup>3–4</sup> and P<sub>4</sub>. The roots of the last two premolars are much larger and more flared than those of the molars. In the maxillary fragment, the mesial border of the zygomatic process is estimated to be above the mesial surface of P<sup>4</sup> (Figure 2C); other cranial features cannot be deduced from the present materials. The

highly robust mandible is broken at the base, so it is impossible to measure its depth (Figure 2H–2I).

P<sup>3</sup> and P<sup>4</sup> are rugose and much larger than M<sup>1</sup> and M<sup>2</sup> (Figure 2A). They are characterized by the flared occlusal outline and the presence of three roots in each. Both in P<sup>3</sup> and P<sup>4</sup>, the paracone and metacone are worn and connected as a single confluent large cusp. The distolingual heel in P<sup>3</sup> is large and distinct. P<sup>3</sup> is mesiodistally longer and buccolingually narrower than P<sup>4</sup>. In P<sup>4</sup>, the enamel wall and root at distobuccal are more flared and larger than those at mesiobuccal (Figure 2C) and the paracone is located distally to the mesial margin of the distobuccal root. The protocone of P<sup>4</sup> is very distinct. The beaded anterior and posterior cingula are well developed in both P<sup>3</sup> and P<sup>4</sup>.

M<sup>1</sup>, M<sup>2</sup>, and M<sup>3</sup> show the typical morphology of teeth of tetraconodontine suids: very thick enamel; four major cusps (paracone, protocone, metacone, and hypocone) with rounded outline and shallow furchen; a well developed anterior cingulum. The minor cusps (protopreconule, hypopreconule and pentapreconule) are clearly outlined. The pentacone is tiny but distinct in all upper molars. A simple and minute talon is present on M<sup>3</sup>. The buccal cingulum is poorly developed on M<sup>1</sup> and M<sup>2</sup>. The distolingual



**Figure 2.** *Tetraconodon irramagnus* sp. nov. **A–C.** YUDG-Mge 089, a right maxillary fragment with  $P^3$ – $M^2$  and mesial half of  $M^3$ : **A.** Occlusal view (stereo pair); **B.** Lingual view; **C.** Buccal view. **D–F.** YUDG-Mge 091, a left maxillary fragment with  $M^2$ – $M^3$ : **D.** Occlusal view (stereo pair); **E.** Lingual view; **F.** Buccal view. **G–I.** YUDG-Mge 090, a left mandibular fragment with  $P_4$ : **G.** Occlusal view; **H.** Lingual view; **I.** Buccal view.

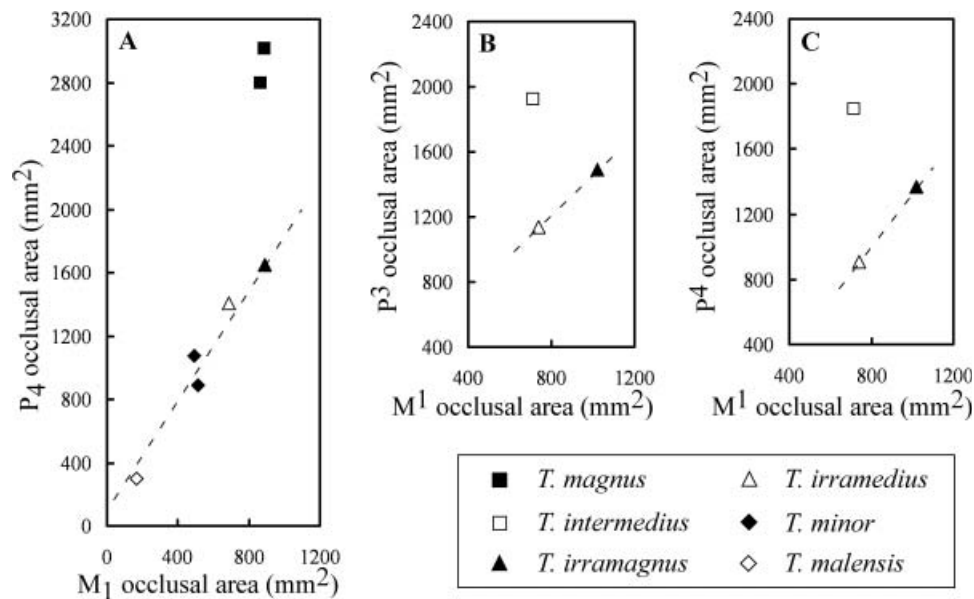
root of  $M^2$  is slightly bifurcate. The buccolingual width of the first lobe is greater than that of the second lobe in upper molars. The occlusal dimensions of  $M^2$  are nearly the same as those of  $M^3$ .  $M^1 < M^2$ .

The large and rugose  $P_4$  is moderately worn, and the morphology of the protoconid and metaconid cannot be investigated. The anterior precristid and prestylid are isolated. The enamel is thick and slightly wrinkled

distally. The hypoconid and posterior cingulum are distinct.

Although no lower molars have been discovered, the alveolus of  $M_1$  remains in one of the specimens, and the approximate length and width were traced (Chit-Sein *et al.*, 2006).

**Comparison.**—The specimens show typical tetracodontine suid features, and their morphological char-



**Figure 3.** Bivariate plots for the dental measurements of *Tetraconodon* specimens from Siwalik and Myanmar. **A.** Occlusal area of  $P_4$  on that of  $M_1$ . **B, C.** Occlusal areas of upper premolars on that of  $M_1$ : **B.**  $P^3$  on  $M^1$ ; **C.**  $P^4$  on  $M^1$ . Comparative measurements are listed in Table 2.

acters (extremely large last two premolars and small  $M^3$  with a minute talon) are congruent with the definition of the genus *Tetraconodon*. The occlusal dimensions of the  $M^1_{/1}$  are similar to those of *T. magnus*, however, the dimensions of  $P^3$ ,  $P^4$ , and  $P_4$  are distinctly smaller than those of the corresponding teeth of *T. magnus* (see Figure 3). Moreover, the size of  $M^3$  (length  $\times$  width = 39 mm  $\times$  34.3 mm) is distinctly smaller than the size of  $M^3$  in the lectotype of *T. magnus* (52 mm  $\times$  37.6 mm).

*T. irramagnus* sp. nov. differs from *T. irramedius* sp. nov. in the following characters: larger size; more flared and larger distobuccal wall and root of  $P^4$ ; distally located paracone of  $P^4$ . *T. irramagnus* sp. nov. differs from *T. intermedius* in its distinctly larger first molar and the smaller last two premolars, and from *T. minor* and *T. malensis* in its much larger size.

***Tetraconodon irramedius* sp. nov.**

Figure 4

*Tetraconodon intermedius*, Thaung-Htike *et al.*, 2005, p. 247, fig. 4.  
*Tetraconodon* sp. cf. *T. intermedius*, Thaung-Htike *et al.*, 2005, pp. 247–248, fig. 5.

**Holotype.**—NMMP-KU-IR 0225, a right maxillary fragment with  $P^3$ – $M^3$  (Figure 3A–3C) (Thaung-Htike *et al.*, 2005, fig. 5).

**Paratype.**—NMM 839/80, a left mandibular fragment with  $P_4$ – $M_3$  (Figure 3D–3E) (Thaung-Htike *et al.*, 2005, fig. 4).

**Type locality.**—Holotype from near Chaungsong Village, about 25 km south of Pauk City, Magway Division, paratype from near Male Village, Sagaing Division (Figure 1). However, the exact locations are unknown (Thaung-Htike *et al.*, 2005).

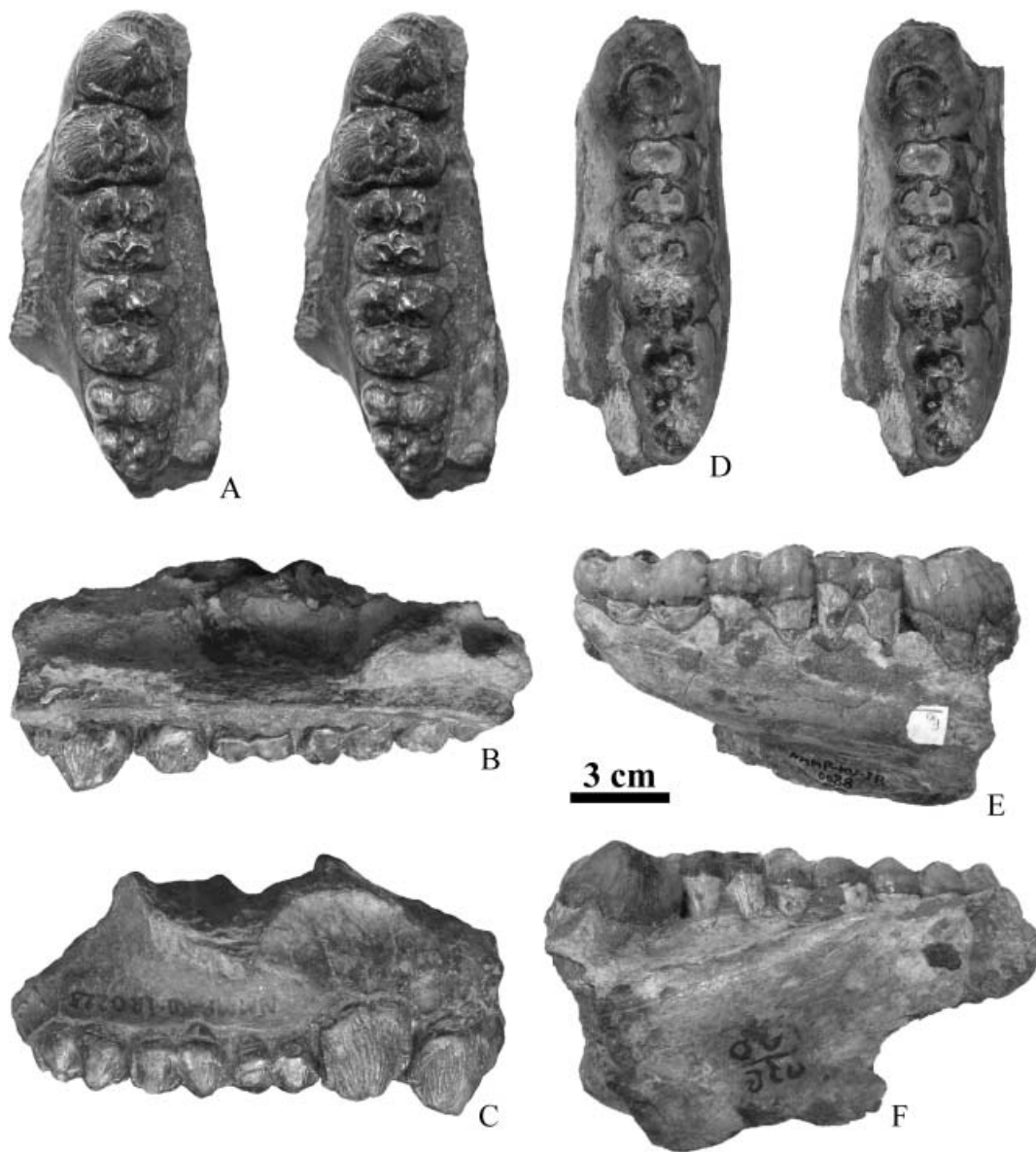
**Type horizon and age.**—Basal part of the ‘Irrawaddy Group’, early late Miocene.

**Etymology.**—Irra-, first four letters of the Irrawaddy Group, from where the type specimen was recovered; -medius, medium, a species intermediate in size between *T. minor* and *T. irramagnus* sp. nov.

**Diagnosis.**—A large species of *Tetraconodon*. The occlusal dimensions of  $M^1$  are congruent with those of *T. intermedius*, however, the dimensions of  $P^{3-4}$  and  $M^3$  are distinctly smaller than those of *T. intermedius*. In  $P^4$ , the mesiobuccal root and distobuccal root are nearly the same size. The paracone of  $P^4$  is distinctly separated from the metacone, and located above the mesiobuccal root. The mesiodistal length of  $M^1$  is 26.5 mm.

**Description.**—We described the detailed dental morphology of specimens in our previous paper (Thaung-Htike *et al.*, 2005), and identified them as *T. cf. intermedius* and *T. intermedius*. Here, we redescribe only the distinct dental characters and add some new characters which were not described in the previous work.

The maxillary and mandibular fragments are known, with well preserved  $P^3$ – $M^3$  and  $P_4$ – $M_3$ . Both the upper and lower cheek teeth are bunodont and brachyodont.



**Figure 4.** *Tetraconodon irramedius* sp. nov. **A–C.** NMMP-KU-IR 0225, a right maxillary fragment with P<sup>3</sup>–M<sup>3</sup>: **A.** Occlusal view (stereo pair); **B.** Lingual view; **C.** Buccal view. **D–F.** NMM 839/80, a left mandibular fragment with P<sub>4</sub>–M<sub>3</sub>: **D.** Occlusal view (stereo pair); **E.** Lingual view; **F.** Buccal view.

The tooth enamel is very thick and highly wrinkled, especially on P<sup>3–4</sup> and P<sub>4</sub>.

The broken edge of the zygomatic process remains on the left maxilla. The mesial border of the zygomatic process can be seen above P<sup>3</sup>, and the distal border can be estimated above the mesial end of M<sup>3</sup>, indicating an elongated junction of the zygomatic process and the maxilla. This character is comparable to those of other tetraconodontine suids, such as *Conohyus sin-diensis* (see Colbert, 1933) (In *Sus*, the junction is

shrunk and appears dorsally between M<sup>2</sup> and M<sup>3</sup>).

P<sup>3</sup> is nearly triangular in occlusal view and wider distally. The paracone is clearly separated from the metacone. The distolingual heel is well developed.

P<sub>4</sub> is wider buccally than lingually. The buccolingual width is greater than the mesiodistal length. The paracone is clearly separated from the metacone. The protocone is distinct, and separated from the paracone and metacone by a protofossa. The paracone and metacone are located above the mesiobuccal and dis-

tobuccal roots, respectively. The sizes of the mesiobuccal and distobuccal roots are nearly the same.

M<sup>1</sup> and M<sup>2</sup> are rectangular in occlusal view. M<sup>3</sup> is nearly triangular in occlusal view and narrower distally. All molars have four major cusps (paracone, protocone, metacone and hypocone) with rounded outline and shallow furchen. The minor cusps (protopreconule, hypopreconule and pentapreconule) are distinct. The pentacone is small but well defined in each molar. The talon of M<sup>3</sup> is quite small. The buccal cingula are well developed in M<sup>1</sup> and M<sup>2</sup>. The occlusal dimension of M<sup>2</sup> is larger than that of M<sup>3</sup>. M<sup>1</sup> < M<sup>2</sup>.

The robustness of the mandible suggests that it belonged to a male. It is broken at the base and impossible to measure the depth of the mandible. The anterior ridge of the ascending ramus is broken at the buccal side of P<sub>4</sub> and the distal side of M<sup>3</sup> (Figure 4F). The outline of the canine cannot be traced.

P<sub>4</sub> is large and rugose. The protoconid and metaconid are worn, and cannot be observed. The hypoconid is distinct. Three clearly separated roots are present.

M<sub>1</sub> and M<sub>2</sub> are nearly rectangular in occlusal view, and smaller than the P<sub>4</sub>. M<sub>3</sub> is elongated and narrows distally. The four major cusps (protoconid, metaconid, hypoconid and entoconid) and three minor cusps (protopreconulid, hypopreconulid and pentapreconulid) are distinct. The pentaconid is well defined in all molars, especially in M<sub>3</sub>. The talonid of M<sub>3</sub> is simple. The anterior cingulum is well developed in all molars, and protrudes at the mesiobuccal corner of the crown. The mesiodistal length of M<sub>2</sub> is shorter than that of M<sub>3</sub> but its buccolingual width is greater. M<sub>1</sub> < M<sub>2</sub>.

**Comparison.**—The characters of the extremely large last two premolars and small M<sup>3</sup>/<sub>3</sub> indicate that the specimens belong to the genus *Tetraconodon*. The occlusal dimensions of M<sup>1</sup>/<sub>1</sub> are congruent with that of *T. intermedius*, however, the Siwalik species *T. intermedius* can be differentiated from *T. irramedius* sp. nov. by its distinctly larger P<sup>3-4</sup> and M<sup>3</sup> (see Figure 3). The other Myanmar species; *T. irramagnus* sp. nov. is clearly distinguished from *T. irramedius* sp. nov. (a detailed comparison is made in the above text); *T. minor* and *T. malensis* are smaller than *T. irramedius* sp. nov. (Figure 3A), and their size differences exceed the limit of individual variation of the sympatric artiodactyl species of the same genus (Made, 1991). *T. magnus* from the Middle Siwalik Group differs from *T. irramedius* sp. nov. by its much larger size.

## Discussion

*Tetraconodon* was first described by Falconer (1868). The type species *Tetraconodon magnus* (= *T. mag-*

*num*) is distinct for its large size (M<sub>1</sub> length is about 33 mm). Pilgrim (1926) grouped *Tetraconodon* with the Asian *Conohyus* (*C. sindiensis* Lydekker, 1878, and *C. indicus* Lydekker, 1884) which is a small tetraconodont, and suggested that the latter genus might be the ancestor of the former. He also described the important distinctions between these two genera such as the much greater relative enlargement of the premolars in *Tetraconodon*. The later-described *T. minor* (Pilgrim, 1910) and *T. intermedius* (Made, 1999) are also large (M<sub>1</sub> length is about 23 mm in *T. minor* and about 27 mm in *T. intermedius*) and large size had been used as a diagnostic character of *Tetraconodon* until we discovered a small species, *Tetraconodon malensis* (M<sub>1</sub> length is about 14 mm) from the middle Miocene of Myanmar (Thaung-Htike *et al.*, 2005).

Among *Tetraconodon* species, *T. intermedius* from the upper Miocene of the Middle Siwalik Group has been known only from its upper dentition. We previously described the discovery of *T. intermedius* and *T. cf. intermedius* from the late Miocene of Myanmar (Thaung-Htike *et al.*, 2005). We classified the mandibular fragment (NMM 839/80) as *T. intermedius* based on similarity between the occlusal dimensions of its M<sub>1</sub> and M<sup>1</sup> of *T. intermedius*, and classified the maxillary fragment (NMMP-KU-IR 0225) as *T. cf. intermedius* because of its distinctly smaller P<sup>3-4</sup> and M<sup>3</sup> compared to those of *T. intermedius*. We mentioned that the smaller last two premolars and third molar in the Myanmar specimens compared to the specimens of *T. intermedius* from Siwalik could be due to individual variability, and it was difficult to classify the Myanmar specimens as a new species rather than as *T. intermedius* and *T. cf. intermedius*.

Recently, Chit-Sein *et al.* (2006) described three new large *Tetraconodon* specimens from the late Miocene of Myanmar. The occlusal dimensions of M<sup>1</sup>/<sub>1</sub> in their materials resemble those of *T. magnus* of the Middle Siwalik Group; however, the last two premolars and M<sup>3</sup> in their specimens are smaller than those of *T. magnus*. Therefore, they attributed their specimens to *T. cf. magnus*.

When reevaluating these three large *Tetraconodon* from Myanmar, *T. cf. magnus*, *T. intermedius*, and *T. cf. intermedius* (Chit-Sein *et al.*, 2006; Thaung-Htike *et al.*, 2005) together with other Myanmar species (*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 (Figure 3). However, the Siwalik species (*T. magnus* and *T. intermedius*) are distinct for



their relatively larger last two premolars and third molars compared to those of Myanmar species (Figure 3).

Finally, we reclassify the large *Tetraconodon* species of Myanmar, redefining *T. cf. magnus* (Chit-Sein *et al.*, 2006) as *T. irramagnus* sp. nov., and *T. intermedius* and *T. cf. intermedius* (Thaung-Htike *et al.*, 2005) as *T. irramedius* sp. nov. Among the Myanmar species (*T. irramagnus*, *T. irramedius*, *T. minor* and *T. malensis*) the most obvious interspecies distinctions are their dental size differences, which exceed the individual variability and sexually dimorphic differences documented in extant suids (Made, 1991).

*Tetraconodon* specimens are rare and discovered only from the Middle Siwalik Group of India/Pakistan and the Miocene sediments of Myanmar. Myanmar species *Tetraconodon irramagnus*, *T. irramedius*, and *T. minor* have been discovered from the basal part of the Irrawaddy Group (early late Miocene), and *T. malensis* has been discovered from the uppermost part of the Pegu Group (late middle Miocene). The known materials of Myanmar species were recovered from different localities, and it is difficult to correlate their stratigraphic levels. However, the larger teeth of the tetraconodontine suids have come from the younger sedimentary strata, which suggests that the large species of Myanmar *Tetraconodon* are chronologically younger than the small species.

Relatively smaller premolars are common in all Myanmar species. In contrast, the Siwalik species (*T. magnus* and *T. intermedius*) have relatively larger premolars with respect to the first molar, and this enlargement could be regarded as a derived character. It suggests that the Siwalik species and Myanmar large species (*T. irramagnus* and *T. irramedius*) evolved from the smaller *T. minor* of Myanmar, and the derived character of the Siwalik species probably occurred after they entered the Indian Subcontinent during the late Miocene. Moreover, the chronological gap between the possible youngest Myanmar species (*T. irramagnus*, early late Miocene) and the oldest species (*T. malensis*, late middle Miocene) is relatively short, which suggests that a rapid evolution of *Tetraconodon* occurred during the middle and late Miocene.

The gradual enlargement in the overall dental size of *Tetraconodon* has been accepted as an evolutionary trend. In addition, larger sizes of the last two premolars and third molar with respect to the first molar in Siwalik species are the most obvious character to distinguish this species from the Myanmar species. In conclusion, the enlargement of the last two premolars and third molar can also be accepted as an evolutionary change that occurred in the Siwalik lineage.

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## References

- Bender, F., 1983: *Geology of Burma*, 293p. Gebrüder Borntraeger, Berlin.
- Chit-Sein, Thaung-Htike, Tsubamoto, T., Tin-Thein, and Rössner, G. E., 2006: New discovery of a large-sized *Tetraconodon* (Artiodactyla, Suidae) from the lower part of the Irrawaddy Formation, Myanmar. *Asian Paleoprimatology, Primate Research Institute, Kyoto University*, vol. 4, p. 186–196.
- Colbert, E. H., 1933: The skull and mandible of *Conohyus*, a primitive suid from the Siwalik Beds of India. *American Museum Novitates*, vol. 621, p. 1–12.
- Colbert, E. H., 1935: Siwalik mammals in the American Museum of Natural History. *Transactions of the American Philosophical Society, Philadelphia*, new series, vol. 26, p. 1–401.
- Colbert, E. H., 1938: Fossil mammals from Burma in the American Museum of Natural History. *Bulletin of the American Museum of Natural History, New York*, vol. 74, p. 255–436.
- Falconer, H., 1868: Description of a fragment of a jaw of an unknown extinct pachydermatous animal, from the Valley of the Murkunda. *Tetraconodon magnum* vel *Choeritherium*. In, Murchison, C. ed., *Palaeontological Memoirs and Notes of the Late Hugh Falconer, A. M., M. D., Fauna Antiqua Sivalensis*, vol. 1, p. 149–156.
- Gray, J. E., 1821: On the natural arrangement of vertebrate animals. *London Medical Repository*, vol. 15, no. 1, p. 296–310.
- Lydekker, R., 1876: Notes on the fossil mammalian faunae of India and Burma. *Records of the Geological Survey of India*, vol. 9, p. 86–106.
- Lydekker, R., 1878: Molar teeth and other remains of Mammalia. *Memoirs of the Geological Survey of India, Palaeontologia Indica*, ser. 10, vol. 1, no. 2, p. 19–69.
- Lydekker, R., 1884: Indian Tertiary and post-Tertiary vertebrata. Siwalik and Narbada bunodont Suina. *Memoirs of*

- the Geological Survey of India, Palaeontologia Indica*, ser. 10, vol. 3, no. 2, p. 35–104.
- Made, J. van der, 1991: Sexual bimodality in some recent pig populations and application of the findings to the study of fossils. *Zeitschrift für Säugetierkunde*, vol. 56, p. 81–87.
- Made, J. van der, 1999: Biometrical trends in the Tetraconodontinae, a subfamily of pigs. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, vol. 89, p. 199–225.
- Owen, R., 1848: Description of teeth and portions of jaw of two extinct anthracotherioid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits of the N.W. coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of Pachyderms by the number of their toes. *Quarterly Journal of the Geological Society of London*, vol. 4, p. 103–141.
- Pickford, M., 1988: Revision of the Miocene Suidae of the Indian Subcontinent. *Münchener Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie*, vol. 12, p. 1–92.
- Pilgrim, G.E., 1910: Notices of new Mammalian genera and species from the Tertiaries of India. *Records of the Geological Survey of India*, vol. 40, p. 63–71.
- Pilgrim, G.E., 1926: The fossil Suidae of India. *Memoirs of the Geological Survey of India, New Series*, vol. 8, no. 4, p. 1–104.
- Takai, M., Saegusa, H., Thaung-Htike, and Zin-Maung-Maung-Thein, 2006: Neogene mammalian fauna in Myanmar. *Asian Paleoprimatology, Primate Research Institute, Kyoto University*, vol. 4, p. 143–172.
- Thaung-Htike, Tsubamoto, T., Takai, M., Natori, M., Egi, N., Maung-Maung, and Chit-Sein, 2005: A revision of *Tetraconodon* (Mammalia, Artiodactyla, Suidae) from the Miocene of Myanmar, and description of a new species. *Paleontological Research*, vol. 9, p. 243–253.