Note on giraffe remains from the Miocene of continental Southeast Asia

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Abstract

Bramatherium (Giraffidae, Artiodactyla) remains were recovered from the Miocene deposits at the Tha Chang sand pit No.8, northeastern Thailand, and from the Irrawaddy sediments, central Myanmar. *Bramatherium* described here is similar to the same genus (or *Hydaspitherium*) from the Upper Miocene of the Siwalik Groups, Indian subcontinent, in terms of dental and metatarsal morphology. The fossil assemblages including *Bramatherium* are attributed probably to the early late Miocene fauna in continental Southeast Asia. *Bramatherium* records may be useful in biostratigraphic comparisons because this genus was widely distributed in Asia, whereas it was restricted to the Late Miocene, at least before 6 Ma.

Keywords: Giraffidae, Bramatherium, Myanmar, Thailand, Neogene.

Introduction

Late Neogene terrestrial sediments in continental Southeast Asia have yielded a variety of vertebrate fossils. The Irrawaddy sediments are well-known fossiliferous beds in central Myanmar and are distributed widely along the Irrawaddy and Chindwin rivers. The Irrawaddy sediments are traditionally divided into lower and upper parts based on paleontological and lithological criteria^{1,2} (see also Figure. 1). The fossil mammals from the lower part are characterized by extinct genera, such as *Hipparion*, *Brachypotherium*, *Tetraconodon*, and *Hydaspitherium*^{3,4}. On the other hand, living genera, such as *Equus*, *Dicerorhinus*, *Sus* and *Cervus*, likely appeared in the upper stage^{1,3,5}.

The geological age of the Irrawaddy fauna has been estimated by comparing with well-dated Siwalik faunas of the Indian subcontinent. The Lower Irrawaddy sediments are correlated with the Dhok Pathan Formation, or the Middle Siwaliks, and possibly with the uppermost part of the Chinji Formation of the Lower Siwaliks, suggesting that the Lower Irrawaddy fauna dates to the latest Middle Miocene to Early Pliocene^{1,3,6,7}. The Upper Irrawaddy fauna is correlated primarily with the Upper Siwalik fauna that is dated to the Late Pliocene and the Early Pleistocene^{1,3,8}, although several endemic taxa, strictly small mammals, appeared in continental Southeast Asia since this period⁹.

Another well-known fossil locality is the Tha Chang sand pits located along the Mun River in northeastern Thailand (Figure. 1). The sand pits are composed of the late Neogene sand/mudstones, ranging from the Middle Miocene to Pliocene and are usually covered by the Quaternary alluvial deposits on the surface^{10,11}. The deposits in the sand pits are separated into two units: the lower sand unit with organic-rich clay (or reduced zone) and the upper sand unit with yellowish sand and gravel (or oxidized zone)^{10,12}. This lithological difference reflects likely to sedimentary matrix with fossils, and most fossils from the lower unit show a black-colored surface and include sulfide minerals, such as pyrite. According to Chaimanee et al. (2007)¹³ and Hanta et al. (2008)¹¹, most mammalian fossils were yielded from clay or sandstone beds in the lower unit.

Vertebrate fossils from the Tha Chang sand pits were preliminarily reported by Suteethorn et al. (1997)¹⁴, and in recent years various remains have been

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collected by villagers working at the sand pits. As for mammals, a lot of fossils were discovered from the sand pit No. 8 (Samsok sandpit), and they included at least 17 genera to date: primates *Khoratpithecus*, artiodactyls *Hippopotamodon*, *Propotamochoerus*, *Merycopotamus*, *Microbunodon* and unidentified genera of bovids and giraffids; perissodactyls *Hipparion*, *Chilotherium*, *Brachypotherium*, *Alicornops* and *Aceratherium*, and proboscideans *Prodeinotherium*, *Deinotherium*, *Gomphotherium*, *Stegolophodon* and *Stegodon*^{10,11,15,16,17}.

The geological age of the Tha Chang fauna was roughly estimated to the Late Miocene based on biogeographic comparisons¹⁰. However, the fossil assemblage that was collected at the sand pit No. 8 is composed possibly of different fauna from at least three ages: Middle Miocene, Late Miocene, and Early Pleistocene^{11,16}.

Both the Irrawaddy fauna and the Tha Chang fauna have been traditionally compared by the biostratigraphy of mammals, with the Siwalik fauna. Biostratigraphic indicators (or index fossils) are usually adopted under the condition that they are widely distributed and have relatively a short lifespan: that is, rapidly evolved within narrow geological time periods. In mammals, proboscideans are one of the good taxa indicating geological age, and also the other large mammals like giraffes are possibly useful to define periods because they had a broad distribution in the past.

Giraffes, or the family Giraffidae, live only in Africa at present, but their fossils have been known commonly in Asia^{1,18}. Colbert (1938)¹ reported two sivatheriin giraffids, *Hydaspitherium birmanicum* and *Vishnutherium iravaticum*, from the Lower Irrawaddy sediments, but these genera have been synonymized with another si vatheriin *Bramatherium*^{19,20,21}. Chaimanee et al. (2006)¹⁰ mentioned the existence of giraffids from the Tha Chang sand pit No. 8, but they have not been taxonomically cleared yet. Thus, in this study, we systematically describe the giraffe remains that were collected from the Irrawaddy sediments and the Tha Chang sand pits, and preliminarily discuss the biostratigraphic relationship with the Siwalik fauna.

Materials and Methods

Fossil materials and locality

All referred specimens are stored in the Northeastern Research Institute of Petrified Wood & Mineral Resources (or Khorat Fossil Museum), Nakhon Ratchasima Rajabhat University, Nakhon Ratchasima Province, northeastern Thailand. A total of 14 specimens of giraffids, which were discovered from two fossil localities, were used in this study.

The specimens catalogued as ONG numbers were donated from a collector, Mr. Ongart, to the Khorat Fossil Museum. This collection is not accompanied with any locality information because the fossils were obtained through fossil traders. However, most of the ONG specimens were surely collected from the Irrawaddy sediments of central Myanmar, and perhaps some of them were brought from a famous fossil locality, Yenangyaung area (Figure 1), known by Colbert (1938, 1943)^{1,22}, Jaeger et al. (2011)²³, and Chavasseau et al. (2013)⁴. The ONG collection includes eight families of mammals: Stegodontidae, Rhinocerotidae, Equidae, Bovidae, Giraffidae, Hippopotamidae, Suidae, and Tragulidae. This faunal composition, except for Giraffidae, is similar to the Lower Irrawaddy fauna reported by Colbert (1938)¹ and Zin-Maung-Maung-Thein et al. (2011)⁶.

The specimens catalogued as RIN numbers were collected from the Tha Chang sand pit No.8 (Samsok sandpit) in Nakhon Ratchasima Province (Figure 1). The specimens were probably found from the lower unit, or the reduced zone, at the sand pit on the basis of the specimens' color and information by collectors. The RIN collection contains a variety of mammals, including both Miocene species (e.g. *Prodeinotherium*) and Pleistocene species (e.g. *Elephas*), but most of them are correlated with the late Miocene Siwalik fauna^{11,17}.

Terminology and measuring method

Tooth materials were measured using a digital caliper (model no. NTD12P-15C) by Mitutoyo Corp., Japan. Lower cheek teeth were measured basically by the maximum length (or width) of their crowns, and the molar widths were obtained at the anterior lobe. Terminology of teeth followed that of Bärmann and Rössner (2011)²⁴ (see also Figure 2).

Institutional abbreviations

AMNH, American Museum of Natural History, New York; BSPG, Bavarian State Collection of Paleontology and Geology of Munich University, Munich; NMB, Natural History Museum of Basel, Basel; NRRU, Nakhon Ratchasima Rajabhat University, Nakhon Ratchasima; ONG, Mr. Ongart's collection; PU, Geology Museum, Panjab University, Chandigarh; RIN, Rajabhat Institute Nakhon Ratchasima.

Systematic paleontology

Order Artiodactyla Owen, 1848²⁵ Family Giraffidae Gray, 1821²⁶ Subfamily Sivatheriinae Zittel, 1893²⁷ Genus *Bramatherium* Falconer, 1845²⁸ *Bramatherium* sp. indet. (Figures 3 and 4)

Materials

Two right M¹ or M² fragments (ONG 182, 192); a right mandible with P_4-M_1 (ONG 228); two right mandibles with M_1-M_2 (ONG 117, 165); a left mandible with P_2-P_4 (RIN 791); a left mandible with M_1 (ONG 571); a left mandible with M_1-M_2 (ONG 164); a left mandible with M_2-M_3 (ONG 606); a left mandible with M_2 (ONG 628); a right M_3 (ONG 213); a right lower molar fragment (ONG 200); a left metatarsal with navicular cuboid (RIN 794); a distal part of right metatarsal (RIN 436).

Measurements

See Tables 1 and 2.

Description

The fragmentary upper molars (ONG 182 and 192) preserve only anterior lobe that is composed primarily of paracone and protocone. The teeth are moderately worn, and the labial point of the paracone is slightly rounded. The parastyle and the mesostyle are relatively small, and their longitudinal ribs on the labial surface are also weak. The labial surface is approximately flat owing to an indistinct rib below the paracone. The anterior fossa shows a sharp V-letter in occlusal view. The cristas or cusps at the labial side are isolated from those at the lingual side by

the anterior fossa. The preprotocrista is broad, expanding anterolingually. The crown width considerably increases from the occlusal surface to the base. Entostyle is absent. The anterior side of each tooth has an interfacet. There are prominent cingulums surrounding the crown base, but these cingulums disappear below the anterior interfacet and the protocone.

 P_2 has the occlusal outline with an isosceles triangle that is composed of the anterior stylid, the posterior stylid, and the posterolabial conid. The mesolabial conid at the center is prominent. This main cusp connects to the anterior stylid and the posterolabial conid by the anterolabial cristid and the posterolabial cristid, respectively. The anterior stylid does not diverge, namely the anterior conid is absent. The anterior valley is very shallow. There is neither the mesolingual conid nor any cristids at the lingual side. The posterolingual conid is so weak that the posterior valley and the back valley are not well-developed.

P, shows the basic premolar pattern of ruminants, which is represented by premolars of oxen or antelopes (see also Figure 2B). The mesolabial conid and the mesolingual conid are prominent. The mesolingual conid extends posteriorly and connects to the posterolingual cristid, while it lacks the anterolingual cristid. The anterior point is diverged into two cusps, the anterior stylid and the anterior conid. The anterior conid is situated slightly inward relative to the anterior stylid. The anterior valley is wide and deep, and has a distinct cingulum at base. The posterior part is composed of the posterolabial conid, the posterolingual conid, and the posterior stylid. This part is slightly wider than the middle part that is composed of the mesolabial conid and the mesolingual conid. The posterior valley and the back valley are anteroposteriorly shallow. The labial surface below the posterolabial conid expands outward strictly at base. The labial cingulums are weakly present at the anterior side.

 P_4 basically has the same enamel patterns with P_3 but approaches a molar-form (molarization) that divides the crown into anterior and posterior lobes. The occlusal surface shows a rectangular shape rather than a triangle because the anterior lobe is almost as wide

as the posterior lobe. The anterior stylid connects with a cristid (probably premetacristid) that extends from the mesolingual conid (or metaconid). An internal cristid from the mesolabial conid, or the internal postprotocristid, approaches the labial wall of the posterolingual cristid (or internal postmetacristid), but they are not fused to each other. The anterior valley is closed and anteroposteriorly elongated. The posterior valley is deep, and its sinus at the lingual side approaches the cervical line. The labial surface is intruded inward as a sinus between the anterior and posterior lobes. The posterior lobe is similar to that of P₂, including the posterolabial conid, the posterolingual conid, and the posterior stylid. The back valley is closed by these cusps. There are cingulums at the anterolingual side and the anterolabial side, and the former is much stronger than the latter.

M₁ has a trapezoidal outline in occlusal view. The anterior lobe is slightly smaller than the posterior lobe. The metaconid and the entoconid are relatively sharp, although all specimens are moderately worn. The mesostylid is indistinct, but instead there is a weak cingulum on the anterolingual side. The anterior cingulid at the base is also very weak. The internal postprotocristid approaches the labial wall of the preentocristid, but is not fused with any cristids. The preentocristid is folded into the anterior fossa between the postprotocristid and the internal postmetacristid. The lamina with the entoconid and its cristids is isolated from the other laminae. There is a deep gap between the anterior and posterior lobes because the prehypocristid is separated from the other cristids. The posthypocristid is connected with the postentocristid at the middle height of the crown. The ectostylid is present in all specimens, and is very short and rounded. The posterior base has a vestigial cingulum. The ribs on the lingual surface are weakly projected at the upper half, but disappear near the base. The crown width increases from the top through base.

 $\rm M_2$ and the anterior part of $\rm M_3$ are the same basically with $\rm M_1$ in terms of enamel patterns, but $\rm M_2$ and $\rm M_3$ are slightly larger than $\rm M_1$. The posterior fossa in $\rm M_2$ opens at the posterolabial corner like a small sinus. Both $\rm M_2$ and $\rm M_3$ have ectostylids between the anterior and pos-

terior lobes. In M_3 (ONG 606), the posterior ectostylid is much stronger than the anterior ectostylid. The cingulum at base is present only at the anterior sides, and that in M_3 is much weaker than that in M_1 or M_2 .

The metatarsal (RIN 794) is completely preserved and connected with the navicular cuboid. The metatarsal body is relatively long (maximum length: 460 mm), but is much shorter than that of living adult *Giraffa*. The distal part is approximately 76 mm wide, and has two phalanges' pulleys, each with a width of 36 mm. The pulleys are close to each other, being situated almost in parallel: their divergence is less than 15 degrees. The narrowest part of the metatarsal body is 48 mm wide, and continues for 150 and 260 mm from the distal end. There is a distinct median ditch on the anterior surface. The proximal part is anteroposteriorly broad, and is connected with the navicular cuboid by sedimentary matrix. The other tarsal bones are not observed in the present specimens.

The navicular cuboid is large and somewhat compressed anteroposteriorly, relative to that of living *Giraffa*. The surface jointing with astragalus and calcaneus is relatively wide. The posterior joint part with the calcaneus projects outward. The projection at the posterointernal side is very strong. There is a small notch, projecting outward, on the anterointernal surface. The maximum anteroposterior and labiolingual widths of the proximal surface are 92 mm and 100 mm, respectively.

Discussion and Conclusion Comparisons

The giraffid remains from the Irrawaddy sediments and the Tha Chang sand pit No. 8 were referred to *Bramatherium* (Sivatheriinae) primarily on the basis of dental and metatarsal size. The Sivatheriinae is known as a large-sized giraffid group that lived in the Miocene to Pleistocene of Eurasia and Africa and includes eight genera: *Helladotherium, Karsimatherium, Vishnutherium, Decennatherium, Birgerbohlinia, Bramatherium, Hydaspitherium*, and *Sivatherium*²⁹. Colbert (1935)¹⁸ included more two genera, *Griquatherium* and *Libytherium*, in the Sivatheriinae, but these genera were synonymized into *Sivatherium* in the classification list of McKenna and Bell (1997)²⁹. Colbert (1935)¹⁸ also suggested the synonymity of *Indratherium* and *Sivatherium*.

The sivatheriins are distinguished from the other subfamilies, such as Giraffinae, in having greater size, relatively hypsodont cheek teeth with rugose enamel, and less elongated but heavy limb bones¹⁸. The referred specimens in this study share these diagnostic characteristics, and are very similar to some species of Sivatheriinae. Colbert (1935)¹⁸ described several species of *Giraffa* from the Middle Siwaliks, but their premolars, strictly P_3 and P_4 , are anteroposterioly compressed relative to the present specimens.

One primitive genera, *Giraffokeryx* Pilgrim (1910)³⁰, had been originally classified into Giraffinae and later replaced into a new clade, Giraffokerycinae, as the sister group of Sivatheriinae by cladogram analysis³¹. *Giraffokeryx* is usually much smaller than any sivatheriin species (Figure 5), but retains symplesiomorphy with the sivatheriins in terms of characteristics of the skull. The cheek teeth patterns of *Giraffokeryx* also resemble those of sivatheriins, when comparing *Giraffokeryx punjabiensis* and *Giraffokeryx anatoliensis* from the Lower Siwaliks and the Middle Miocene of Turkey, respectively^{18,32}. On the other hand, metapodials of *Giraffokeryx* are relatively long and slender, and are close to those of living *Giraffa* in shape³¹.

Sivatheriin genera were classified basically by cranial morphology, while their teeth shapes and measurements are probably not useful for identification among the genera. For example, *Hydaspitherium* and *Vishnutherium* from the Siwaliks were originally described as different genera from *Bramatherium*^{18,33}, but the former two genera are likely junior synonyms of *Bramatherium*^{19,20,21}. In fact, cheek teeth measurements among these genera are not significantly different from each other (Table 1 and 2; Figure 5).

Sivatherium and *Bramatherium*, including their synonyms, have been found previously from the Upper Miocene of the Siwalik Groups and the Lower Irrawaddy sediments^{1,18}. Dental comparisons indicated that the teeth measurements of the RIN and ONG specimens are almost

as large as *Bramatherium* or *Hydaspitherium* from the Siwaliks, and also that occlusal patterns of *Bramatherium* are considerably similar between the specimens from Southeast Asia and from the Siwaliks (Figures 3 and 5).

Sivatherium is much larger than *Bramatherium* or *Hydaspitherium* (Figure 5). Moreover, *Sivatherium* is characterized by relatively short and stout metapodials^{31,34}. However, the metatarsal of RIN 794 is much longer than that of *Sivatherium*, which supports the similarity between the present specimens and *Bramatherium* rather than *Sivatherium*. Metatarsals of *Bramatherium* or *Hydas pitherium* were also described by Colbert (1935)¹⁸, and they are almost as long as RIN 794.

Helladotherium, another medium sized sivatheriin, from the Late Miocene of Europe, is also similar to *Bramatherium* in teeth measurements (Figure 5). Although we cannot define the difference between *Bramatherium* and *Helladotherium* by the present materials, we believe that the sivatheriin specimens found in Southeast Asia are attributed to *Bramatherium* because *Helladotherium* has never found in South to East Asia.

Geographical and stratigraphic distribution

Bramatherium, including *Hydaspitherium* and *Vishnutherium*, has been found from the Upper Miocene of Turkey, Indo-Pakistan, and Myanmar^{1,18,21,35,36}. Giraffe remains have also listed in the mammalian fossil assemblage from the Upper Miocene of the Tha Chang sand pits¹³, and they were classified to *Bramatherium* in this study. Thus, *Bramatherium* species were widely distributed during central Asia and continental Southeast Asia.

The occurrence of *Bramatherium* is restricted mostly to the Late Miocene, ranging approximately from 10.3 to 7.1 Ma³⁷. Khan et al. (2014)³⁶ recently reported two species of *Bramatherium* from the latest Miocene or early Pliocene of the Siwalik Groups (Dhok Pathan Formation), Hasnot. Biostratigraphically they suggested that *Bramatherium* had survived likely until the end of the late Miocene in the Indian subcontinent, but chronological and taxonomic data that Khan et al. (2014)³⁶ referred have been revised in the recent studies³⁹. Chavasseau et al. (2013)⁴ reviewed the middle and late Miocene fauna from the Irrawaddy sediments, and suggested that giraffids in Myanmar appeared at least in the early Late Miocene on the basis of fossils from Yenangyaung area. On the other hand, a huge amount of mammalian fossils have been collected from the latest Miocene/early Pliocene (ca. 6–4 Ma) and late Pliocene/early Pleistocene (ca. 4–2 Ma) localities in central Myanmar, but giraffids have never been found from such periods to date^{3,4,6,9}. Montoya and Molares (1991)³⁸ also mentioned that the sivatheriin group disappears outside Africa and Siwaliks in the latest Miocene. Therefore, the presence of *Bramatherium* remains from Myanmar and Thailand indicated that both fossil assemblages contained the late Miocene fauna, strictly before 6 Ma.

In conclusion, *Bramatherium* remains were recovered from the Irrawaddy sediments and the Tha Chang sand pit No. 8, and suggested that this genus existed widely in Asia during the late Miocene. The collected specimens in this study were fragmentary, so that their taxonomic status at species level should be examined from additional material in the future and discussed with phylogenetic relationships among species between the Indian subcontinent and continental Southeast Asia.

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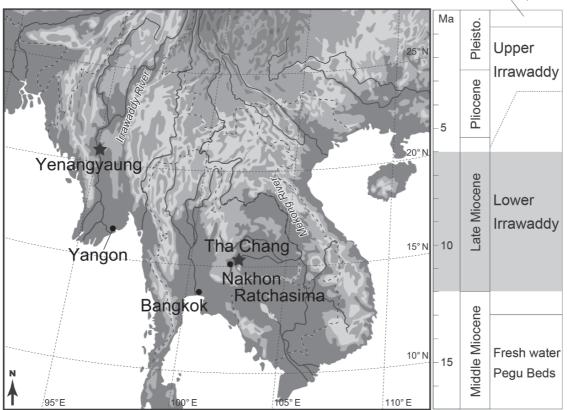
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River terrace deposits

Figure 1 Locations of the Tha Chang sand pits (Nakhon Ratchasima Province, northeastern Thailand) and the Irrawaddy sediments near Yenangyaung area, central Myanmar, with the stratigraphic column that shows chronological ranges of the localities (gray part).

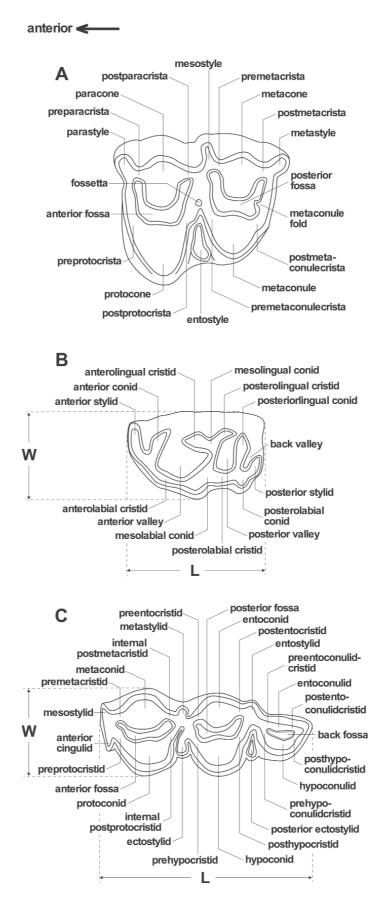


Figure 2 Terminology and measuring method of ruminant teeth, modified after Bärmann and Rössner²⁴. A, left M³.
B, left P₄. C, left M₃.

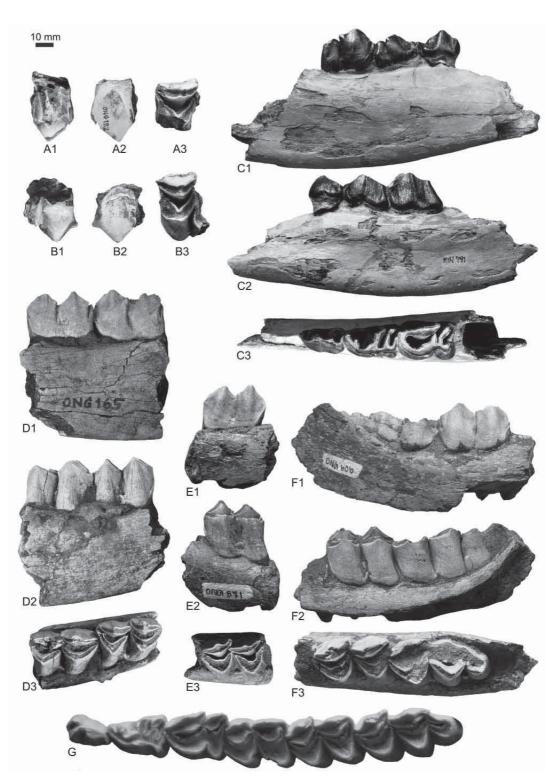


Figure 3 Dental specimens of *Bramatherium* sp. indet. from the Tha Chang sand pit No. 8 (RIN) and the Irrawaddy sediments (ONG), with the Siwalik species. **A**, right M¹ or M² fragment (ONG 182): **A1**, lingual view; **A2**, labial view; **A3**, occlusal view. **B**, right M¹ or M² fragment (ONG 192): **B1**, lingual view; **B2**, labial view; **B3**, occlusal view. **C**, left mandible with P_2-P_4 (RIN 791): **C1**, lingual view; **C2**, labial view; **C3**, occlusal view. **D**, right mandible with M_1-M_2 (ONG 165): **D1**, lingual view; **D2**, labial view; **D3**, occlusal view. **E**, left mandible with M_1 (ONG 571): **E1**, lingual view; **E2**, labial view; **E3**, occlusal view. **F**, left mandible with M_2-M_3 (ONG 606): **F1**, lingual view; **F2**, labial view; **F3**, occlusal view. **G**, occlusal view of left mandible with P_2-M_3 (AMNH 19684, P_2 is connected by the wrong way round).



Figure 4 Metatarsals of *Bramatherium* sp. indet. from the Tha Chang sand pit No. 8. A, left metatarsal with navicular cuboid (RIN 794): A1, internal view; A2, anterior view; A3, posterior view; A4, proximal view. B, left metatarsal (RIN 436): B1, anterior view; B2, schematic drawing of the proximal cross-section. Abbreviations: an, anterior; ex, external; di, distal; pr, proximal.

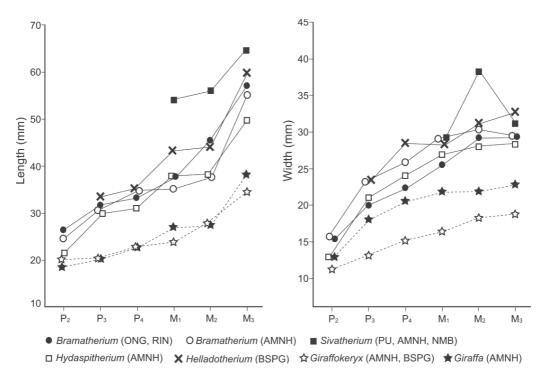


Figure 5 Mean values of length and width of lower cheek teeth among six genera of giraffids. Specimens and their measurements are listed in Tables 1 and 2. Solid and broken lines show the groups of Sivatheriinae and others, respectively.

Table 1 Premolar measurements of giraffid fossils from Myanmar and Thailand, comparing with those from Europe	
and Indo-Pakistan. L, maximum length of crown. W, maximum width of crown.	

	Р	P ₂		P ₃) 4
	L	W	L	W	L	W
Bramatherium sp. indet.						
RIN 791	26.40	15.52	31.53	20.06	33.39	22.72
ONG 228	_	_	_	_	33.60	21.98
Bramatherium sp. indet.						
AMNH 19684	24.30	15.62	30.86	23.17	34.62	25.93
Hydaspitherium megacephalum						
AMNH 1966918	21.00	13.00	30.00	21.00	31.00	24.00
Helladotherium duvernoyi						
BSPG ASII645	_	_	33.55	23.44	34.93	28.59
Giraffokeryx punjabiensis						
AMNH 19587	18.0018	9.0018	20.55	12.39	23.25	15.60
BSPG Zu160	20.42	11.17	20.13	13.86	22.61	14.63
Giraffa punjabiensis						
AMNH 19318	20.30	12.50	21.21	17.73	22.24	21.83
Giraffa camelopardalis						
AMNH (no number)	16.84	13.36	19.63	18.46	23.24	19.58

	M ₁		Ν	N ₂	M ₃	
	L	W	L	W	L	W
Bramatherium sp. indet.						
ONG 228	38.01	25.44	_	_	_	_
ONG 117	34.42	23.66	_	_	_	_
ONG 165	38.88	29.47	48.69	31.30	_	_
ONG 571	36.75	24.74	—	—	—	_
ONG 164	38.55	24.70	41.18	28.36	—	_
ONG 606	_	—	45.47	28.71	57.08	29.38
Bramatherium sp. indet.						
AMNH 19684	35.12	28.97	37.74	30.46	55.35	29.43
Hydaspitherium megacephalum						
AMNH 19669*	38.00	27.00	38.00	28.00	50.00	28.50
Helladotherium duvernoyi						
BSPG ASII645	43.29	28.41	31.23	33.64	32.87	32.82
Sivatherium giganteum						
PU A/542	54.26	29.48	_	_	_	_
AMNH 1980218	_	_	58.00	38.00	67.00	33.00
AMNH 19797 ¹⁸	_	_	54.00	39.00		_
AMNH 2983518	_	—	—	—	68.00	33.00
AMNH 19828 ¹⁸	_	_	_	_	57.00	29.00
NMB K21/574 Jn297	_	—	—	—	67.51	31.19
PU H/533	_	_	_	_	64.88	31.27
Giraffokeryx punjabiensis						
AMNH 19587	24.28	16.05	27.86	17.30	34.71	18.09
BSPG Zu160	23.51	16.63	_	19.28	_	19.46
Giraffa punjabiensis						
AMNH 19318	27.13	22.62	25.90	_	_	_
Giraffa camelopardalis						
AMNH (no number)	27.00	21.43	28.95	21.89	38.22	22.93

Table 2 Molar measurements of giraffid fossils from Myanmar and Thailand, comparing with those from Europe and
Indo-Pakistan. L, maximum length of crown. W, maximum anterior width of crown.